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Late Pleistocene large mammal faunas from the Urals

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Abstract

The 121 local faunas of large mammals from Late Pleistocene sites of the South (56–51°N), Middle (59–56°N) and North (64–59°N) Urals have been studied. All local faunas were combined into eight chronological groups on the basis of radiocarbon dates and the evolutionary level of rodents present in them. On the basis of species composition analysis of the faunas, three chronological complexes have been distinguished: Mikulino, Early–Middle Valdai and Late Valdai. The first is characterized by the presence of *Hystrix vinogradovi* and *Ursus thibetanus*; the second, by the presence of a large form of horse (*Equus* (*E.*) cf. *latipes*), *Crocuta crocuta*, *Ursus spelaeus* and *U. savini*; the third, by the presence of a small horse (*E. uralensis*) and absence of *U. spelaeus*, *U. savini* and *C. crocuta*. The latter two complexes were represented by three geographical variants: southern (South Urals), northern (North Urals) and transitional (Middle Urals). Differences between theriocomplexes are related to changes in morphology and areas and extinctions of a series of species. The existence of chronological theriocomplexes and their geographical variants was determined by chronological and geographical change in structure of paleophytocoenoses. It should be noted that the role of human in changes of chronological complexes and species extinctions in the Late Pleistocene has not been demonstrated in the Urals. In the Urals *U. savini* probably became extinct at the end of the Middle Valdai, *C. crocuta* at the beginning of the last glacial maximum (LGM), *U. spelaeus* at the end of the LGM, *Coelodonta antiquitatis* at the beginning of the Preboreal and *Megaloceros giganteus* at the middle of the Atlantic.

1. Introduction

A series of works is dedicated to the history of the large mammal fauna of some regions of the Urals (Dubrovo, 1966; Kosintsev, 1996; Kuzmina, 1971, 1975, 2000; Smirnov et al., 1990). In addition, much new data from sites with clear stratigraphy and series of radiocarbon dates have appeared in recent years. At present, they allow a more complete picture of the large mammal faunal history of the whole Urals. However, data from the Polar Urals are scarce and are not considered here.

2. Materials and methods

Within the territory of the North (NU) (64–59°N), Middle (MU) (59–56°N) and South (SU) (56–51°N) Urals, more than 150 sites in karst cavities and more than 100 alluvial sites, containing large mammal remains of the Late Pleistocene age, are known. Many sites consist of several sediment units of different age and, accordingly, contain several local faunas. A total of 121 AMS and conventional radiocarbon dates have been obtained on mammal bones. All dates cited below are not calibrated. On the basis of these dates, local faunas were combined into chronological groups. Faunas for which finite dates have been not obtained were attributed to stratigraphical subdivisions of the Pleistocene on the basis of evolutionary level and species composition of rodents present in these faunas. Eight faunal groups characterizing the following stratigraphical subdivisions were distinguished:

1. Mikulino (Eemian Interglacial; MIS5): MU—1 local fauna;
2. Early Valdai (Early Weichselian; MIS4): NU—3 local faunas, MU—3 local faunas, SU—4 local faunas.
3. Middle Valdai 1 (Middle Weichselian I; early MIS3; 46–34 kyr BP): NU—2 local faunas, MU—9 local faunas, SU—8 local faunas.
4. Middle Valdai 2 (Middle Weichselian II; late MIS3; 34–24 kyr BP): NU—4 local faunas, MU—11 local faunas, SU—5 local faunas.

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5. Late Valdai 1 (LGM; Late Weichselian I; early MIS2; 24–15 kyr BP): NU—2 local faunas, MU—17 local faunas, SU—9 local faunas.
6. Late Valdai 2 (Late Weichselian II; late OJS2; 15–12.4 kyr BP): NU—4 local faunas, MU—16 local faunas, SU—8 local faunas.
7. Bølling-Allerød (Late Weichselian II; late MIS2; 12.4–10.9 kyr BP): NU—3 local faunas, MU—4 local faunas, SU—2 local faunas.
8. Dryas III (Late Weichselian II; late MIS2; 10.9–10.2 kyr BP): NU—1 local fauna, MU—3 local faunas, SU—2 local faunas.

As the list above shows, not all chronological periods are characterized BY data on large mammal faunas. Comparisons were restricted to chrono-geographical fauna groups that included several local faunas because only their species lists can be considered as sufficiently complete. Chronological faunal complexes were distinguished on the basis of peculiarities of species composition and morphology of species present in these faunas. Geographical faunal complexes were distinguished on the basis of species composition peculiarities (Fig. 1).

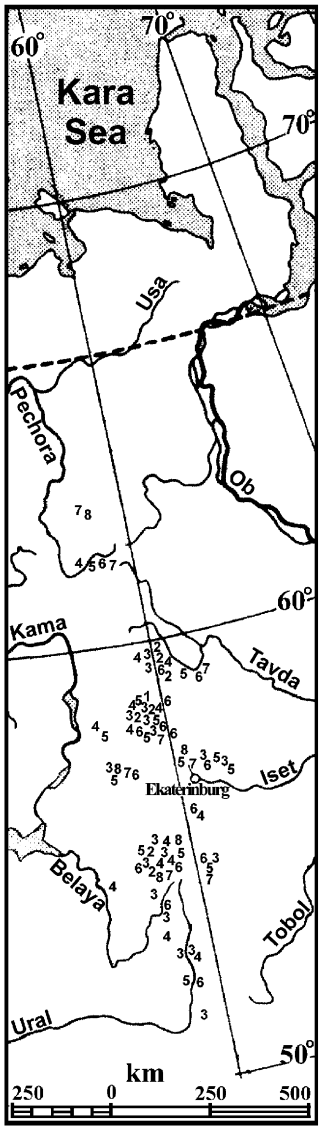

Fig. 1. Location of Late Pleistocene local faunas in the Urals (N 1–8 denote numbers of chronological groups).

3. Area dynamics and extinction time of individual species

Don's hare—*Lepus tanaiticus* Gureev, 1964. This is a typical species of the North Eurasian mammoth fauna (Averianov, 1995). It inhabited the Urals throughout the whole of the Late Pleistocene (Tables 1–3) and began to disappear only in the Holocene. Its replacement by Alpine hare (*L. timidus*) occurred gradually from south to north. Don's hare inhabited the South Urals until the end of the Boreal, the Middle Urals until the middle of the Atlantic and at the North Urals until the middle of the Subboreal. These are the latest records of Don's hare in Eurasia. The systematic relationship between Don's hare and Alpine hare is not sufficiently clear. If it is a distinct species, then extinction of this mammoth fauna representative occurred in the Urals in the middle of the Subboreal. If Don's hare is a geographical subspecies of Alpine hare, then phyletic evolution of *L. tanaiticus* to *L. timidus* has occurred. It is not possible to solve this problem at present.

Table 1
Species composition of Late Pleistocene chronological groups of large mammals in the North Urals

Species	Chronological groups[a]					
	2	3	4	5	6	7
Lepus tanaiticus Gureev	+	+	+	+	+	+
Marmota bobak Müller	+	+	+	–	+	+
Castor fiber L.	+	–	–	–	+	+
Canis lupus L.	+	+	+	+	+	+
Alopex lagopus L.	+	+	+	+	+	+
Vulpes vulpes L.	+	+	+	+	+	+
Ursus arctos L.	+	+	+	+	+	+
U. spelaeus Rose et Hein	+	+	+	–	–	–
Martes sp.	+	+	+	+	+	+
Gulo gulo L.	+	+	+	+	+	+
Mustela erminea L.	+	+	+	+	+	+
M. nivalis L.	+	+	+	+	+	+
M. eversmanni Lesson	+	+	+	+	+	+
Meles meles L.	+	–	–	–	–	–
Panthera spelaea Goldfuss	+	+	+	+	+	+
Mammuthus primigenius Blüm	+	+	+	+	+	+
Equus cf. *latipes* Gromova	+	+	+	–	–	–
Equus uralensis Kuzmina	–	–	–	+	+	+
Coelodonta antiquitatis	+	+	+	+	+	+
Cervus elaphus L.	+	+	–	–	–	–
Alces alces L.	+	+	–	–	+	+
Rangifer tarandus L.	+	+	+	+	+	+
Bison priscus Bojanus	+	+	+	+	+	+
Saiga tatarica L.	+	–	+	+	+	+
Ovibos pallantis H. Smith	–	–	+	+	+	+

[a]Here and below NN 1–8 denote numbers of chronological groups.

Table 2
Species composition of Late Pleistocene chronological groups of large mammals at the Middle Urals

Species	Chronological groups							
	1	2	3	4	5	6	7	8
Lepus tanaiticus Gureev	+	+	+	+	+	+	+	+
Marmota bobak Müller	–	–	+	+	+	+	+	+
Castor fiber L.	–	–	–	+	–	–	+	–
Hystrix vinogradovi Argiropulo	+	–	–	–	–	–	–	–
Canis lupus L.	+	+	+	+	+	+	+	+
Alopex lagopus L.	–	+	+	+	+	+	+	+
Vulpes vulpes L.	–	+	+	+	+	+	+	+
Ursus thibetanus	+	–	–	–	–	–	–	–
U. arctos L.	–	–	–	+	+	+	+	+
U. spelaeus Rose et Hein	–	+	+	+	+	–	–	–
U. savini Andrews	–	–	+	+	–	–	–	–
Martes sp.	–	–	+	+	+	+	+	+
Gulo gulo L.	–	+	+	+	+	–	+	+
Mustela erminea L.	–	+	+	+	+	+	+	+
M. nivalis L.	–	+	+	+	+	+	+	+
M. eversmanni Lesson	–	+	+	+	+	+	+	+
Meles meles L.	–	–	+	+	–	+	+	–
Crocuta crocuta Erxleben	–	–	+	–	–	–	–	–
Panthera spelaea Goldfuss	+	+	+	+	+	+	+	–
Lynx lynx L.	–	–	+	–	–	+	–	–
Mammuthus primigenius Blüm	+	+	+	+	+	+	–	–
Equus cf. *latipes* Gromova	+	+	+	+	–	–	–	–
Equus uralensis Kuzmina	–	–	–	–	+	+	+	–
Coelodonta antiquitatis Blüm	–	+	+	+	+	+	+	+
Cervus elaphus L.	+	–	+	+	–	–	–	–
Megaloceros giganteus Blüm	–	–	–	+	–	–	+	–
Alces alces L.	+	–	+	+	+	+	+	–
Rangifer tarandus L.	–	+	+	+	+	+	+	+
Bison priscus L.	+	+	+	+	+	+	+	+
Saiga tatarica L.	–	–	+	+	+	+	+	+
Ovibos pallantis H. Smith	–	–	+	+	+	+	–	–

Table 3
Species composition of Late Pleistocene chronological groups of large mammals at the South Urals

Species	Chronological groups						
	2	3	4	5	6	7	8
Lepus tanaiticus Gureev	+	+	+	+	+	+	+
Marmota bobak Müller	+	+	+	+	+	+	+
Castor fiber L.	+	+	+	–	+	+	–
Canis lupus L.	+	+	+	+	+	+	+
Alopex lagopus L.	+	+	+	+	+	+	+
Vulpes vulpes L.	+	+	+	+	+	+	+
Vulpes corsac L.	+	+	+	+	+	+	+
U.arctos L.	–	–	–	+	+	+	+
U. spelaeus Rose et Hein.	+	+	+	+	–	–	–
U. savini Andrews	+	+	–	–	–	–	–
Martes sp.	+	+	+	+	+	+	+
Gulo gulo L.	–	+	–	+	+	–	–
Mustela erminea L.	+	+	+	+	+	+	+
M. nivalis L.	+	+	+	+	+	+	+
M. eversmanni Lesson	+	+	+	+	+	+	+
Meles meles L.	–	–	+	–	+	–	–
Crocuta crocuta Erxleben	+	+	+	–	–	–	–
Panthera spelaea Goldfuss	+	+	+	+	+	+	–
Mammuthus primigenius Blüm	+	+	+	+	+	+	–
Equus cf. *latipes* Gromova	+	+	+	–	–	–	–
Equus uralensis Kuzmina	–	–	–	+	+	+	+
E. (*asinus*) *hydruntinus* Regalia[a]	–	+	+	–	–	–	–
Coelodonta antiquitatis Blüm	+	+	+	+	+	+	–
Camelus ferus Przewalski[a]	–	+	+	–	–	–	–
Cervus elaphus L.	+	+	+	+	+	+	+
Megaloceros giganteus Blüm	–	+	+	–	–	–	+
Alces alces L.	–	–	+	+	+	+	–
Rangifer tarandus L.	+	+	+	+	+	+	+
Bison priscus Bojanus	+	+	+	+	+	+	+
Saiga tatarica L.	+	+	+	+	+	+	+
Ovis ammon L.	+	+	+	–	–	–	–

[a]Southern part of South Ural only.

Vinogradov's porcupine—*Hystrix vinogradovi* Argyropulo, 1941. The remains of this species have been found from the only site that is dated to the Mikulino Interglacial, on the basis of species composition and molar morphology of rodents. In later sites of the remains of this species are not found in the Urals. At the beginning of the Early Valdai, the geographical distribution of the porcupine retreated to the south.

Large cave bear—*Ursus spelaeus* Rossenmüller et Heinroth, 1794. This species inhabited the Urals throughout the greater part of the Late Pleistocene. It probably appeared in the Urals at the beginning of the early Valdai, when the area of forests had become substantially reduced in this region. Radiocarbon dates have been obtained on cave bear bones from Urals sites, of which the latest is $16\,470 \pm 560$ yr BP (SOAN-4516) (Kosintsev et al., 2003). Cave bear became extinct in the Urals in the Middle Valdai and did not survive through the last glacial maximum (LGM).

Small cave bear—*Ursus savini* Andrews, 1922. This species' remains have only been found in the Early and Middle Valdai sites of the Middle and South Urals (Tables 2, 3). Two radiocarbon dates have been obtained on its bones: $\geqslant 37\,890 \pm 1200$ (SOAN-4528) and $33\,980 \pm 400$ (LE-2334) yr BP. This species probably became extinct in the Urals in the beginning of the LGM.

Spotted hyena—*Crocuta crocuta* Erxleben, 1777. Hyena remains were found in sites of early–middle Valdai age in the South Urals and in the only site of this age, in the Middle Urals (Tables 2, 3). Three AMS dates were obtained on its bones—$35\,650 \pm 450$ (OxA-10 890) yr BP and two others which were not finite. This species probably became extinct in the Urals at the beginning of the LGM.

Cave lion—*Panthera spelaea* Goldfuss, 1810. This species inhabited the Urals throughout nearly the whole of Late Pleistocene time (Tables 1–3). Ten AMS dates were obtained on its bones, the latest of which are: $13\,570 \pm 70$ (OxA-10 908) $13\,560 \pm 70$ (OxA-10 909) and $13\,500 \pm 65$ (OxA-11 349) yr BP. The extinction of cave lion at the Urals occurred in the end of the Late Valdai.

Woolly mammoth—*Mammuthus primigenius* Blumenbach, 1799. Mammoth was present in the Urals throughout nearly the whole of Late Pleistocene time (Tables 1–3). The majority of its remains have been recovered from alluvial sequences. The largest is a 'mammoth cemetery' on the river Sosva, where several thousand mammoth bones were found. Thirty-five AMS and conventional radiocarbon dates were obtained on mammoth bones, of which the latest is 11 080 ± 160 (SOAN-4842) yr BP. This species became extinct in the Urals at the end of the Late Valdai.

Horse—*Equus* (*E.*) cf. *latipes* Gromova, 1949 and *E.* (*E.*) *uralensis* Kuzmina, 1975. In the Late Pleistocene, two forms of horses existed in the Urals: the larger (*E.* cf. *latipes*) ranging from the Mikulino Interglacial to the Middle Valdai II, and the smaller from Late Valdai I to the Younger Dryas Chronozone (Dryas III). The status of these forms as independent species is now being questioned. Probably, these are chronological subspecies of the same species—*E. caballus* (Bachura and Podoprigora, 2003). Horse survived the Pleistocene–Holocene boundary in the Urals, and known by the name 'tarpan' persisted till the 18th century in the South Urals (Geptner, 1955).

Pleistocene ass—*Equus* (*Asinus*) *hydruntinus* Regalia, 1907. The remains of this species were found in two faunas Middle Valdai in the southern part of the South Urals (Kuzmina, 2000). The time of its extinction in the Urals is unknown.

Woolly rhinoceros—*Coelodonta antiquitatis* Blumenbach, 1799. This species inhabited the Urals throughout nearly all of the Late Pleistocene (Tables 1–3). Fifty-two AMS and conventional radiocarbon dates were obtained on its bones. Eight bones among them are dated from 14 845 ± 75 (OxA-11 350) to 12 330 ± 120 (LU-1668) yr BP. The latest date was obtained on the scapula bone from Lobvinskaya cave at the Middle Urals—9510 ± 260 (IPAE-93) yr BP (Kosintsev, 1995). A relict population of woolly rhinoceros probably persisted here until the beginning of the Holocene.

Giant deer—*Megaloceros giganteus* Blumenbach, 1803. In the Urals this species persisted until the end of the Pleistocene (Tables 2–3). AMS dates testify that the giant deer became extinct in the Middle Urals in the Atlantic (Stuart et al., 2004).

Extinct bison—*Bison priscus* Bojanus, 1827. This species inhabited the Urals throughout the Late Pleistocene (Tables 1–3). Forty AMS and conventional ^{14}C dates were obtained on its bones. The latest, 8040 ± 210 (SOAN-5754) yr BP, is from the South Urals. The last populations of this species disappeared in this region by the end of the early Holocene.

Musk ox—*Ovibos pallantis* H. Smith, 1827. The latest remains of this species were found at the North Urals in fauna dated by radiocarbon to 12 230 ± 100 (LE-3059) and 11 840 ± 50 (GIN-8400) yr BP (Sinitsin et al., 1997; Svezhentsev and Popov, 1993). Musk ox, probably became extinct in the Urals during Allerød—Younger Dryas (Late Valdai) time.

Analysis of species lists and radiocarbon dates from individual bones of some species (Kosintsev et al., 2003; Orlova et al., 2004; Sinitsin et al., 1997; Svezhentsev and Popov, 1993) allow us to distinguish several groups of species. The first group includes species that disappeared from the Urals in the Late Pleistocene: *H. vinogradovi* and *U. thibetanus* (Mikulino–Valdai border); *U. savini*, *C. crocuta*, *Ovis ammon* (Middle–Late Valdai border); *U. spelaeus* (LGM); *P. spelaea*, *M. primigenius* and *O. pallantis* (Bølling-Allerød).

The second group consists of species that became extinct during the Holocene: a relict population of *L. tanaiticus* persisted in the North Urals until the end of the middle Holocene (Kosintsev, 1996); a population of *C. antiquitatus* in the Middle Urals persisted until the early Holocene (Kosintsev, 1995); a population of *M. giganteus* survived the Middle Urals until the middle Holocene (Stuart et al., 2004) and a population of *B. priscus* lived at the South Urals until the early Holocene.

The third group includes species that succeeded each other in time. These are chronological forms of horses—the large *Equus* (*E.*) cf. *latipes*, existed throughout the Late Pleistocene until the end of the Middle Valdai; the small *E.* (*E.*) *uralensis* existed in the Late Valdai and was succeeded in Holocene by *E.* (*E.*) *gmelini*.

The fourth group includes species that lived in the Urals only during some periods of the Late Pleistocene: *Meles meles* and *Lynx lynx*. The fifth group consists of species that considerably shifted distributions during the Late Pleistocene: *Castor fiber*, *U. arctos*, *Cervus elaphus* and *Alces alces*.

The sixth group includes species which did not undergo considerable distributional changes in the Late Pleistocene: *Marmota bobac*, *Canis lupus*, *Vulpes vulpes*, *Alopex lagopus*, *Martes* sp., *Gulo gulo*, species of genus *Mustela*, *Rangifer tarandus*, *Saiga tatarica*. In a strict sense this group also includes *L. tanaiticus*, *P. spelaea*, *M. primigenius*, *Equus* (*E.*) sp., *C. antiqutatis*, *B. priscus* and *O. pallantis*, in which distributional areas varied little until the Bølling-Allerød (Late Valdai) period.

4. Faunal complexes

4.1. Chronological complexes

Three faunal complexes can be distinguished in the Late Pleistocene of the Urals. The Mikulino Complex is represented by a single site on the boundary between the North and Middle Urals. It is distinguished by the presence of *H. vinogradovi* and *U. thibetanus*. Later these species became absent from the Urals (Tables 1–3).

The Early and Middle Valdai Complex is represented at many sites over the whole territory of the Urals. It is characterized by presence of large horse (*E.* cf. *latipes*), and

large cave bear (*U. spelaeus*), and also for southern faunas *U. savini* and *C. crocuta*.

The Late Valdai Complex is represented by multiple sites throughout the Urals. It is characterized by the presence of the small form of horse (*E. uralensis*), an absence of cave bears (*U. spelaeus* and *U. savini*) and spotted hyenas. In this complex an early stage corresponding with the LGM can be distinguished, when extinction of cave bear and, probably, spotted hyena was taking place. This complex terminated at the beginning of the Younger Dryas, when cave lion, woolly mammoth and woolly rhinoceros become extinct over nearly the whole Urals (Tables 1–3).

4.2. Geographical variants

Within the chronological complexes geographical variants can be distinguished. Within the Early and Middle Valdai complex a southern variant (South Urals) is clearly recognized. It is characterized by presence of *V. corsac*, *C. crocuta*, *O. ammon* and absence of *O. pallantis*. In the south of this region *E. hydruntinus* and *Camelus ferus* were also present (Tables 2, 3). A northern variant (North Urals) stands out clearly. It is characterized by limited species list from which *C. fiber*, *U. savini*, *M. meles*, *C. crocuta* and *M. giganteus* are absent (Tables 1, 2). The Middle Urals fauna is transitional between southern and northern variants. Its characteristic feature is the presence of lynx (Tables 1–3).

In the Late Valdai geographical variants are less distinct than in the previous complex. This is a result of extinction and the changing distributions of some species. In the LGM, the southern variant is distinguished by the presence of *C. fiber*, *V. corsac*, *C. elaphus* and the absence of *O. pallantis* (Tables 2, 3). The northern variant is characterized by the absence of *U. spelaeus* and *A. alces* (Tables 1, 2). The Middle Urals fauna retains its transitional character: it includes *U. spelaeus*, *A. alces* and *O. pallantis*. In the Last Glacial event distinctions are even less marked. The southern variant is distinguished by the presence of *V. corsac* and *C. elaphus* and absence of *O. pallantis* (Tables 2, 3). The northern variant is characterized by the absence of *M. meles* and *M. giganteus* (Tables 1, 2). The Middle Urals fauna complex retains its transitional character by the presence of *M. meles*, *M. giganteus* and *O. pallantis* and is distinguished by the presence of *L. lynx* (Tables 1–3).

4.3. Theriocomplexes and paleophytocoenoses

For two of the chronological periods considered here—the Mikulino and the LGM, reconstructions of vegetation have been made for the territory of the Urals (Grichuk, 2002). The presence of *H. vinogradovi* and *U. thibetanus* in theriocomplex of Mikulino Interglacial is associated with the area of dark coniferous forests with oak and lime and coniferous—broadleaf (mainly lime) forests at the Urals in this time. In the later time, forests of this type were not present in the Urals. During the LGM period in the South Urals pine forests with spruce, pine and birch forests, pine open forests with steppe communities were present and most of the area was covered with pine–oak forests and mixed broadleaf forests of oak, lime, maple and elm. The presence of *C. fiber*, *V. corsac*, *A. alces* and *C. elaphus* in the theriocomplex of the South Urals is associated with these paleophytocoenoses. At this time in the Middle Urals pine forests with spruce and fir and meadow steppe with birch and spruce forests with some tundra communities were present. *O. pallantis* and *A. alces* are associated with these paleophytocoenoses. Tundra and cold-tolerant xerophyte communities and spruce and birch open woodlands were distributed at the North Urals. *Alces* could not exist *in these paleophytocoenoses*, but musk ox was able to colonise.

5. Conclusion

The analysis of the large mammal species composition of local faunas from Late Pleistocene sites revealed that throughout this period in the Urals three chronological theriocomplexes replaced each other consecutively: Mikulino, Early–Middle Valdai and Late Valdai. The last two were represented by three geographical variants: southern (South Urals), northern (North Urals) and transitional (Middle Urals). Differences between theriocomplexes are connected with changes in morphology, areas and extinctions of a series of species. The existence of chronological theriocomplexes and their geographical variants was distinguished by the chronological and geographical change in structure of paleophytocoenoses. At the Pleistocene–Holocene boundary not all the species of mammoth complex became extinct. Several species disappeared from the Urals in the Holocene: *C. antiquitatis*, *B. priscus* (Early Holocene), *L. tanaiticus* and *M. giganteus* (Middle Holocene). It should be noted that the role of human in changes of chronological complexes and species extinctions in the Late Pleistocene in the Urals cannot be demonstrated.

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Appendix A

Mammal species composition and remains numbers from sites and radiocarbon age on collagen from fossil mammal bones in the Urals are given in Tables A.1 and A.2.

Table A.1
Mammal species composition and remains numbers from sites in the Urals

Species	Sites																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Lepus tanaiticus	121	10	55	13	50	19	8	2828	81	37	119	15	291	2594	191	172	48		1709	74	16
Marmota bobak	1	–	5	–	–	–	1	1	–	–	–	–	2	1	1	7	18		44	28	239
Castor fiber	–	–	–	–	–	–		–	–	–	3	–	–	–	–	–	–		–	–	–
Hystrix vinogradovi	–	12	–	–	–	–		–	–	–	–	–	–	–	–	–	–		–	–	–
Canis lupus	–	5	2	–	3	1	3	30	–	–	12	1	3	5	5	11	36		39	19	1
Alopex lagopus	4	1	33	5	5	3	5	302	14	4	5	2	11	132	11	18	29		104	32	15
Vulpes vulpes	2	–	–	–	–	–		3	–	2	6	–	–	–	5	1	9		7	9	5
Vulpes corsac	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–		–	–	–
Ursus arctos	1	–	–	4	–	–	2	7	–	–	16	–	–	–	–	–	–		2	–	–
Ursus spelaeus	–	–	–	10	–	5		–	2	–	2666	–	–	–	–	62	1163		–	604	351
Ursus thibetanus	–	27	–	–	–	–		–	–	–	–	–	–	–	–	–	–		–	–	–
Martes sp.	1	–	–	–	–	–		2	–	–	24	–	1	–	1	5	3		11	7	14
Gulo gulo	–	–	1	–	–	–	1	2	–	–	1	1	–	1	1	1	1		3	1	–
Mustela eversmanni	–	–	7	–	–	–		3	–	–		–	2	–	–	–			–	–	–
Mustela erminea	9	–	1	–	–	–		183	–	–	1	–	3	38	–	–	1		14	–	–
Mustela nivalis	43	–	–	–	–	–		453	38	1	–	–	–	4	–	–	–		1	–	–
Meles meles	–	2	–	–	–	–		–	–	–	3	–	–	–	–	–	3		–	8	5
Crocuta crocuta	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	2		–	–	–
Lynx lynx	–	–	–	–	2	–		1	–	–	–	–	–	–	–	–	–		2	–	–
Panthera spelaea	–	1	–	1	–	–	1	1	–	7	5	2	–	1	6	–	2		–	–	–
Mammuthus primigenius	–	1	1	14	14	11	1	2	1	1	2	2	–	1	–	1	–		4	14	2
Equus cf. *latipes*	–	12	–	–	–	234		–	3	–	41	–	–	–	–	6	–		–	31	11
Equus cf. *uralensis*	–	–	79	282	427	–	250	75	–	166	–	84	19	140	23	–	–		239	–	–
Equus hydruntinus	–	–	–	–	–	–			–	–	–	–	–	–	–	–	–		–	–	–
Coelodonta antiquitatis	2	–	17	56	104	56	40	5	2	22	6	14	5	5	7	–	–		62	17	8
Camelus ferus	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–		–	–	–
Cervus elaphus	–	12	–	–	–	–		–	2	–	3	–	–	–	–	3	–		–	8	3
Megaloceros giganteus	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–		–	–	–
Alces alces	–	–	1	–	–	3		–	–	4	2	–	–	–	–	3	–		–	–	–
Rangifer tarandus	5	8	211	394	457	159	560	966	15	271	144	283	109	854	85	47	154		734	93	98
Bison priscus	–	6	1	19	37	46	42	7	2	16	17	22	2	16	4	2	–		95	68	12
Saiga tatarica	–	–	15	3	3	1	2	13	1	2	2	–	8	2	–	–	–		116	10	6
Ovibos pallantis	–	–	6	3	4	–	30	1		3	–	–	–	–	–	–	–		20	19	7
Ovis ammon	–	–	–	–	–	–		–		–	–	–	–	–	–	–	–		–	–	–

Species	Sites																	
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Lepus tanaiticus	47	34	13	129	1	338	117	15	389	264	21	162	114	95	66	620	–	2
Marmota bobak	19	55	10	181	1	116	48	3	12	72	7	61	199	130	79	66	–	49
Castor fiber	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
Hystrix vinogradovi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Canis lupus	8	–	2	6	5	95	43	11	17	3	–	14	4	11	55	2	–	18
Alopex lagopus	15	5	14	5	2	41	5	1	8	11	3	28	37	18	28	7	–	5
Vulpes vulpes	7	–	–	1	1	30	12	1	44	4		5	7	1	35	4	–	6
Vulpes corsac	–	–	–	–	–	–	–	–	–	–	–	2	2	4	–	–	–	–
Ursus arctos	7	–	15	–	–	–	–	–	–	3	–	–	–	1	–	3	–	–
Ursus spelaeus	–	–	–	–	2627	566	2993	–	37	–	–	50	30	–	54	–	–	9
Ursus thibetanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Martes sp.	–	–	–	–	–	3	2	3	6	–	–	2	–	–	1	38	–	–
Gulo gulo	2	–	–	–	–	–	1	–	–	–	–	–	–	1	2	–	–	–
Mustela eversmanni	–	–	1	–	–	1	2	–	2	–	–	1	–	–	–	–	–	–
Mustela erminea	–	–	–	–	–	2	3	–	4	1	2	11	2	3	–	62	–	–
Mustela nivalis	–	–	–	–	–	1	–	–	1	1	–	19	9	1	–	36	–	–
Meles meles	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	45
Crocuta crocuta	–	–	–	?	–	14	4	–	–	–	–	1	–	–	25	–	–	5
Lynx lynx	–	–	–	–	–	–	–	–	–	–	–	–	–		5	–	–	–
Panthera spelaea	–	–	–	–	–	11	–	–	1	–	–	1	1	2	–	–	–	2
Mammuthus primigenius	–	–	–	–	–	–	1	1	–	–	–	1	–	3	7	1	2	460
Equus cf. *latipes*	–	–	–	–	–	71	4	–	2	–	–	21	35	–	120	–	29	–

Table A.1 (*continued*)

Species	Sites																	
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Equus cf. *uralensis*	96	94	472	12	–	–	–	58	–	1	4	–	–	266	–	–	–	16
Equus hydruntinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	126
Coelodonta antiquitatis	8	5	17	?	–	29	2	9	4	–	–	3	5	144	84	–	1	–
Camelus ferus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Cervus elaphus	–	–	–	–	–	30	5	–	1	–	–	4	2	28	85	–	2	–
Megaloceros giganteus	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–
Alces alces	–	–	–	–	–	–	–	–	–	–	–	–	–	7	1	–	–	3
Rangifer tarandus	123	111	134	33	1	44	12	34	2	8	12	27	80	171	82	2	–	75
Bison priscus	21	4	46	4	1	8	3	20	1	–	4	9	7	294	47	5	476	11
Saiga tatarica	25	20	37	9	1	6	1	–	1	1	2	9	9	8	3	–	–	–
Ovibos pallantis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ovis ammon	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–

1.—Lobvinskaya cave (strata 3); 2.—Makhnevskaya cave; 3.—Grotto Blyznetsova; 4.—Ivaka; 5.—Sur'ya 1–7 (strata 2); 6.—Sur'ya 1–7 (strata 3); 7.—Verkhnegubakhinskaya; 8.—Rasik (strata 10); 9.—Rasik (strata 12); 10.—Viasher (pit 4,5); 11.—Viasher (pit 1, 2, 3); 12.—Kholodny; 13.—Stolbovoy; 14. Dyovaty Kamen' (Chusovaya); 15.—Kotel; 16.—Bolshoy Glukhoy (strata); 17.—Bolshoy Glukhoy (strata); 18.—Talytskogo cave; 19.—Bobilek (strata 4); 20.—Bobilek (strata 5); 21.—Bobilek (strata 6); 22.—Bezymyany; 23.—Shaitanoozersky (strata 5); 24.—Zotinsky; 25. Ustinivo; 26. Ignat'evskay, pit 1(strata 3); 27. Ignat'evskay, pit 5 (strata 3); 28. Ignat'evskay, pit 5 (strata 8); 29. Serpievskaya-1 (strata 2); 30.—Serpievskaya-2 (strata 3); 31.—Pryzhim 2; 32. Sikiyaz-Tamak 7, (strata 8); 33.—Sikiyaz-Tamak 7 (strata 9); 34.—Sikiyaz-Tamak 7 (strata 11); 35.—Nykolskaya (strata 2); 36.—Ust'- Katavskaya; 37.—Bayslantash (strata 4); 38.—Gornovo; 39.—Smelovskaya 2 (strata 3–4).

Table A.2
Radiocarbon age on collagen from fossil mammal bones in the Urals

Locality, strata	Latitude °N	Longitude °E	Dated object	Date $\pm\sigma$[a]	Lab No.[b]
1	2	3	4	5	6
Grotto Lobvinsky, strata 3	59,28	60,04	Bone	12 275 ± 55	KIA-5670
Grotto Bliznetsova	59,20	57,49	Bone	28 540 ± 300	LE-2766
Grotto Ivaka	59,17	57,30	Bone	26 730 ± 200	OxA-10 925
Grotto Ivaka	59,17	57,30	Bone	16 460 ± 185	SOAN-5142
Grotto Sur'ya 1–7, strata 2	59,10	57,31	Bone	14 500 ± 240	SOAN-5146
Grotto Sur'ya 1–7, strata 2	59,10	57,31	Bone	14 815 ± 75	OxA-11 299
Grotto Sur'ya 1–7, strata 2	59,10	57,31	Bone	14 845 ± 75	OxA-11 350
Grotto Sur'ya 1–7, strata 2	59,10	57,31	Bone	16 810 ± 65	OxA-12 122
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	29 500 ± 140	OxA-12 987
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	34 470 ± 350	OxA-10 914
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	42 550 ± 800	OxA-
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	45 700 ± 900	OxA-11 300
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	55 400 ± 1800	OxA-12 991
Grotto Sur'ya 1–7, strata 3	59,10	57,31	Bone	> 61 300	OxA-12 988
Grotto Verchnegubakhinsky	58,53	57,37	Bone	13 560 ± 70	OxA-10 908
Grotto Rasik, strata 10	59,04	57,33	Bone	12 680 ± 180	GIN-10 569
Grotto Rasik, strata 10	59,04	57,33	Bone	13 250 ± 180	GIN-10 568
Grotto Rasik, strata 10	59,04	57,33	Bone	13 330 ± 120	GIN-105567
Grotto Rasik, strata 11	59,04	57,33	Bone	31 540 ± 260	OxA-10 931
Grotto Rasik, strata 11	59,04	57,33	Bone	47 050 ± 750	OxA-12 985
Grotto Rasik, strata 11	59,04	57,33	Bone	> 34 490	IEMEG-1374
Grotto Rasik, strata 11	59,04	57,33	Bone	> 38 400	GIN-10 566
Grotto Viasher 1–3	59,05	57,39	Bone	13 570 ± 70	OxA-10 908
Grotto Viasher 1–3	59,05	57,39	Bone	16 130 ± 150	SOAN-5230
Grotto Viasher 1–3	59,05	57,39	Bone	16 900 ± 115	SOAN-5231
Grotto Kholodny	58,40	57,34	Bone	14 750 ± 70	OxA-10 910
Grotto Kholodny	58,40	57,34	Bone	16 370 ± 80	OxA-10 927
Grotto Kholodny	58,40	57,34	Bone	26 330 ± 120	OxA-12 988
Grotto Kholodny	58,40	57,34	Bone	25 000 ± 100	OxA-12 990
Grotto Kholodny	58,40	57,34	Bone	29 060 ± 140	OxA-12 987
Grotto Stolbovoy	58,40	57,34	Bone	22 890 ± 200	LE-2773
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 610 ± 60	CAMS-35 896
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 620 ± 60	CAMS-35 897
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 793 ± 122	IEMEG-1370

Table A.2 (*continued*)

Locality, strata	Latitude °N	Longitude °E	Dated object	Date ± σ[a]	Lab No.[b]
1	2	3	4	5	6
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 810 ± 60	CAMS-35 898
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 820 ± 60	CAMS-35 894
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	12 960 ± 60	CAMS-35 899
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	13 013 ± 135	IEMEG-1368
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	13 620 ± 60	CAMS-35 895
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	13 757 ± 250	IEMEG-1140
Grotto Dyrivaty Kamen'	57,39	58,54	Bone	15 200 ± 140	SOAN-5228
Grotto Kotel	57,45	58,45	Bone	13 245 ± 65	OxA-10 921
Grotto Bolshoy Glukhoy, strata 9	58,16	57,59	Bone	38 200 ± 900	GIN-8404
Grotto Bolshoy Glukhoy, strata 6	58,16	57,59	Bone	33 900 ±	LE-4201
Talitskogo	58,10	56,36	Bone	18 700 ± 200	GIN-1907
Grotto Bobylek, strata 4	56,19	57,39	Bone	14 200 ± 200	IERG-164
Grotto Bobylek, strata 4	56,19	57,39	Bone	14 630 ± 80	OxA-11 296
Grotto Bobylek, strata 4	56,19	57,39		16 720 ± 365	IERZ-142
Grotto Bobylek, strata 5	56,19	57,39	Bone	> 33 000	IERZ-137
Grotto Bobylek, strata 5	56,19	57,39	Bone	> 34 490	IEMEG-1374
Grotto Bobylek, strata 6	56,19	57,39	Bone	> 24 000	IERZ-138
Grotto Bezymyanny	56,54	62,05	Bone	19 240 ± 265	SOAN-2212
Grotto Shaitanoozersky	57,20	60,13	Bone	22 460 ± 340	SOAN-3824
Grotto Shaitanoozersky	57,20	60,13	Bone	23 179 ± 1420	SOAN-3825
Grotto Zotinsky	56,11	61,42	Bone	13 615 ± 215	SOAN-2467
Grotto Ustinovo	54,52	59,58	Bone	12 400 ± 30	IERZ-49
Ignatievskaya cave, pti 2, strata 3	54,54	57,47	Bone	> 27 500	IEMEG-723
Ignatievskaya cave, pti 5, strata 3	54,54	57,47	Bone	> 27 620	IERZ-59
Ignatievskaya cave, pti 5, strata 8	54,54	57,47	Bone	> 27 500	IERZ-21
Grotto Serpievsky-1, strata 2	54,50	57,50	Bone	16 585 ± 598	IEMEG-722
Grotto Serpievsky-1, strata 2	54,50	57,50	Bone	14 300 ± 110	SOAN-5307
Grotto Serpievsky-1, strata 2	54,50	57,50	Bone	13 870 ± 180	IERZ-46
Grotto Serpievsky-2, strata 3	54,50	57,50	Bone	25 200 ± 1800	SOAN-5308
Grotto Pryzhim II	55,60	57,45	Bone	16 650 ± 400	IERZ-32
Grotto Pryzhim II	55,60	57,45	Bone	17 070 ± 1017	IEMEG-700
Grotto Pryzhim II	55,60	57,45	Bone	21 085 ± 630	IERZ-37
Grotto Sikiyaz-Tamak 7, strata 8	55,11	58,38	Tooth	10 775 ± 75	OxA-10 704
Grotto Sikiyaz-Tamak 7, strata 9	55,11	58,38	Bone	> 57 300	OxA-10 916
Grotto Sikiyaz-Tamak 7, strata 11	55,11	58,38	Bone	> 47 600	OxA-10 889
Grotto Nikolsky	55,28	59,27	Bone	14 450 ± 75	OxA-10 920
Grotto Nikolsky	55,28	59,27	Bone	16 130 ± 310	SOAN-4804
Grotto Nikolsky	55,28	59,27	Bone	18 100 ± 215	SOAN-5310
Grotto Nikolsky	55,28	59,27	Bone	21 080 ± 205	SOAN-5144
Ust-Katavskay cave	54,56	58,08	Bone	35 650 ± 450	OxA-10 890
Grotto Baislantash, strata 4	52,54	56,52	Bone	13 560 ± 250	GIN-10 853
Gornovo	54,53	55,53	Wood	28 800 ± 1250	BASHGI-36
Gornovo	54,53	55,53	Wood	29 700 ± 1250	H-1856/1287
Gornovo	54,53	55,53	Teeth	> 33 670	LU-3712
Smelovskaya II, strata 3–4	54,53	52,16	Bone	31 000 ± 1500	GIN-8401
Smelovskaya II, strata 3–4	54,53	52,16	Bone	41 000 ± 800	GIN-8402

[a]Dates not calibrated.

[b]Lab Codes for dates: BASHGI—Cenozoic Laboratory of the Institute of Geology Scientific Centre of Ufa RAS, Ufa; CAMS—Centre for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA, USA; GIN—Geological Institute, Russian Academy of Sciences (RAS), Moscow; IEMEG—Institute of Animal Evolution Morphology and Ecology, RAS, Moscow; IERZ—Institute of Plant and Animal Ecology, Ural Branch RAS, Ekaterinburg; 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.

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