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Late Pleistocene and Holocene small mammal faunas from the South Trans-Urals

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ABSTRACT

Bone remains of rodents and small lagomorphs (c. 24,000 cheek teeth) extracted from unconsolidated sediments of five karst cavities of the South Trans-Urals have been examined. On the basis of ^{14}C dates, two of these sites, the Syrtinsky and Alexeevsky caves, are regarded as key localities for the region; thus the main conclusions regarding the regional fauna composition and structures have been based on the fossil assemblages from these two sites. The species richness of rodent communities was calculated; the number of species changed over time. The total number of species found in the sequences amounted to 21; 15 of which occurred in both Late Pleistocene and Holocene assemblages. Four species appeared only in the beginning of the Holocene; the yellow steppe lemming and small jerboa (*Pygeretmus*) were noted to disappear at the end of the Sub-Boreal and do not occur in the modern fauna of the region. In the Late Pleistocene communities, *Lagurus lagurus*, *Eolagurus luteus* and *Microtus gregalis* were dominant. In the Holocene faunas, the narrow-skulled vole began to dominate and the steppe lemming decreased significantly in numbers, while the percentage of the common vole (*Microtus arvalis*) increased, though this species can be regarded as an azonal element in steppe associations. The proportions of xerophilic and mesophilic rodent species changed significantly during the interval examined: from 90% and 2% in Late Pleistocene communities to 30% and 35%, respectively, by the end of the Holocene.

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1. Introduction

The history of modern small mammal faunas cannot be understood without a detailed examination of their development in the Late Pleistocene and Holocene. This relatively short time interval (from a geological point of view) is peculiar, providing us with an opportunity to follow the development of recent animal species occurring under conditions of an extremely variable environment with regard to both biotic and abiotic components.

The problems with the changes in the animal population structure in different groups of mammals during the Late Pleistocene have been widely discussed by different scientists. It was shown that due to specific environmental conditions existing in Northern Eurasia in the Late Pleistocene, vast territories were occupied by special mammal communities; different authors named them “tundra-steppe”, “hyper-boreal” or “disharmonious” faunas (Smirnov, 2001). However, there are still both geographical and chronological ‘white spots’ with no information on this issue, and one of such regions is the South Trans-Urals. The region lies east of the Ural ridge, covering elevated and plain territories in the forest-steppe and steppe zones. The climate is arid here (precipitation not more than 350–400 mm per year) and the snow cover

reaches a depth of 0.3–0.4 m. The mean annual temperature ranges from +1 °C to +3 °C, and the winter minimum and summer maximum differ about 70–75 °C; the warm period (with no frosts) lasts c. 200 days. The vegetation is mainly of the forest-steppe and steppe types (Gerasimov, 1968; Mordkovich et al., 1997).

The mammals of this territory were examined by A. Maleeva (1982), Smirnov et al. (1990), Smirnov (1992), T. Strukova (Stephanovskiy et al., 2003), and S. Kuzmina (2000). Their studies provided numerous data on small mammal faunas, but they usually had no ^{14}C dates (except Ustinovo, which has two radiocarbon dates) and the faunas were preliminarily dated on the basis of morphological features of the dominant animal species.

Starting in 2000, researchers of the laboratory of historical ecology (Institute of Plant and Animal Ecology, RAS, in Ekaterinburg, Russia) made regular studies in steppe and forest-steppe regions of the Trans-Urals. The author of this paper, with collaborators, has examined mammal fossils from about 10 cave sites (Kuzmina et al., 2001; Kuzmina, 2002, 2003a). Data from 5 sites (Fig. 1) are presented below, two of which have been ^{14}C -dated (Kuzmina, 2003b). All these localities are cave sites situated in the valleys of small rivers flowing into the upper reaches of the Ural River. Due to the compact concentration of the localities under study and the number of ^{14}C dates, we have denoted this region the Magnitogorsk key territory for the steppe part of the South Trans-Urals. The study was carried out to examine the composition and

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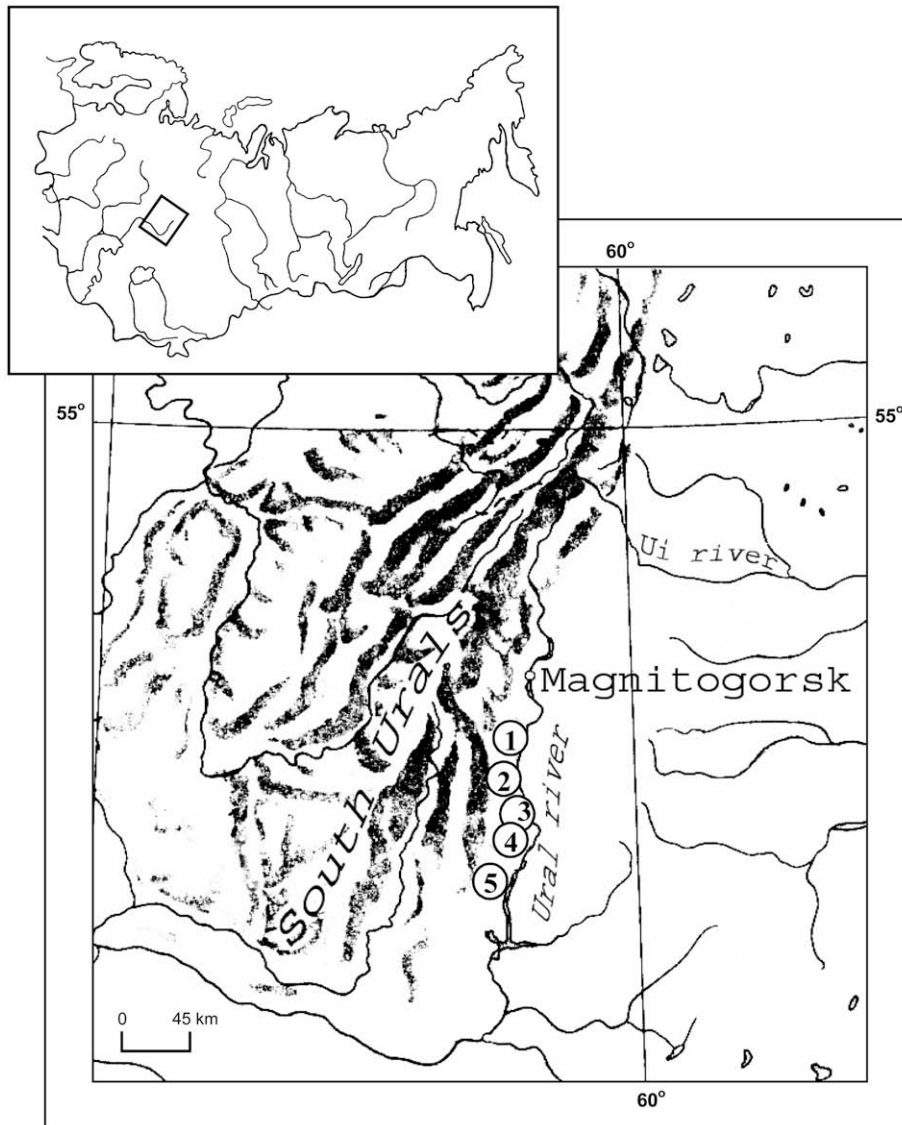


Fig. 1. The cave sites of the Magnitogorsk key territory of the South Trans-Urals: 1 – Syrtinsky; 2 – Cernishevsky-III; 3 – Khudolaz; 4 – Chernishevsky-V; 5 – Alexeevsky.

structure of animal populations of the Magnitogorsk key territory, in order to trace the dynamics of their development during the Late Pleistocene and Holocene.

2. Materials and methods

Bone remains of small mammals were extracted from unconsolidated cave sediments washed through 1 mm sieves. Among the small mammals in this study we examined all rodent remains and those of a lagomorph animal, genus *Ochotona* (that is, the level of primary consumers in ecosystems), not taking into consideration bones of insectivores, small carnivores, chiropterans, etc. Bone fossils collected from one lithological layer (and one horizon) are regarded as an elementary oryctocoenosis taking into account the species diversity and their proportion in the fossil assemblage (Smirnov, 2003).

Animal species were identified on the basis of their cheek teeth. Proportions of the species were calculated using the method proposed by Smirnov and Markova (1996). The basis of the method is the highest number of fossils of a specific element of a certain species. These numbers are added up and the sum is regarded as 100%. The resulting figure is considered to indicate the proportional

representation of species in the community (Smirnov and Markova, 1996). An example of such a calculation is shown in Table 1. Table 2 presents the total number of bone fossils excavated in the karst cavities of the Magnitogorsk key territory of the South Trans-Urals. A total of 20 elementary oryctocoenoses (assemblages) from five cave sites have been examined, the number of identified molars totalling 23,800. Seven elementary assemblages have been ^{14}C -dated; three of these indicate a Late Pleistocene age (Syrtinsky cave) and four have a Holocene age (Alexeevsky cave).

3. Fossil small mammal species in the Magnitogorsk key territory of the South Trans-Urals

The assemblages of the investigated territory are subdivided into Late Pleistocene and Holocene faunas based on ^{14}C data. A complete overview of the data is presented in Table 3.

3.1. The Late Pleistocene

During the late Valdai maximum glaciation interval (Late Weichselian), c. 24–17,000 years BP, glaciers covered only the higher parts of the South Ural mountains, spreading down river

Table 1

Late Pleistocene elementary oryctocoenoses of horizon 32 from the V lithological layer of the Syrtinsky cave, South Trans-Urals

Species	Cheek teeth						Percentage
	M ¹	M ²	M ³	M ₁	M ₂	M ₃	
<i>Microtus gregalis</i>	1	5	1	3	2	1	9.38
<i>Lagurus lagurus</i>	9	5	10	16	12	6	50.00
<i>Marmota</i> sp.	–	–	–	1	–	–	3.13
<i>Ochotona pusilla</i>	1	–	–	–	–	–	3.13
<i>Spermophilus major</i>	–	–	–	2	–	–	6.25
<i>Eolagurus luteus</i>	7	4	4	8	8	2	25.00
<i>Pygeretmus (Alactagulus) pumilio</i>	–	–	–	1	–	–	3.13
Summed maximum quantity of the same molars	34						100
Total number of identified molars	109						

plains, and the region under study was rather far from the extended northern inland ice sheets. Annual mean temperatures range from -3 to -5 °C; the permafrost thickness reached 200 m; the vegetation type could be described as sagebrush and herb steppes, both on the plains and in the low mountains, combined with sagebrush deserts and areas of pine-and-birch forests and pine open forests with steppe communities (Velichko, 2002).

The Late Pleistocene stage of the small mammal fauna history is represented by seven assemblages (elementary oryctocoenoses) from the Syrtinsky cave; the total number of cheek teeth amounted to over 3300. Fifteen species of rodents and 1 pika are recorded in the Late Pleistocene interval examined (Table 3). For the time of the Late Valdai glacial maximum, c. 24–17,000 years ago, 13 species of these two orders were recorded, and during the Late Glacial (17–12,000 years BP) the species number decreased to 10 taxa. The taxa lists of all assemblages include steppe lemmings (*Lagurus lagurus*), narrow-skulled voles (*Microtus gregalis*), yellow steppe lemmings (*Eolagurus luteus*), suslik (*Spermophilus major*), marmot (*Marmota bobak?*), and steppe pika (*Ochotona pusilla*). Almost all assemblages also included molars of a small jerboa (genus *Pygeretmus*) similar to the modern species *Pygeretmus (Alactagulus) pumilio* (Shenbrot et al., 1995). The occurrence of a number of species in the Late Pleistocene assemblages is irregular; their presence varied over time. For example, the mole vole *Ellobius talpinus* occurred only during the LGM (Table 3).

Two lower molars of the collared lemming *Dicrostonyx* found in the sample from horizon 24 of the Syrtinsky cave are dated to 22,050 years BP (Table 3). This find probably derived from birds of prey bringing their quarry from the elevated region of the South

Ural eastern slope, where different environments were present. The tundra-type group of animal species was marked in the samples from the Ustinovo cavity situated in an elevated region, the lower layer of which is dated to the Late Glacial ($12,400 \pm 300$ years BP), and included molars of *Dicrostonyx gulielmi* and *Lemmus* sp. (Smirnov et al., 1990).

3.2. The Holocene

The faunal history during the Holocene was characterized by data from 13 elementary oryctocoenoses (assemblages from five cave sites; the total number of molars amounted to more than 20,000). In the Boreal period (^{14}C -dated to 8450 years BP), small mammal communities included 20 species (of rodents and pika); subsequently, the number of species decreased, totalling 18 in the Sub-Boreal (2550 years BP) and 16 in the Sub-Atlantic (1470 years ago). In the beginning of the Holocene, four new species (not recorded previously) were found in rodent assemblages: the common hamster (*Cricetus cricetus*), smaller suslik (*Spermophilus pygmaeus*), field vole (*Microtus agrestis*), and the birch mouse (*Sicista* sp.). At the boundary of the Sub-Boreal and Sub-Atlantic, about 2500 years ago, two species were shown to disappear from the faunas, the yellow steppe lemming and small jerboa (*Pygeretmus*); this time interval was recorded for the first time in the region. In modern times, the small mammal fauna of the South Trans-Urals numbers 21 species, four of which have not been observed in sediments of the examined cave sites. They are: the harvest mouse (*Micromys minutus*), two rats (*Rattus rattus*, *Rattus norvegicus*), and an introduced species, *Ondatra zibethicus*.

Table 2

Number of fossilized rodent molars from different sites of the Magnitogorsk key territory of the South Trans-Urals

Geological Age	Site	Layer	Horizon (depth in cm)	Number of remains (max. quantity of identical elements)	Years BP (^{14}C date)	Laboratory index	
Holocene	Khudolaz	I	1 (0–5)	2 110 (508)			
	Chernishevsky-III	I	1 (0–5)	653 (176)			
	Alexeevsky	I	1 (0–10)	4 279 (819)	1 470 \pm 90	GIN-11330	
	Alexeevsky	I	2 (–10 to 20)	2 982 (637)	2 550 \pm 100	GIN-11331	
	Syrtinsky	I	1 (0–5)	470 (112)			
	Syrtinsky	I	2 (–5 to 10)	245 (59)			
	Syrtinsky	I	3 (–10 to 20)	203 (62)			
	Syrtinsky	I	5 (–30 to 40)	1 136 (272)			
	Chernishevsky-V	I	1 (0–10)	727 (221)			
	Chernishevsky-V	I	2 (–10 to 25)	1 251 (255)			
	Alexeevsky	II	4 (–30 to 40)	3 414 (787)	8 100 \pm 240	GIN-11333	
	Syrtinsky	I	7 (–45 to 50)	1 390 (328)			
	Alexeevsky	II	5 (–40 to 50)	1 643 (350)	8 450 \pm 200	GIN-11334	
	Late Pleistocene	Syrtinsky	II	11 (–70 to 80)	240 (55)		
			II	13 (–90 to 100)	501 (113)	13 990 \pm 340	SBRAS-5134
		II	15 (–110 to 120)	614 (152)	(?)		
		III	18 (–140 to 150)	1 209 (207)	17 160 \pm 190	SBRAS-5132	
		III	24 (–200 to 210)	517 (146)	22 050 \pm 200	SBRAS-5133	
		IV	28 (–240 to 250)	130 (34)			
		V	32 (–280 to 290)	107 (32)			

Table 3
Species composition dynamics of rodent faunas from different sites of the Magnitogorsk key territory of the South Trans-Urals

No	List of species	Late Pleistocene – Holocene time, years BP (by ¹⁴ C dates)							Modern state ^a
		22 050	17 160	13 990	8 450	8 100	2 550	1 470	
Lagomorpha									
Ochotonidae									
1	<i>Ochotona pusilla</i>	+	+	+	+	+	+	+	+
Rodentia									
Sciuridae									
2	<i>Spermophilus major</i>	+	+	+	+	+	+	+	+
3	<i>Spermophilus pygmaeus</i>	–	–	–	+	+	+	–	+
4	<i>Marmota bobak</i> (?)	+	+	+	+	+	–	–	+
Dipodidae									
5	<i>Sicista</i> sp.	–	–	–	+	+	+	+	+
6	<i>Allactaga jaculus</i>	+	+	–	+	+	+	+	+
7	<i>Pygeretmus</i> (<i>Alactagulus pumilio</i>)	+	+	+	+	+	+	–	–
Muridae									
8	<i>Apodemus (Sylvaemus)</i> sp.	–	–	–	+	+	+	+	+
9	<i>Micromys minutus</i>	–	–	–	–	–	–	–	+
10	<i>Rattus rattus</i>	–	–	–	–	–	–	–	+
11	<i>Rattus norvegicus</i>	–	–	–	–	–	–	–	+
Cricetidae									
12	<i>Ellobius talpinus</i>	–	+	–	+	+	+	+	+
13	<i>Allocricetulus eversmanni</i>	+	+	–	+	+	+	+	+
14	<i>Cricetulus migratorius</i>	–	+	+	+	+	–	+	+
15	<i>Cricetus cricetus</i>	–	–	–	+	+	+	+	+
16	<i>Ondatra zibethicus</i>	–	–	–	–	–	–	–	+
17	<i>Clethrionomys</i> ex gr. <i>rutilus-glareolus</i>	+	–	–	+	+	+	+	+
18	<i>Lagurus lagurus</i>	+	+	+	+	+	+	+	+
19	<i>Eolagurus luteus</i>	+	+	+	+	+	+	–	–
20	<i>Dicrostonyx</i> sp.	+	–	–	–	–	–	–	–
21	<i>Arvicola terrestris</i>	+	+	+	+	+	+	+	+
22	<i>Microtus gregalis</i>	+	+	+	+	+	+	+	+
23	<i>M. oeconomus</i>	–	+	+	+	+	+	+	+
24	<i>M. agrestis</i>	–	–	–	+	–	+	+	–
25	<i>M. arvalis</i>	+	–	–	+	+	+	+	+

^a Data on the extant fauna is after Marvin (1969), and also from the author's own analyses of pellets and carnivore faeces collected in the study region.

However, rat remains (*Rattus* sp.) were found in the site of Verkhny Gussikha (Smirnov and Kuzmina, 2001), which is also situated within the Magnitogorsk key territory. In contrast, the field vole (*M. agrestis*) was not noted in modern steppe faunas of the Urals (Marvin, 1969); it is also not found in pellets and faeces, nor among the animals trapped around the nature reserve of Arkaim (Markova, 2003).

4. Structure of the fossil small mammal assemblages of the Magnitogorsk key territory of the South Trans-Urals

Not only the presence of species is relevant for our analyses but also the structure of the fossil communities is important. The proportion of the different species in the fauna is significant.

During the Late Valdai, the steppe lemming dominated the communities, making up more than 30% of all small mammal remains. The yellow steppe lemming occupied the second place by abundance, followed by the narrow-skulled vole (Fig. 2). Four species (Eversman's and gray hamsters, steppe pika, root vole) were common, representing 1–9.9% of the fauna. Several species were rare (0.2–0.9%): big jerboa, steppe marmot, big suslik, common and *Clethrionomys* (ex gr. *rutilus-glareolus*) voles, mole vole, small jerboa (*Pygeretmus*), and water vole. The collared lemming from horizon 24 of the Syrtinsky cave may also be referred to this group. In the Boreal period, about 8000 years BP, the narrow-skulled vole began to dominate, and the steppe lemming moved into second place (Fig. 2). The third place was occupied by the common vole with 6.9%. The percentage of *E. luteus* decreased to 4.22%. Common species were Eversman's and gray hamsters, steppe pika, big jerboa,

water and root voles, common hamster, and mole vole. Both suslik species, marmot, field vole, wood and birch mice, *Clethrionomys* voles (ex gr. *rutilus-glareolus*), and small jerboa were rare in these faunas. By the end of the Sub-Boreal, the percentage of yellow steppe lemming remains decreased to 0.31%, and in the Sub-Atlantic deposits they were not found at all, like the *Pygeretmus* jerboa. During the Sub-Atlantic, the narrow-skulled vole remained dominant, but the next position was occupied by common vole remains (13.19%), the animal which should be regarded as an azonal element in steppe communities. The number of steppe lemming remains took third position with 11.6%. Steppe pika, water, root and field voles, common hamster, birch mouse, forest voles and mole vole were common in these faunas. Eversman's hamster, big jerboa and wood mice were rare. Some animals are extremely rare (gray hamster, the two suslik species, *S. major* and *S. pygmaeus*, and marmot).

Many explorers agree that the main factor in the extant steppe ecosystems is humidity (Odum, 1986; Mordkovich et al., 1997). That is why we tried to divide the assemblages into two groups, according to their dependency on this factor: xerophilic and mesophilic species (Fig. 3). The narrow-skulled vole, *M. gregalis*, is regarded as a separate group (the cryoxerophilic one), due to its extremely wide polyzonal distribution, both in the Late Pleistocene and in modern times. *Dicrostonyx* remains are also referred to this group. The group of xerophilic animals included the following species: *O. pusilla*, *S. major*, *S. pygmaeus*, *M. bobak*, *Allactaga jaculus*, *Pygeretmus (Alactagulus) pumilio*, *E. talpinus*, *Allocricetulus eversmanni*, *Cricetulus migratorius*, *L. lagurus*, and *E. luteus*. The species *Sicista* sp., *Apodemus (Sylvaemus)* sp., *C. cricetus*, *Clethrionomys* ex gr. *rutilus-glareolus*, *Arvicola terrestris*, *Microtus oeconomus*,

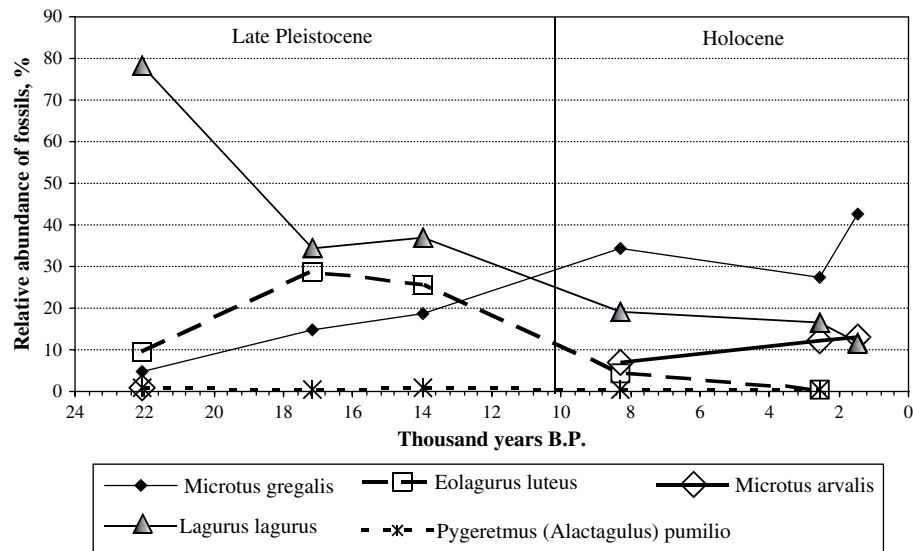


Fig. 2. Changes through time in the relative abundance of species forming the bulk of rodent faunas in the Magnitogorsk key territory of the South Trans-Urals.

M. agrestis, and *M. arvalis* are included in the mesophilic group. The changes in time of the relative abundance of the remains of these two ecological mammal groups is shown in Fig. 3. One can observe that during the Late Pleistocene, xerophilic species dominate heavily in the region (70–90%). The proportions of cryoxerophilic animals increased gradually, from 5 to c. 19%, and those of mesophilic species varied between 2 and 15%.

At the beginning of the Holocene, the Boreal, the percentages of xerophilic species decreased significantly (down to 40%), whereas the proportion of mesophilic animals increased to 25%. At the end of the Holocene, the Sub-Atlantic, the cryoxerophilic group began to dominate (35.36%), led by only one species, the narrow-skulled vole. Mesophilic species showed almost the same value (35.15%), and xerophilic forms showed a further decrease in abundance (30%). In the latter group, two species were noted to disappear entirely, and steppe rodents in the small mammal assemblages became rare or extremely rare. At present, steppe ecosystems are more mesophitic. This is not only the result of changes in climate (Dinesman, 1999), but steppe ecosystems are also heavily affected

by the expansion of cultivated landscapes and the reduction of the primary steppe areas.

5. Conclusions

The data obtained indicate that during the period examined in the South Trans-Urals, the population of small mammals showed no significant changes in both composition and structure. Even the Pleistocene – Holocene transition interval affected the population of small mammals of this region to a much smaller extent than those found further north and west. Zonal fauna type (steppe – semi-desert) during this time interval remained the same. The quality of the fauna composition remained the same during the whole period studied, but percentages of *Lagurus–Eolagurus* remains were noted to decrease gradually, whereas those of *Microtus* voles (especially *M. gregalis* and *M. arvalis*) increased. Such conservatism was probably due to the specific geographic position of the South Trans-Urals. First of all, this region is situated continentally, at the eastern edge of Europe, thus maximally distant from

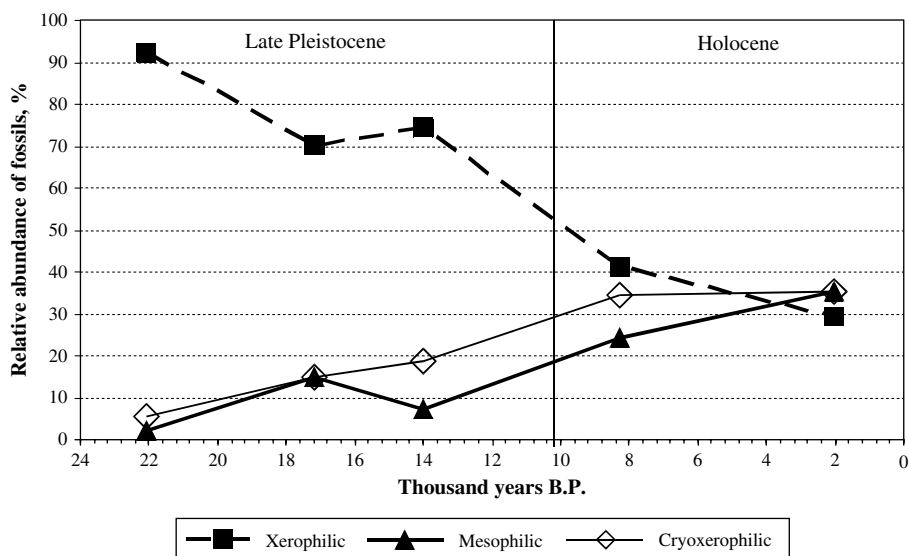


Fig. 3. Changes in time of the relative abundance of different ecological groups of rodents from the South Trans-Urals.

both Arctic and Atlantic coasts. Second, this territory remained far enough from the Valdai ice sheets and hence was affected by those to a lesser extent than areas lying further north and west. In the third place, the Ural mountain barrier closed off the South Trans-Urals from the influence of humid air masses moving eastwards from the Atlantic. This caused the high aridity of the climate, which also affected the small mammal communities of the region.

An important feature of the Late Pleistocene complexes of small mammals found in the South Trans-Urals steppe region is the absence of tundra species. The latter were widely represented in the faunas 200–250 km north of this region. For example, during the LGM, the small mammal communities of the Middle Trans-Urals were dominated in equal proportions by the steppe lemming (*L. lagurus*) and the narrow-skulled vole (in rare cases – *E. luteus*), followed by a tundra form – the collared lemming (*Dicrostonyx*) (Strukova, 2000). In the South Ural mountain sites situated farther to the west, small mammal communities also included tundra elements such as *Dicrostonyx* sp. and *Lemmus* sp. (Smirnov et al., 1990). In the Pre-Urals, areas in about the same latitude as the region studied but west of the ridge, also revealed tundra elements, and besides, wider represented mesophilic elements, namely forest, meadow, and river-side ones (Yakovlev et al., 2005), which were probably due to the stronger influence of Atlantic air masses and the relative proximity of ice sheets.

The small mammal communities of the South Trans-Urals remained conservative in the Holocene too. Desert and semi-desert species continued to live in the region as relics almost until the late Holocene. Only at the end of the Sub-Boreal was this group, represented by *E. luteus* and *Pygeretmus (Alactagulus) pumilio*, observed to disappear from the region, moving south-eastwards to Asia.

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