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Late Pleistocene and Holocene small- and large-mammal faunas from the Northern Urals

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Abstract

Data from the mammal fauna of the North Urals during the Late Pleistocene and Holocene are synthesised. Analysis of differentiation the degree of small- and large-mammal faunas during this time has been undertaken. Only differences of mammal species composition were significant between the Late Pleistocene and Holocene complexes, and within these complexes, the distinction between faunas was insignificant. The transition from the Late Pleistocene to the Holocene complex small-mammal faunas occurred in the Middle Late Valdai due to expansion of the forest species. In large-mammal faunas, the process was recorded later (in Dryas 3-Early Holocene) because of the extinction of some species and others that changed their areas of occupation.

1. Introduction

The Northern Urals extend from 64°N to 59°N. A series of investigations have examined the Late Quaternary mammal faunas of the Northern Urals region, including Kuzmina (1971), Kosintsev and Borodin (1990), Kosintsev (1996), Smirnov (1996), Smirnov et al. (1999b), Borodin et al. (2000), Kosintsev et al. (2000), Bachura and Strukova (2002), Teterina (2002, 2003), Bachura and Plasteeva (2005) and Kosintsev and Bachura (2005). These articles describe both the small- and large-mammal faunas of separate periods during the Late Pleistocene and Holocene.

In the present work mammal faunal evidence from the Late Pleistocene and Holocene from the Northern Urals is summarised. Analysis of the differentiation between the small- and large-mammal fauna assemblages during this time has been undertaken.

2. Materials and methods

Data collected from mammalian assemblages from 10 alluvial, 23 cave and 5 archaeological sites provide the basis for this synthesis (Fig. 1). The radiocarbon dates, the evolutionary stages of individual species, and archaeological artifacts allow the combination of these local faunas to 8 faunal groups, and are assigned to chronological periods (Tables 1 and 2; Appendix Tables A1 and A2):

1. Early Valdai (Early Weichselian; MIS4)—EW; 3 local faunas (Zhiliche Sokola—2, Usolcevskaya and Shaitanskaya caves).
2. Middle Valdai (Middle Weichselian II; Late MIS3; 34–24 kyr BP)—3 local faunas (Cheremukhovo pit 1, 2, 4).
3. Late Valdai 1 (LGM; Late Weichselian I; Early MIS2; 24–15 kyr BP)—5 local faunas (Medvezhaya, Studenaya and Shaitanskaya caves, Cheremukhovo pit 2, 4).
4. Late Valdai 2 (LGE; Late Weichselian II; Late MIS2; 15–12.4 kyr BP)—1 local fauna (Shaitanskaya cave).
5. Bølling-Allerød (Late Weichselian II; Late MIS2; 12.4–10.9 kyr BP)—3 local faunas (Medvezhaya and Shaitanskaya caves, Kakva-4).
6. Early Holocene (Early MIS1; 10.2–8.0 kyr BP)—4 local faunas (Medvezhaya and Shaitanskaya caves, Cheremukhovo pit 1, Kamen' Pisany).
7. Middle Holocene (Middle MIS1; 8.0–2.5 kyr BP)—11 local faunas (Zhiliche Sokola—1, Cheremukhovo pit 1, Burmantovo—1, Burmantovo—2, Shaitanskaya and Ushminskaya caves, Ivdel'—2, Lisia, Kamen' Pisany, Kaninskaya and Uninskaya caves).

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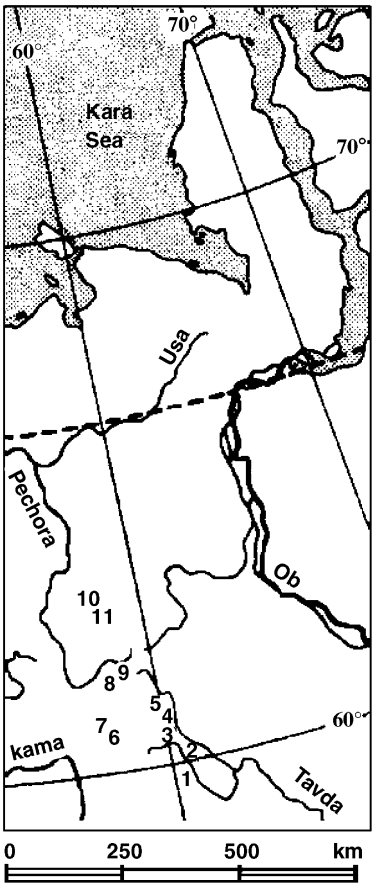

Fig. 1. Fossil fauna localities in the Northern Urals. 1—Zhiliche Sokola, Kakva-4; 2—Cheremukhovo; 3—Usolcevskaya cave; 4—Shaitanskaya cave; 5—Burmantovo; 6—Kamen' Pisany; 7—Dyrovaty Kamen'; 8—Kaninskaya cave; 9—Uninskaya cave; 10—Medvezhaya cave; 11—Arka.

8. Late Holocene (Late MIS1; 2.5 kyr BP—precent)—16 local faunas (Zhiliche Sokola—1, Cheremukhovo pit 1, Burmantovo—1, Cheremukhovo-2, Shaitanskaya and Ushminskaya caves, Ivdel'—2, Lisia—2, Vizhay, Lozvinsky gorodok, Atym'a—2, Atym'a—7, Kamen' Pisany, Kaninskaya cave, Dyrovaty Kamen', Arka).

In Tables 1 and 2 and on Fig. 2, indexes W (3W–8W) and E (1E—8E) indicate faunas of the corresponding period from the western and eastern slopes of the Northern Urals.

3. Changes of mammals species composition

Analysis of the species lists allows six species groups to be distinguished.

Group 1: Species are present in all faunal complexes including *Microtus oeconomus*, *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Martes zibellina*, *Gulo gulo*, *Mustela erminea*, *Mustela nivalis* and *Rangifer tarandus* (Tables 1 and 2).

Group 2: Species that have replaced each other at certain periods. On the Middle Valdai 2 and the Late Valdai 1 boundary, the large form of horse (*Equus latipes*) was replaced by a small form (*Equus uralensis*). During the Bølling-Allerød, *Dicrostonyx gulielmi* was replaced by *Dicrostonyx torquatus* (Smirnov et al., 1999b), and during the Middle Holocene, *Lepus tanaiticus* was replaced by *Lepus timidus* (Tables 1 and 2).

Group 3: Species that inhabited the Northern Urals during the Late Pleistocene and disappeared during the Holocene. *Spermophilus sp*. and *Mustela eversmanni* lived here until the middle part of the mid-Holocene. *Ochotona pusilla, Lagurus lagurus*, *Dicrostonyx torquatus, Lemmus sibiricus* and *Alopex lagopus* disappeared from this region during the Late Holocene.

Table 1
Species composition of Late Pleistocene mammal faunas from North Urals

Species	Faunas						
	1E[a]	2E	3W	3E	4E	5W	5E
Lepus tanaiticus Gureev	+	+	+	+	+	+	+
Ochotona pusilla Pallas	+	+	+	+	+	+	+
Sciurus vulgaris L.	+	–	–	–	–	–	+
Spermophilus sp.	+	+	–	+	+	–	+
Castor fiber L.	+	–	–	–	–	+	–
Marmota bobak Műller	+	+	–	+	+	–	+
Sicista sp.	–	–	–	–	–	–	–
Cricetulus migratorius Miline-Edwards	+	+	–	+	+	–	–
Clethrionomys rufocanus Sundervall	+	–	–	–	+	+	+
Cl. rutilus Pallas	+	–	–	–	+	+	+
Lagurus lagurus Pallas	+	+	–	+	+	–	+
Dicrostonyx gulielmi Sanford	+	+	+	+	+	–	–
D. torquatus Pallas	–	–	–	–	–	+	+
Lemmus sibiricus Kerr	+	+	+	+	+	+	+
Myopus schisticolor Lilljeborg	+	–	+	?	+	+	+
Arvicola terrestris L.	+	–	–	+	+	+	+
M. gregalis Pallas	+	+	+	+	+	+	+
M. oeconomus Pallas	+	+	–	+	+	+	+
M. agrestis L.	–	–	–	–	+	+	+
M. middendorffi Poljakov	+	+	+	+	–	–	–
Canis lupus L.	+	+	+	+	+	+	+
Alopex lagopus L.	+	+	+	+	+	+	+
Vulpes vulpes L.	+	+	+	+	+	+	+
Ursus arctos L.	+	+	?	+	+	?	+
Martes zibellina L..	+	+	+	+	+	+	+
Gulo gulo L.	+	+	+	+	+	+	+
M. erminea L.	+	+	+	+	+	+	+
M. nivalis L.	+	+	+	+	+	+	+
M. eversmanni Lesson	+	+	+	+	+	+	+
Meles meles L.	+	–	–	–	–	–	–
Panthera spelaea Goldfuss	+	+	+	+	+	+	?
Mammuthus primigenius Blüm	+	+	+	+	+	+	+
Equus latipes Gromova	+	+	–	–	–	–	–
E. uralensis Kuzmina	–	–	+	+	+	+	+
Coelodonta antiquitatis Blumenbach	+	+	+	+	+	+	+
Cervus elaphus L.	+	–	–	–	–	–	–
Alces alces L.	+	–	–	–	–	+	–
Rangifer tarandus L.	+	+	+	+	+	+	+
Bison priscus Bojanus	+	+	+	+	+	+	+
Saiga tatarica L.	+	+	+	+	+	+	+
Ovibos pallantis H.Smith	–	–	+	+	+	+	+

[a]Indices indicate faunas from the western slope (W) and eastern slope (E);N 1–5 denote numbers of faunal groups in the text.

Table 2
Species composition of Holocene mammal faunas from North Urals

Species	Faunas					
	6W[a]	6E	7W	7E	8W	8E
Lepus tanaiticus Gureev	+	+	+	+	–	–
Lepus timidus L.	–	–	–	–	+	+
Ochotona pusilla Pallas	+	+	–	+	–	+
Pteromys volans L.	–	–	–	–	+	+
Sciurus vulgaris L.	+	+	+	+	+	+
Tamias sibiricus Laxmann	–	–	–	+	+	+
Spermophilus sp.	+	+	–	+	–	–
Castor fiber L.	+	+	+	+	+	+
Sicista sp.	–	–	–	+	+	+
Clethrionomys rufocanus Sundervall	+	+	+	+	+	+
Cl. rutilus Pallas	+	+	+	+	+	+
Lagurus lagurus Pallas	–	+	?	+	–	+
Dicrostonyx torquatus Pallas	+	+	?	+	+	+
Lemmus sibiricus Kerr	+	+	?	+	+	+
Myopus schisticolor Lilljeborg	+	+	?	+	+	+
Arvicola terrestris L.	+	+	?	+	+	+
M. gregalis Pallas	+	+	?	+	+	+
M. oeconomus Pallas	+	+	?	+	+	+
M. agrestis L.	+	+	?	+	+	+
Canis lupus L.	+	+	+	+	+	+
Alopex lagopus L.	+	+	+	+	–	–
Vulpes vulpes L.	+	+	+	+	+	+
Ursus arctos L.	+	+	+	+	+	+
Martes zibellina L.	+	+	+	+	+	+
Martes martes L.	–	–	–	–	+	+
Gulo gulo L.	+	+	+	+	+	+
Mustela erminea L.	+	+	+	+	+	+
Mustela nivalis L.	+	+	+	+	+	+
Mustela eversmanni Lesson	–	+	–	+	–	–
Meles meles L.	–	–	+	+	–?	–
Lutra lutra L.	+	+	+	+	+	+
Lynx lynx L.	?	?	+	+	+	+
Equus uralensis Kuzmina	?	+	–	–	–	–
Cervus elaphus L.	–	–	–	+	–	–
Capreolus pygargus L.	–	–	–	–	–	+
Alces alces L.	+	+	+	+	+	+
Rangifer tarandus L.	+	+	+	+	+	+

[a]Indices indicate faunas from the western slope (W) and eastern slope (E);N 6–8 denote numbers of faunal groups in the text.

Group 4: Species that inhabited the Northern Urals only during the Late Pleistocene. *Ursus spelaeus* disappeared from this area at the end of the Middle Valdai 2. Also included are *Panthera spelaea, Coelodonta antiquitatis, Bison priscus, Ovibos pallantis* and *Mammuthus primigenius,* that died out at the end of the Pleistocene (Table 1). The occupation areas of *Marmota bobak* and *Saiga tatarica* shifted southward and that of *Microtus middendorffi* shifted northwards from the Northern Urals at the end of the Pleistocene.

Group 5: Species which appeared during the Northern Urals in the Holocene: *Lutra lutra* appeared in the Early Holocene, *Tamias sibiricus*, *Sicista sp*. and *Lynx lynx* appeared in the Middle Holocene, while *Pteromys volans* and *Martes martes* appeared in the Late Holocene.

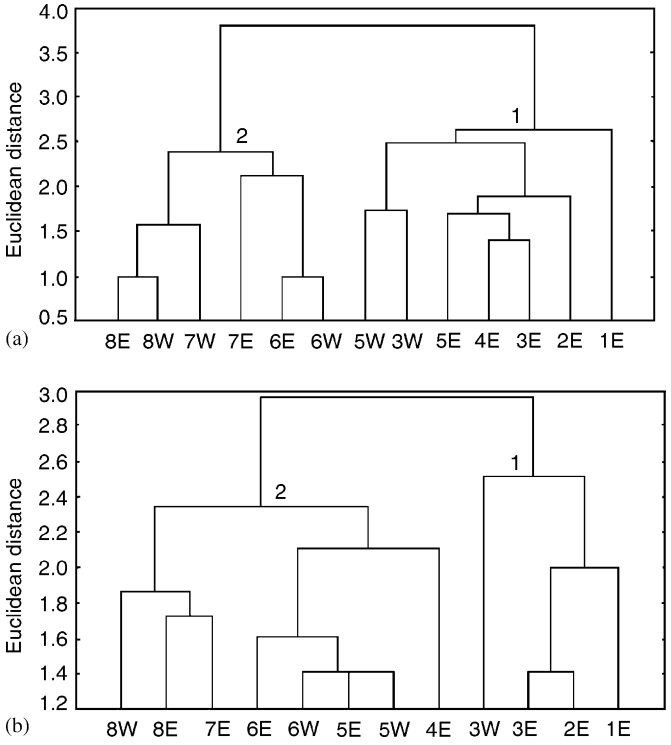

Fig. 2. Dendrogram of large- (a) and small-mammal faunas (b) Indices indicate faunas from the western slope (W) and eastern slope (E); N 1–8 denote numbers of faunal groups mentioned in the text.

Group 6: Species that occur episodically in faunal assemblages. In the Late Pleistocene they were: *Sciurus vulgaris*, *Castor fiber*, *Cricetulus migratorius*, *Clethrionomys rufocanus*, *Clethrionomys rutilus*, *Myopus schisticolor*, *Arvicola terrestris*, *Microtus agrestis*, *Mustela lutreola*, *Meles meles* and *Cervus elaphus*. In the Holocene they were: *Meles meles*, *Cervus elaphus* and *Capreolus pygargus*.

Faunal assemblages from the western and eastern slopes of the Northern Urals show geographical distinctions. On the western slope, remains of *Marmota bobak, Lagurus lagurus, Cricetulus migratorius* and *Spermophilus sp*. were absent during the Late Pleistocene, while on the eastern slope, no remains of *Ursus spelaeus* are known. The times of the disappearance of some species in the two regions were different: *Panthera spelaea* died out on the eastern slope at the beginning of Dryas 1, while on the western side this species remained until the end of the Pleistocene. Likewise, *Ochotona pusilla* disappeared from the eastern slope in the Late Holocene, and *Mustela eversmanni* disappeared during the Middle Holocene. On the western side, pika disappeared from the fauna during the Late Holocene, whilst the steppe polecat is absent after the Early Holocene.

4. Analysis of faunas

Cluster analysis of mammal species lists was undertaken to determine character changes in the small-mammal faunas that occurred during the Late Quaternary to allow

comparison with that of the large mammals. Various cluster analysis methods (complete linkage, UPGM, Ward's method) have shown a stable amalgamation of faunas into two clusters in both cases (Figs. 2a and b). The distance between the objects in these plots is the Euclidean distance.

In the analysis of the large-mammal faunas, the first cluster includes all faunas of Late Pleistocene age from Northern Urals, whilst the second includes all faunas from the Holocene (Fig. 2a). In first cluster, the Early Valdai fauna stands apart from others. Other faunas of the Late Pleistocene are combined in two geographical variances: western and eastern. In cluster 2, Holocene faunas are united in two chronological variances: Early and Late. The Middle Holocene fauna of the western slope was similar to the Late Holocene fauna. The Middle Holocene fauna of the eastern slope was similar to the Early Holocene fauna, because it included a significant amount of Pleistocene species.

Thus, during the Holocene there were more significant changes in the large-mammal composition of the fauna than during the Late Pleistocene.

In the analysis of small-mammal faunas, cluster structures differ from those seen for the large mammals (Fig. 2b). Cluster 1 consists of faunas of Early Valdai, Middle Valdai and the Late Valdai 1. Cluster 2 includes faunas from the Bølling-Allerød and the Holocene. Thus, rearrangement of the North Urals small-mammal faunas occurred during the transition from the Late Valdai 1 to Late Valdai 2. The small-mammal faunas were represented by two geographical variants, one on the western and the other on the eastern slopes during the Late Pleistocene. Cluster 2 includes two chronological variants of the faunas: Bølling-Allerød (Late Valdai)–Early Holocene, and Middle Holocene–Late Holocene (Fig. 2b).

Thus cluster analysis has shown that differences in mammal-species composition were significant between the Late Pleistocene and Holocene complexes, but within these complexes distinction between faunas was insignificant. The transition from the Late Pleistocene to the Holocene complex in the small-mammal fauna took place at the boundary of the Late Valdai 1 and Late Valdai 2 due to an expansion of forest species. The same process in the large-mammal fauna occurred later (in Dryas 3–Early Holocene) when some species died out and others changed their distributions.

5. Discussion

Comparison of Late Pleistocene mammal species composition of the Northern Urals with that of North Eurasia was undertaken (Table 3). Mammal fauna of the North Urals during Late Pleistocene was a northern variant of the periglacial mammal-fauna in the North Eurasia. The mammal faunas of the Polar Ural and adjacent territories of Eastern Europe and Western Siberia included 27 species (Kuzmina, 1977; Smirnov, 1986; Kochev, 1993; Smirnov et al., 1999a; Borodin and Kosintsev, 2001; Ponomarev, 2003). The mammal faunas of the Northern Urals and adjacent territories of Eastern Europe (Kochev, 1993; Ponomarev, 2003) and Western Siberia (Borodin and

Table 3
Species composition of the Late Pleistocene mammal faunas from the Northern Urals and adjacent territories

Species	Territories		
	1	2	3
Lepus tanaiticus Gureev	+	+	+
Ochotona pusilla Pallas	+	+	+
Spermophilus sp.	–	+	+
Castor fiber L.	–	+	+
Marmota bobak Műller	–	+	+
Allactaga jaculus Pallas	–	–	+
Apodemus sylvaticus L.	–	–	+
Apodemus flavicollis Melchior	–	–	+
Allocricetullus eversmanii Brandt	–	–	+
Cricetulus migratorius Miline-Edwards	–	+	+
Cricetus cricetus L.	–	–	+
Clethrionomys rufocanus Sundervall	?	+	+
Cl. ex gr. rutilus-glareolus	+	+	+
Lagurus lagurus Pallas	–	+	+
Eulagurus luteus Eversmann	–	–	+
Dicrostonyx gulielmi Sanford	+	+	+
D. torquatus Pallas	–	+	–
Lemmus sibiricus Kerr	+	+	+
Myopus schisticolor Lilljeborg	–	+	?
Arvicola terrestris L.	+	+	+
M. gregalis Pallas	+	+	+
M. oeconomus Pallas	+	+	+
M. agrestis L.	+	+	+
M. arvalis Pallas	–	–	+
M. middendorffi Poljakov	+	+	–
M. hyperboreus Vinogradov	+	–	–
Canis lupus L.	+	+	+
Alopex lagopus L.	+	+	+
Vulpes vulpes L.	+	+	+
Ursus arctos L.	+	+	+
Ursus spelaeus Rosenmüller et Heinroth	–	+	+
Martes ex. gr. martes-zibellina	+	+	+
Gulo gulo L.	+	+	+
M. erminea L.	+	+	+
M. nivalis L.	+	+	+
M. eversmanni Lesson	?	+	+
Meles meles L.	–	+	+
Crocuta spelaea Goldfuss	–	–	+
Panthera spelaea Goldfuss	+	+	+
Mammuthus primigenius Blüm	+	+	+
Equus ex. gr. latipes-uralensis	+	+	+
Coelodonta antiquitatis Blumenbach	+	+	+
Cervus elaphus L.	–	+	+
Alces alces L.	–	+	+
Rangifer tarandus L.	+	+	+
Bison priscus Bojanus	+	+	+
Saiga tatarica L.	+	+	+
Ovibos pallantis H.Smith	+	+	+

*1—Polar Urals and adjacent territories of the East Europe and West Siberia.
2—North Urals and adjacent territories of the East Europe and West Siberia.
3—Middle Urals and adjacent territories of the East Europe and West Siberia.

Kosintsev, 2001; Bobkovskaya, 2002) included 39 species. The mammal faunas of the Middle Urals (Smirnov, 1993; Kosintsev, 2003; Fadeeva, 2003; Razhev et al., 2005) and adjacent territories of Eastern Europe (Yakovlev, 2003) and Western Siberia included 44 species. Consequently, by species abundance mammal fauna of the North Urals during the Late Pleistocene differed from that of the Polar Urals, and was similar to the Middle Urals.

The large-mammal faunal composition of the Late Pleistocene at the North Urals was similar to that of the Central Russian Plain (Markova et al., 1995; Sablin, 2001) and the Central Yakutia (Lazarev et al., 1998). The mammal faunas of North Urals and Central Russian Plain mainly differed by small-mammal species assemblages. *Desmana moschata*, *Sicista subtilis, Allactaga major, Eolagurus luteus* and *Microtus arvalis* were not present in the Northern Ural and *Myopus schisticolor*, *Martes zibellina, Ursus spelaeus* in the Central Russian Plain.

The fauna of Yakutia differed from that of the North Urals in three ways. Ural and Yakutia faunas are characterized by the presence of species which are ecological vicariates. *Ochotona pussilla*, *Marmota bobak*, *Microtus middendorffi*, *Equus latipes* and *Equus uralensis* existed in the North Urals and *O. hyperborea*, *M. camtchatica*, *M. hyperboreus* and *E. lenensis* in Yakutia. Secondly, the fauna of Yakutia included less 'steppe species' than the fauna of the North Urals. *Lagurus lagurus* and *Cricetulus migratorius* did not inhabit Yakutia. Finally, one European species (*Ursus spelaeus)* was absent from Yakutia, and one Asiatic species (*Ovis nivicola*) was absent from the North Urals (Markova, et al., 1995).

Mammal faunas of the North Urals and northern regions of Central and Western Europe differ in much greater degrees. The species list of large-mammal fauna of the Northern Urals during the Late Pleistocene was significantly longer than that of the northern Scandinavian peninsula (Hufthammer, 2001) and significantly shorter than that of northern regions of Europe and Great Britain (Stuart, 1982; Musil, 1985; Turner, 1991; Kahlke, 1994; van Kolfschoten, 2001; Stewart et al., 2003). The greatest differences were in small-mammal fauna. In the North Urals, Insectivora are represent by 1–2 species and Chiroptera are absent, as well as Hystricidae, Gliridae, Dipodidae, Spalacidae and Muridae. The Family Cricetidae included only representatives of subfamilies Cricetinae (1 species) and Arvicolinae (11 species). The differences in large-mammal fauna were not so significant. Order Carnivora included 17 species in northern Europe and 12 species in the Urals; order Proboscidea—2 and 1 species; order Perissodactyla—4 and 2 species; and order Artiodactyla—13 and 6 species. The degree of these differences varied during the Late Pleistocene. The differences were maximal during interglacial and minimal during glacial periods. The majority of warmth-requiring species: insectivores, bats, mice, dormice, roe deer, wild boar, aurochs, and others were absent in faunas during cold periods. This species group was comparatively numerous in northern European fauna and absent from the North Urals during the interglacial.

Changes of the fauna composition and structure probably began simultaneously in Europe and the North Urals. However, the rates of these changes were different.

The transition from the Pleistocene to Holocene occurred at a greater rate in Europe than in the North Urals (Aaris-Sørensen, 1992; Coard and Chamberlain, 1999; Street and Baales, 1999). The Pleistocene relicts (*Ochotona pusilla*, *Lagurus lagurus*, *Dicrostonyx torquatus* and *Lemmus sibirica*) lived until the Sub-Atlantic in the North Urals. A similar phenomenon is found in Yakutia (Boeskorov, 2006).

6. Conclusion

Species composition of mammal faunas from the North Urals revealed significant differences between the Late Pleistocene and Holocene complexes. These distinctions were the result of two processes: extinction and distributional changes in some species. Reorganisation of the small-mammal fauna occurred at the end of the Pleistocene, whilst that of the large-mammal fauna occurred at the transition from the Pleistocene to Holocene. Such distinctions may be related to ecological factors for both the small and large mammals. Small-mammal populations require specific biotopes, whereas the character of landscapes is more important for large-mammal populations. At the end of the Pleistocene, during deglaciation of the Eurasian ice sheet in the Northern Urals, areas of forest vegetation increased, resulting in expansion of species which were connected to such biotopes. A great rearrangement of environment took place later, at the Pleistocene–Holocene boundary. This process caused changes of the structure and composition of large-mammal fauna.

Species composition of the Late Pleistocene mammal fauna from the North Urals was similar to that of the Central Russian Plain and Yakutia. Faunas of these regions were a northern variant of the mammoth fauna of the periglacial zone of North Eurasia. This variant differed significantly from northward arctic and from northern Europe and Great Britain faunas.

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Appendix A

Radiocarbon age determined on collagen from fossil mammal bones from the Northern Ural is given in Table A1.

Table A1
Radiocarbon age determined on collagen from fossil mammal bones from the Northern Urals

Sites	Date[a]	±; (>) infinite dates	Laboratory No.[b]	Lat °N	Long °E	Species	Dated object
Cheremukhovo, pit 1 (stratum 5)	4930	75	SOAN-5137	60.24	60.03	*Mammal*	Bones
Lisia cave	5073	173	IEMEG-1339	60.25	60.05	Mammal	Bones
Lisia cave	7213	60	IEMEG-1338	60.25	60.05	Mammal	Bones
Cheremukhovo, pit 2 (stratum 1-2)	8030	120	SOAN-5138	60.24	60.03	*Equus* sp.	Bone
Kakva – 4 (horizons 7)	10 555	65	SOAN-5140	59.35	60.00	Mammal	Bones
Shaitanskaya cave, pit 2 (stratum 5b)	11 220	200	SOAN-5305	60.42	60.22	*Bison priscus*	Metatarsal
Medvezhaya cave (grey loamy soil)	11 840	50	GIN-8400	62,20	59.0	*Rangifer tarandus*	Bone
Medvezhaya cave (greyish-brown "A" loamy soil))	12 230	100	LE-3059	62.20	59.0	Mammal	Bones
Kakva – 4 (horizon 8)	12 630	80	SOAN-5141	59.35	60.00	Mammal	Bones
Medvezhaya cave (grey loamy soil)	12 670	90	GIN-8398	62.20	59.0	*Rangifer tarandus*	Bone
Kakva-4 (horizon 4)	12 800	300	GIN-9444	59.35	60.00	Mammal	Bones
Medvezhaya cave (greyish-brown "A" loamy soil)	13 260	230	T-13476	62.20	59.0	Mammal	Bones
Shaitanskaya cave, pit 1 (stratum 2)	14 480	650	SOAN-2212	60.42	60.22	*Equus, Rangifer tarandus*	Bones
Medvezhaya cave (greyish-brown "B" loamy soil)	16 130	150	LE -3060	62.20	59.0	mammal	Bones
Medvezhaya cave (greyish-brown "B" loamy soil)	17 980	200	LE-3061	62.20	59.0	Mammal	Bones
Medvezhaya cave (greyish-brown "B" loamy soil)	18 700	180	GIN-8399	62.20	59.0	*Rangifer tarandus*	Bones
Cheremukhovo, pit 4 (stratum 1)	18 780	379	IEMEG- 1259	60.24	60.03	Mammal	Bones
Cheremuchovo, pit 1 (stratum 9)	18 900	320	SOAN-4531	60.24	60.03	*Mammuthus primigenius*	Femur
Shaitanskaya cave, pit 1 (stratum 2)	19 050	200	SOAN-5225	60.42	60.22	*Bison priscus*	Humerus
Shaitanskaya cave, pit 1 (stratum 2)	19 140	205	SOAN-5224	60.42	60.22	*Coelodonta antiquitatis*	Tibia
Shaitanskaya cave, pit 1 (stratum 2)	22 650	670	SOAN-4529	60.42	60.22	*Mammuthus Primigenius*	Tibia
Cheremukhovo, pit 2 (stratum 1-2)	24 580	355	SOAN-5223	60.24	60.03	*Coelodonta antiquitatis*	Humerus
Cheremukhovo, pit 1 (stratum 10)	25 150	500	SOAN-5302	60.24	60.03	*Coelodonta antiquitatis*	Pelvis
Cheremuchovo, pit 1 (stratum 10)	26 480	840	OxA-10926	60.24	60.03	*Coelodonta antiquitatis*	Thoracic vertebra
Cheremukhovo, pit 1 (stratum 9)	27 000	710	AA-36471	60.24	60.03	Mammal	Bones
Cheremuchovo, pit 4 (stratum 2)	27 350	255	SOAN-5139	60.24	60.03	Mammal	Bones
Cheremukhovo, pit 4 (stratum 2)	28 140	350	SOAN-5303	60.24	60.03	*Coelodonta antiquitatis*	Scapula
Medvezhaya cave, Inner gallery	28 390	890	SOAN-4799	62.20	59.0	*Ursus spelaeus*	Bone
Cheremukhovo, pit 1 (stratum 12)	28 520	840	AA-36469	60.24	60.03	Mammal	Bones
Cheremukhovo, pit 1 (stratum 9)	29 120	230	OxA-10894	60.24	60.03	*Panthera spelaea*	Metacarpal
Cheremukhovo, pit 2 (stratum 3)	30 140	240	OxA-10895	60.24	60.03	*Panthera spelaea*	Tooth
Cheremukhovo, pit 1 (stratum 10)	31 500	1200	AA-36470	60.24	60.03	*mammal*	Bones
Cheremukhovo, pit 2 (stratum 2)	33 650	600	OxA-10891	60.24	60.03	*Coelodonta antiquitatis*	Bone
Cheremukhovo, pit 1 (stratum 12)	> 34 140	—	GIN-101152	60.24	60.03	*Mammal*	Bones
Shaitanskaya cave, pit 1 (stratum 3)	34 310	580	SOAN-5304	60.42	60.22	*Bison priscus*	Tibia
Cheremukhovo, pit 2 (stratum 2)	42 700	800	OxA-10911	60.24	60.03	*Mammuthus primigenius*	Femur
Zhiliche Sokola, pit 2	> 50 000	—	GIN-8500	59.35	60.00	mammal	Bones
Shaitanskaya cave, pit 1 (stratum 3)	54 500	2600	OxA-10907	60.42	60.22	*Panthera spelaea*	Bone

[a]Uncalibrated dates.
[b]Laboratory codes for dates: AA—University of Arizona, Tucson, USA; GIN—Geological Institute, Russian Academy of Sciences (RAS), Moscow; IEMEG—Institute of Animal Evolution Morphology and Ecology, RAS, Moscow; LE—Institute of Archeology, Leningrad Branch (currently Institute of the History of Material Culture), St.—Petersburg; OxA—Oxford Accelerated, University of Oxford, UK; SOAN—Institute of Geology and Geophysics, Siberian Branch RAS, Novosibirsk; T—Trondheim, Radiological Dating Laboratory, Norway.

Appendix B

Mammal-species composition and remain numbers from sites in the Northern Ural are given in Table A2.

Table A2
Mammal-species composition and remain numbers from sites in the Northern Urals

Species	Late pleistocene												Holocene												
	Early Valdai			Middle Valdai			Late Valdai 1			Bølling-Allerød			Early		Middle					Late					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Ochotona pusilla	9	—	—	163	1	985	269	101	—	9	43	—	1	10	6	22	5	—	—	—	3	—	1	—	—	—	—
Lepus tanaiticus	764	400	78	283	109	1254	4343	345	209	194	386	188	—	48	76	161	187	32	34	53	—	—	—	—	—	—	—

Table A2 (*continued*)

Species	Late pleistocene												Holocene														
	Early Valdai			Middle Valdai			Late Valdai 1			Bølling-Allerød			Early		Middle						Late						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Lepus timidus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	141	52	108	6	16	21	121
Pteromys volans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	20	—	—	—	—
Sciurus vulgaris	1	—	—	—	—	—	—	—	—	—	4	—	1	41	371	1801	1051	15	16	72	2288	68	1205	13	19	28	95
Tamias sibiricus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	5	—	—	—	11	1	4	—	—	—	—
Spermophilus sp.	1	2	—	1	—	1	—	3	—	—	34	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Castor fiber	2	—	—	—	—	—	—	—	—	2	—	—	—	1	7	26	3	—	43	214	68	—	—	32	21	58	173
Marmota bobak	26	2	1	2	4	2	—	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sicista sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	3	—	—	—	—	—	—
Cricetulus migratorius	1	—	—	10	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Clethrionomys rufocanus	1	—	—	—	—	—	1	—	—	2	1	—	7	289	132	—	98	5	—	—	403	3	—	5	—	—	—
Cl. rutilus	—	—	—	—	—	—	—	—	—	—	4	—	—	159	165	—	—	—	—	—	638	—	—	—	—	—	—
Clethrionomys sp.	2	13	—	—	—	—	1	—	—	3	—	—	11	—	—	—	111	5	—	—	—	5	—	9	—	—	—
Lagurus lagurus	6	—	—	34	10	46	—	—	—	—	6	—	—	12	56	—	—	—	—	—	4	7	—	—	—	—	—
Dicrostonyx gulielmi	35	372	—	4304	1130	6795	146	4245	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dicrostonyx torquatus	—	—	—	—	—	—	—	—	—	27	76	—	6	678	1920	—	—	5	—	—	78	37	—	1	—	—	—
Lemmus sibiricus	30	410	—	711	529	4428	20	1096	—	42	23	—	12	54	—	—	54	—	—	—	—	9	—	—	—	—	—
Myopus schisticolor	—	—	—	—	—	—	2	68	—	6	1	—	3	245	1970	—	18	3	—	—	259	1	—	5	—	—	—
Arvicola terrestris	—	—	—	—	—	—	—	1	—	2	1	—	5	5	5	—	10	1	—	—	19	2	—	—	—	—	—
M. gregalis	28	253	—	404	125	4400	27	1539	—	51	89	—	8	148	185	—	120	2	—	—	14	20	—	—	—	—	—
M. oeconomus	7	159	—	2	—	177	—	205	—	10	5	—	4	160	64	—	75	—	—	—	92	2	—	1	—	—	—
M. agrestis	—	—	—	—	—	—	—	—	—	8	3	—	6	17	179	—	29	3	—	—	79	2	—	1	—	—	—
M. middendorffi	15	23	—	49	5	800	1	229	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Canis lupus	79	52	4	4	—	27	208	—	5	32	11	1	—	—	1	2	1	—	2	16	1	—	—	—	—	—	14
Alopex lagopus	513	125	14	92	75	297	1003	42	16	74	1507	11	—	5	5	2	7	—	4	3	—	—	—	—	—	—	—
Vulpes vulpes	50	—	2	—	—	8	10	1	—	—	1	5	—	2	2	38	19	—	5	—	9	1	7	2	1	10	5
Ursus arctos	338	62	8	—	—	3	—	5	—	—	13	2	—	—	—	48	43	38	25	181	2	2	1	486	27	61	1210
Martes zibellina	1	4	—	—	3	20	9	19	1	—	5	1	—	7	53	126	57	3	13	254	135	1	5	1	6	91	61
Gulo gulo	—	—	2	—	—	—	11	—	2	—	86	—	—	—	—	—	—	—	—	26	2	—	—	—	—	—	—
Mustela lutreola	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mustela eversmanni	18	1	—	—	—	2	21	2	1	2	10	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—
Mustela erminea	28	3	—	16	1	86	32	54	—	4	184	9	—	—	4	1	9	—	—	—	34	5	2	—	—	—	—
Mustela nivalis	26	1	—	15	—	49	18	32	—	2	136	2	—	4	14	1	13	—	—	—	49	8	5	3	—	—	—
Meles meles	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	7	—	—	—	—	—	—	—	—	—	—
Lutra lutra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	12	4	4	39	6	—	—	6	4	13	—
Lynx lynx	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	4
Panthera spelaea	—	—	1	2	29	1	6	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Equus latipes	84	23	154	40	16	166	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Equus uralensis	—	—	—	—	—	—	337	—	40	26	—	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coelodonta antiquitatis	13	4	67	13	4	47	77	—	12	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cervus elaphus	4	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Capreolus pygargus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—
Alces alces	4	4	—	—	—	—	—	—	—	2	—	—	—	—	13	14	2	69	426	73	59	228	—	151	118	50	161
Rangifer tarandus	265	198	251	138	102	387	3198	—	221	86	2	59	—	6	27	1	1	4	71	242	119	6	—	4	28	31	129
Bison priscus	17	19	65	6	1	6	11	—	5	2	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Saiga tatarica	4	5	4	1	—	—	40	—	5	4	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ovibos pallantis	—	—	12	—	4	—	18	—	—	8	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mammuthus primigenius	4	1	1	1	—	4	109	—	—	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

1—Zhiliche Sokola, pit 2; 2—Usolcevskaya cave; 3—Shaytanskaya, pit 1 (stratum 3); 4—Cheremukhovo pit 1 (stratum 9—12); 5—Cheremukhovo pit 2, 3; 6—Cheremukhovo pit 4 (stratum 2); 7—Medvezhaya cave (greyish-brown "B" loamy soil); Cheremukhovo pit 4 (stratum 1); 9—Shaitanskaya, Shaitanskaya cave, pit 1 (stratum 2); 10—Medvezhaya cave (greyish-brown "A" and grey loamy soil); 11—Kakva-4; 12—Shaitanskaya cave, pit 2 (stratum 5b); 13—Medvezhaya cave (green sandy loam) ; 14—Cheremukhovo, pit 1 (stratum 6—7); 15—Cheremukhovo pit 1 (stratum 5); 16—— Burmantovo—1, 2; 17—Lisia; 18—Ushminskaya cave (stratum 3); 19—Zhiliche Sokola, pit 1 (stratum 2); 20—Uninskaya; 21—Cheremukhovo pit 1 (stratum 1-4); 22—Shaitanskaya cave, pit 2 (stratum 1); 23—Lisia-2; 24—Ushminskaya cave (stratum 1-2); 25—Zhiliche Sokola, pit 1 (stratum 1); 26—Kamen' Pisany; 27—Kaninskaya cave.

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