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Carnivores (Mammalia, Carnivora) of the Urals in the Late Pleistocene and Holocene

P.A. Kosintsev*, V.V. Gasilin, D.O. Gimranov, O.P. Bachura

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Russian Federation

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ABSTRACT

Carnivore assemblages from localities of the Late Pleistocene and Holocene of Northern, Middle and Southern Urals were studied. Analysis of species composition of the carnivore fauna was performed for seven chronological periods: MIS 5e, MIS 3, mid-MIS2 (LGT), late MIS 2 (BAIC), early MIS 1 (Preboreal-Boreal), mid-MIS 1 (Atlantic-Subboreal), late MIS 1 (Subatlantic). In the Urals, changes in carnivore fauna were occurring during the Late Pleistocene and Holocene. Faunal composition included the species from European, Siberian and European–Siberian faunal complexes throughout the Late Pleistocene and Holocene, dominated by the species from European–Siberian faunal complexes. The general trend of fauna changes is represented by a decreasing percentage of species from the European faunal complex and an increasing percentage of those from the Siberian faunal complex. Faunal composition has changed due to two main reasons, range shifts and extinction. Sixteen out of 24 species that inhabited the Urals during the Late Pleistocene and Holocene underwent range shifts. The ranges shifted in different directions: reduction, increased and fluctuations. The ranges of several species have not changed. Three species became extinct.

1. Introduction

The Ural region has overlapping ranges of species from the different geographical fauna complexes: European, Siberian, and Euro-Siberian (Kuznetsov, 1950; Kulik, 1980). It is located on the border between Europe and Asia, and crosses tundra, taiga, and steppe natural zones. At present, the Urals is inhabited by 16 species of carnivores belonging to four families (Canidae, Ursidae, Mustelidae, and Felidae) (Marvin, 1969).

The Urals is known for its well-studied Late Pleistocene and Holocene localities, yielding numerous fossil mammal assemblages, including fossil carnivores. The results of these studies have been presented in a considerable number of papers dedicated either to the description of the history of large mammals of selected areas of the Urals (Kuzmina, 1971, 1975; Smirnov et al., 1990; Kosintsev and Bachura, 2005, 2013, 2014; Ulitko, 2006; Bachura and Kosintsev, 2007; Kosintsev, 2007; Kosintsev and Plasteeva, 2009; Danukalova et al., 2011; Ponomarev et al., 2013; Smirnov et al., 2014) or to the description of the fauna of certain localities (Bachura and Strukova, 2002; Bachura and Plasteeva, 2005; Gimranov, 2009; Kosintsev, 1996; Kosintsev and Orlova, 2002; Petrov, Kosintsev, 2005; Kuzmina et al., 1999; Kuz'mina, 2000; Razhev et al., 2005; Strukova et al., 2006; Svendsen et al., 2010; Ulitko et al., 2011; Yakovlev et al., 2006). In these works, carnivores are studied together with other large mammals. Some articles devoted to the history of certain carnivore species of the Urals have been published (Baryshnikov, 2001, 2007; Gasilin and Kosintsev, 2010; Gasilin et al., 2014; Gimranov and Kosintsev, 2015; Kosintsev and Bachura, 2015; Kosintsev and Gasilin, 2011; Kosintsev, Vorob'ev, 2001; Kuzmina, 2002). The purpose of this paper is to reconstruct the history of carnivore fauna of the Urals in the Late Pleistocene and Holocene.

The most ancient carnivore fossils have been found in the Southern Urals. At the site of Baturino, remains of *Ursus* sp. and *Mustela* (small forma) whose size is close to that of *M. erminea* and *M. nivalis*, have been found in the deposits dating to the middle stages of the Early Pleistocene, while the *Mustela* remains (small form) date to the end of the Early Pleistocene (Stefanosvkiy and Borodin, 2002). The Middle Pleistocene deposits of the Ignatievsky cave contain remains of *Canis lupus* and *Canis* sp. (small form), *Vulpes vulpes*, *V. lagopus*, *Ursus savini*, *Martes* sp., *Gulo gulo*, *Mustela erminea*, and *M. nivalis* (Smirnov et al., 1990). The Late Pleistocene deposits yield other Uralian carnivore remains.

2. The modern situation: some components of the Urals biota

Four regions are traditionally distinguished within the Urals: the Polar (from 67°30′N to 64°00′N), Northern (from 64°00′N to

* Corresponding author.
E-mail address: kpa@ipae.uran.ru (P.A. Kosintsev).

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59°15′N), Middle (from 59°15′N to 55°54′N), and Southern Urals (from 55°54′N to 51°00′N) (Urals and Pre-Urals, 1968). Although this division is based on the orography of the Ural Range, each of these regions has its specific natural and climatic features. Here, we consider the Middle and Southern Urals in a broad sense, including the mountains and parts of the Trans-Urals peneplain. We do not have data on the carnivore fauna history in the Polar Urals, so we do not consider this region in this article.

The climate of the Northern, Middle, and Southern Urals is temperate continental. The Urals is disposed across the direction of the prevailing westerly winds, so this western slope is moister than the east slope. The territories of Northern and Middle Urals are located in the taiga where pine and spruce dominate. In the south part of the Middle Urals, there is a large proportion of birch in the composition of vegetation. Almost all the mountainous part of the Southern Ural territory lies in the zone of coniferous small-leaf and coniferous broadleaf forests. Pine, birch, linden, elm and oak (in the south) dominate among vegetation. The southern part of the Southern Urals is located in the steppe zone. In the peneplain of the Middle and Southern Urals, steppe vegetation is present. The mountains of the Northern, Middle and Southern Urals are not high so the altitudinal belt in vegetation is not expressed (Gorchakovskiy, 1975).

Fauna of carnivore of the Urals consist of three main complexes: tundra, forest, and steppe. The carnivores which inhabit the entire territory of Urals are *Canis lupus*, *Vulpes vulpes*, *M. nivalis*, *M. erminea*. A typical tundra species is *Vulpes lagopus* which inhabits the Polar Urals and the extremely northern part of the Northern Urals. The forest complex of carnivores inhabits territory of Northern and Middle Urals as well as mountain-forest zone of Southern Urals. This complex is represented by the taiga (*Ursus arctos*, *Gulo gulo*, *Martes zibellina*, *Martes martes*, *M. putorius*, *M. sibirica*, *Lynx lynx*) and taiga-wetland species (*M. lutreola*, *M. vison*, *Lutra lutra*). The species of forest-steppe species (*Meles leucurus)* inhabits the southern Northern Urals, the Middle, and Southern Urals. Distribution of carnivores of the steppe mammal complex is limited by the southern part of the Middle Urals and Southern Urals (*M. eversmanni*) and the Southern Trans-Urals peneplain area (*V. corsac*) (Urals and Pre-Urals, 1968).

3. Materials and methods

We studied data on carnivore species composition from 287 sites located (Table A.1.) in the Urals between 64° and 51°N (Fig. 1). The carnivore remains have been found in localities of several types, i.e. alluvial, swamp, cave, and archaeological localities.

All faunas have been dated. The MIS 5 faunas have been dated on the basis of the species composition of the associated mammal fauna. All the MIS 3 and MIS 2 faunas have been dated using radiocarbon. The MIS 1 fauna has been dated using radiocarbon and archaeological methods. Radiocarbon dates from the Uralian localities were obtained from the bones of several carnivore species (Table A.2.). We use uncalibrated radiocarbon dates.

All radiocarbon dates with indices GIN, LE, LU, SOAN were obtained by conventional radiocarbon dating, while the dates with other indices by accelerator mass spectrometer (AMS) method. Some localities were radiocarbon-dated by both methods. The comparison of radiocarbon dates obtained by different methods for the cave bear bones indicates that sometimes these methods do not give consistent results (Table A.2.). For example, a conventional radiocarbon date of 26980 BP and some AMS dates, ranging between 37190 BP and 47600 BP, were obtained for the Tayn cave. The bones from the Geologov 3 cave were a source for two conventional radiocarbon dates of 27070 BP and 27580 BP, as well as a single AMS date of 38480 BP. The bones from the Zapovednaya cave gave two conventional dates of 28700 BP and 37250 BP and three infinite AMS dates. The general trend is that the conventional ^{14}C dates (i.e., produced by liquid scintillation counting) yield older ages compared to the AMS ^{14}C values from the same strata. Therefore, we will use AMS dates to determine the dates of species extinction.

The available data allowed us to perform the analysis of the species composition of the carnivore fauna for seven chronological periods: MIS 5e, MIS 3, mid-MIS 2 (LGT), late MIS2 (BAIC), early MIS 1 (Preboreal-Boreal, Early Holocene), mid-MIS 1 (Atlantic-Subboreal, Middle Holocene), late MIS 1 (Subatlantic, Late Holocene). Data for the other periods are not sufficient.

In the Late Interglacial (MIS 5e, Eemian, Mikulino, Streletsk, Kazantsevo), the climate was warmer than now, and forest vegetation was more widespread (Mangerud, 1989; Grichuk, 2002; Kühl, Litt, 2003). The mega-interstadial of the Last Glaciation (MIS 3, Middle Weichselian, Bryansk Interstadial, Karginsk Interstadial) with an age of 60–24 ka BP is characterized by relatively warm climate but also by the occurrence of a large number of climatic fluctuations which differ in intensity (Zagwijn, 1974; Vanderberge, 2002; Rasmussen et al., 2006; Svensson et al., 2008; Velichko and Faustova, 2009). As for the end of the Late Pleistocene (MIS 2, Late Weichselian, Late Valdai, Sartan), we have studied two periods that occurred after the Last Glacial Maximum (LGM), i.e. Deglaciation or Late Glacial Transition (LGT; 17–12.4 ka BP) and the Bølling – Allerød interstadial warming divided by short and weak pronounced Older Dryas Stadial (BAIC; Late Weichselian, Late Valdai, Late Sartan; 12.4–10.3 ka BP) (Markova et al., 2008; Faustova, 1994). At the onset of the Holocene, the climate became warmer (Svensson et al., 2008) and the forests spread rapidly (Chotinsky and Klimanov, 2002). The chronology of the localities examined in the paper covers the entire the Late Pleistocene and Holocene, from MIS 5e to late MIS 1. The boundaries of the chronological periods are given as radiocarbon years.

The faunas of separate localities within one area (Northern, Middle and Southern Urals) have been chronologically classified into several groups (Table A.1.). The Southern Urals includes two large geomorphologic units: the mountain region and the Trans-uralian peneplain. Within the territory of the Southern Urals, all the Late Pleistocene localities are situated in mountains region. Therefore, we consider them as one geographical group. The Holocene localities are situated in both regions. Thus, the localities of each Holocene period form two geographical groups, namely the “mountain” and the “peneplain” groups.

The analysis of the Late Pleistocene and Holocene and modern ranges of each species allowed us to assign all the carnivore species to one of three faunal complexes, European, Siberian, or European–Siberian complex. The ranges of many species cover the territory of both Europe and Asia. The European faunal complex is represented by the species whose range lies mostly in Europe, and its eastern margin in Asia is restricted to the Yenisei River. The Siberian faunal complex contains the species whose range lies mostly in Asia and its western margin in Europe is restricted to the Volga basin. The European–Siberian faunal complex includes the species with their ranges represented mostly in both Europe and Asia. It is difficult to assign the Asiatic black bear (*Ursus tibethanus*) and dhole (*Cuon alpinus*) to a particular faunal complex. At present, their ranges lie entirely in Asia, though their Pleistocene ranges were different. During the Saalian glaciation the Asiatic black bear's range covered central (Musil, 2005–2006; Nagel, Rabeder, 2000) and southern Europe and extended into the Iberian Peninsula (Torres, 1988; Crégut-Bonnoure, 1997). This range apparently remained unchanged until the end of the Eem interglacial and was drastically reduced at the onset of the Weichselian Stage. The dhole's range covered southern and central Europe in the Late Pleistocene (Sommer and Benecke, 2005). The dhole persisted in

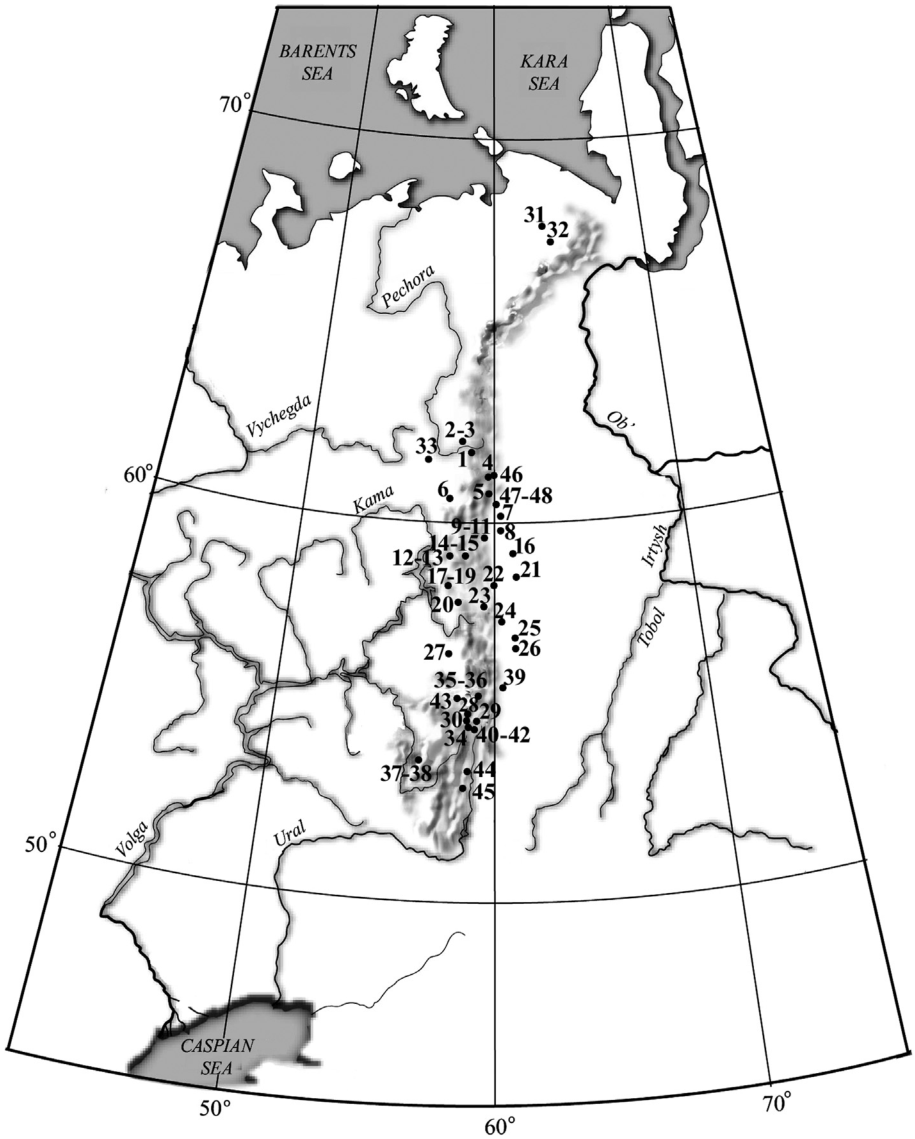

Fig. 1. The main localities of carnivore remains from the Urals. 1 – Medvezhaya cave; 2 – Kaninskaya cave; 3 – Uninskaya cave; 4 – Burmantovo; 5 – Usoltsevskaya cave; 6 – Kamen' Pysannyj; 7 – Cheremukhovo-1; 8 – Zhilische Sokola; 9 – Makhnevskaya-Ledyanaya cave; 10 – Tayn cave; 11 – Kizelovskaya cave; 12 – Rasik; 13 – Verkhnegubakhinskaya cave; 14 – Lun'evka III cave; 15 – Viasher cave; 16 – Lobvinskaya cave; 17 – Grotto Bolshoj Glukhoj; 18 – Dyrovatyj-na-Chusovoj; 19 – Ust'-Katavskaya cave; 20 – Turistov cave; 21 – Koksharovsko-Ur'inskaya; 22 – Shigirskoe gorodische; 23 – Georgievskaya cave; 24 – Pershinskaya cave; 25 – Bezymaynnyj; 26 – Zotinskij; 27 – Grotto Bobylek; 28 – Barsuchij Dol; 29 – Ust'-Katavskaya cave; 30 – Ignat'evskaya cave; 31 – Pymva-Shor; 32 – Mamontova Kyr'ya; 33 – Pizhma-1; 34 – Pobeda cave; 35 – Nikol'skaya cave; 36 – Sikiyaz-Tamak; 37 – Bayslan-Tash; 38 – Balatukaj; 39 – Ustinovo; 40 – Zapovednaya cave; 41 – Imanaj cave; 42 – Verkhnyaya cave; 43 – Asha-1; 44 – Smelovskaya cave; 45 – Syrtinskaya cave; 46 – Severnaya cave; 47 – Laksejskaya cave; 48 – Shajtanskaya cave.

the Iberian Peninsula until the Early Holocene (Ripol et al., 2010). Thus, European–Siberian geographical distribution was characteristic of both Asiatic black bear and dhole in the Pleistocene. That is why we consider them to be part of the European–Siberian faunal complex.

The ranges of several species with quite similar skeleton structure overlap or used to overlap each other in the Urals. We applied special methods for species identification of fossil remains of the following species: *Vulpes vulpes*, *V. lagopus* and *V. corsac* (Monchot and Gendron, 2010), *Canis lupus* and *Cuon alpinus* (Ripol et al., 2010; Pionnier-Capitan et al., 2011), *Meles meles* and *M. leucurus* (Aristov and Baryshnikov, 2001; Gasilin and Kosintsev, 2012), *Martes martes*, *M. zibellina* and *M. foina* (Gasilin and Kosintsev, 2013; Gimranov, 2015; Gimranov and Kosintsev, 2015).

The analysis of ancient DNA from the cave bear bones from the Northern Urals showed that the *Ursus* (*Spelaearctos*) *ingressus* form inhabited this area (Knapp et al., 2009). No DNA analysis has been performed for the bears from other Uralian areas. Pending data for other areas, we assign the cave bear of the Urals to *Ursus* (*Spelaearctos*) *spelaeus*. The approach representing order Carnivora follows Wilson and Reeder (2005).

4. Discussion

The most ancient Late Pleistocene carnivore remains have been found in the faunas of the Bobylek caves (Smirnov, 1993; Razhev et al., 2005) and the Makhnevskaya Ledyanaya in the Middle Urals (Barysnikov, 2001; Fadeeva et al., 2011), as well as in the Barsuchii Dol in the Southern Urals (Fig. 1). As these faunas comprise forest species (*Lynx lynx*, *Ursus tibethanus*, *Sciurus vulgaris*, *Apodemus flavicollis*, *Dryomys nitedula*) and those that inhabit the areas with relatively warm climate (*Desmana moshata*, *Talpa europaea*, *Lutra lutra*, *Meles meles*, *Hystrix brachyura*), they have been assigned to an interglacial time. Simultaneously the typical Late Pleistocene species were found with these species as part of the fauna – *Ursus spelaeus*, *U. savini*, *Panthera spelaea*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bison priscus*, *Microtus gregalis* and *Lemmus sibiricus* (Baryshnikov, 2001; Razhev et al., 2005; Fadeeva et al., 2011). This evidence allows us to allocate this interglacial to the Late Pleistocene and to date the faunas to Streletsk interglacial (MIS 5e, Eemian, Mikulino, Kazantsevo). Species composition of the Middle and Southern Uralian faunas was nearly the same at that time (Table 1). Asiatic black bear (*Ursus tibethanus*) (Barysnikov, 2001) and wolverine (*Gulo gulo*) (Razev et al., 2005) were present in the interglacial time fauna of the Middle Urals. The absence of these species in fauna of the Southern Urals can be explained by insufficient numbers of well-studied localities of this period. This might also explain the absence of some species of the genera *Martes* and *Mustela* in the composition of these faunas. The faunal composition is dominated by the species of the European–Siberian faunal complex. The species of the European faunal complex are not abundant, and the species of the Siberian faunal complex are absent (Table 2). The presence of the Asian black bear in the fauna of this period is regarded as its peculiarity (Table 1), as this species is absent from later faunas. *Meles meles* was part of the faunal composition of this period, though it is absent from the fauna of the subsequent periods.

Faunas from some dozens of the localities in the Northern, Middle and Southern Urals are known from the mega-interstadial of the Last Glaciation (MIS 3). These faunas comprised the species of the European–Siberian, European and Siberian faunal complexes (Table 1). All these faunas were dominated by the species of the European–Siberian faunal complex, while European and Siberian complexes were represented by rare species (Table 2). This period is characterized by differences in the species composition of the fauna typical of different areas. The number of species decreased from south to north. Eighteen species inhabited the Southern Urals, 14 species were common for the Middle Urals and 12 species occurred in the Northern Urals. The fauna of the Southern Urals was distinguished by the dhole (*Cuon alpinus*), lynx (*Lynx lynx*), otter (*Lutra lutra*), pine marten (*Martes martes*) and European mink (*Mustela lutreola*). These species were absent from the Middle Uralian fauna (Table 1). As for the Northern Urals, besides the above listed species, cave hyena (*Crocuta crocuta spelaea*) and corsac (*Vulpes corsac*) were also absent from its fauna (Table 1). In contrast to the fauna of the Southern Urals, faunal composition of the Middle and Northern Urals was distinguished by the sable (*Martes zibellina*). Forest (lynx, and semi-aquatic (otter, European mink) species were the first to disappear from the fauna from south to north, followed by relatively "thermophilic" species (corsac, cave hyena) in passing northwards. The faunal composition included several species (*Cuon alpinus*, *Crocuta crocuta spelaea*, *Ursus spelaeus*, *Ursus savini*) which were absent from later periods. The ranges of the first two species

Table 1
Species composition of carnivore fauna from the Ural during the Late Pleistocene

Species	Faunal complex	MIS 5e		MIS 3			LGT			BAIC		
		MU[a]	SU	NU	MU	SU	NU	MU	SU	NU	MU	SU
Lynx lynx	European–Siberian	+	+	–	–	+	–	+	–	–	+	–
Panthera spelaea	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Crocuta crocuta spelaea	European–Siberian	–	–	–	+	+	–	–	–	–	–	–
Canis lupus	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Cuon alpinus	European–Siberian	–	–	–	–	+	–	–	–	–	–	–
Vulpes corsac	Siberian	–	–	–	+	+	–	–	+	–	–	+
Vulpes lagopus	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Vulpes vulpes	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Ursus arctos	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Ursus tibethanus	European–Siberian	+	–	–	–	–	–	–	–	–	–	–
Ursus spelaeus	European	+	+	+	+	+	–	–	–	–	–	–
Ursus savini	European–Siberian	+	+	+	+	+	–	–	–	–	–	–
Lutra lutra	European–Siberian	+	+	–	–	+	–	–	–	–	–	–
Gulo gulo	European–Siberian	+	–	+	+	+	+	+	+	+	+	+
Martes martes	European	–	–	–	–	+	–	–	+	–	–	+
Martes zibellina	Siberian	–	–	+	+	–	+	+	–	+	+	–
Meles leucurus	Siberian	–	–	–	–	–	–	–	–	–	–	–
Meles meles	European	+	+	–	–	–	–	–	–	–	+	–
Mustela erminea	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Mustela eversmanii	European–Siberian	+	+	+	+	+	+	+	+	+	+	+
Mustela lutreola	European	+	+	–	–	+	–	–	–	–	–	–
Mustela nivalis	European–Siberian	+	+	+	+	+	+	+	+	+	+	+

[a] NU – Northern Urals, MU – Middle Urals, SU – Southern Urals.

Table 2
Species ratio of the European–Siberian, European and Siberian faunal assemblages in the carnivore fauna of the Urals during the Late Pleistocene (%%)

Faunal complex	NU[a]				MU				SU			
	MIS 5e	MIS 3	LGT	BAIC	MIS 5e	MIS 3	LGT	BAIC	MIS 5e	MIS 3	LGT	BAIC
European–Siberian	–	84	90	90	81	79	91	84	79	77	82	82
European	–	8	0	0	19	7	0	8	21	17	9	9
Siberian	–	8	10	10	0	14	9	8	0	6	9	9
Number of species	–	12	10	10	15	14	11	10	13	18	11	11

[a] NU – Northern Urals, MU – Middle Urals, SU – Southern Urals.

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reduced and they did not inhabit the Urals later (Table 1). Two other species became extinct.

After the Last Glacial Maximum, the number of carnivores decreased. In the Late Glacial Transition (LGT) the fauna of the Northern Urals contained 10 species. There were 11 species in the Middle and the Southern Urals during this period (Table 1). The Late Glacial Transition fauna did not contain otter (*Lutra lutra*) and European mink (*Mustela lutreola*) whose ranges contracted. The faunas of the Northern and Middle Urals included the species of the European–Siberian and Siberian faunal complexes, while the Southern Urals contained the species of all the three complexes (Table 2). While sable, which is assigned to the Siberian faunal complex, inhabited the Northern and Middle Urals, the Southern Urals was distinguished by the presence of pine marten, which is assigned to the European faunal complex, and corsac, part of the Siberian faunal complex (Table 2).

European–Siberian and Siberian faunal complex, while the fauna of the Middle and Southern Urals contained those from all the three faunal complexes (Table 2). At the end of this period, cave lion (*Panthera spelaea*) went extinct.

The Early Holocene faunas have been studied in the Middle and Southern Urals (Table 3). The Early Holocene faunal composition of the Middle Urals and that of forest and steppe zones of the Southern Urals included the species of the European–Siberian, Siberian, and European faunal complexes (Table 4). The species from the European–Siberian complex dominated the faunas of all the areas. Range expansion resulted in reappearance of the otter (*Lutra lutra*) and European mink (*Mustela lutreola*) in the Uralian fauna. In the Early Holocene the Arctic fox (*Vulpes lagopus*) range began to decrease northwards, while the range of the steppe polecat (*Mustela eversmanii*) southwards. The Arctic fox disappeared from the fauna of the Southern Urals, but it persisted in the Middle Urals. The remnant population of the steppe polecat survived (Table 3).

Table 3
Species composition of carnivore fauna from the Urals during the Holocene and modern

Species	Faunal complex	NU[a]				MU			SU							
									"Mountain"				"Peneplain"			
		EH[b]	MH	LH	R	MH	LH	R	EH	MH	LH	R	EH	MH	LH	R
Lynx lynx	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–
Canis lupus	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Vulpes corsac	Siberian	–	–	–	–	–	–	–	+	+	–	–	+	+	+	+
Vulpes vulpes	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ursus arctos	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lutra lutra	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Gulo gulo	European–Siberian	+	+	+	+	+	+	+	+	+	+	–	–	+	–	–
Martes foina	European–Siberian	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Martes martes	European	–	–	+	+	+	+	+	+	+	+	+	–	+	+	–
Martes zibellina	Siberian	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–
Meles anakuma	Siberian	–	–	+	+	–	+	+	–	–	+	+	–	–	+	+
Meles meles	European	+	+	–	–	+	–	–	+	+	–	–	+	+	–	–
Mustela erminea	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mustela eversmanii	European–Siberian	+	–	–	–	–	–	–	+	+	+	+	+	+	+	+
Mustela lutreola	European	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mustela nivalis	European–Siberian	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mustela putorius	European	–	–	–	–	+	+	+	–	+	+	+	–	–	–	–
Mustela sibirica	Siberian	–	–	–	+	–	–	+	–	–	–	+	–	–	–	+

[a] NU – Northern Urals, MU – Middle Urals, SU – Southern Urals.
[b] EH – Early Holocene, MH – Middle Holocene, LH – Late Holocene, R – recent.

Table 4
Species ratio of the European–Siberian, European and Siberian faunal assemblages in the carnivore fauna of the Urals during the Holocene and modern (%%)

Faunal complex	NU[a]			MU				SU							
								«Mountain»				«Peneplain»			
	MH[b]	LH	R	EH	MH	LH	R	EH	MH	LH	R	EH	MH	LH	R
European–Siberian	75	66	62	77	58	61	58	69	64	71	64	70	73	70	64
European	17	17	15	15	33	23	21	23	29	22	22	20	18	10	9
Siberian	8	17	23	8	9	16	21	8	7	7	14	10	9	20	27
Number of species	12	12	13	13	12	13	14	13	14	14	14	10	11	10	11

[a] NU – Northern Urals, MU – Middle Urals, SU – Southern Urals.
[b] EH – Early Holocene, MH – Middle Holocene, LH – Late Holocene, R – recent.

During the Bølling – Allerød interstadial (BAIC), the faunas of the Northern and Southern Urals remained unchanged in comparison with those of the LGT (Table 1). Certain changes occurred in the faunal composition of the Middle Urals. It contained European badger (*Meles meles*). As a result, the faunal composition of the Northern Urals consisted of the species from the

During the Middle Holocene, the species of the European–Siberian faunal complex dominated the fauna of all the areas, but its share was noticeably smaller in the Middle Urals, than in the Northern and Southern Urals (Tables 3 and 4). The species of the European faunal complex closely follow those of the European–Siberian complex. As for the Siberian complex, it was represented by one species only in all the areas, the sable (*Martes zibellina*) in the Northern and Middle Urals, and corsac (*Vulpes corsac*) in the Southern Urals. The Arctic fox (*Vulpes lagopus*) suffered further range contraction and eventually disappeared from the Middle Uralian fauna, though its remnant population still survived in the Northern Urals. Remnant population of the corsac (*Vulpes corsac*) still persisted in the forest zone of the Southern Urals. Range expansion led to appearance of the polecat (*Mustela putorius*) in the fauna of the Middle Urals and the forest zone of the Southern Urals. At the same time, the pine marten (*Martes martes*) range started to spread fast and led to its appearance in the Middle Urals (Gasilin et al., 2014). Only during the Middle Holocene, wolverine (*Gulo gulo*) appeared in the faunal composition of the steppe zone of the Southern Urals (Table 3).

In the Late Holocene, the species of all three faunal complexes were represented in the faunas of all areas. The species of the European–Siberian complex dominated all the faunas (Table 3). The Siberian and European faunal complexes were represented by 1–4 species (Table 4). This period witnessed the end of a long process of range contraction of the steppe and tundra species. Thus, the Arctic fox (*Vulpes lagopus*) disappeared from the Northern Urals, while corsac (*Vulpes corsac*) dropped out of the forest zone of the Southern Urals (Table 3). Wolverine (*Gulo gulo*) withdrew from the steppe zone of the Southern Urals. Beach marten (*Mates foina*) appeared in fauna of forest part of Southern Urals only in the Late Holocene (Kosintsev, Gasilin, 2011; Gimranov, Kosintsev, 2015). At the onset of the Late Holocene, the Asian badger (*Meles leucurus*) forced out European badger (*Meles meles*) from the entire area of the Urals (Gasilin, Kosintsev, 2010).

The transition to modern fauna of the Uralian carnivores (Table 3) has taken place over the last 200 years. At this time the Siberian weasel (*Mustela sibirica*) appeared in the Urals. Northward range extension of the pine marten (*Martes martes*) led to its appearance in the Northern Urals. At the same time wolverine (*Gulo gulo*) and Beach marten (*Mates foina*) disappeared from the forest zone of the Southern Urals (Table 3). Modern fauna is still characterized by the dominance of the species from the European–Siberian faunal complex, though the share of the species from the Siberian faunal complex has increased (Table 4).

The analysis revealed that the carnivore faunal composition of the Urals in general and of its separate areas in particular underwent changes through the Late Pleistocene (Table 1) and Holocene (Table 3). The numbers of species and the shares of species assigned to European–Siberian, European, and Siberian faunal complexes changed in the faunal composition (Tables 2 and 4). The «megainterstadial» of the Last Glaciation (MIS 3) is characterized by the most prominent diversification of species, while in the Late Glacial Transition and the Bølling – Allerød interstadial the lowest number of species was recorded (Table 1). Species from the European–Siberian faunal complex dominated the faunas through the entire the Late Pleistocene and Holocene. The Late Pleistocene and Holocene show a general trend of fauna changes to a decreasing percentage of species from the European faunal complex and an increasing percentage of those from the Siberian faunal complex (Tables 2 and 4).

Changes in the carnivore faunal composition resulted from several processes. Eight species (*Crocuta crocuta spelaea*, *Cuon alpinus*, *Vulpes corsac*, *V. lagopus*, *Ursus thibetanus*, *Gulo gulo*, *Meles meles*, *Mustela eversmanii*) suffered from range contraction. Today, the ranges of four species (*Crocuta crocuta spelaea*, *Cuon alpinus Ursus thibetanus Meles meles*) are beyond the Urals completely. Four species (*Martes martes*, *Meles leucurus*, *Mustela putorius*, *Mustela sibirica*) expanded their ranges. Four species (*Lynx lynx*, *Lutra lutra*, *Martes foina*, *Mustela lutreola*) inhabited the Urals in some periods, but were absent in others. Thus, their ranges fluctuated. Five species (*Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela erminea*, *Mustela nivalis*) appeared consistently in the faunas of all the periods of study. One species (*Panthera spelaea*) was found in all the Late Pleistocene faunas, whereas two species (*Ursus spelaeus*, *Ursus savini*) persisted in the Uralian fauna only till the middle stage of the Late Pleistocene. The last three species went extinct. Thus, 16 out of 24 species underwent range shifts during the Late Pleistocene and Holocene. Range dynamics is apparently the principal cause of fauna changes, though species extinction also contributed to this process. These were exactly the same reasons for alterations of carnivore faunas in Europe (Sommer, Benecke, 2004, 2005; Turner, 2009; Stuart, 2014).

Considering the carnivore distribution in the Urals in the Late Pleistocene and Holocene, the range limits of certain species here were a bit further north than in other areas. Here, we found for the Eem interglacial period the northernmost localities of *Ursus thibetanus*, *U. savini*, *Meles meles* (Makhnevskaya Ledyanaya cave, 59°26′N, 57°41′E), *L. lynx* (Bobylek grotto, 56°23′N, 57°37′E). There are for the second half of the MIS 2 (Late Glacial Transition and the Bølling – Allerød interstadial) the northernmost localities of *Ursus spelaeus* and *U. savini* (Medvezh'ya cave, 62°00′N, 58°44 E), *Crocuta crocuta spelaea* (Makhnevskaya cave, 59°26′N, 57°41′E), *Martes zibellina* (Tain cave, 59°25′N, 57°38′E), *Mustela lutreola* (Viasher cave, 59°05′N, 57°39′E), *Meles meles* (Viasher cave, 59°05′N, 57°39′E), *Vulpes corsac* (Georgievskaya cave, 57°02′N, 59°34′E), *Cuon alpinus* (Ignatievskaya cave, 54°54′N, 57°47′E) dating the MIS 3 (Fig. 1). In the Urals there are northernmost localities of *Mustela eversmanii* (Medvezh'ya cave, 62°00′N, 58°44′E) and *M. meles* (Lun'evka III cave, 59°10′N, 57°36′E) (Fig. 1.). The eastern limit of the *U. spelaeus* range lay in the Urals in the Late Pleistocene: its remains were found only on the western slope of the Urals and were absent on the eastern slope. In the Urals are the extreme north-eastern Holocene localities of *M. foina* (Podpornaya cave, 52°57′N, 55°59′E), *M. eversmanii* (Koksharovsko-Yurinskaya, 1, 58°10′N, 61°20′E) and *M. lutreola* (Kaninskaya cave, 62°02′N, 58°10′E) (Fig. 1).

The time of extinction or range shifts of isolated species can be determined by radiocarbon dates obtained from their bones (Table A.2.). The available radiocarbon dates allow us to determine the time of the cave hyena (*Crocuta crocuta spelaea*) range contraction. Its bones gave 13 AMS dates (Table A.2.). 6 out of 13 dates are infinite. The latest dates were obtained from the bones of the Makhnevskaya cave (37700 ± 360, OxA-17003) in the Middle Urals and Ust-Katavskaya cave (35650 ± 450, OxA-10890) in the Southern Urals (Stuart, Lister, 2014). These dates are more ancient than those obtained from the localities situated in Central and Southern Europe and Britain (Stuart, Lister, 2014). This gives us good evidence to assume that the cave hyena's range contracted in the Urals earlier than in Europe.

The carnivore fauna of the Urals is distinguished by three species that went extinct in the Late Pleistocene, namely *Ursus spelaeus*, *Ursus savini* and *Panthera spelaea*. The cave lion (*Panthera spelaea*) gave 11 AMS dates. The latest dates were obtained from the bones of the Pymva-Shor 2 locality (12995 ± 90, Ua-14006) in the Northern Urals and localities Podzemnyskh okhotnikov (13500 ± 65, OxA-11349), Verkhnegubakhinskaya cave (13560 ± 70, OxA-10909) and Viasher cave (13570 ± 70, OxA-10908) in the Middle Urals (Table A.2.). These dates are close to the dates obtained from the cave lion bones from the localities of France, Yakutia and Alaska (Stuart and Lister, 2011). These data show that the extinction of the cave lion in the Urals was synchronous with its extinction in northern Eurasia and North America. The cave bear bones provided 16 AMS dates (Table A.2.). The latest dates were obtained from the bones from the Tayn cave (37190 ± 680 BP) and Geologov 3 cave (38480 ± 360, OxA-19669) in the Middle Urals and from the Asha 1 cave (47100 ± 900, OxA-16959) in the Southern Urals. These dates are more ancient than those obtained from the cave bear bones from Western Europe (Pacher and Stuart, 2008). The cave bear apparently went extinct in the Urals earlier than in Western Europe. Bones of the third extinct species, small cave bear *Ursus savini*, yielded only a few radiocarbon dates (Table A.2.). Of them, two AMS dates (31870 ± 190, OxA-16960; 36390 ± 270, OxA-16964) were obtained from the bones from the Kizelovskaya cave in the Middle Urals. These dates allow us to infer that the small cave bear became extinct in the Urals at the end of Bryansk Interstadial (Middle Weichselian, MIS 3). Generally, extinction of the carnivores in the Urals was synchronous with their extinction in northern Eurasia (Stuart, 2014).

5. Conclusions

We have studied the carnivore assemblages from the Late Pleistocene and Holocene localities of the Northern, Middle and Southern Urals. Analysis of the species composition of the carnivore fauna was performed for seven chronological periods: MIS 5e, MIS 3, mid-MIS 2 (LGT), late MIS 2 (BAIC), early MIS 1 (Preboreal-Boreal), mid-MIS 1 (Atlantic-Subboreal), late MIS 1 (Subatlantic). The MIS3 fauna consisted of 12 species in the Northern Urals, 14 species in the Middle Urals and 18 species in the Southern Urals. The Late Glacial Transition and the Bølling – Allerød interstadial faunas included 10–11 species. The faunal diversity and numbers increased in the Holocene: from 10 to 15 species inhabited different Uralian areas through different Holocene periods. Faunal composition comprised the species from European, Siberian and European–Siberian faunal complexes throughout all the Late Pleistocene and Holocene periods. Throughout all the periods it was dominated by the species from European–Siberian faunal complexes. The general trend of fauna changes is represented by a decreasing percentage of species from the European faunal complex and an increasing percentage of those from the Siberian faunal complex.

Faunal composition has changed due to two main reasons, range shifts and extinction. Sixteen out of 24 species that inhabited the Urals during the Late Pleistocene and Holocene underwent range shifts. Their ranges shifted in different directions. Eight species (*Crocuta crocuta spelaea*, *Cuon alpinus*, *Vulpes corsac*, *V. lagopus*, *Ursus thibetanus*, *Gulo gulo*, *Meles meles*, *Mustela eversmanii*) suffered from range contraction. Four (*Crocuta crocuta spelaea*, *Cuon alpinus*, *Ursus thibetanus*, *Meles meles*) are no longer found in the Urals. The ranges contracted during the Late Pleistocene (*Crocuta crocuta spelaea*, *Cuon alpinus*, *Ursus thibetanus*) and Holocene (*Vulpes corsac*, *V. lagopus*, *Gulo gulo*, *Meles meles*, *Mustela eversmanii*). Ranges of four species (*Martes martes*, *Meles leucurus*, *Mustela putorius*, *Mustela sibirica*) expanded. Three out of these four species (*Meles leucurus*, *Mustela putorius*, *Mustela sibirica*) appeared in the Urals for the first time. Range expansion occurred in the Holocene. Four species (*Lynx lynx*, *Lutra lutra*, *Martes foina*, *Mustela lutreola*) exhibited range fluctuations: while their ranges expanded during some periods and they were present in the Uralian fauna, during other periods their ranges contracted and they disappeared from the faunal composition. These fluctuations occurred both in the Pleistocene and Holocene. Five species (*Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela erminea*, *Mustela nivalis*) did not exhibit any range shifts throughout Late Pleistocene and Holocene. Three more species (*Panthera spelaea*, *Ursus spelaeus*, *Ursus savini*) did not undergo any range shifts, but these species went extinct during the Late Pleistocene. Two (*Ursus spelaeus*, *Ursus savini*) became extinct at the end of MIS 3 and one (*Panthera spelaea*) at the end of MIS 2.

Because the presence of some species in the Urals was restricted to certain periods or certain areas, these species lend themselves to biostratigraphy and relative dating of the deposits. The remains of the Asiatic black bear (*Ursus thibetanus*), dhole (*Cuon alpinus*), cave bear (*Ursus spelaeus*), small cave bear (*Ursus savini*), cave hyena (*Crocuta crocuta spelaea*) and cave lion (*Panthera spelaea*) can be used for relative dating of the Late Pleistocene deposits all over the Urals. The remains of the polecat (*Mustela putorius*) are useful for relative dating of the Middle and Late Holocene, while those of the Asian badger (*Meles leucurus*) for relative dating of the Late Holocene all over the Urals. The remains of the corsac (*Vulpes corsac*), Arctic fox (*Vulpes lagopus*), wolverine (*Gulo gulo*), beech marten (*Martes foina*), pine marten (*Martes martes*), European badger (*Meles meles*) and steppe polecat (*Mustela eversmanii*) are appropriate for relative dating of the deposits from different Holocene periods in some Uralian areas.

The history of the carnivore fauna in the Urals can be divided into the following principal stages: the MIS 5e fauna, the MIS 3 fauna, the fauna of the second half of the MIS 2, the MIS 1 fauna, and modern fauna. The changes in the carnivore fauna of the Urals, as well as of other European and Asian areas, occurred through the Late Pleistocene and Holocene to the present day.

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Appendix

Table A.1
Carnivore species composition and remains numbers from the main localities in the Urals

Species	Northern Urals														
	MIS3					Mid-MIS 2	Late MIS2	Mid-MIS 1				Late MIS 1			
	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Lynx lynx	–	–	–	–		–	–	2	–	–	1	–	3	–	1
Panthera spelaea	3	–	–	2	1	6	7	–	–	–	–	–	–	–	–
Crocuta crocuta spelaea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Canis lupus	–	79	52	4	27	208	103	14	2	1	1	16	13	–	1
Cuon alpinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vulpes corsac	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vulpes lagopus	–	513	125	92	297	1003	103	20	2	7	5	3	12	–	–
Vulpes vulpes	–	50	–	–	8	10	1	5	37	19	2	–	6	10	9
Ursus arctos	1	338	62	–	3	–	3	1210	40	43	–	–	1128	61	2

(continued on next page)

Table A.1 (*continued*)

Species	Northern Urals														
	MIS3					Mid-MIS 2	Late MIS2	Mid-MIS 1				Late MIS 1			
	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ursus tibetanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ursus spelaeus	253	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ursus savinii	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lutra lutra	–	–	–	–		–	–	16	–	12	3	39	43	13	6
Gulo gulo	–	–	–	–	–	11	–	33	–	–	–	26	76	–	2
Martes foina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Martes martes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Martes zibellina	–	1	4		20	9	6	61	16	62	53	–	77	99	146
Meles leucurus	–	–	–	–		–	–	–	–	–	–	–	2	–	–
Meles meles	–	–	–	–		–	–	6	–	7	1	–	–	–	–
M. erminea	–	28	3	16	86	32	–	–	1	9	4	–	–	–	34
M. eversmanni	–	18	1	–	2	21	2	–	–	6		–	–	–	–
M. lutreola	–	–	–	–	–	–	–	2	–	–	–	–	–	1	–
M. nivalis	–	26	1	15	49	18	2	–	–	13	14	–	–	–	49
M. putorius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Species	Middle Urals																		
	MIS 5e		MIS3		Mid-MIS 2						Late MIS2			Early MIS 1					
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Lynx lynx	–	–	–	–	1	–	–	–	2	–	–	–	–	1	–	–	–	–	–
Panthera spelaea	1	–	2	–	1	10	–	–	–	–	–	–	–	–	–	–	–	–	–
Crocuta crocuta spelaea	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Canis lupus	7	20	30	4	13	17	8	11	39	34	–	2	–	–	1	5	21	20	1
Cuon alpinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vulpes corsac	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Vulpes lagopus	1	47	27	5	123	44	15	24	104	162	8	64	4	8	2	12	–	8	16
Vulpes vulpes	3	14	9	–	–	5	7	11	7	29	–	1	2	1	7	4	–	–	5
Ursus arctos	2	–	–	–	4	92	7	15	2	2	4	1	1	2	–	11	5	–	2
Ursus tibetanus	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Ursus spelaeus	23	955	1080	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ursus savinii	41	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lutra lutra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Gulo gulo	–	1	–	–	–	–	2	1	3	9	–	–	–	–	–	1	–	3	–
Martes foina	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–
Martes martes	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–
Martes zibellina	–	21	3	2	2	7	–	–	11	8	–	4	1	228	23	–	4	6	1
Meles leucurus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Meles meles	8	13	–	–	–	–	–	–	–	–	2	–	–	–	–	1	8	1	1
M. erminea	–	–	1	–	88	–	–	–	14	4	2	5	9	–	14	5	–	10	1
M. eversmanni	–	–	3	–	–	2	–	3	–	4	–	5	–	–	–	–	1		2
M. lutreola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
M. nivalis	–	–	1	–	200	–	–	–	1	1	–	5	43	–	17	4	–		2
M. putorius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Species	Middle Urals				Sothern Urals											
	Mid-MIS 1		Late MIS 1		MIS 5e	MIS3			Mid-MIS 2					Mid-MIS 1	Late MIS 1	
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Lynx lynx	–	–	1	2	1	–	–	–	–	–	–	–	–	1	–	–
Panthera spelaea	–	–	–	–	–	5	4	–	2	–	–	–	–	–	–	–
Crocuta crocuta spelaea	–	–	–	–	–	28	4	45	–	–	–	–	–	–	–	–
Canis lupus	1	2	5	26	3	55	61	18	11	2	1		2	1	11	–
Cuon alpinus	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Vulpes corsac	–	–	–	–	–	–	–	–	4	–	–	1	9	–	–	–
Vulpes lagopus	–	–	–	–	–	28	30	5	18	7		4	18	–	–	–
Vulpes vulpes	–	3	62	15	7	35	11	6	1	6	1	2	39	3	19	1
Ursus arctos	13	8	11	95	–	3	–	9	1	–	–	3	2	–	26	79
Ursus tibetanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ursus spelaeus	–	–	–	–	457	54	343	–	–	–	–	–	–	–	–	–
Ursus savinii	–	–	–	–	16	–	–	–	–	–	–	–	–	–	–	–
Lutra lutra	5	–	7	11	–	1	–	–	–	–	–	–	–	–	6	3
Gulo gulo	–	1	5	1	–	2	–	–	1	–	–	–	1	–	–	–
Martes foina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Martes martes	1	5	–	13	–	1	2	–		–	1	–	–	1	24	27
Martes zibellina	41	21	105	1201	–	–	–	–	–	–	–	–	–	–	–	–
Meles leucurus	–	–	–	4	–	–	–	–	–	–	–	–	–	–	2	–
Meles meles	1	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–
M. erminea	–	2	1	4	1	–	2	–	3	1	21	24	–	67	86	–
M. eversmanni	–		–	–	–	–	–	–	–	2	–	1	1	1	18	–

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Table A.1 (*continued*)

Species	Middle Urals				Sothern Urals											
	Mid-MIS 1		Late MIS 1		MIS 5e	MIS3			Mid-MIS 2					Mid-MIS 1	Late MIS 1	
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
M. lutreola	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
M. nivalis	–	–	–	1	1	–	–	–	1	6	23	4	1	38	9	1
M. putorius	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–

*1 – Medvezhaya cave (inside gallery); 2 – Zhilische Sokola (pit 2); 3 – Usoltsevskaya cave; 4 – Cheremukhovo 1-1 (strata 9–12); 5 – Cheremukhova 1–4; 6 – Medvezhaya cave (strata grayish-brown "B" loamy soil); 7 – Medvezhaya cave (strata grey loamy soil); 8 – Kaninskaya cave (layer of Bronze age); 9 – Burmantovo (pit 1); 10 – Lisiy; 11 – Cheremukhovo 1-1 (strata 6); 12 – Uninskaya cave; 13 – Kaninskaya cave (layer of Iron age); 14 – Kamen' Pysannyi; 15 – Cheremukhovo 1-1 (strata 1–4); 16 – Makhnevskaya-Ledyanaya cave; 17 – Bobylek (srata 5–6); 18 – Grotto Bolshoj Glukhoj (strata 9); 19 – Grotto Bolshoj Glukhoj (strata 8); 20 – Rasik; 21 – Verkhnegubakhinskaya cave; 22 – Bezymaynnyj; 23 – Zotinskij; 24 – Bobylek (strata 4); 25 – Pershinskaya cave; 26 – Lun'evka III cave; 27 – Dyrovatyj-na-Chusovoj; 28 – Lobvinskaya cave; 29 – Grotto Bolshoy Glukhoy (strata 2); 30 – Lobvinskaya cave; 31 – Dyrovatyj-na-Serge; 32 – Koksharovsko-Ur'inskaya; 33 – Bobylek (strata 3); 34 – Ust'-Koyvinskaya; 35 – Shigirskoe gorodische; 36 – Bobylek (strata 2); 37 – Turistov cave; 38 – Bobylek (strata 2); 39 – Barsuchyi dol; 40 – Ust'-Katavskaya cave; 41 – Ignat'evskaya cave; 42 – Smelovskaya cave; 43 – Nikol'skaya cave; 44 – Ignat'evskaya cave; 45 – Bayslan-Tash (strata 4); 46 – Balatukay; 47 – Syrtinskaya cave (strata 3); 48 – Bayslan-Tash (strata 3); 49 – Bayslan-Tash (strata 2); 50 – Podpornaya cave.

Appendix

Table A.2
Radiocarbon dates for Quaternary carnivore remains from the localities of the Urals

Species	Date(a)	±; (>) infinite dates	Lab. No (b)	Lat °N	Long °E	Localities	Dated object
Panthera spelaea	12995	90	Ua-14006	67,10	60,51	Pymva-Shor 2	Bone
Panthera spelaea	54500	2600	OxA-10907	60,42	60,22	Shaytanskaya cave	Metapodia
Panthera spelaea	29120	230	OxA-10894	60,24	60,03	Cheremuchovo 1-1 cave	Metapodia
Panthera spelaea	30140	240	OxA-10895	60,24	60,03	Cheremuchovo 1–4 cave	Dentes
Panthera spelaea	>49600		OxA-10888	59,25	57,46	Tayn cave	Pelvis
Panthera spelaea	13500	65	OxA-11349	59,17	57,50	Podzemnykh okhotnikov	Calcaneus
Panthera spelaea	13570	70	OxA-10908	59,05	57,40	Viasher cave	Vertebrae
Panthera spelaea	13560	70	OxA-10909	58,53	57,38	Verkhnegubakhinskaya cave	Scapula
Panthera spelaea	14750	70	OxA-10910	58,40	57,34	Kholodniy grotto	Bone
Panthera spelaea	41900	1200	OxA-10887	54,54	57,47	Ignatievskaya cave	Dentes
Panthera spelaea	>39800		OxA-10845	54,10	56,51	Pobeda cave	Bone
Crocuta crocuta spelaea	37700	360	OxA-17003	59,26	57,41	Makhnevskaya cave	Mandibula
Crocuta crocuta spelaea	>47600		OxA-10889	55,11	58,38	Sikiyaz-Tamak 7	Dentes
Crocuta crocuta spelaea	35650	450	OxA-10890	54,56	58,08	Ust'-Katavskaya cave	Bone
Crocuta crocuta spelaea	>59200		OxA-19533	54,56	58,08	Ust'-Katavskaya cave	Dentes
Crocuta crocuta spelaea	>40100		OxA-10846	54,54	57,47	Ignatievskaya cave	Bone
Crocuta crocuta spelaea	40240	380	OxA-19660	54,54	57,47	Ignatievskaya cave	Mandibula
Crocuta crocuta spelaea	44300	600	OxA-19659	54,54	57,47	Ignatievskaya cave	Dentes
Crocuta crocuta spelaea	47500	900	OxA-19537	54,54	57,47	Ignatievskaya cave	Dentes
Crocuta crocuta spelaea	>62300		OxA-19658	54,54	57,47	Ignatievskaya cave	Cranium
Crocuta crocuta spelaea	51400	1500	OxA-19536	54,51	59,58	Ustinovo grotto	Dentes
Crocuta crocuta spelaea	46200	1500	OxA-17004	53,20	59,00	Smelovskaya 2 cave	Dentes
Crocuta crocuta spelaea	>59800		OxA-19535	53,20	59,00	Smelovskaya 2 cave	Dentes
Crocuta crocuta spelaea	>60800		OxA-19534	53,20	59,00	Smelovskaya 2 cave	Dentes
Canis lupus	40035	1825	TUa-3525	66,34	62,25	Mamontovaya Kur'ya	Bone
Canis lupus	13675	70	AAR11385	59,00	58,00	Caves from r. Kos' va	Radius
Vulpes corsac	25220	130/120	GrA-41244	57,02	59,34	Georgievskaya cave	Pelvis
Vulpes lagopus	10180	50/45	GrA-42216	64,55	51,44	Pizhma 1	Calcaneus
Ursus savini	>37890	1200	SOAN-4528	59,25	57,46	Tayn cave	Bone
Ursus savini	31870	190	OxA-16960	59,06	57,65	Kizelovskaya cave	Mandibula
Ursus savini	33980	400	LE-2334	59,06	57,65	Kizelovskaya cave	Bone
Ursus savini	36390	270	OxA-16964	59,06	57,65	Kizelovskaya cave	Cranium
Ursus savini	>48500		no.?	59,06	57,65	Kizelovskaya cave	Cranium
Ursus savini	22750	1210	LU-3714	54,33	57,16	Verkhnyaya cave	Bone
Ursus savini	26320	1790	GIN-14244	54,33	57,16	Imanaj cave	Vertebrae, humerus
Ursus spelaeus	28390	890	SOAN-4799	62,05	58,05	Medvezh'ya cave	Femur
Ursus spelaeus	>48600		no.?	62,05	58,05	Medvezh'ya cave	Bone
Ursus spelaeus	>16470	560	SOAN-4516	59,25	57,46	Tayn cave	Humerus
Ursus spelaeus	26980	710	SOAN-4527	59,25	57,46	Tayn cave	Femur
Ursus spelaeus	37190	680	no.?	59,25	57,46	Tayn cave	Bone
Ursus spelaeus	39190	360	OxA-16961	59,25	57,46	Tayn cave	Cranium
Ursus spelaeus	39580	360	OxA-16965	59,25	57,46	Tayn cave	Cranium
Ursus spelaeus	39630	360	OxA-16962	59,25	57,46	Tayn cave	Cranium
Ursus spelaeus	40340	370	OxA-16963	59,25	57,46	Tayn cave	Cranium
Ursus spelaeus	47600	900	OxA-16958	59,25	57,46	Tayn cave	Mandibula
Ursus spelaeus	19550	230	SOAN-4526	59,06	57,65	Viasher cave	Bone
Ursus spelaeus	22650	670	SOAN-4515	59,06	57,65	Viasher cave	Humerus
Ursus spelaeus	27070	810	SOAN-4517	58,46	57,43	Geologov 3 cave	Femur
Ursus spelaeus	27580	950	SOAN-4518	58,46	57,43	Geologov 3 cave	Femur
Ursus spelaeus	38480	360	OxA-19669	58,46	57,43	Geologov 3 cave	Mandibula

(*continued on next page*)

Table A.2 (*continued*)

Species	Date(a)	±; (>) infinite dates	Lab. No (b)	Lat °N	Long °E	Localities	Dated object
Ursus spelaeus	>64400		no.?	58,16	57,59	Bolshoi Glukhoy	Bone
Ursus spelaeus	29040	385	SOAN-7043	55,00	57,18	Asha 1	Bone
Ursus spelaeus	47100	900	OxA-16959	55,00	57,18	Asha 1	Mandibula
Ursus spelaeus	>55500		OxA-19666	55,00	57,18	Asha 1	Dentes
Ursus spelaeus	>61500		OxA-19667	55,00	57,18	Asha 1	Metacarpus
Ursus spelaeus	>35900		AA-90659	54,55	57,53	Serpievskaya 2 cave	Bone
Ursus spelaeus	44050		no.?	54,55	57,53	Serpievskaya 2 cave	Bone
Ursus spelaeus	>27500		IPAE-25	54,54	57,47	Ignatievskaya cave	Bone
Ursus spelaeus	>27500		IEMEZ-723	54,54	57,47	Ignatievskaya cave	Bone
Ursus spelaeus	28700	1050	LU-3715	54,33	57,16	Zapovednaya cave	Bone
Ursus spelaeus	37250		LU-3876	54,33	57,16	Zapovednaya cave	Bone
Ursus spelaeus	>46600		LU-5135	54,33	57,16	Zapovednaya cave	Bone
Ursus spelaeus	>50200		LU-5134	54,33	57,16	Zapovednaya cave	Bone
Ursus spelaeus	>62400		OxA-19670	54,33	57,16	Zapovednaya cave	Bone
Ursus spelaeus	27500	350	SOAN-5145	54,10	56,51	Pobeda cave	Bone
Ursus spelaeus	47600	900	OxA-19679	54,10	56,51	Pobeda cave	Metatarsus
Ursus spelaeus	60600	3600	OxA-19678	54,10	56,51	Pobeda cave	Metacarpus
Ursus arctos	12045	79	NSKA-AA-847	62,05	58,05	Medvezh'ya cave	Phalanx 2
Ursus arctos	29527	320	NSKA-AA-846	62,05	58,05	Medvezh'ya cave	Humerus
Ursus arctos	2046	33	NSKA-848	62,00	58,09	Kaninskaya cave	Mandibula
Ursus arctos	27100	250	SOAN-7916	61,55	60,05	Severnaya cave	Bone
Ursus arctos	8350	750	OxA-no.?	60,43	60,17	Lakseyskaya cave	Mandibula
Ursus arctos	15840	70/60	GrA-39266	57,27	61,27	Pershinskaya cave	Ulna
Ursus arctos	2816	35	no.?	54,54	57,47	Zhemchuzhnaya cave	Bone
Martes zibellina	5600	70	Ua-15104	67,10	60,51	Pymva-Shor 1	Bone
Meles meles	7359	79	AA-102248	62,00	58,09	Kaninskaya cave	Mandibula
Meles meles	11340	50	GrA-39271	59,10	57,55	Lunievka III	Mandibula
Meles meles	11570	50	GrA-39270	59,05	57,39	Viasher cave	Bone

[a] Dates are not calibrated.
[b] Laboratory codes for dates: AA – University of Arizona, Tucson, USA; AAR – University of Aarhus AMS Laboratory; GIN – Geological Institute, Russian Academy of Sciences (RAS); GrA – Groningen Rad. Lab., The Netherlands; IEMEG – Institute of Animal Evolution Morphology and Ecology, RAS; IPAE – Institute of Plant and animal Ecology, Ural division of RAS; LE – Institute of Archeology, Leningrad Branch (currently Institute of the History of Material Culture), RAS; LU – St. Petersburg Univ., RAS; NSKA – AMS pretreatment laboratory Centre of Cenozoic Geochronology Institute of Archaeology & Ethnography Siberian Branch of Russian Academy of Sciences; OxA – Oxford Accelerated, University of Oxford, UK; SOAN – Institute of Geology and Geophysics, Siberian Branch, RAS; TUa – Prepared in Trondheim, measured in Uppsala Univ., Sweden; Ua – Laboratory University of Uppsala, Sweden.

References

Aristov, A.A., Baryshnikov, G.F., 2001. The Mammals of Russia and Adjacent Territories. Carnivores and Pinnipeds. Zoological Institution of RAS Press, St. Petersburg (in Russian).

Bachura, O., Kosintsev, P., 2007. Late Pleistocene and Holocene small- and large-mammal faunas from the Northern Urals. Quaternary International 160, 121–128.

Bachura, O.P., Plasteeva, N.A., 2005. Holocene mammal fauna from Burmantovskiy cave deposits at the North Urals. In: Kosintsev, P.A. (Ed.), Ural and Siberia Faunas at Pleistocene and Holocene Times. Riphey Press, Chelyabinsk, pp. 38–55 (in Russian).

Bachura, O.P., Strukova, T.V., 2002. Mammal bone remains from the site Cheremukhovo-1 (pit 4). In: Kosintsev, P.A. (Ed.), Urals Fauna at Pleistocene and Holocene Times. University Press, Ekaterinburg, pp. 37–56 (in Russian).

Baryshnikov, G.F., 2001. The Pleistocene Black Bear (Ursus Thibetanus) from the Urals (Russia), vol. 32, pp. 33–44. Lynx (Praha).

Baryshnikov, G.F., 2007. Ursidae. Mammals. V. I, Issue 5. Fauna of Russia and Neighbouring Countries, New Series, vol. 147 (in Russian).

Chotinskiy, N.A., Klimanov, V.A., 2002. The Holocene Vegetation. Dynamics of Terrestrial Landscape Components and Inland and Marginal Seas of Northern Eurasia during the Last 130000 Years. Atlas-monograph "Evolution of Landscape and Climates of Northern Eurasia. Late Pleistocene – Holocene – Elements of Prognosis. II General Paleogeography". Geos Press, Moscow, pp. 89–105 (in Russian).

Crégut-Bonnoure, E., 1997. The Saalian *Ursus thibetanus* from France and Italy. Geobios 30, 285–294.

Danukalova, G., Yakovlev, A., Osipova, E., Alimbekova, L., Yakovleva, T., Kosintcev, P., 2011. Biostratigraphy of the Late Upper Pleisticene (Upper Neopleisticene) to Holocene deposits of the Belaya River Valley (Southern Urals, Russia). Quaternary International 231, 28–43.

Fadeeva, T.V., Kosintsev, P.A., Kadebskaya, O.I., Maksimova, E.G., 2011. Resalts of research of zoogene deposits of Makhnevskaya Ledyanaya (Perm region). In: Maksimovich, N.G. (Ed.), Caves, Issue 34. Perm State University, Perm, pp. 71–99 (in Russian).

Faustova, M.A., 1994. Deglaciation and the types of glacial relief on the territory of European Soviet Union. In: Palaeogeographic Base of Modern Landscapes. Nauka Press, Moscow, pp. 30–40 (in Russian).

Gasilin, V.V., Kosintsev, P.A., Razhev, D.I., Fadeeva, T.V., 2014. The Geographic Ranges of *Martes* Species (Carnivora, Mustelidae) in the Middle Urals in the Late Pleistocene and Holocene. Biology Bulletin 41 (8), 672–680.

Gasilin, V.V., Kosintsev, P.A., 2010. Replasement of the European Badger (*Meles meles* L., 1758) by the Asian Badger (*Meles leucurus* Hodgson, 1847) at the Boundary between Europe and Asia in the Holocene Epoch. Doklady Biological Sciences 432, 227–229.

Gasilin, V.V., Kosintsev, P.A., 2012. Identification of the badgers (Carnivora, Mustelidae) Europe (*Meles meles* L. 1758) and North Asia (Meles leucurus L. Hodgson, 1847) according to cranium and mandibula. Zoologicheskiy Zhurnal 91 (4), 475–485 (in Russian).

Gasilin, V.V., Kosintsev, P.A., 2013. Diagnosis species of the subgenus Martes str. (Carnivora, Mustelidae) on the metric characteristics of mandibles. Zoologicheskiy Zhurnal 92 (2), 221–230 (in Russian).

Gimranov, D.O., 2009. Stratigraphy and taphonomy of hunting sites of Palaeometal and Early Iron Age periods in Podpornaya cave (river Nugush, the Southern Urals). In: Mazhitov, N.A. (Ed.), XLI International Ural-Volga Archeological Conference of Students and Young Scientists. RIC Bash. State Univ. Press, Ufa, pp. 87–90 (in Russian).

Gimranov, D.O., 2015. Morphotypical variability of teeth in *Martes martes* and *Martes zibellina* (Carnivora, Mustelidae). Zoologicheskiy Zhurnal 94 (5), 560–569 (in Russian).

Gimranov, D.O., Kosintsev, P.A., 2015. Differentiation of three *Martes* species (*M. martes*, *M. zibellina*, *M. foina*) by tooth morphotypes. Comptes Rendus Palevol. http://dx.doi.org/10.1016/j.crpv.2015.06.007.

Gorchakovskiy, P.L., 1975. Vegetative World of Mountain Ural. Moscow. (In Russian).

Grichuk, V.P., 2002. The Late Pleistocene Vegetation. Dynamics of Terrestrial Landscape Components and Inland and Marginal Seas of Northen Eurasia during the Last 130000 Years. Atlas-monograph "Evolution of Landscape and Climates of Northern Eurasia. Late Pleistocene – Holocene – Elements of Prognosis. II Ceneral Paleogeography". Geos Press, Moscow, pp. 64–89 (in Russian).

Knapp, M., Roland, N., Weinstock, J., Baryshnikov, G., Sher, A., Nagel, D., Rabeder, G., Pinasi, R., Schmidt, H.A., Hofreiter, M., 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Molecular Ecology 18, 1225–1238.

Kosintsev, P.A., 1996. Large mammal fauna of the North Urals in the Late Pleistocene and Holocene. In: Smirnov, N.G. (Ed.), Materials and Research on History of the Recent Urals Fauna. Yekaterinburg Press, Yekaterinburg, pp. 84–109 (in Russian).

Kosintsev, P., 2007. Late Pleistocene large mammal faunas from the Urals. Quaternary International 160, 112–120.

Kosintsev, P.A., Bachura, O.P., 2013. Late Pleistocene and Holocene mammal fauna of the Southern Urals. Quaternary International 284, 161–170.

Kosintsev, P.A., Bachura, O.P., 2014. Formation of recent ranges of mammals in the Urals during the Holocene. Biology Bulletin 41 (7), 629–637.

Kosintsev, P.A., Bachura, O.P., 2005. New Holocene sites of large mammals remains at the Northern Urals. In: Kosintsev, P.A. (Ed.), Urals Fauna at Pleistocene and Holocene Times. University Press, Yekaterinburg, pp. 148–168 (in Russian).
Kosintsev, P.A., Bachura, O.P., 2015. A mass burial of brown bears (*Ursus arctos* L., 1758) from the Upper Pleistocene of the Northern Urals. Doklady Biological Sciences 462, 128–130.
Kosintsev, P.A., Gasilin, V.V., 2011. Historical change of North-East boundary of the Stone Marten (*Martes foina Erxleben, 1777*). Doklady Biological Sciences 436, 139–141.
Kosintsev, P.A., Orlova, M.V., 2002. Large mammals from the deposits in the caves "Lobva" and "Lobva 1" (Mamyachenkova). In: Kosintsev, P.A. (Ed.), Urals Fauna at Pleistocene and Holocene Times. University Press, Ekaterinburg, pp. 136–145 (in Russian).
Kosintsev, P.A., Plasteeva, N.A., 2009. Holocene large mammals of the Kama Cisural region. Bulletin of Moscow Society of Naturalists. Biological series 114 (5), 36–42 (in Russian).
Kosintsev, P.A., Vorob'ev, A.A., 2001. Biology of Large Cave Bear (*Ursus spelaeus* Ros. Et Hein.) in the Ural Mountains. In: Rozanov, A. Yu (Ed.), Mammoth and its Environment: 200 Years of Investigations. GEOS Press, Moscow, pp. 266–278 (in Russian).
Kühl, N., Litt, T., 2003. Quantitative time series reconstruction of Eemian temperature at three European sites using pollen data. Vegetation History and Archaeobotany 12, 205–214.
Kulik, I.L., 1980. The interosculation of mammal faunal assemblages. In: Voronov, A.G., Drozdov, N.N. (Eds.), Modern Problems of Zoogeography. Nauka Press, Moscow, pp. 272–284 (in Russian).
Kuzmina, I.E., 1971. Forming of theriofauna of the North Urals during the Late Anthropogene. In: Vereshchagin, N.R. (Ed.), Materials on the Faunas of Anthropogene of the USSR. Proceedings of the Zoological Institute, vol. 49, pp. 44–122. Leningrad. (in Russian).
Kuzmina, I.E., 1975. Some data on mammals of the Middle Urals in the Late Pleistocene. Bulletin of the Commission on Study of Quaternary Period 43, 63–77 (in Russian).
Kuzmina, I.E., 2002. Cave bears of the urals. In: Kosintsev, P.A. (Ed.), Urals Fauna at Pleistocene and Holocene Times. University Press, Ekaterinburg, pp. 3–23 (in Russian).
Kuzmina, I.E., Sablin, M.V., Tsyganova, S.A., 1999. Species composition and morphological characteristics of mammals from the grotto Big Blind in the Middle Urals. issue 3. In: Chairkin, S.E. (Ed.), Protection of the Archaeological Research in the Middle Urals. Bank kulturnoy informatsii Press, Yekaterinburg, pp. 4–14 (in Russian).
Kuzmina, S.A., 2000. Faunal data from the Late-Palaeolithic site Smelovskaya II in the South Urals. In: Kosintsev, P.A. (Ed.), Pleistocene and Holocene Urals Faunas. Rifey Press, Chelyabinsk, pp. 137–153 (in Russian).
Kuznetsov, B.A., 1950. Studies in Zoogeographical Zoning of the USSR. Moskovskoe Obschestvo Ispytatelej Prirody Press, Moscow (in Russian).
Mangerud, J., 1989. Correlation of the Eemian and the Weichselian with deep sea oxygen isotope stratigraphy. Quaternary International 314, 1–4.
Markova, A.K., Kolfschoten, T., van Bohncke, S., Kosintsev, P.A., Mol, J., Puzachenko, A. Yu, Simakova, A.N., Smirnov, N.G., Verpoorte, A., Golovachev, I.B., 2008. Evolution of European Ecosystems during Pleistocene – Holocene Transition (24–8 kyr BP). KMK Scientific Press, Moscow (in Russian).
Marvin, M. Ya, 1969. Terrestrial Vertebrate Fauna of the Urals. Uralskiy Gos. Universitet Press, Sverdlovsk (in Russian).
Monchot, H., Gendron, D., 2010. Disentangling long bones of foxes (*Vulpes vulpes* and *Alopex lagopus*) from arctic archaeological sites. Journal of Archaeological Science 37, 799–806.
Musil, R., 2005-2006. Die Bärenpopulation von Bilzingsleben – eine neue mittelpleistozäne Art. Munibe 57, 67–101.
Nagel, D., Rabeder, G., 2000. Mittelpleistozäne Säugetierreste aus einer Spaltenfüllung bei Mannersdorf am Leithagebirge (Niederösterreich). Beiträge zur Paläontologie 25, 1–9.
Pacher, M., Stuart, A.J., 2008. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas 38, 189–206.
Petrov, A.N., Kosintsev, P.A., 2005. Mammal fauna from cave "Turistov" (Middle urals). In: Kosintsev, P.A. (Ed.), Ural and Siberia Faunas at Pleistocene and Holocene Times. Riphey Press, Chelyabinsk, pp. 169–189 (in Russian).
Pionnier-Capitan, M., Bemilli, C., Bodu, P., Celerier, G., Ferrie, J.G., Fosse, Ph, Garcia, M., Vigne, J.D., 2011. New evidence for Upper Palaeolithic small domestic dogs in South-Western. Europe. Journal of Archaeological Science 38, 2123–2140.
Ponomarev, D., Puzachenko, A., Bachura, O., Kosintsev, P., van der Plicht, J., 2013. Mammal fauna during the Late Pleistocene and Holocene in the far northeast of Europe. Boreas 42, 779–797.
Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.-L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. Journal of Geophysical Research 111, 2156–2202.
Razhev, D.I., Kosinsev, P.A., Ulitko, A.I., 2005. Large mammal fauna of the Late Pleistocene and Holocene from cave Bobilek (Middle Urals). In: Kosintsev, P.A. (Ed.), Ural and Siberia Faunas at Pleistocene and Holocene Times. Riphey Press, Chelyabinsk, pp. 190–211 (in Russian).
Ripol, M.P., Peretz, J.V.M., Serra, A.S., Tortosa, J.E.A., Montañana, I.S., 2010. Presence of the genus, Cuon in upper Pleistocene and initial Holocene sites of the Iberian Peninsula: new remains identified in archaeological contexts of the Mediterranean region. Journal of Archaeological Science 37 (3), 437–450.
Smirnov, N.G., Bolshakov, V.N., Kosintsev, P.A., Panova, N.K., Korobeynikov, Yu.I., Olshvang, V.N., Erokhin, N.G., Bikova, G.V., 1990. Historical Ecology of Animals of the South Urals Mountains. Uralskoe Otd. Akademyi Nauk SSSR Press, Sverdlovsk (in Russian).
Smirnov, N.G., 1993. Small Mammals of the Middle Urals in the Late Pleistocene and Holocene. UIF Nauka Press, Yekaterinburg (in Russian).
Smirnov, N.G., Kosintsev, P.A., Kuzmina, E.A., Izvarin, E.P., Kropacheva, Yu.E., 2014. The ecology of quaternary mammals in the urals. Russian Journal of Ecology 45 (6), 449–455.
Sommer, R., Benecke, N., 2005. Late-Pleistocene and early Holocene history of the canid fauna of Europe (Canidae). Mammalian Biology 70 (4), 227–241.
Sommer, R., Benecke, N., 2004. Late- and Post-Glacial history of the mustelid fauna of Europe (Mustelidae). Mammalian Reviews 34, 249–284.
Stephanovskiy, V.V., Borodin, A.V., 2002. Reference Eopleistocene–Lower Neopleistocene Section of the South Transurals Region. Stratigraphy and Geological Correlation 10 (4), 391–401.
Strukova, T.V., Bachura, O.P., Borodin, A.V., Stefanovskii, V.V., 2006. Mammal Fauna First Found in Alluvial-Speleogenic Formations of the Late Neopleistocene and Holocene, Northern Urals, Locality Cheremukhovo-1. Stratigraphy and Geological Correlation 14 (1), 91–101.
Stuart, A.J., 2014. Late Quaternary megafaunal extinctions on the continents: a short review. Geological Journal. http://dx.doi.org/10.1002/gj.2633.
Stuart, A.J., Lister, A.M., 2011. Extinction chronology of the cave lion *Panthera spelaea*. Quaternary Science Reviews 30, 2329–2340.
Stuart, A., Lister, A., 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. Quaternary Science Reviews 96, 106–116.
Svendsen, J.I., Heggen, H.P., Hufthammer, A.K., Mangerud, J., Pavlov, P., Roebroeks, W., 2010. Geo-archaeological investigations of Palaeolithic sites along the Ural Mountains – on the northern presence of humans during the last Ice Age. Quaternary Science Reviews 29, 3138–3156.
Svensson, A., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Davies, S.M., Johnsen, S.J., Muscheler, R., Parrenin, F., Rasmussen, S.O., Rothlisberger, R., Seierstad, I., Steffensen, J.P., Vinther, B.M., 2008. A 60,000 year Greenland stratigraphic ice core chronology. Climate of the Past 4, 47–57.
Torres, T. de, 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Ibérico: I. Filogenia; Distribución estratigráfica y geográfica. Estudio anatómico y métrico del cráneo (Bears (Mammalia, Carnivora, Ursidae) from Pleistocene of the Iberian peninsula: I. Phylogeny; Stratigraphical and geographical distribution; Morphometrical studies on the skull). Boletin Geológico y Minero 99, 3–46 (in Spanish).
Tuner, A., 2009. The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. Journal of Quaternary Science 24, 991–1005.
Ulitko, A.I., 2006. Holocene mammals from karst cavities of the Middle Urals. In: Savinetsky, A.B. (Ed.), Dynamics of the Recent Ecosystems over the Holocene. KMK Scientific Press, Moscow, pp. 243–247 (in Russian).
Ulitko, A.I., Kuzmina, E.A., Kropachova, Yu.E., 2011. Mammals the Late Paleolithic Southern Ural (based on Syrtinskaya caves). In: Matveeva, N.P., Bagashev, A.N. (Eds.), Ecology of Ancient and Traditional Societies, Issue 4. IPDN SB RAS Press, Tumen, pp. 80–83 (in Russian).
Urals and Pre-Urals, 1968. Nauka Press, Moscow.
Vandenberghe, J.F., 2002. The relation between climate and river processes, landforms and deposits during the Quaternary. Quaternary International 91, 17–23.
Velichko, A.A., Faustova, M.A., 2009. The development of glaciations in Late Pleistocene. In: Velichko, A.A. (Ed.), Palaeoclimates and Palaeolandscapes of Extratropical Space of Northern Hemisphere. Late Pleistocene – Holocene. GEOS Press, Moscow, pp. 32–41 (in Russian).
Wilson, D.E., Reeder, D.M., 2005. Mammal Species of the World: a Taxonomic and Geographic Reference, 2005. Johns Hopkins University Press, Baltimore, Maryland.
Yakovlev, A., Danukalova, G., Kosintcev, P., Alimbekova, L., Morozova, E., 2006. Biostratigraphy of the Late Palaeolithic site of "Bajslan-Tash cave": (the Southern Urals). Quaternary International 149, 115–121.
Zagwijn, W.H., 1974. Vegetation, climate and radiocarbon datings in the late Pleistocene of the Netherlands: Part II: Middle Weichselian (Mededelingen – Netherlands). Mededelingen van de Geologische Stichting 25 (3), 15–45.