Late Pleistocene and Holocene Faunas of Small Mammals of the Urals

Nikolai G. Smirnov
Institute of Plant and Animal Ecology, Russian Academy of Sciences, Ekaterinburg

ABSTRACT.–This paper presents a regional summary of small mammal faunas of the Urals during the Late Pleistocene and Holocene. It proposes a comparative analysis of the structure and composition of the Quaternary faunas that have been studied (and previously described in Russian) from the South, Middle, and North Urals during the last several years. The data discussed were obtained during excavations of several dozens of cave sites. The analysis of materials utilized the ratio of species remains and proportions in the local faunas of species having different biotopic preferences. To describe the faunal structure, indices of species diversity and equitability were used. Differing combinations of species composition and structure of the faunas based on these indices are shown to exist for different Late Pleistocene/Holocene time intervals and for different regions of the Urals.

ПОЗДНЕПЛЕЙСТОЦЕНОВЫЕ И ГОЛОЦЕНОВЫЕ ФАУНЫ МЕЛКИХ МЛЕКОПИТАЮЩИХ УРАЛА

Н. Г. Смирнов

АБСТРАКТ.–Данная работа представляет собой региональную сводку по фаунам мелких млекопитающих Урала в позднем плейстоцене и голоцене. В ней приведен сравнительный обзор состояния изученности состава и структуры фаун Южного, Среднего и Северного Урала, описанных за последние годы в литературе на русском языке. Материал, обсуждаемый в работе, получен из раскопок нескольких десятков пещерных местонахождений. Анализ материала базируется на соотношении долей остатков видов и количества видов с разной биотопической приуроченностью в локальных фаунах. При описании структуры фауг использованы индексы видового разнообразия и степени выровненности долей остатков видов. Показана специфика состава и структуры фаун по этим показателям в разных частях Урала.

Quaternary Paleozoology in the Northern Hemisphere. J. J. Saunders, B. W. Styles, and G. F. Baryshnikov (Editors). 1998. Illinois State Museum Scientific Papers, Vol. XXVII. Springfield.

INTRODUCTION

Studies of the history of small mammal faunas by I. M. Gromov and his disciples started widely in the former Soviet Union in the 1950s (e.g., Gromov 1983; Vereshchagin and Gromov 1977; and numerous other references). Not until the 1980s, however, did these studies include the elevated regions of the Urals. Quaternary history of small mammal faunas of the adjacent territories (Pre-Urals, Trans-Urals) have been studied by Maleeva (e.g., 1982) and by Sukhov (e.g., 1970), but they did not include Holocene data.

The Ural Mountains form the boundary between Europe and Asia. The Urals cross all the natural zones of North Eurasia: tundra, taiga, broad-leaved forests, forest-steppes, steppes, and semideserts. The Ural ridge stretches for about 2,000 km, starting beyond the polar circle in the north and reaching the semideserts in the south. Nearly the whole length of the ridge is marked with numerous karst cavities, many of which are full of Quaternary mammal remains.

If desired one can find sites with similar taphonomy and thus obtain a fully comparable picture of the dynamics of the fauna and other biotic characteristics across this vast latitudinal gradient. For the purpose of comparison, I selected several relatively compact tracts in the South, Middle, and North Urals, where a series of cave sites have been found containing well preserved faunal material of Pleistocene and Holocene age.

In order to describe the full chronological succession of small mammals one must possess data from no less than several thousand molars. After the molars have been identified to species, taxa lists are compiled and the species proportions are calculated, as are indices of species diversity and equitability.

Especially interesting for the Urals is the problem of the transformation of disharmonious periglacial associations into the zonal associations of the Holocene period. This problem is of utmost importance for the Middle and South Urals where there are relatively large tracts of azonal insular forest-steppes, among the inhabitants of which there are no vertebrate animals typical of steppe biotopes.

MATERIALS AND METHODS

The materials studied are from sites that are broadly distributed both geographically and chronologically (Fig. 1).

The descriptions of sites and taxa lists are omitted in the text, as the majority of them have been published earlier: the main part of the data from the South Urals may be found in Smirnov, et al. (1990, 1992). Data from the Middle Urals are available in a previous paper (Smirnov 1993). Dating was done by the radiocarbon method. The strata shown to be aged beyond the limit of radiocarbon dating were considered to date to the first part of the Late Pleistocene. Such layers were represented in the Ignatievsky cave and the First Serpievsky Cave in the South Urals (Smirnov et al.1990) and Bobyliok cavity in the Middle Urals. The full collection from these layers includes approximately 6,000 cheek teeth of small mammals. Unfortunately it is not yet possible to determine the age of these materials more exactly. All of these strata include faunas similar in species lists and species proportions. All of them are viewed to characterize one and the same stage of faunal development around the time of the Mikulino interglacial.

The stage of faunal development shown between 25,000 and 12,000 years B.P. appeared to be the richest in both the number of sites and abundance of animal remains. The characteristics of this time interval are considered to be similar to those of the Late Valdai stage of the European stratigraphic chart or to the Sartansky horizon of the Siberian scheme. Four sites with small mammal remains of this faunal stage have been studied for the Middle Urals (Krasnoufimsky area). The whole collection includes about 6,000 molars of small mammals. Six sites of this age were studied in the South Urals. These sites contained about 3,000 small mammal molars.

Only two sites containing faunas of the Late Pleistocene - Holocene transition period (dated to 11,000 - 9,000 years B.P.) are known at the present time and both occur only in the Middle Urals. They are richly fossiliferous and the collection includes about 25,000 small mammal molars.

The small mammal fauna of the Atlantic period was represented in only one site in the Middle Urals, the cavity named Oleniy, where some 5,500 molars have been studied.

Two sites in the South Urals (Sim III, Ustinovo; about 7,000 molars) and two others in the Middle Urals (Tavra, Sukhorechensky; 1,500 cheek teeth) contained the data for the small mammal fauna of the Sub-Boreal period.

INTRODUCTION

Studies of the history of small mammal faunas by I. M. Gromov and his disciples started widely in the former Soviet Union in the 1950s (e.g., Gromov 1983; Vereshchagin and Gromov 1977; and numerous other references). Not until the 1980s, however, did these studies include the elevated regions of the Urals. Quaternary history of small mammal faunas of the adjacent territories (Pre-Urals, Trans-Urals) have been studied by Maleeva (e.g., 1982) and by Sukhov (e.g., 1970), but they did not include Holocene data.

The Ural Mountains form the boundary between Europe and Asia. The Urals cross all the natural zones of North Eurasia: tundra, taiga, broad-leaved forests, forest-steppes, steppes, and semideserts. The Ural ridge stretches for about 2,000 km, starting beyond the polar circle in the north and reaching the semideserts in the south. Nearly the whole length of the ridge is marked with numerous karst cavities, many of which are full of Quaternary mammal remains.

If desired one can find sites with similar taphonomy and thus obtain a fully comparable picture of the dynamics of the fauna and other biotic characteristics across this vast latitudinal gradient. For the purpose of comparison, I selected several relatively compact tracts in the South, Middle, and North Urals, where a series of cave sites have been found containing well preserved faunal material of Pleistocene and Holocene age.

In order to describe the full chronological succession of small mammals one must possess data from no less than several thousand molars. After the molars have been identified to species, taxa lists are compiled and the species proportions are calculated, as are indices of species diversity and equitability.

Especially interesting for the Urals is the problem of the transformation of disharmonious periglacial associations into the zonal associations of the Holocene period. This problem is of utmost importance for the Middle and South Urals where there are relatively large tracts of azonal insular forest-steppes, among the inhabitants of which there are no vertebrate animals typical of steppe biotopes.

MATERIALS AND METHODS

The materials studied are from sites that are broadly distributed both geographically and chronologically (Fig. 1).

The descriptions of sites and taxa lists are omitted in the text, as the majority of them have been published earlier: the main part of the data from the South Urals may be found in Smirnov, et al. (1990, 1992). Data from the Middle Urals are available in a previous paper (Smirnov 1993). Dating was done by the radiocarbon method. The strata shown to be aged beyond the limit of radiocarbon dating were considered to date to the first part of the Late Pleistocene. Such layers were represented in the Ignatievsky cave and the First Serpievsky Cave in the South Urals (Smirnov et al.1990) and Bobyliok cavity in the Middle Urals. The full collection from these layers includes approximately 6,000 cheek teeth of small mammals. Unfortunately it is not yet possible to determine the age of these materials more exactly. All of these strata include faunas similar in species lists and species proportions. All of them are viewed to characterize one and the same stage of faunal development around the time of the Mikulino interglacial.

The stage of faunal development shown between 25,000 and 12,000 years B.P. appeared to be the richest in both the number of sites and abundance of animal remains. The characteristics of this time interval are considered to be similar to those of the Late Valdai stage of the European stratigraphic chart or to the Sartansky horizon of the Siberian scheme. Four sites with small mammal remains of this faunal stage have been studied for the Middle Urals (Krasnoufimsky area). The whole collection includes about 6,000 molars of small mammals. Six sites of this age were studied in the South Urals. These sites contained about 3,000 small mammal molars.

Only two sites containing faunas of the Late Pleistocene - Holocene transition period (dated to 11,000 - 9,000 years B.P.) are known at the present time and both occur only in the Middle Urals. They are richly fossiliferous and the collection includes about 25,000 small mammal molars.

The small mammal fauna of the Atlantic period was represented in only one site in the Middle Urals, the cavity named Oleniy, where some 5,500 molars have been studied.

Two sites in the South Urals (Sim III, Ustinovo; about 7,000 molars) and two others in the Middle Urals (Tavra, Sukhorechensky; 1,500 cheek teeth) contained the data for the small mammal fauna of the Sub-Boreal period.

MAIN SITES OF FOSSIL MATERIAL (number of molars)

	MIDDLE URALS	SOUTH URALS
SA	Sukhorechensky, Tavra, Bazhukovo III (42,000)	Simsky fauna: (7,000) Serpievsky cave I, rock-shelters, Sim I, II, III
SB	Sukhorechensky, Tavra (1,500)	
AT	Oleniy cavity (5,500)	
BO	Dyrovaty cave (2,000)	
PB	Bolshoi Glukhoi (7,500) Dryovaty cave (18,000)	
Q $\frac{4}{3}$	Arakaevsky fauna: (6,000) Arakaevo cave, Bobyliok cave, Dryovaty, Alikaev Kamen'	Ignatievsky fauna: (3,000) Ignatievsky cave, Serpievsky caves, I, II, Idrisovsky, Prizhim
Q $\frac{3}{3}$ Q $\frac{2}{3}$		
Q $\frac{1}{3}$	Sargainsky fauna: (1,700) Bobyliok cave	Serpievsky fauna: Ignatievsky o. (4,000) Serpievsky II

Figure 1. Main sites of fossil material (number of molars) in the Middle and South Urals. SA = Sub-Atlantic; SB = Sub-Boreal; AT = Atlantic; BO = Boreal; PB = Pre-Boreal; Q 4/3 = Late Valdai; Q 1/3 = first half of Late Pleistocene; Q 2/3 and Q 3/3 = intervening intervals.

The Sub-Atlantic period is represented by four sites in the Middle Urals, with a combined sample of 42,000 molars of small mammals.

Some of the most interesting sites are described below.

In the Simsky area, 10 sites with Quaternary fauna were excavated from karst cavities of different types. The maximum distance between sites is about 15 km. The area is situated in the mountain belt of mixed forests with broad-leaved elements present. In its northern part the Simsky area adjoins the insular Mesyagutovsky forest-steppe tract. The main site studied in this area is Ignatievsky Cave. This cave was excavated for five years, with the participation of archaeologists. The cave included a cultural layer of Late Paleolithic age and numerous rock paintings were discovered on the walls (Petrin 1992). This cave does not contain Holocene deposits; all the sediments, with a maximum depth exceeding four meters, are dated to different periods of the Late Pleistocene. A series of pits was discovered in different parts of the cave, and it was possible to correlate the deposits in these pits.

In the Middle Urals (Krasnoufimsky area) we have discovered a cave, named Bobyliok, that includes a succession of unconsolidated deposits about 4 m deep, dated to the Late Pleistocene and Holocene (Volokitin et al. 1992). The lowermost strata contained fauna similar to those dated to the Mikulino interglacial. The middle layers contained faunas of intermediate type, and in their upper part included a stratum corresponding to the Late Valdai main phase, with a cultural layer and Upper Paleolithic megafauna. The uppermost layers in the cave dated to the Holocene and included archaeological materials and megafauna of the Mesolithic, Neolithic, Bronze and Early Iron Ages, and the Middle Ages.

Data on small mammal species composition (percentage for each stratum) for all cave sites were compared and grouped, taking into consideration the stratigraphy, radiocarbon dates, and ages based on associations with archaeological materials. Based on the results of grouping the data obtained for contemporaneous layers at sites situated in neighboring territories, we distinguished a series of local faunas.

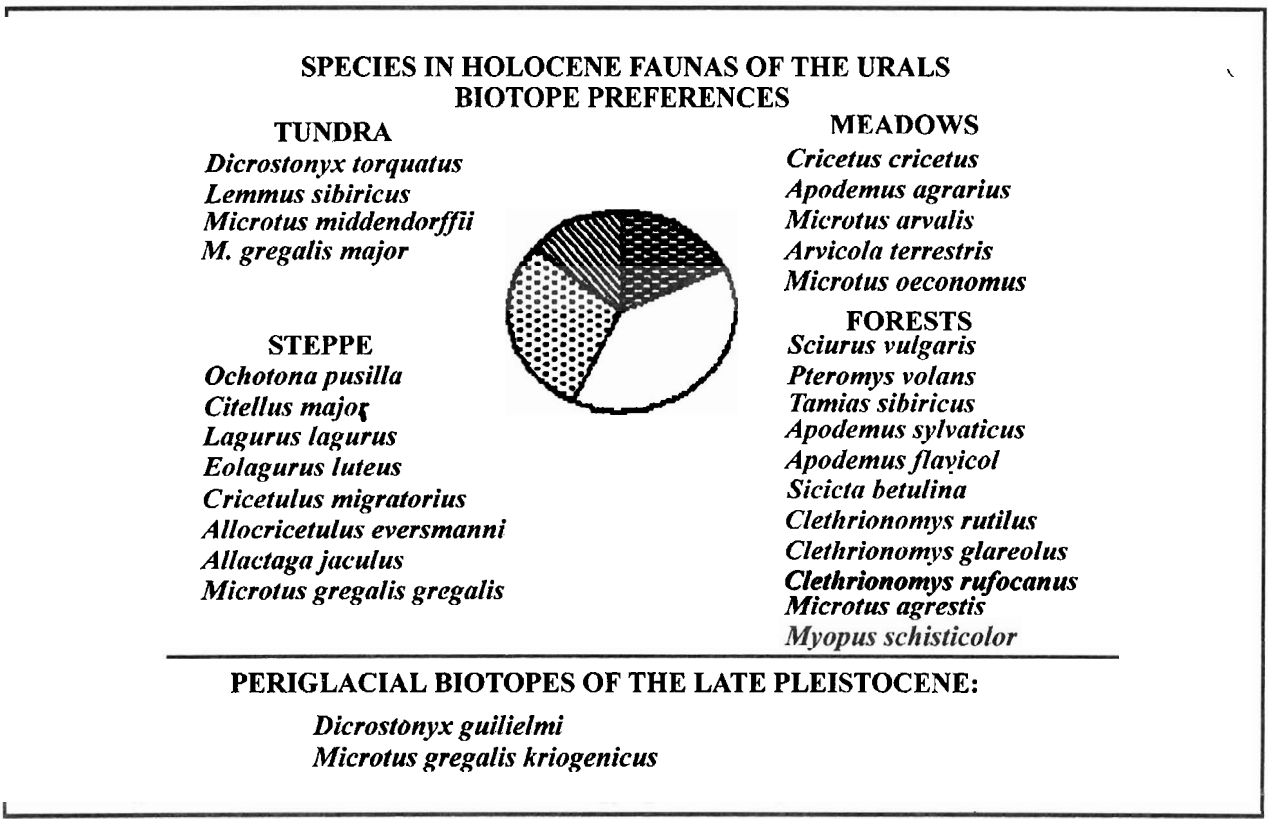

Figure 2. Species in Holocene faunas of the Urals: Biotope preferences.

In some cases we designated geographical variants and chronological stages within the local faunas. These faunas were named for geographical reference points (usually settlements) situated in the vicinity of the sites. Each local fauna was characterized by several parameters: species list, proportion of species by abundance, diversity index ("d"), equitability index ("e"), and level of "disharmony" shown by the faunal structure.

The species abundance groups were established according to the following criteria: the species was considered to be "extremely abundant" if the proportion of its remains in the stratum was 30% or more; the species was classified as "numerous" if the proportion was between 10 and 29.9%. Abundance of the species was viewed as "ordinary" if the proportion was between 1 and 9.9%. Species with proportions between 0.2 and 0.9% were considered to be "rare," and those species contributing less than 0.2% of remains are classified as "extremely rare."

The indices of equitability and species diversity were calculated as shown in Figures 5 and 8.

The index of disharmony, or the degree of faunal differences when compared to modern zonal complexes, was evaluated based upon the association (in every local fauna) of remains of extant species that appear to be ecologically incompatible today. Use of the term "disharmonious" follows Semken (1974).

BIOTOPIC DISTRIBUTION OF SMALL MAMMALS

All small mammals species that inhabited the Urals during the Holocene can be discriminated according to their preferences for different biotopes (Fig. 2). Thus, *Sciurus vulgaris*, *Pteromys volans*, *Tamias sibiricus*, *Apodemus sylvaticus* et *flavicollis*, *Sicista betulina*, *Clethrionomys* voles, *Microtus agrestis*, and *Myopus schisticolor* form the group of "forest species." Species showing preference for open meadow biotopes include *Cricetus cricetus*, *Apodemus agrarius*, and *Microtus arvalis*. Near-water biotopes and wet meadows are occupied by the water (*Arvicola terrestris*) and tundra voles (*Microtus oeconomus*).

Ochotona pusilla, *Citellus major*, *Cricetulus migratorius*, *Lagurus lagurus*, and *Microtus gregalis* (subspecies *M. g. gregalis*) prefer steppe biotopes. In the tundra zone, arid tracts are inhabited by *Dicrostonyx torqvatus* and the narrow-skulled voles (subspecies *M. g. major*), while tundra wetlands are inhabited by *Lemmus sibiricus* and *Microtus middendorffii*. Specific biotopes of the rocky deposits of the Polar Urals are occupied by mousehares (*Ochotona hyperborea uralensis*).

Earlier, I (Smirnov 1990, 1992) have discussed the problem of identifying species preferences for biotopes during the Pleistocene based only on the facts known for their Holocene descendants. It was concluded that such interpretations would be inadequate for at least two reasons. First, the biotopes and conditions in them were not the same during the Pleistocene and Holocene (e.g., see Graham 1985). Second, the ecological preferences of animal species and subspecies do not remain constant through time. This phenomenon is termed "ecogenesis." It has been shown that change in biotopes and in ecological preferences for species are expressed to different extent for different species and different ecosystem types. Thus, the now stenotopic genus *Dicrostonyx*, represented in Eurasian tundras by the species *D. torquatus*, is clearly distinct from the form *D. guilielmi*, which inhabited the so-called periglacial forest-steppes of the Late Pleistocene. The degree of these differences was perhaps as great as that between modern tundra conditions and the environment of Late Pleistocene periglacial forest-steppes. Biotope preferences of the Late Pleistocene narrow-skulled vole (subspecies *M. g. kriogenicus* Rekovets, 1978) were similar to those of the Pleistocene collared lemmings but differed from those of both extant vole subspecies (either inhabiting steppes or tundras). These two Late Pleistocene mammals, the collared lemming and the narrow-skulled vole (*M. gregalis kriogenicus*), may perhaps be considered as indicative of the specific biotopes characterizing the now-extinct periglacial forest-steppes. In addition to these two species, these now-extinct communities included low percentages of species that now inhabit meadows, steppe, and forest biotopes. I have shown, using factor analysis, (Smirnov 1992) that the biotopic groups described above may be distinguished not only in Holocene but in periglacial faunas, too, and with few exceptions, they are analogous to those of the Holocene. The exceptions include the water and tundra voles. Their association with wet meadows during the Pleistocene was perhaps not as close or obligatory as during the Holocene. The most difficult problem is to distinguish the species of tundra biotopes in the periglacial faunas. There are probably no direct analogs to the tundra ecosystems of the Middle and South Urals during the Late Pleistocene. Perhaps, the relatively wet habitats occupied today by the Siberian lemming are most similar to the tundra ecosystems of the Late Pleistocene. In the factor analyses, in all the cases studied this species kept a specific position invariably distant from that of the collared lemming, but usually close to species that dwell in wet forest or meadow environments.

STAGES OF SMALL MAMMAL FAUNAL DEVELOPMENT IN THE URALS DURING THE LATE PLEISTOCENE AND HOLOCENE

The most ancient Late Pleistocene small mammal faunas in the Middle Urals were recovered from the bottom layers in the cavity Bolshoi Glukhoi (Guslitser and Pavlov 1987). They were dated to the Middle Pleistocene cold epoch based on archaeological data and occurrence of remains of Early Pleistocene *Dicrostonyx simplicior* in them.

Faunas that are confidently assigned to the Mikulino interglacial have not been found in the Middle Urals. The most "thermophilous" fauna among all the Late Pleistocene faunas studied in the Middle Urals was excavated from the bottom layers of the cavity Bobyliok; this has been named the "Sargainsky" fauna. The only extremely abundant species in the Sargainsky fauna was the tundra vole; the narrow-skulled and common voles were numerous. *Clethrionomys glareolus* et *rutilus*, *Microtus agrestis*, *Arvicola terrestris*, and *Lemmus* appeared to be the ordinary species. The remains of *Sciurus*, *Apodemus sylvaticus*, *Cricetus cricetus*, and *Ochotona pusilla* were rare, and those of *Apodemus flavicollis*, *Clethrionomys rufocanus*, *Citellus major*, and *Dicrostonyx* were extremely rare. The proportion of the insectivorous remains was relatively large, 5.4%.

The pollen record from the deposits containing the Sargainsky fauna has shown the presence of only a few grains of tree pollen (*Pinus*, *Betula*, *Abies*, *Larix*, *Tilia*, and *Quercus*), and abundant pollen of different herbs, especially those of the compositae family, including sage-brushes. Spores of ferns and mosses occurred infrequently. The pollen spectrum, like the fauna, has no analog among modern ecosystems.

In the South Urals at a time contemporaneous with the Sargainsky fauna, was a fauna that we named "Serpievsky." It appeared to be extremely disharmonious, with the occurrence of *Apodemus sylvaticus* et *flavicollis* and the Russian desman, on the one hand, together with the remains of *Dicrostonyx*, *Lemmus,* and *Lagurus* on the other. Yet the collared lemmings were represented by the species *D.* cf. *simplicior*, the latter being the ancestral form of the typical Late Pleistocene lemming *D. guilielmi*. The narrow-skulled voles identified there were also designated as a specific subspecies distinct from that occurring in the "cold" faunas of the terminal Late Pleistocene. The important features of the Serpievsky fauna as compared to those that lived later, were the relatively larger proportions of remains of *Lemmus sibiricus* and *Microtus agrestis*. The Serpievsky fauna differed from the contemporaneous Sargainsky fauna of the Middle Urals in the large number of steppe taxa accompanied with a larger proportion of forms having both steppe and periglacial affinities. Remains of forest-dwellers comprised a smaller proportion, both in abundance and in species. Squirrels were not identified (Fig. 3).

From the bottom layers of Studeny Cave in the North Urals (Guslitcer, Pavlov, and Panyukova 1989) has come a fauna that, probably, is correlated with the Sargainsky and Serpievsky faunas. It included only 7 - 8 species (named in sequence from most to least abundant): *Lemmus*, *Dicrostonyx*, *Microtus gregalis*, *M. oeconomus*, *Arvicola agrestis*, *Ochotona*, *M. agrestis*, and *Clethrionomys* sp. This fauna, thus, appears to be disharmonious, as well, but with a reduced taxa list when compared to those in the contemporaneous faunas of the Middle and South Urals. The group of forest inhabitants in this fauna also was significantly less abundant, both in the number of species and proportion of taxa represented (Fig. 3).

The main phase of the Valdai, named the Sartansky horizon according to the Siberian chart and Evlatkinsky horizon in the local stratigraphic scheme, is dated to the interval of 25,300 - 12,300 years B.P. Faunas of this period have been found in several sites in the Middle Urals. The most abundant and well-dated material has been excavated from two sites, the cavity Bobyliok (layer 2a) and the cave Arakaevo (layer 12). The species list and species proportions in both sites were very similar, and all the data have been united into one local fauna called "Arakaevsky" (Fig. 4). In the composition of this fauna, the narrow-skulled vole (*M. g. kriogenicus*) was extremely abundant. The group of numerous species included *M. oeconomus*, *Dicrostonyx*, and *Lagurus lagurus*. *Cricetulus migratorius*, *M. arvalis*, all three *Clethrionomys* voles, and *Ochotona* appeared to be the ordinary species. Two species, *Lemmus sibiricus* and *Citellus major* were rare and Eversmann's hamster was extremely rare. The remains of *Arvicola terrestris*, *Cricetus cricetus*, *M. agrestis*, and *Eolagurus luteus* were identified only in Arakaevo cave (the proportions of the first three not exceeding 1% each and about 3% for the latter). They did not occur in the Bobyliok cavity fauna. The differences may be explained as geographical variation within the local fauna. One can clearly see that the Arkaevsky fauna is also disharmonious.

We can get some idea about the vegetation existing during the time of the Arakaevsky fauna based on pollen data from the Bobyliok deposits. More than half of the total amount was composed of different fern spores; pollen of different herbs accounted for about 40% and only some 4.3% of the grains were produced by trees (*Abies*, *Picea*, and *Larix*). Such a pollen spectrum points to a non-forested setting with rare groups of trees along river valleys.

It is concluded that the Arakaevsky fauna and its environmental conditions differed significantly from those of the preceding Sargainsky fauna. The two faunas can be discriminated in terms of both the taxa represented and the proportions of species of various biotope preferences. In the earlier, Sargainsky fauna the remains of forest-inhabiting species were recorded at 25% (including *Sciurus*, *Apodemus sylvaticus* et *flavicollis*, *Clethrionomys rutilus* et *glareolus*, and *Microtus agrestis)*, while in the later, Arakaevsky fauna they constituted no more than 3%, and only *Clethrionomys* voles were identified. On the other hand, the steppe species (there were only two, *Ochotona* and *Citellus*) occurred in low numbers in the earlier fauna (not exceeding 1%) but increased to 26% in the later period, and the taxa list added *Lagurus*, *Eolagurus*, and Eversmann's and migratory hamsters. The remains of meadow-dwellers (*M. oeconomus*, *Cricetus cricetus*, *M. arvalis*, and *Arvicola terrestris*) dominated the Sargainsky fauna (about 50%); their proportion falls to 15% in the Arakaevsky fauna. As for the typically "periglacial" species, the narrow-skulled voles and collared lemmings were recorded in both faunas, their proportions increased with time from 18% to 55% (i.e., became dominant in the Arakaevsky fauna).

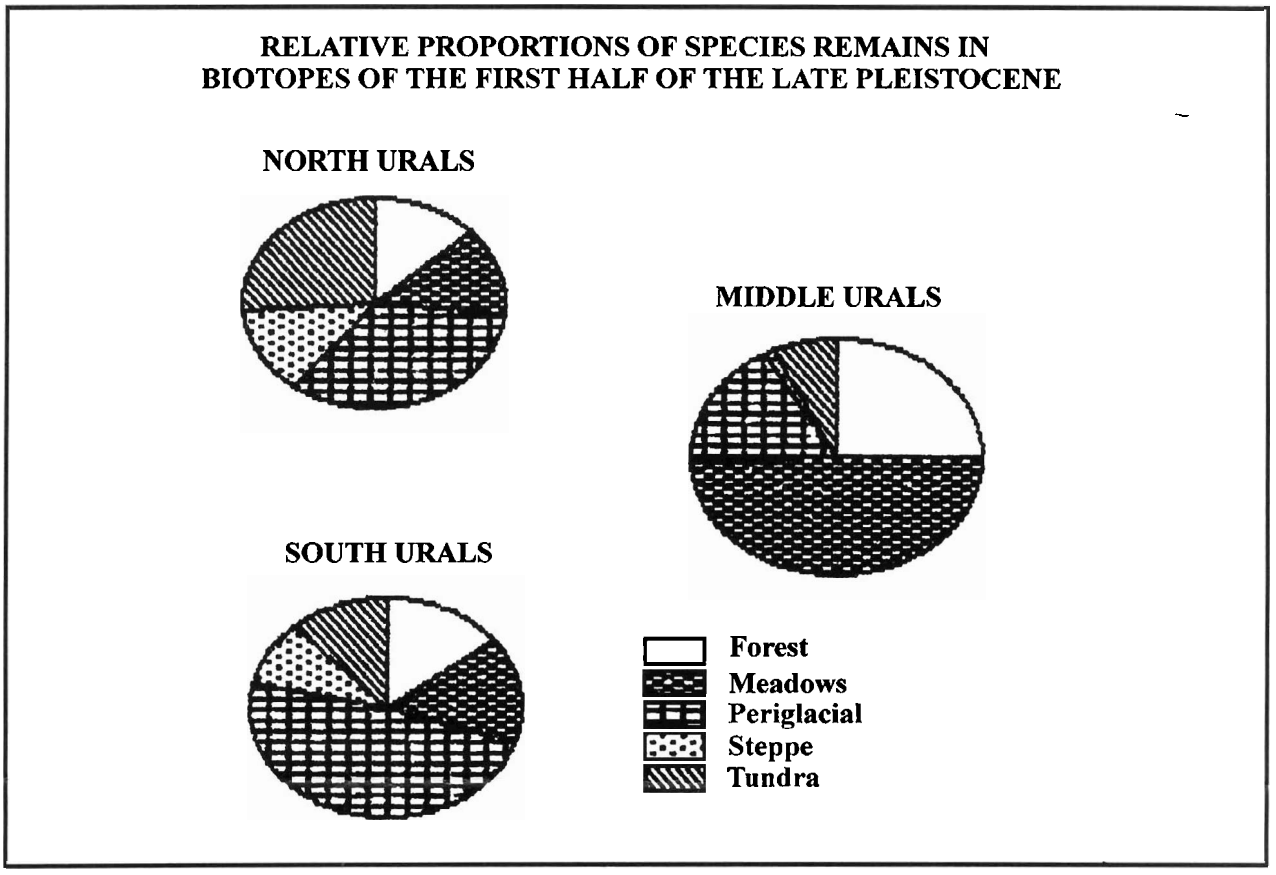

Figure 3. Shares of species remains in biotopes of the Late Pleistocene: First half.

Contemporaneous with the Arakaevsky fauna, in the South Urals was the Ignatievsky fauna that was not significantly distinct from faunas in the Middle Urals. The dominant species was the narrow-skulled vole, *M. g. kriogenicus*. The remains of *D. guilielmi* occurred there, together with those of jerboas (not found in the Middle Urals), and the proportion of steppe taxa (steppe lemmings, mousehares, and migratory and Eversmann's hamsters) was high. Mice remains were not recovered, and proportions of *Cricetus cricetus*, *Lemmus*, and insectivores were extremely low, the latter being represented only by shrews (*Sorex*).

From the Medvezhy (Bear) Cave in the North Urals, one additional fauna contemporaneous with both Arakaevsky and Ignatievsky has been described (Kotchev 1991) (Fig. 4).

These differences in faunal composition of the North, Middle, and South Urals add to the picture of geographical variation within the boreal pattern of the mammoth faunal complex described by Baryshnikov and Markova (1990).

I have discussed changes in taxa lists and in proportions of species groups that have different biotope preferences. Now I discuss the dynamics of faunal structure revealed by variation in two indices: species diversity and equitability (Fig. 5).

The Ignatievsky fauna of the South Urals, dated to the main phase of the Late Valdai, appeared to show the greatest difference from the other faunas in both indices; the diversity value was high enough and accompanied with low equitability.

During the Late Pleistocene, disharmonious faunas changed against a background of disappearing forest biotopes. The process was undoubtedly caused by decrease in precipitation. One can see that the diversity index for the Ignatievsky fauna is higher than that for the Serpievsky fauna, but possibly does not reflect better environmental conditions since the simultaneous significant decrease in the equitability value would, perhaps, lead to the opposite conclusion. The forest group of species disappeared due to the absence of the biotopes required, yet the taxa list increased as species

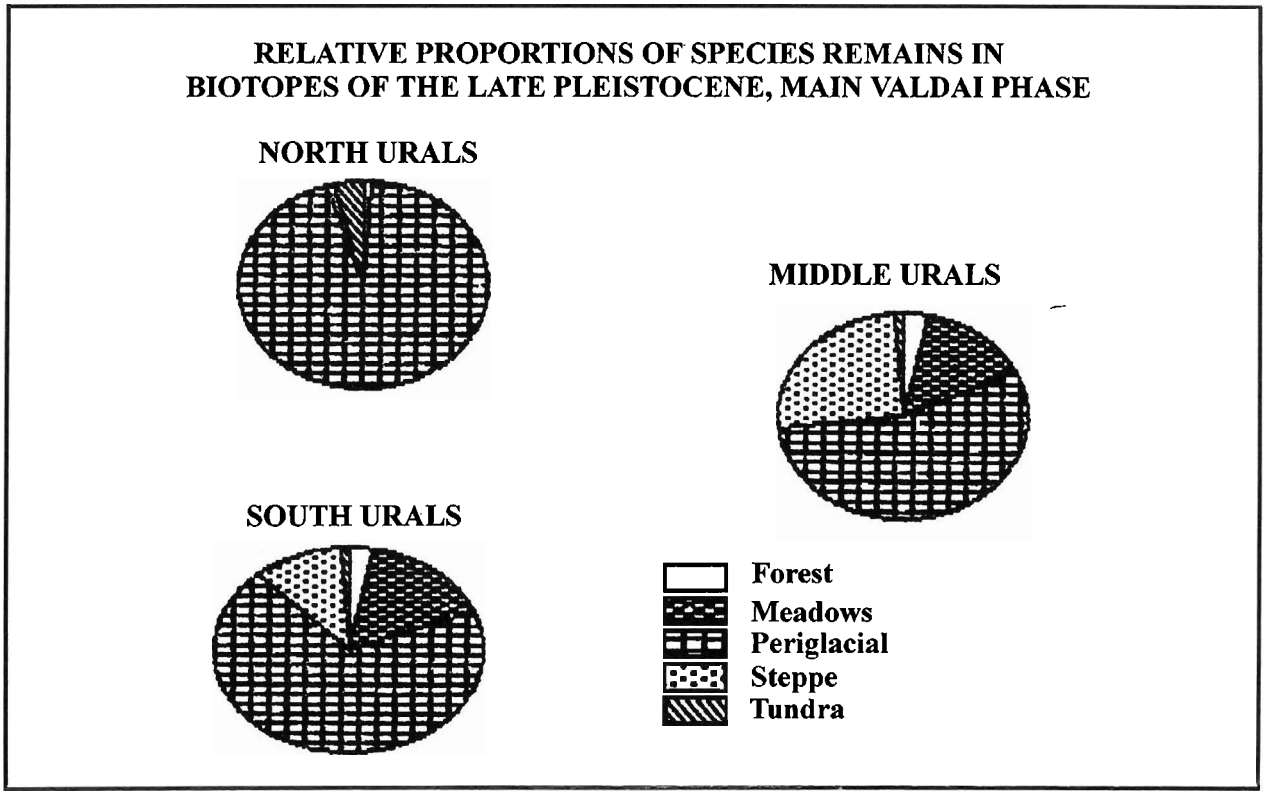

Figure 4. Shares of species remains in biotopes of the Late Pleistocene: Main Valdai Phase.

preferring arid conditions appeared. But conditions seemed to appear favorable only for the narrow-skulled vole, the remains of which dominated among those of all other taxa. At the same time, conditions were perhaps near to the extreme tolerance limits for other animals.

In the Middle Urals the Sargainsky fauna, dated to the first phase of the Late Pleistocene, showed a higher diversity index value as compared to that in the fauna that replaced it. On the contrary, the equitability index was low in the preceding fauna and increased through time (Fig. 5). The transformation of relatively warm and humid conditions to cold and arid led to reduced species diversity, but the cold and arid conditions appeared to be more favorable for a larger number of animals (taxa).

Thus, during the first half of the Late Pleistocene, disharmonious faunas of the South and Middle Urals showed similar values for the structure indices, and afterwards, during the Valdai main phase they differed significantly in both diversity and equitability. Actually the fauna became more diverse in the South Urals, but the diversity index decreased in the Middle Urals, while equitability became more uniform (the proportions of taxa were similar) in the latter area, and in the South Urals species occurred in extremely unequal numbers.

For the North Urals, I only have data to suggest the development of the same tendency (but not yet to quantify the trend). When moving northward I have found only reduced numbers of species in disharmonious communities (usually due to the fact that the "steppe" taxa disappeared in the majority), but the species proportions in them becomes more uniform. Looking a bit forward we can say that the same tendency is noted for the Holocene communities.

Thus we see that the species diversity index shows the highest values during the Valdai main phase of the Late Pleistocene and, also, at the southern limits of the disharmonious faunal distribution.

The next stage in the development of the small mammal fauna in the Middle Urals is that of the transformation of the Late Pleistocene disharmonious faunas into the faunas of the Holocene (those of modern zonal types). This period can be studied based on data from two sites: Bolshoi Glukhoi cavity (layers 12 - 13; the fauna named Tchusovsky) and the cavity Dyrovaty Kamen' on the Serga River (horizon 11; the fauna

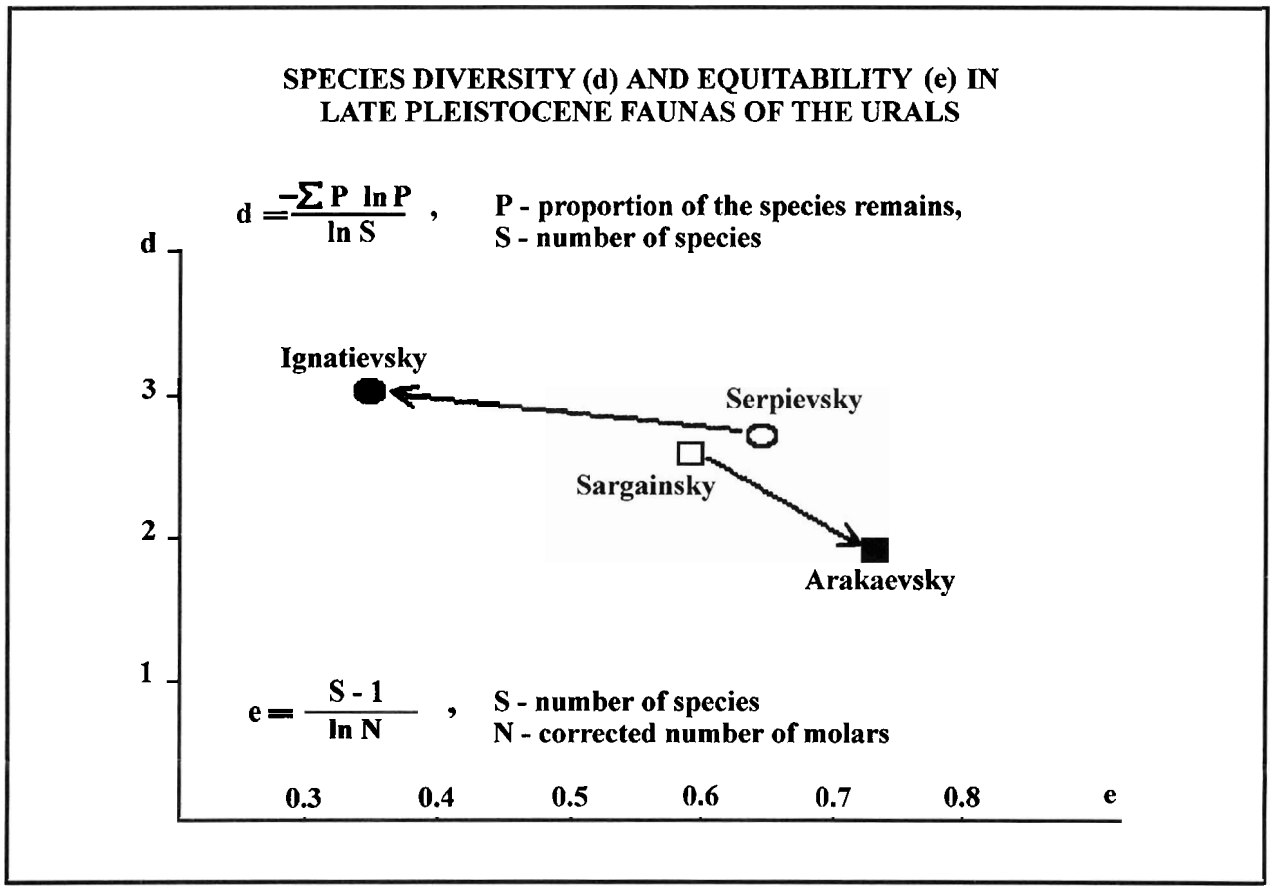

Figure 5. Species diversity (d) and equitability (e) in Late Pleistocene faunas of the Urals.

named Serginsky). The faunas of these two sites were very similar in the taxa represented but the proportions of "steppe" and "forest" species in them differed to some extent. We cannot combine the data for the two faunas because the sites are geographically distant.

The species represented in these two faunas, dated to the Early Holocene, were nearly the same as that in the Late Pleistocene Arakaevsky fauna (with squirrels and *Apodemus sylvaticus* and Eversmann's hamster missing), but the species proportions differed significantly. It was during this time interval that the dominant species, the narrow-skulled vole, changed in subspecies status.

The traits that distinguish the Late Pleistocene subspecies *M. g. kriogenicus* from the modern forms are expressed on the first lower molars: size and morphotype proportions (Figs. 6, 7). Based on both traits the voles from the Serginsky and Tchusovsky faunas are referred to the modern steppe subspecies, and thus, in turn suggest steppe environments.

Thus the structure of the Serginsky fauna as compared to that of the Arakaevsky is as follows: The most abundant species in the Serginsky fauna was the narrow-skulled vole, which changed in subspecies status to *M. g. gregalis*. *Microtus agrestis* (practically not recorded in the Arakaevsky fauna) and *M. oeconomus* were numerous (the latter, however, in lower numbers). Remains of these taxa and *Clethrionomys* voles occur in similar proportions. These species, together with *Ochotona,* formed the main portion of the Serginsky fauna. Remains of *Dicrostonyx* and *Lagurus* are very rare (while in the Arakaevsky fauna they were abundant).

The proportion of species preferring different biotopes changed significantly, too. First, I have nothing to say about animals that inhabit periglacial biotopes. The narrow-skulled vole became a steppe form, and we failed to identify the collared lemmings to the species. If we do not take those lemmings into consideration, then species of steppe biotopes composed about 60%,

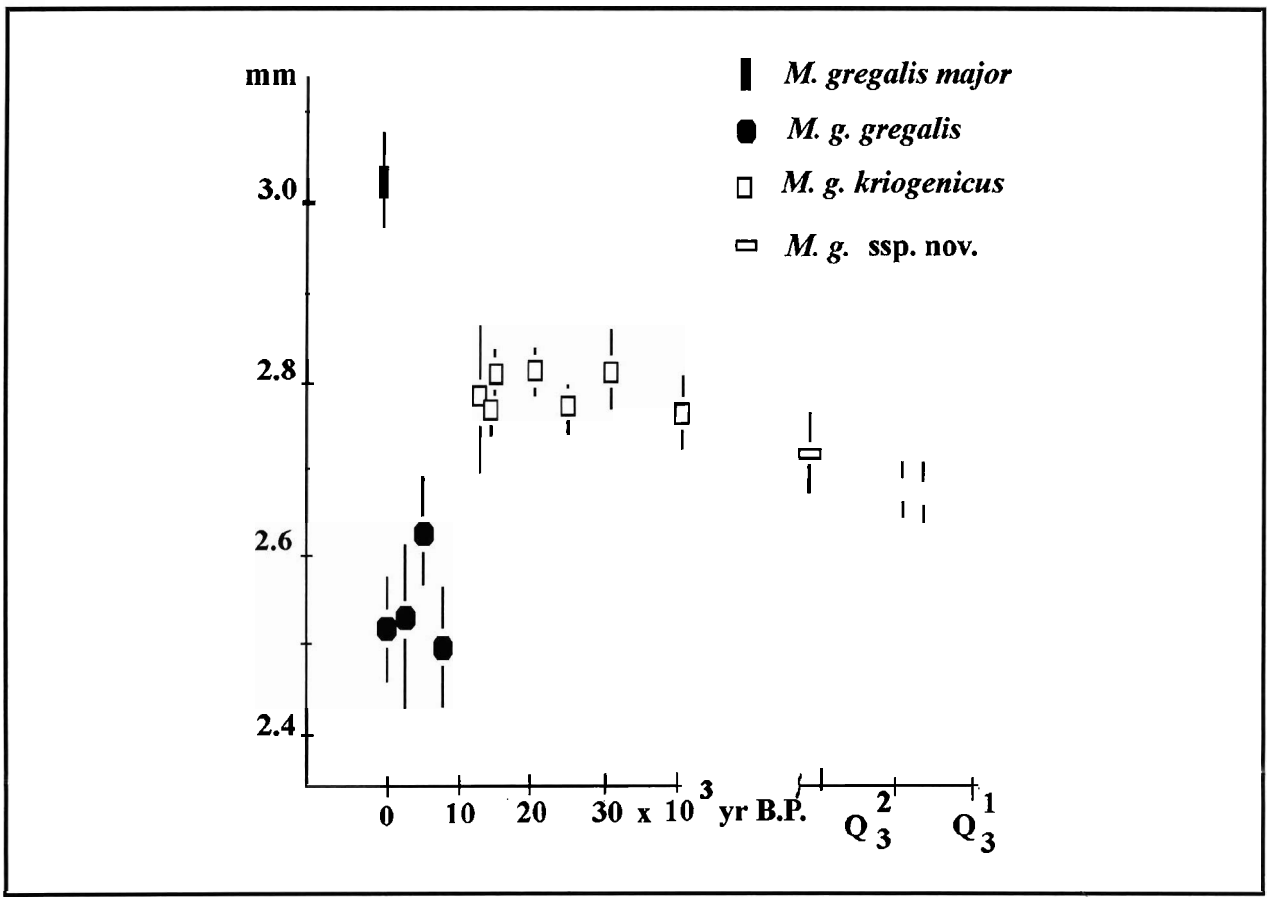

Figure 6. Length of the first lower molar in Holocene and Late Pleistocene subspecies of *Microtus gregalis*.

forest-dwellers about 30%, and species inhabiting meadows nearly 10%. In the Tchusovsky fauna the corresponding figures are 40%, 40%, and 20%. The larger share of steppe forms in the Serginsky fauna may be explained by its more southerly geographical position (about 200 km south).

Just above the deposits that contained the Serginsky fauna another fauna has been discovered, the age of which has not yet been determined. Certainly it is younger than the Serpievsky fauna, but clearly older than the fauna dated to the Atlantic. Probably the proper age is about 8,000 - 9,000 years B.P. (the Boreal period). The list of taxa represented in this fauna is actually the same as in the Serginsky fauna, but the species proportions differ. The remains of "steppe" forms composed only 30% (compared to 60% in the Serginsky fauna), while those of the forest-dwellers and inhabitants of meadows were higher, at 48% and 22%, respectively. It is important that the proportion of *M. agrestis* remained the same and that the proportion of *Clethrionomys* voles increased (resulting in the higher proportional representation of the total "forest group").

The Atlantic period of the Holocene was a separate stage in the development of the climate and biota, but in the Middle Urals the small mammal fauna dated to this time has not been sufficiently studied. During this period, in sites in the Krasnoufimsky area, the remains of forest, meadow, steppe and, strange as it seems, tundra inhabitants have been recovered. The tundra dwellers are represented by collared and brown lemmings. Among the recorded steppe-dwellers were mousehares, migratory hamsters, steppe lemmings, and narrow-skulled voles. The total for their remains is about equal to those of the "tundra" taxa. The majority of the faunal remains consisted of "forest" (about 40%) and "meadow" species (a bit more than 50%). The structure of the "forest" group remained nearly the same as for the preceding fauna. *Clethrionomys* remains dominated the forest group.

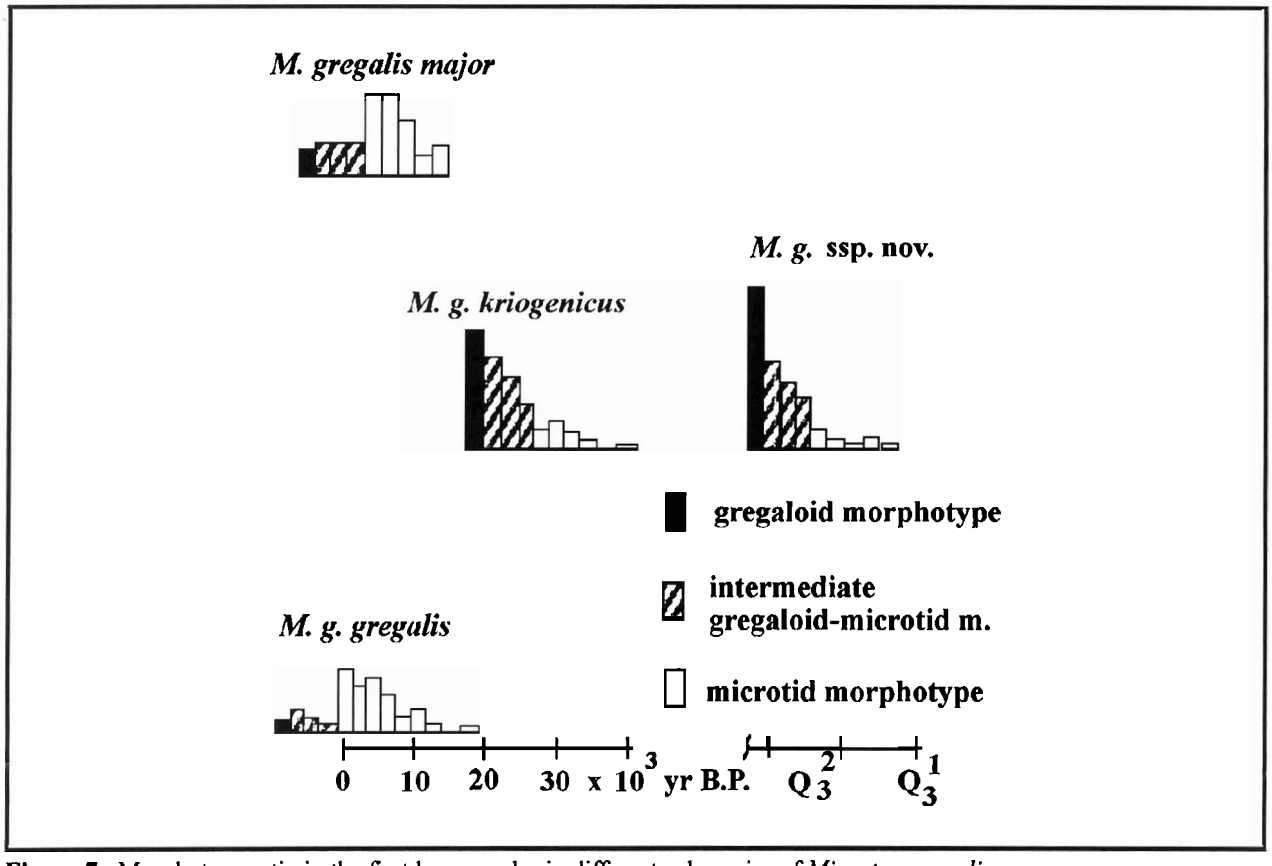

Figure 7. Morphotype ratio in the first lower molar in different subspecies of *Microtus gregalis*.

During the Sub-Boreal, steppe elements were identified in the faunas of the Middle and South Urals, but both the narrow-skulled voles and mousehares became very rare. The majority of the remains were represented by meadow and forest species, the latter gradually decreased in numbers after the Atlantic.

During the Sub-Atlantic the process of forest species reduction develops further, though the taxa list remained the same in both the "forest" and "meadow" species groups. During the Sub-Atlantic, the last steppe forms in the faunal assemblages disappeared. The remains of mousehares were already missing in the strata of the Sub-Atlantic; those of the narrow-skulled voles were last recorded in deposits dated to 800 years B.P. During the same period, bones of the Norway rat, a synanthropic species, occurred for the first time.

The other feature that reflects the influence of human activities upon the fauna is the local reduction of species diversity and the sharp dominance of remains of *Microtus arvalis* in the regions of developed agriculture.

For the South Urals only the fauna of the Sub-Atlantic has been described. It included the remains of the following species: *Tamias*, *Pteromys*, *Eliomys quercinus*, *Apodemus sylvaticus* et *flavicollis*, numerous *Microtus arvalis*, *M. agrestis*, *Arvicola terrestris*, *Clethrionomys glareolus*, and *Cricetus cricetus*. At the early stages of its development, very rare molars of three steppe taxa were identified: *Cricetulus migratorius*, *Eolagurus lutescens*, and *Citellus major*.

The Late Holocene forest faunas of the South Urals showed high species diversity values and relatively uniform distribution of species proportions (equitability). The same combination of these index values has been found in the Late Holocene fauna of the central forest-steppe regions of the Trans-Urals. Modern tundras of the Middle Yamal show low species diversity and medium equitability. A strange combination of index values was observed in the Late Holocene faunas situated at the boundary of steppes and forest-steppes of the Trans-Urals: medium species diversity and low equitability, that may be a result of effects of human activities upon the fauna (Fig. 8).

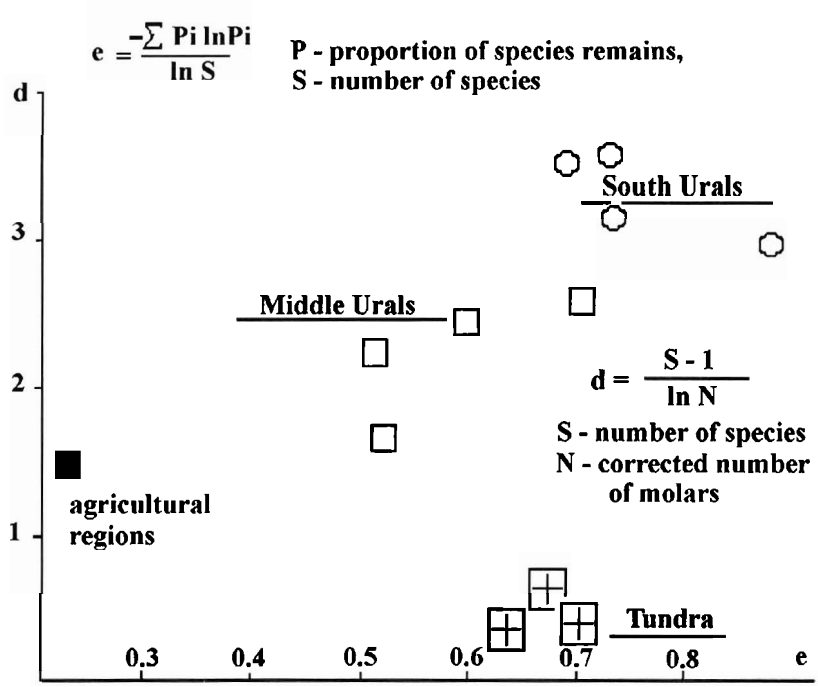

Figure 8. Species diversity (d) and equitability (e) in Late Holocene faunas of the Urals.

CONCLUSIONS

As the history of the small mammal fauna in the Urals has been studied based on varying sample sizes for different regions and time intervals, it is not possible to describe the whole picture of faunal development during the Late Pleistocene and Holocene. Based on the materials reviewed above, the following conclusions are offered:

1. The faunas in the North, Middle, and South Urals dated to the first half of the Late Pleistocene possess some features in common, namely relatively high proportions of remains of brown lemmings and species of the "forest" group. The highest number of "forest" taxa and the maximum proportional representation of remains of the forest group were observed in the Middle Urals.

In the Middle and South Urals the structure of faunas (described by the combination of species diversity "d" and species equitability "e" indices) was similar to those in modern forest-steppe faunas. Yet the peculiarities of the taxa list and especially the occurrence of *Lemmus* remains make the faunas disharmonious.

2. Faunas correlated with the Valdai main phase showed the most unusual combination of the species representation and structure. In the South Urals there were high diversity and low equitability values. In the Middle Urals diversity values were relatively lower, but those for equitability were high. In the North Urals diversity values decreased even more. All of this may suggest that during this severe period, it was in the Middle Urals where the conditions were more favorable for the existence of disharmonious periglacial faunas.

3. The most important features of the faunas of the Early Holocene were the change of the subspecies status in the narrow-skulled vole and the sharp increase in the proportion of all forest taxa (especially due to the remains of *Microtus agrestis*).

4. The Holocene history has been studied in greatest detail for the faunas of the Middle Urals. The proportion of forest taxa remains increased at that time. The dominant *M. agrestis* was replaced by *Clethrionomys* voles (*glareolus* + *rutilus*) by the second half of the Sub-Atlantic.

5. In portions of the Middle Urals now occupied by insular forest-steppes, the remains of steppe-dwelling species were recorded until the second half of the

Sub-Atlantic. Steppe-dwellers became extinct there in succession, as follows: *Citellus major*, *Cricetulus migratorius* (Boreal time), *Lagurus lagurus*, *Ochotona pusilla* (Sub-Boreal), and *Microtus gregalis* (the second half of the Sub-Atlantic).

6. It was surprising to find that remains of collared and brown lemmings occurred in Holocene deposits in the Middle Urals until the Atlantic period. This finding needs more study.

The faunas of the Late Holocene, influenced by agricultural development, appear to possess a distinctive structure. They show low species diversity and very low equitability values.

ACKNOWLEDGMENTS

I would like to express my thanks to the collaborators of the Laboratory of Historical Ecology, Institute of Plant and Animal Ecology, Russian Academy of Sciences, for their assistance in preparation of this paper. T. P. Kourova helped with analysis and identification of faunal remains; G. V. Bykova translated the text into English and, in addition, helped with the preparation of the manuscript. Special thanks go to Dr. G. F. Baryshnikov, Zoological Institute, Russian Academy of Sciences and to Dr. R. B. McMillan, Director of the Illinois State Museum, who invited the author to take part in the Workshop on Russian/Ukrainian/American Quaternary Paleozoology and inspired him to prepare this paper. This work has been fulfilled thanks to the financial aid supplied by a G. Soros stipend on the problem "Biodiversity" provided by the International Science Foundation and the Academy of Natural Sciences.

REFERENCES CITED

Baryshnikov, G. F., and A. K. Markova
1990. Zoogeographia i paleoecologia teriofauni vnetropicheskoi chasti severnogo polusharia v epokhu maximalnogo razvitia poslednego oledenenia. (Zoogeography and paleoecology of theriofauna of the non-tropical regions of the northern hemisphere during the time of the last glaciation maximum). In *Chronostratigraphia paleolita severnoi, centralnoi i vostochnoi Azii i Ameriki (Dokl. Mezhdunarodnogo Symp.).* Novosibirsk:51-54. (in Russian)

Graham, R. W.
1985. Diversity and community structure of the late Pleistocene mammal fauna of North America. *Acta Zool. Fennica* 170:181-192.

Gromov, I. M.
1983. Introduction to: *Istoria i evolutsia sovremennoi fauni gryzunov SSSR (neogene-sovremennost).* Moscow, Nauka:3-8. (in Russian)

Guslitser, B. I., and P. Yu. Pavlov
1987. O pervonachalnom zaselenii Severo-Vostoka Evropi. (On the primary settlement of the European northeast). *Ser. preprintov "Nauchnye Dokladi" AN SSSR, Komi Filial*, 172:35 pp. (in Russian)

Guslitser, B. I., P. Yu. Pavlov, and N. N. Panyukova
1989. Biostratigraphia i vozrast otlozhenii peshcheri Studenoi na verkhnei Pechore. (Biostratigraphy and age of sediments in the cave Studenaya at the upper Pechora). In *Biostratigraphia fanerozoya Timano-Pechorskoi provintsii.* Syktyvkar:92-100. (in Russian)

Kochev, V. A.
1991. Razvitie pleistocenovoi fauni gryzunov Severo-Vostoka Evropeiskoi chasti SSSR. (Development of the Pleistocene fauna of rodents of the European northeast USSR). (Preprint). Syktyvkar, Geonauka, 82 pp. (in Russian)

Maleeva, A. G.
1982. Melkie mlekopitayushchie verkhnealabugskoi pozdnepleistocenovoi fauni, Yuzhnoe Zauralie. (Small mammals in the Verkhnealabugsky late Pleistocene fauna, South Trans-Urals). In: *Pliocene i Pleistocene Urala*, P. 2. Sverdlovsk:9-38. (in Russian)

Petrin, V. T.
1992. *Paleolithicheskoe svyatilishche v Ignatievskoi peshchere na Yuzhnom Urale. (Paleolithic ritual encampment in the Ignatievsky Cave in the South Urals).* Novosibirsk. VO Nauka. Sibirskaya Izdatelskaya Firma. 207 pp. (in Russian)

Rekovets, L. I.
1978. Novii podvid uzkocherepnoi polevki (*Microtus gregalis* Pall.) iz pozdnepleistocenovykh otlozhenii Ukraini. (A new subspecies of the narrow-skulled vole (*Microtus gregalis* Pall.) from the late Pleistocene deposits of the Ukraine). *Dokladi Akademii Nauk Ukrainskoi SSR*, Ser.B, 6:563-567. (in Russian)

Semken, H. A., Jr.
1974. Micromammal distribution and migration during the Holocene. *Abstracts and Program Amer. Quat. Assoc. 3rd Bienn. Mtg.* Univ. Wisc.: 25.

Smirnov, N. G.
1990. Paleoecologicheskie metodi v reconstruktsii paleogeographicheskikh obstanovok pleistocena. (Paleoecological methods in reconstruction of natural environments of Pleistocene). In *Chronostratigraphia paleolita severnoi, centralnoi i vostochnoi Azii i Ameriki (Dokladi Mezhdunarod. Symp.).* Novosibirsk:275-280 (in Russian)

Smirnov, N. G.
1992. Problemy istoricheskoi ecologii mlekopitayushchikh Severnoi Evrazii. (Problems of historical ecology of mammals in North Eurasia). In *Vekovaya dinamika biogeocenozov.* Chtenia pamyati akademika V. N. Sukacheva, N 10. Moscow, Nauka:17-35. (in Russian)

Smirnov, N. G.
1993. *Melkie mlekopitayushcihck Srednego Urala v pordnem Pleistocene i Holocene.* (*Small mammals of the Middle Urals in Late Pleistocene/Holocene*). Ekaterinburg. 65 pp. (in Russian/English)

Smirnov, N. G., V. N. Bolshakov, P. A. Kosintsev, N. K. Panova, Yu. I. Korobeinikov, V. N. Olshwang, N. G. Erokhin, and G. V. Bykova
1990. *Istoricheskaya ecologia zhivotnykh gor Yuzhnogo Urala.* (*Historical ecology of animals in the mountains of the South Urals*). Sverdlovsk. 244 pp. (in Russian)

Smirnov, N. G., V. N. Bolshakov, P. A. Kosintsev, N. K. Panova, and V. N. Olshwang
1992. *Late Pleistocene/Holocene mammals and biota history in the South Urals.* Ekaterinburg. 25 pp.

Sukhov, V. P.
1970. *Pozdnepliocenovie melkie mlekopitayushchie Akkulaevskogo mestonakhozhdenia v Bashkirii.* (*Late Pleistocene micromammals from the Akkulaevsky site in Bashkiria*). Moscow, Nauka. 93 pp. (in Russian)

Vereshchagin, N. K., and I. M. Gromov
1977. Formirovanie teriofauni SSSR v chetvertichnom periode. (Formation of mammalian fauna of the USSR during the Quaternary period). In *Uspekhi sovremennoi teriologii*, pp. 32-45. Moscow, Nauka. 296 pp. (in Russian)

Volokitin, A. V., N. G. Smirnov, V. N. Shyrokov, and N. R. Tikhonova
1992. The cavity Bobyliok, a new site dated to the terminal Upper Paleolithic in the Middle Urals. [Abstr.] Pp. 36 - 39, In *Paleoekologia i rasselenie drevnego cheloveka v Severnoi Azii i Amerike, Abstr.* Krasnoyarsk. (in Russian)