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Late Pleistocene megamammals of the Urals

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Abstract. An analysis of the species and the ratio of the remains of megamammals from 16 Late Pleistocene localities of the Urals is reported. The faunas of the early interstadial (Q_{III}, earlier than 33 000 years) include *Cervus elaphus* and *Equus* aff. *latipes*. The faunas of the Late Glacial have no *C. elaphus* and horses are represented by *E. uralensis*. In the northern Urals, *Rangifer tarandus* dominates in the faunas of the late Glacial, while in the central and southern Urals both *R. tarandus* and *E. uralensis* are abundant. In the late Glacial (Q_{III4}) the percentage of *Marmota bobac* and *Lepus tanaiticus* increases in the faunas from north to south. This fact indicates the existence of a climatic gradient in the Urals at that time.

Key words: Mammalia, Late Pleistocene, palaeoecology, Urals, Russia.

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I. INTRODUCTION

Megamammals have previously been described from a number of Late Pleistocene localities in the southern (SMIRNOV et al. 1990), central (KUZMINA 1975; PETRIN & SMIRNOV 1977) and northern (KUZMINA 1971; KOSINTSEV & BORODIN 1990) Urals. Analysis of the faunas from localities in the southern Urals has shown their heterogeneity in space and time. In this region, faunas of different ages reflect the chronological development of the faunistic complex of megamammals. Comparison of faunas of the same age but from different regions allowed us to identify faunistic complexes that reflect the differences between the climatic conditions of the western and eastern foothills and mountains of the southern Urals (SMIRNOV et al. 1990). The existence of chronological and geographical variants of faunistic complexes in the Late Pleistocene in the southern Urals allows us to formulate a hypothesis of heterogeneity of the Late Pleistocene faunas of the Urals as a whole. The aim of this work is to study chronological and geographical changes in the qualitative and quantitive structures of the Late Pleistocene megamammal faunas of the Urals.

II. MATERIAL AND METHODS

Data concerning bone remains from the loose strata of nine grottos, five inlets of caves and one interior part of a cave have been used in this work. The geographical locations of the caves is shown in Fig. 1.

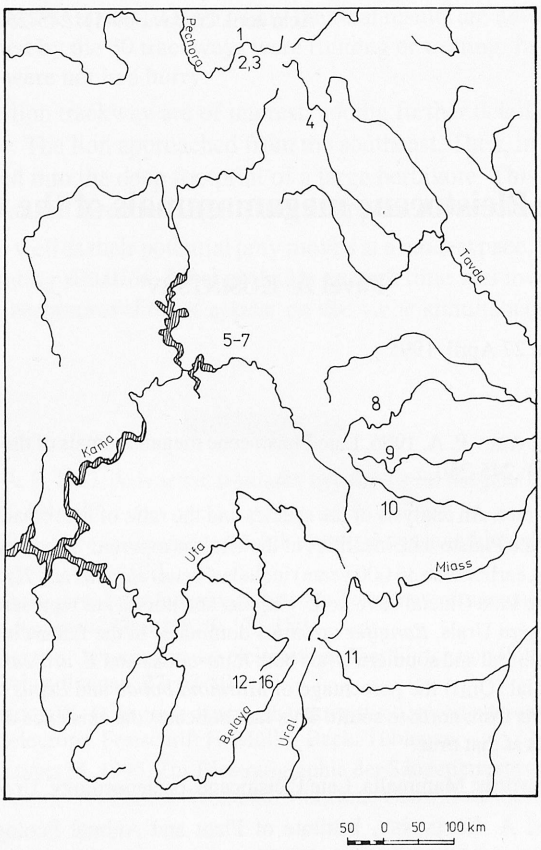

Fig. 1. The geographical localition of the caves. Western part of the northern Urals: 1 – Medvezhya cave; 2 – Uniynskaya cave; 3 – Kaninskaya cave (KUZMINA 1971). Eastern part of the Northern Urals: 4 – the Shaitansky rock-shelter (KOSINTSEV & BORODIN, 1990). Western part of the Middle Urals: 5 – Bliznetsova rock-shelter; 6 – Chornie Kosty rock-shelter; 7 – Stolbovoy (KUZMINA 1975). Eastern part of the Middle Urals: 8 – Shaitanoozersky rock-shelter; 9 – Bezimyanny rock-shelter; 10 – Zotinsky I rock-shelter (PETRIN & SMIRNOV 1977). Eastern part of the southern Urals: 11 – Ustinovo (SMIRNOV et al. 1990). Western part of the southern Urals: 12 – Serpievskaya I cave; 13 – Pryzhim II rock-shelter; 14 – Ignatievskaya (sites 1-3) cave; 15 – Ignatievskaya (site 5) cave; 16 – Idrisovskaya cave (SMIRNOV et al. 1990).

Localities 1-4 and 11-14 have several bone-bearing strata. Of these, only the faunas from the Late Pleistocene strata have been used in the analysis. The faunas from three different strata of locality I, two strata of locality 4 and one stratum from each of the other localities have been analysed. The age determination of the faunas was carried out through C^{14} dating of artefacts and faunistic complexes of rodents and other mammals.

Taphonomic analysis showed that the main agent of accumulation of the bone remains was predator activity. Artefacts have been found in nine localities, though only in small numbers, indicating the negligible role of man in the accumulation of the mammal bones.

The number of remains of each species from the different areas of the Urals in different chronological periods is shown in Table I. The geographical and chronological changes in the megamammal faunas have been analysed for three groups of species: *A. lagopus* and *V. vulpes*, *L. tanaiticus* and *M. bobac*, and the ungulates.

These groups were chosen for the following reasons: 1) Quantity; the remains of these species are usually the most numerous; 2) Taphonomic homogeneity; the similar sizes of the bones, as well

Table I

Megamammal remains (number of identified specimens) from the Late Pleistocene of the Urals

Species	North Urals		Middle Ural	South Urals	
	Q_{III}^{2-3}	Q_{III}^{4}	Q_{III}^{4}	Q_{III}^{2-3}	Q_{III}^{4}
Lepus tanaiticus GUREEV	43	5023	308	2440	1101
Lepus cf. *europaeus* PALLAS	–	–	–	5	–
Marmota bobac MULLER	–	1	36	684	302
Castor fiber L.	–	8	–	1	–
Canis lupus L.	14	355	15	183	28
Alopex lagopus L.	7	1211	73	270	71
Vulpes vulpes L.	–	16	7	103	34
Vulpes corsac L.	–	–	–	17	–
Ursus arctos L.	–	18	–	–	2
Ursus (*S.*) *spelaeus* ROS. & HEIM.	8	1182	25	4064	1755
Martes sp.	–	27	1	63	9
Gulo gulo L.	2	11	3	1	–
Mustela sp.	–	95	12	107	34
Crocuta spelaea GOLD.	–	–	–	17	3
Panthera spelaea GOLD.	1	14	–	12	–
Lynx lynx L.	–	–	–	5	–
Mammuthus primigenius BLUM.	1	43	393	1	1
Equus aff. *latipes* GROMOVA	143	–	–	100	–
Equus uralensis KUZMINA	–	560	682	–	85
Coleodonta antiquitatis BLUM.	66	130	54	52	15
Cervus elaphus L.	4	–	–	54	–
Capreolus capreolus L.	–	34	–	–	–
Alces alces L.	–	20	3	–	–
Rangifer tarandus L.	220	8318	639	107	81
Brison priscus BOJANUS	62	58	81	14	31
Saiga tatarica L.	3	42	91	27	13
Ovibos pallantis SMITH	12	231	8	–	–

as the similar roles of the species in each group in the ecosystems leads one to expect similar processes of accumulation; 3) Indicators of environmental conditions; the two latter groups are directly associated with the vegetation. For the groups *A. lagopus-V. vulpes* and *L. tanaiticus-M. bobac* only geographical changes in the percentage of remains in the localities from the end of the Late Pleistocene (Tables II and III) were examined. For the ungulates, quantitative and qualitative changes in their remains in all the localities of the last Glacial epoch were studied. For quantitative comparisons, the "*r*" criterion of similarity was used:

$$r = \sum p_i q_i,$$

where p_i and q_i are the frequencies of the corrected numbers of remains of species i in the two faunas to be compared (ZHYVOTOVSKY 1979). As a result, a matrix of values of r is obtained. This matrix forms the basis for the dendrogramme of similarity between the ungulate component of different localities (Fig. 2).

III. RESULTS AND DISCUSSION

The localities were divided into two groups on the basis of their species composition: those including *C. elaphus* and *E.* aff. *latipes* and those lacking these species. The first group includes

Table II

Geographic variation in the ratio of *L. tanaiticus* and *M. bobac* from late Würmian localities

Species	North Urals					
	Western regions 5 localities			Eastern regions 1 locality		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Lepus tanaiticus	4974	–	100.0	49	–	98.0
Marmota bobac	–	–	0.0	1	–	2.0
	Middle Urals					
	Western regions 3 localities			Eastern regions 3 localities		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Lepus tanaiticus	247	91.7-100.0	97.0	61	56.5-100.0	75.9
Marmota bobac	7	0.0-8.3	3.0	29	0.0-43.5	24.1
	South Urals					
	Western regions 3 localities			Eastern regions 1 locality		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Lepus tanaiticus	972	78.6-94.9	88.4	129	–	41.6
Marmota bobac	121	5.1-21.4	11.6	181	–	58.4

Table III

Geographic variation in the ratio of remains of *A. lagopus* and *V. vulpes* from late Würmian localities

Species	North Urals					
	Western regions 5 localities			Eastern regions 1 locality		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Alopex lagopus	1198	99.0-100.0	99.6	13	–	81.3
Vulpes vulpes	13	0.0-1.0	0.4	3	–	18.7
	Middle Urals					
	Western regions 3 localities			Eastern regions 2 localities		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Alopex lagopus	44	100.0	100.0	29	80.6-100.0	90.3
Vulpes vulpes	–	0.0	0.0	7	0.0-19.4	9.7
	South Urals					
	Western regions 3 localities			Eastern regions 1 locality		
	remains	Min-Max %	M %	remains	Min-Max %	M %
Alopex lagopus	66	50.0-73.3	60.2	5	–	83.3
Vulpes vulpes	33	26.4-50.0	39.8	1	–	16.7

three localities: Shaitansky grotto in the eastern part of the northern Urals (no. IV) and the Ignatievskaya (site 5) (no. XV)and Idrisovskaya (nos. XVI) caves in the western part of the southern Urals. Thus, this grouping is not based on the geographical position of the localities, but instead reflects their chronological position in the development of the faunistic complexes of Ural megamammals. Radiocarbon dating gives the age of the upper stratum in site 5 of Ignatievskaya cave as greater than 33 000 years. This date suggests an allocation to the early or middle part of the last Glacial, and the presence of *C. elaphus* and a massive horse indicate that it may be placed in one of the early interstadials.

The second group includes all the remaining localities. All the C^{14} dates from these localities give ages of less than than 29 000 years, and all the artefact complexes in them can be referred to the Upper Palaeolithic. Thus, this group of localities characterises the faunistic complex of Ural megamammals in the last Glacial (Q_{III4}). Our material allows us to examine geographical changes in the species structure of Ural megamammals during this period. Remains of *C. capreolus* and *C. fiber* have been found only in the northern Urals, while remains of *A. alces*, *O. pallantis* and *G. gulo* have been found only in the northern and central Urals and remains of *C. spelaea* only in the southern Urals (Table I).

The peculiarities of the species mentioned above are reflected in the structure of the ungulate fauna (Fig. 2). Three groups can be identified. The first group includes faunas of all the localities from the western part of the northern Urals. Typical of these is their domination by *R. tarandus* (Table II). This can be explained by severe climatic conditions. The second group includes faunas

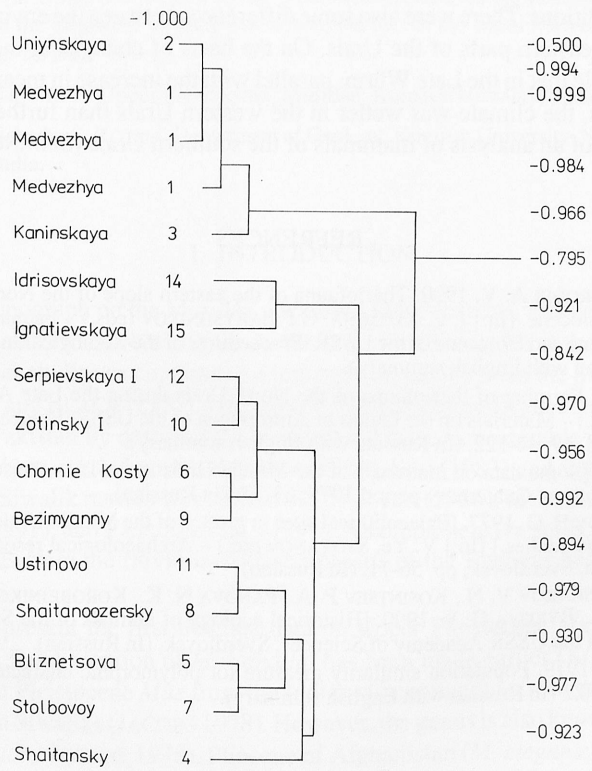

Fig. 2. Dendogram of the similarity in the ungulate faunas from Late Pleistocene localities of the Urals. The locality numbers in the dendogram correspond to the map numbers.

from the localities of the early interstadial (Q_{III2-3}) in the southern Urals. They are characterised by equal proportions of remains of all species of ungulates and by abundant remains of *C. elaphus* and *E.* aff. *latipes* (Table I). The third group includes faunas from all the localities of the late last Glacial (Q_{III4}) of the central and southern Urals and one fauna from the early interstadial (Q_{III2-3}) of the eastern part of the northern Urals. The ungulate complex of the late last Glacial is characterised by two dominant species, *R. tarandus* and *E. uralensis* (Table I). Because of its northerly position, the ungulate fauna from the early interstadial of the western part of the northern Urals was not associated with the faunas of the southern Urals that were dated to the same time interval. Its structure was closer to the faunas of the cold Late Würm from more southerly areas. The climatic conditions to which the faunas of the second group were subject could be considered to be relatively temperate. As for the faunas of the third group, their climatic conditions were relatively severe.

Analysis of changes in the correlation between the remains of *L. tanaiticus* and *M. bobac* from localities of the northern, central and southern Urals shows that *M. bobac* increases in relative abundance from north to south (Table III). Along the western slope of the Urals it increases from 0% to 11.6%, while along the eastern slope it increases from 2% to 50.9%. A similar, though not so clearly expressed, change is seen in the correlation between the remains of *A. lagopus* and *V. vulpes*. The proportion of *A. lagopus* remains decreases from north to south, while the proportion of *V. vulpes* remains increases (Table III).

Analysis of geographical changes in the correlation between the remains in the groups *A. lagopus-V. vulpes*, *L. tanaiticus-M. bobac* and the ungulates from the localities of the late last Glacial (Q_{III4}) of the Urals shows that at that time there was a strong north to south gradient in environmental conditions. There were also some differences between the environmental conditions in the western and eastern parts of the Urals. On the basis of changes in the number of marmot remains, it is possible that in the Late Würm, parallel with the increase in mean annual temperature from north to south, the climate was wetter in the western Urals than further east, as was found earlier on the basis of an analysis of mammals of the southern Urals (SMIRNOV et al. 1990).

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