

Urals Scientific Centre  
Russian Academy of Sciences  
Institute of Plant and Animal Ecology

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N.K.Panova, V.N.Olshwang

LATE PLEISTOCENE / HOLOCENE MAMMALS  
AND BIOTA HISTORY IN THE SOUTH URALS

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For several years the authors work to study different aspects of biota history in the Urals. One of the large pieces of that was published as the book the contents of which one can find below.

If anyone is interested in the publication on the theme, it can be received (but in Russian) from the Institute of Plant and Animal Ecology, the address as follows:

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HISTORICAL ECOLOGY OF ANIMALS  
OF THE SOUTH URALS MOUNTAINS

(English summary)

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## INTRODUCTION

In 1990 the book "Historical ecology of animals in the South Urals Mountains" was published in Russian. After that there came another article on the theme: N.G.Smirnov "Paleoecological methods in reconstruction of Pleistocene paleoenvironments" (In: Chronostratigraphy of Paleolithic. North, Central and Eastern Asia and America. Novosibirsk, 1990; in Russian ).Thus, the English summary below covers the materials and results described both in the book and the article, with the main idea of those to study the

ways of formation of the modern biota of the South Urals during the late Pleistocene and Holocene and, besides, to study the changes of morphological and ecological characteristics occurring in some mammal species in the course of evolution process during this time period.

The main materials the work was based upon had been got while examination of two types of fossil remains, from peatbogs and loose deposits in caves. The peat bogs were studied by N.K.Panova, now working in Institute of Forest, Urals Branch of Russian Academy of Sciences. Excavations in caves were carried out by the working groups of the Laboratory of Historical Ecology, Institute of Plant and Animal Ecology, Russian Academy of Sci., in close collaboration with the group of archaeologists lead by Dr.V.T.Petrin, from the Institute of History, Philosophy and Philology of the Siberian Branch, Russian Academy of Sci.(Novosibirsk). Excavations were started when palaeolithic drawings had been discovered in the Ignatievsky Cave. The results of archaeological studies will be published in separate edition, soon.

#### Chapter 1. PROBLEMS AND METHODS OF HISTORICAL ECOLOGY.

The authors understand historical ecology as the part of ecology dealing with the study of dynamics of ecosystems characteristics and ecological characteristics of species being considered in the historical scale of biological time. This scale is just the intermediate one between the evolutionary and actual scales.

The process of temporal alteration of species ecological characteristics is termed by the authors as ecogenesis and considered to need careful examination. It has been shown that transference of ecological properties of the recent species to their extinct ancestors appears to be incorrect, and not only when one compares forms belonging to different species of the same phyletic line, but also, in some cases, the forms that belong to the same species but lived during the different periods of Late Cenozoic. The authors, too, discuss the methods to study historical dynamics of some ecological characteristics in small rodents (based on paleontological materials): attachment to the certain phytogeographical zone or to the definite biotops, affiliation to a certain faunistic complex, ratio in fauna contents, numbers, nutrition spectrum. When small rodents communities are described,

the main characteristics used are: species contents, species equitability index, index of dis-harmony of communities, index of species diversity.

## Chapter 2.1 MODERN CLIMATIC CONDITIONS AND VEGETATION OF THE REGION OF STUDY.

Climate of the South Urals (in the limits of the Chelyabinsky district) is characterized as temperate and warm, continental. In the mountains it is more cool and humid, near the highest peaks (Iremel, Zigalga, etc., maximum height being 1640 m) it may be referred to the taiga-forest and subarctic types. Mean annual rainfall equals to 500 - 700 mm, in the high-elevated regions it may exceed 800 mm per year. On the whole, the Western slopes get more precipitation than those Eastern.

Resulting from the jagged relief, variety of mountain soil-forming grounds, temperature inversions, the South Urals is characterized with complicacy and heterogeneity of vegetation cover. Submeridional disposition of mountain ridges and their barrier role in precipitation distribution act to form asymmetrical landscape structure. Along the ridge all vegetation zones are shifted to the south for about 200 km, as compared to the adjacent plain territories. In the South Urals different altitude belts are represented: they are mountain-steppe, mountain-forest-steppe, mountain-forest, subalpic and alpic.

Montane-steppe belt occurs only in the south-eastern regions of the South Urals. Mountain-forest-steppe zone is manifested as fragments in some regions of the eastern and partly - western macroslopes. Montane-forest zone forms the main part of landscapes in the South Urals mountains. Forests cover the lower zones of middle-high mountains, low hills, foot-hills and depressions. High-elevated axial part is occupied by dark-coniferous (south taiga) forests of *Picea obovata*, and *Abies sibirica*. At the western slope there goes the boundary of the east-european broad-leaved forests of oak and basswood, sometimes with addition of *Acer platanoides*, *Ulmus scabra*, *U. laevis*. At the eastern slope there are spread the forests of "pre-foreststeppe" type, consisting of *Pinus sylvestris*, *Larix sibirica*, in some places added by *Betula pendula*. At the western slope in the interval between dark-coniferous and broad-leaved forests there goes the stripe of mixed

deciduous and coniferous forests of basswood, oak, larch and fir trees, with addition of *Acer* and *Ulmus*. Along river valleys there grow pine forests and those of pines and larches. Birch forests, both at the eastern and western slopes, are usually derivative; indigene birch forests are very rare, being formed mainly by *Betula pubescens*.

Forest-grassland zone (similar to subalpic belt in Europe) occupies the upper parts of slopes of the highest tops, it is represented by open woodlands consisting of fir and larch-fir forests of the park type, and the fir elfin woodlands at the upper limit of forests.

Zone of mountain tundras (analogue of the alpic belt in Europe) is developed only as fragments at the highest mountain ridges (altitudes exceeding 1300 m). Grass-mossy tundras prevail there, arctic and alpic species dominating among plants. Lichen and stony tundras are typical, too.

Upstreams of the Sim-river, where the main caves and rock-shelters at study are situated, the territories are occupied with broad-leaved and coniferous forests and the secondary aspen and birch groves. Right bank is covered with light-coniferous pine forests, the Sim plato - with broad-leaved forests. From the north the band of coniferous forests is interrupted by the island of forest-steppe vegetation, where the Idrisovsky cave is situated. Rock-shelter named Ustinovo is situated at the eastern slope, at the line dividing south taiga pine forests from the forest-steppe zone with birch and aspen-birch groves and steppe-like grasslands.

#### Chapter 2.2. DISTRIBUTION ON SMALL MAMMALS

Chapter represents the modern picture of small mammals distributions in the region at study. Total 34 rodent species have been recorded in the region. Peculiarities of the animals distribution by the biotopes and species numbers are described.

#### Chapter 2.3. GEOGRAPHICAL ANALYSIS OF THE SOUTH URALS HIGHLANDS FOREST ENTOMOFAUNA WITH HISTORICAL ASPECTS.

The Ural mountains is an interesting region in regard to entomofauna. Its originality consists of peculiar combination of insect species with different types of geographical distribution. Apart from widespread holarctic and transpalearctic insect species, there are European and Siberian species, and mountain-boreal, arcto-alpine species were found in the Urals, too.



Some species were contemporaries to Pleistocene epochs (for example: white admiral *Limenitis camilla* Schiff., capricorn beetle *Rosalia alpina* L.).

There are few insect species endemic of the Urals. For example: ground beetles *Carabus karpinski* Kryzh., *Pterostichus urengaius* Glas., leaf beetle *Chrysolina kuznetzovi* Jack., scale insect *Puto borealis* Borschs.. All of them were found in high-elevated regions of the South or Polar Urals and had the Quaternary age.

The largest part of the Urals entomofauna refer to widespread boreal species. Glacial remnants (tiger moth *Holarctia cervini* Fell. scale insect *Arctothezia cataphracta* Shaw., crane-fly *Tipula tristriata* Lund., etc.) occupy tundra islands at the highest tops of the South Urals: Yaman-tau, Iremel, Zigalga, Urenga. Now these insect species live in peculiar refugia just as ever the remnants of Pleistocene entomofauna survived the glacial temperature depression.

Interglacial remnants (peak whites *Synchlora callidice* Hb., satyrid butterfly *Tryphisa phryne* Pall., crane fly *Nephrotoma stackelbergi* Sav.) survive now in the steppe plots on some South Urals peaks.

South Urals entomofauna is related with different Eurasian regions: North and Central Europe, North and Polar Urals, Caucasus, alpine regions of the Altai and other mountains of the South Siberia and Far East. The map of this relations is appended (Fig.2).

The detailed analysis of South Urals entomofauna in the context of its genesis was made on carabids fauna. The list of carabid beetle species and short remarks on arcto-alpine species are adduced.

Side by side with research and discussions on the present entomofauna, we studied the palaeoentomofauna from several cave sites. More than 80 species of insects of the Holocene age have been found (radiocarbon date - 2790<sup>±</sup>207 B.P.). The list of fossil insect species is adduced. Carabid beetles, weevils and leaf beetles are dominating.

Zoogeographical analysis of the South Urals entomofauna proved that insect populations of high-elevated forests refer to several ecological groups. Their areas reflect the basic moments of

history of landscapes in this region: 1 - nemoral group, related with broad-leaved and mixed coniferous-broad-leaved forests; 2 - alpine endemics; 3 - boreo-montane species (in the extreme - arcto-alpine species); their interrupted distribution is a result of glacial and postglacial periods; 4 - steppe species, remnants of Holocene, having penetrated to the South Urals in the middle of the period, during the thermal maximum. The most ancient elements of the invertebrates fauna of the South Urals are soil inhabitants (carabid beetles, *Lumbricidae*).

### Chapter 3. DESCRIPTION OF SITES AND METHODS OF STUDY.

Methods of field work, operations with paleoremaines and dating are described. The table of radiocarbon dates is given, too. The karst sites are described indicating their geographical position (shown at Fig.1) and geomorphological characteristics, using drawings and photo. Stratigraphy of sites is described usually accompanied with the pollen spectra analysis and tables of remains including both small and megamammals. Besides that data on the small mammals are shown on a serie of figures indicating the ratio of different species in the sites.

### Chapter 4.1 VEGETATIONAL HISTORY OF THE HIGH-ELEVATED REGIONS OF THE SOUTH URALS DURING PLEISTOCENE AND HOLOCENE BY POLLEN DATA.

Vegetational history of the high-elevated regions of the South Urals was studied by pollen analyses of loose deposits of the Caves: Ignatievsky and Serpievsky I & II, rock-shelters Pryzhim I & II (radio-carbon dates refer all of these layers to the period of Valdai glaciation) and of some peatbogs of Holocene age.

Pollen spectra of the Late Pleistocene deposits show the dominance of pratal and steppe-like vegetation (more than 90% of the total number of grains), mainly of different grasses (*Asteraceae* pollen prevailing, the others referring to: *Polygonaceae*, *Geraniaceae*, *Apiaceae*, *Caryophyllaceae*, *Fabaceae*, *Ranunculaceae*, *Onagraceae*, *Dipsacaceae*, with many grains of *Chenopodiaceae*, *Cyperaceae*, *Artemisia*) and some tundra elements (*Betula nana*, *B. humilis*, *Salix* bushes). In several more favourable habitats islands of forest vegetation appeared to retain, with *Pinus*, *Betula*, *Larix* and *Picea* represented.

Ratio between different components in plant communities during

the whole period at study varied.

Thus, by the end of the Karghinsky (Mologo-Sheksninsky) interstadial, judging by the results of pollen analysis of the deposits dated by  $C^{14}$  to 25-27 thousand years B.P., only 10-12 % of pollen was produced by trees, the share of *Picea* being at the first place; *Abies*, *Alnus* and *Tilia* were present, too. Grasses were more diverse, including *Sanguisorba officinalis*, *Valeriana officinalis*, *Polygonum bistorta*, *Thalictrum*, *Scabiosa*, *Knautia* and others growing at wet meadow glades. *Polypodiaceae* ferns were in abundance.

Later on, during the Polar-Urals glaciation ( $C^{14}$  date about 17 th. years ago, Table 6), both quota of wooden plants and species diversity of herbs decreased. Quantity of trees pollen in the spectra fell to 5 %, share of grasses composed about 90 %. Number of *Artemisia* plants increased. Ferns spores were still numerous.

During the final, cold and arid period of the last glaciation characterized by pollen spectra of the cultural layer of the Ignatievsky Cave ( $C^{14}$  date = 14000 B.P.), forest vegetation was depressed, with full dominance of grasses (*Asteraceae*, including many *Artemisia* plants, *Chenopodiaceae*, *Poaceae*, *Cyperaceae*, etc.), accompanied with elements of the shrubby tundras.

Holocene vegetation was reconstructed, mainly, by pollen data of the deposits of high-elevated peatbogs and, besides, the upper layers of the Serpievsky-I Cave and the sites Sim II & III (Table 29). During the upper Dryas period vegetation, to the larger part, retained the features of that of the Late Pleistocene time. Yet the quota of arboreal plants increased, and larch was the main forest-forming species.

During the Preboreal period the two phases were determined: the earlier warm period, when forest vegetation (with *Picea*, *Pinus*, *Abies*) dominated, and the later and cooler period, when herbaceous and shrubby assemblages were restored.

In the Boreal Period (during the first half of it) vegetation was represented by forest - steppe complexes with larch, pine, birch. By the end of the period close forests were formed, mainly of pines and birches. In the central high-elevated regions there appeared the belt of dark-coniferous (fir) forests with a touch of *Pinus sibirica*.

During the first part of the Atlantic the pine forests were

dominating, with presence of *Picea*, *Tilia cordata*, *Ulmus scabra*, *Ulmus laevis*, *Quercus robur*. During the second part there were spread mixed broad-leaved and coniferous forests, with *Carpinus betulus* and *Ulmus campestris* being present in them, too.

In the Subboreal period quota of the broad-leaved species decreased.

During the Subatlantic, dark-coniferous forests of *Abies* and *Picea* became widely distributed.

Thus, pollen data have shown that in the high-elevated regions of the South Urals even during the most cold periods of the Upper Pleistocene there were present the foci of forest vegetation. In some of them, in the South-West foothills, the retreats of nemoral flora existed, and the latter began to distribute from them around the whole territory when it grew warmer in Holocene.

#### Chapter 4.2 STAGES OF DEVELOPMENT OF SMALL MAMMALS FAUNA DURING THE LATE PLEISTOCENE AND HOLOCENE

Data on small mammals species composition (percentage for every stratum) for all cave sites at study were compared and grouped, with taking into consideration the layers stratigraphy, radiocarbon dates and archaeological dating of materials. Based on the results of grouping of the data received for synchronous layers of sites situated at the neighbouring territories, we came to distinguish a serie of local faunas. In some cases there were designated some geographical variants and chronological stages inside of the local faunas. These faunas were named by the geographical points (usually settlements) situated in the vicinity of sites. Each fauna was characterized by several parameters: species composition, distribution of species by their abundance, equitability index "e", level of "disharmony" of fauna composition.

The abundance groups were established according to the following gradations: the species was concerned to be "extremely numerous" if the share of it's remains in the stratum composed 30% or more; the class was named "numerous" for the frequency figures lying between 10 and 29.9%. Animals were thought to be "ordinary" if the share of those among the remains was from 1 to 9.9%. Those in between 0.2 - 0.9 % were considered to be "rare", and less than 0.2 % - "extremely rare".

Index of equitability was calculated as follows:

$$e = \frac{H}{\ln S} ,$$

where S is the total number of species, and H is Shannon index (calculated as  $H = -\sum p_i \ln p_i$ ,  $p_i$  being the share of remains referring to the i-th species).

Index of species diversity was calculated using two parameters: the number of the found species (S) and the number of the specimens studied (N) (instead of the latter we used the corrected number of teeth):

$$d = \frac{S-1}{\ln N}$$

Index of disharmony, or the distance of the fauna differences as compared to the modern zonal complexes, was evaluated based upon the simultaneous presence (in every local fauna) of bones of animals representing the genera which are now characteristic to different modern zonal complexes (for example, those of tundra and steppes, taiga and deserts, etc.). If we have marked animals of different genera, inhabiting now all the different zones, from tundra up to that of nemoral forests (i.e., *Dicrostonyx*, *Lagurus*, *Apodemus*, *Myopus*, *Clethrionomys*, *Eolagurus*), we considered this fauna to be "extremely disharmonious". "Disharmonious" fauna was that which included together both the animals, partly dwelling now at the conditions of tundra and the others inhabiting now only steppes, or, in another variant, those which are now characteristic for the taiga and desert faunistic complexes (for example: *Dicrostonyx*, *Lagurus*, *Myopus*, *Clethrionomys*, *Eolagurus*). Fauna of intrazonal type included the elements, now belonging to adjacent zonal complexes.

The materials received allow to describe the history of small mammals fauna in two regions of the South Urals, at the eastern and western slopes.

From the eastern slope where the forest-steppe landscapes are spread now, we have described the fauna we named Ustinovsky, that existed about 12 th.years ago, and, besides, two development stages of the terminal Holocene fauna we named Myassky.

From the western slope of the Urals (now occupied by coniferous and broad-leaved forests), based on cave materials we

have described the faunas we named Serpievsky, Aratsky and Ignatievsky, characterizing the consequent stages of the Late Paleolithic complex development, from the terminal latest interglacial to the terminal Pleistocene. For the latest Holocene of this region the Simsky fauna was distinguished, based on the materials from the serie of caves situated in the watershed of the Sim-river. Besides that, from the watershed of the Yuruzan'-river, northwards from the Sim, we have described regional variants of the Ignatievsky and Aratsky faunas. Data on species composition and distribution by abundance for all the faunas studied are given in Tables 31, 32.

Undoubtedly, the greatest step in development of faunas both of big and small mammals, was the boundary between Pleistocene and Holocene. That was the interval when chronological faunistic complexes were changed, the Late Palaeolithic complex was removed by the Holocene one.

Similarity between local faunas was evaluated with the help of "r" criterium calculated as:

$$r = \frac{m}{\sum_{i=1}^m \sqrt{p_i q_i}} \text{ , where } p_i \text{ and } q_i \text{ are the frequencies of the}$$

corrected numbers of remains of the same species in the two faunas to be compared, and  $m$  is the quantity of the common species.

This figure was the minimum and equaled to 0.35 when comparing the Simsky fauna of late Holocene with it's Pleistocene ancestor, the Ignatievsky fauna. The similar figure. (0.42) was received when the two faunas of the eastern slope of the Urals were compared, those named Myassky (Holocene aged) and Ustinovsky (Pleistocenic one).

The much higher similarity was found to exist between the faunas referring to the different chronological stages in the late Palaeolithic complex development: 0.88 between Ignatievsky and Aratsky; 0.89 between Aratsky and Serpievsky; 0.88 between Ignatievsky and Serpievsky faunas.

Geographically different but synchronic faunas of the South Urals, referring to the same late palaeolithic complex, show the similarity figures about the same as the faunas of different chronological development stages of that very complex: 0.78 (Ustinovsky-Ignatievsky); 0.80 (Ustinovsky - Yuruzansky variant of

the Ignatievsky fauna); 0.95 (Ignatievsky fauna and it's Yuruzansky variant); 0.82 (Aratsky fauna and it's Yuruzansky variant).

In all Late Pleistocene faunas of the South Urals western slope the share of the narrow-skulled vole remains prevailed sharply ; and all these faunas must be referred to the group of disharmonious or even extremely disharmonious. This feature is expressed to the most extent in the oldest fauna of those discussed, the Serpievsky one. There were marked such forms as the yellow-necked and common forest mice, together with Russian desman, from one side, - and the lemmings, collared, siberian and steppe forms, from the other. However, collared lemmings were represented with the remains designated as a distinct species, which must be considered to be the ancestor form for the late Pleistocene typical species, *Dicrostonyx gullielmi*. Narrow-skulled voles, too, were designated as a dissent subspecies.

The Ignatievsky fauna, 14-C dated to 14 th.years B.P., is marked for the following peculiarities :

- 1) Sharp prevalence of the narrow-skulled vole referring to the dissent late pleistocenic subspecies;
- 2) Combination of remains of *Dicrostonyx gullielmi* with those of the jerboas, accompanied with relatively high ratio of the species, modern descendants of which now inhabit steppes, as steppe lemmings, haymakers, *Cricetulus* and *Allocricetulus* hamsters;
- 3) Mice remains missed in it; the share of remains of the common hamster and that of insectivores (only shrews species) being extremely low.

The late Holocene Simsky fauna showed significantly more uniform distribution of species according to their abundance. There were found the remains of forest-dwelling animals, as chipmunk, Siberian flying squirrel, garden dormouse, yellow-necked and common field mice. Remains of the short-tailed and common voles, water vole, bank vole and common hamster were numerous. Share of the insectivores remains was significantly higher than those in all Late Pleistocene faunas. At the early stages of this fauna existence rare remains of 3 steppe species, grey hamster, steppe lemming and red-cheeked suslik, were recorded.

Faunas of the eastern Urals slope are notable for the greater share of the steppe animal species, among which, both during Holocene and Late Pleistocene, the mole-vole remains were recorded

- the species not marked in the faunas of the western slope.

Besides the differences in the faunas quality it was important to study the dynamics of the communities structure of different regions and of the different age. To describe the communities structure we used the combination of two indexes: equitability (to show the level of the species distribution uniformity in the communities) and species diversity (to show, how many species are there in the community). These parameters were calculated for all of the studied Pleistocene and Holocene faunas of the South Urals, and, besides, for the serie of recent faunas of the steppe, forest-steppe and tundra regions adjacent to the Urals.

As for the faunas of the same region of the South Urals, but dated to the different periods of the Late Pleistocene and Holocene, the index of species diversity varied only slightly, though the qualitative contents of faunas and the whole biota differed significantly. Thus, species diversity values for the Late Pleistocene Ignatievsky, Aratsky and Serpievsky faunas equalled to 2.96; 2.60; 2.63, correspondingly; and for some sites of the Simsky fauna they varied from 2.63 to 3.31. This small variation looks especially insignificant when compared to the huge modern latitude gradient between species diversity values: from 0.34 to 3.31. The minimum values are found for the recent tundra rodent faunas (0.34-0.65), and those the largest describe the recent faunas of the broad-leaved forests of the South Urals (3.31).

The second parameter, equitability, varied significantly both in the recent geographical gradient and in time (Pleistocene and Holocene faunas of the South Urals). For the faunas studied the values varied from 0.37 to 0.89 (theoretically possible figures lying between 0 and 1). The highest values were shown to describe the faunas with the most uniform species shares, and they were marked both for the richest recent forest faunas of the South Urals (0.89) and for the poorest northern, tundra-like, Pleistocene faunas of the West Siberia (0.74). The minimal values were found for the recent steppe faunas (0.37; 0.48) and for the Late Pleistocene Ignatievsky fauna of the South Urals (0.45). The recent forest-steppe faunas and some faunas of disharmonious character dated to the first half of the Late Pleistocene were found to show the intermediate values of equitability index.

Thus, the recent and Late Holocene faunas of the South Urals



dwelling in the mixed-broad-leaved forests show the maximum values of both species diversity index and equitability. For the Ignatievsky fauna dated to the terminal Late Pleistocene cold period, combination of these two factors looks quite different as compared to all of the faunas studied. Index of species diversity being high enough, the equitability value is very low. That is, the conditions the fauna existed at, were sufficient to provide many species to live there, but the majority of the species could develop only low numbers, and the only narrow-skulled vole proved to become the absolute dominant. Among the recent zonal faunas studied, the most similar combination of both indexes was found to describe the steppe faunas but the species diversity values in them were smaller. When using these fauna characteristics, one can see that the comparison of the cold Late Pleistocene faunas with the tundra communities is of little sense as the latter show quite dissent combination of both indexes (extremely low species diversity combined with average equitability values).

The Aratsky and Serpievsky faunas dated to the first half of the Late Pleistocene, which existed at the conditions, perhaps, not so severe as those of the Ignatievsky fauna time being, were characterized with the combination of both indexes similar to that in the recent forest-steppe faunas. That is, species diversity indexes were relatively high, and equitability values were near to the average.

Thus one can come to the conclusion about high specificity of the Late Pleistocene cold faunas, - not only in their quality contents but in their ecological structure, too, and that is why it is of little or no sense to draw the direct analogy between these faunas and modern zonal communities.

#### Chapter 4.3. HISTORY OF DEVELOPMENT OF MEGAMAMMALS FAUNA.

Stages of fauna development were studied based at the analysis of species contents of bone remains from taphonomically uniform sites.

During the Late Pleistocene 3 stages of theriofauna have been distinguished. The first stage (referring perhaps to the end of the Riss-Wurm period) is represented by the only site where the following species were determined: *Spelaearctos rossicus* Boriss., *Cervus*

*elaphus* L., small forms of *Canis lupus* L. and *Gulo gulo* L.

The second stage (earlier Wurm interstadial, older than 33 thousand years ago) is demonstrated by 4 sites. There were found the remains of *Equus cf. latipes* Gromova, *C. elaphus* L., *S. spelaeus* Ros. and Hein., *Canis lupus* L. (large form), *Lynx lynx* L., *Castor fiber* L. Two geographical variants may be distinguished with the fauna. Three sites, situated in the mountains, showed dominating among the remains horse and reindeer, numerous red deer and woolly rhinoceros, rare bison and saiga. The only site situated at the boundary between plain and western mountain slopes, offered the different fauna contents, with prevalence of reindeer, numerous remains of saiga, red deer, woolly rhinoceros and horse, bison remains being rare.

The third stage (dated by radiocarbon to the end of the Wurm, about 13-14 thousand years ago) is represented by two sites; the bone remains revealed *Equus uralensis* Kuzm., *S. spelaeus* Ros. and Hein., big form of *Canis lupus* L., the remains of *C. elaphus* L. missing; species quota differing between sites.

At the boundary of Pleistocene and Holocene seven species of big mammals perished, the majority of others changed their areas and numbers. Holocene theriofauna included *Lepus timidus* L., *Ursus arctos* L., *Meles meles* L., *Capreolus pygargus* Pall., *Alces alces* L. Significant changes in theriofauna occurred, too, when the domestic forms appeared (II millenium B.C.) and when industrial era started (18-19 centuries A.D.).

## Chapter 5. DYNAMICS OF MORPHOLOGICAL AND ECOLOGICAL CHARACTERISTICS IN RODENT SPECIES.

### 5.1 The narrow-skulled vole (*Microtus gregalis*).

The narrow-skulled vole was recorded in all of the described ancient faunas of the South Urals, but now does not inhabit the studied regions of the mountain part of the South Urals. The nearest plots of the modern area lie in about 150 km to the west and east, in the zonal forest-steppes in the Pre-Urals and Trans-Urals. Now the narrow-skulled voles inhabit all the steppes and the large part of the forest-steppe zone of Asia, from the Ural river in the west up to the Amur river in the east. Besides that, the species is spread in the tundra zone, from the North Dvina river up

to the river of Anadyr'. The whole species is divided into a series of subspecies, and the tundra populations of the different subspecies demonstrate the common properties distinctive from the steppe forms. First of all, the northern narrow-skulled voles are discerned for the larger sizes leading to some morphophysiological peculiarities (Schwartz, 1963, Gromov, Polyakov, 1977).

In our study we have analyzed the paraconid forms and dimensions (length and width) of the first lower molars of more than 1500 specimens from 21 sites of the South Urals dated to the Late Pleistocene and Holocene, comparing them with recent tundra and steppe narrow-skulled voles. The data are represented at Fig. 43 and Tab. 34 & 35.

Special methodical variational analysis of several paraconid parameters has shown that for the quantitative assessment of the teeth shape it is sufficient to measure the only trait - the expressiveness of the recess at the buccal side of the front loop. This trait was estimated by measuring the corresponding angle as one can see from Fig. 42. Teeth of the most simple variant (with no recess) were marked as corresponding to  $0^{\circ}$  (so called "gregaloid morphotype"); the recess being equal to  $5^{\circ}$ ,  $10^{\circ}$ ,  $15^{\circ}$ , teeth were referred to an intermediate type ("gregaloid-microtid"); when the angle measure exceeded  $20^{\circ}$  - they were considered as the "microtid" morphotype.

The narrow-skulled voles from the most ancient fauna, the Serpievsky one, had the  $M_1$  length a bit larger than that in the recent steppe forms and quite another morphotype ratio. Teeth of the "gregaloid" morphotype composed 40-50%, the intermediate "gregaloid-microtid" group included some 40%, and only the minimal part of teeth (below 20%) referred to the "microtid" morphotype.

The later voles aged to the cold phase of the Late Pleistocene (the Ignatievsky fauna), had the larger teeth length and the better-expressed recess at the front loop buccal side. The share of the "gregaloid" morphotype teeth composed 20-30%, that of the "gregaloid-microtid" group - about 40-50%, and of the "microtid" morphotype teeth - some 20%. These voles are to be designated as *M. gregalis krigenicus*, described by L.I. Rekovetz for the Late Pleistocene faunas of the East Europe.

During Holocene the narrow-skulled voles of the South Urals showed the sharp decrease of size and significantly different

morphotype ratio. Thus, in the recent steppe subspecies *M.g.gregalis*, inhabiting the territories near to the South Urals, the "gregaloid" morphotype teeth run to 3% only, those of the "gregaloid-microtid" group - less than 20%, and the molars of the "microtid" morphotype occurred as the dominating group (about 80%).

In the recent tundra subspecies *M.g.major* inhabiting the Yamal peninsula as compared to the recent steppe subspecies, the share of teeth with the small recess at the front loop was a bit larger ("gregaloid" morphotype composed 8%, the "gregaloid-microtid" one - about 30%, the teeth of the "microtid" morphotype exceeding 60%). The dimensions of this form were found to be significantly larger than those in both the steppe voles and the remains of the animals of the Pleistocene age.

Thus, during the Late Pleistocene the narrow-skulled voles of the South Urals showed the shift of morphological traits (equal to the subspecies rank) towards the increase of the molars size and the complication of the paraconid part. At the boundary of Pleistocene and Holocene one can see not only the change of size variation trend towards the decrease of molars, but the rate of variation increased sharply. On the contrary to that, the trend towards the complication of teeth remained, though the rate of this process increased sharply, too.

So, one can come to conclude that temporal dynamics of size characteristics in this species lies inside the species cold reaction norm whereas the temporal variation of morphological traits occurred independently of any environment parameters changes.

## 5.2. Tundra vole (*Microtus oeconomus*)

The tundra vole was recorded in all described faunas of the South Urals dated to both the Late Pleistocene and Holocene. Now this species inhabits the vast areas of the larger part of the North Eurasia, being spread in the tundra, forest-tundra, taiga, and, partly, the forest-steppe, zones. The region at study is now inhabited by this species, too.

The share of the tundra vole remains in the Pleistocene faunas of the South Urals (those named Serpievsky, Aratsky and Ignatievsky) was very large. As to the classification we use, the remains of this species in all these faunas appeared to refer to

the category of numerous or extremely numerous species, being inferior in numbers only to the narrow-skulled vole. In the Holocene-aged Simsky fauna the share of *Microtus oeconomus* reduced significantly, not exceeding 10%.

We have analyzed about 600 first lower molars from 19 samples dated to both Late Pleistocene and Holocene (Tab.36). It was shown that during the discussed interval of time teeth sizes in the tundra voles increased, and the morphotypes ratio changed, too (see Fig.45). Yet the scope of these changes was significantly smaller as compared to that in the narrow-skulled vole. The other important moment is the fact that at the boundary between Pleistocene and Holocene the narrow-skulled voles demonstrated the change of the trend in size variation, while in the tundra vole the trend did not change, and the latter species during Holocene showed the same trend of size increase which was found to exist in both species during Pleistocene.

#### 5.4. Collared lemmings.

*Dicrostonyx* remains have been recorded in all Pleistocene faunas of the South Urals. The moment of the genus occurrence and extinction in this region has not yet been established. However, it is known for sure that during the Late Holocene the collared lemmings did not inhabit the South Urals. Among the small mammals remains from the rock shelter named Sim III of the middle Holocene age we have found one *Dicrostonyx* molar, but one can not exclude the possibility that it was re-buried from the previously-formed deposits. As the faunas of the early Holocene have not been found in the South Urals yet, nobody can say whether the collared lemmings inhabited these territories at that time, but it is possible to propose that it was just at that time when these animals ceased to occupy their prominent place in the communities that they had in the Late Pleistocene ecosystems.

In the Ignatievsky fauna of the Late Pleistocene age *D.guilielmi* was an ordinary species, just as the steppe lemming and the grey hamster were (Tab.32). In the older Aratsky fauna the share of remains of this species decreased significantly and turned to the group of rare species, again together with steppe lemmings and grey hamsters. In even more ancient Serpievsky fauna the collared lemmings remains quota was relatively small, yet falling

into the group of the ordinary species. It is important, that in the Serpievsky fauna the *Dicrostonyx* remains were designated as *D. cf. simplicior*. The conclusion was drawn based on the  $M^1$  and  $M^2$  pattern, the latter being fully represented (100%) by the "simplicior" morphotype (Fig.48). Lemmings from the Aratsky fauna showed about 50% molars of this pattern, and, besides those, teeth of the "henseli" morphotype and a few molars of the "torquatus" type. In the contents of the Ignatievsky fauna the lemmings were represented having mostly the molars of the "henseli" morphotype; the smaller share of teeth showed the "torquatus" pattern and only the minimum part of them revealed the "simplicior" variant. In the recent collared lemmings inhabiting tundras of Eurasia the "simplicior" pattern is extremely rare, the "henseli" morphotype numbers about 10%, and the "torquatus" type dominates sharply. Dentition evolution in the collared lemmings was discussed in a serie of special publications. As for the lemmings of the South Urals, specifics of this process is connected with the fact that *Dicrostonyx cf. simplicior* only rather lately was substituted by *D.guittelmi*. It had been shown that at the territories adjacent to the North Urals both to the east and west, this process took place during the middle Pleistocene, and at the South Urals territories it drew till the end of the Late Pleistocene.

*Dicrostonyx* remains being recorded in a community, this community is usually associated with the tundra conditions, but such a conclusion is to be considered wrong for the South Urals. Numerous data indicate that *D.simplicior* from the Serpievsky fauna in the South Urals were a part of the communities of the forest-steppe type, the flora of which included the broad-leaved trees, and among the animals recorded there were mice, desmans and some other forms that can hardly be imagined to dwell at tundra conditions.

*D.guittelmi* recorded in the contents of the Ignatievsky fauna dwelt perhaps in the landscapes more cold and arid usually determined as periglacial steppes. It is known that in the regions northwards both *D.simplicior* and *D.guittelmi* inhabited the tundra communities, as modern *D.torquatus* do. To the author's opinion this is a feature to indicate the decrease of ecological plasticity of the collared lemmings in the course of evolution.

#### 5.5. Steppe lemming (*Lagurus lagurus*)

The steppe lemming (sagebrush vole) is a steppe-dwelling species and now is not recorded in the mountain-forest regions of the South Urals. Few bones of this species were found in the Simsky fauna of the middle Holocene age. At the eastern slope during this time interval the remains of the steppe lemmings were numerous, and in the Miassky fauna it was one of the ordinary species. In the same region, in the Ustinovsky fauna of the Late Pleistocene age, the steppe lemmings were the most numerous species among the rodents (exceeding 30% of remains). At the western slope, in the Yuruzan'-river valley (Yuruzan' variants of the Ignatievsky and Aratsky faunas) these animals were inferior in numbers only to the narrow-skulled and tundra voles, thus being one of the numerous species. In the Sim'-river basin the share of this species remains appeared to be the largest in the Ignatievsky fauna, somewhat lower it was in the Serpievsky fauna (one of the ordinary species there), and in the Aratsky fauna it was one of the rare species.

Molar sizes in the steppe lemmings did not stay constant during the period at study (Fig.49). The trend of  $M_1$  size variation was similar to that in the narrow-skulled vole: from the first half to the terminal Late Pleistocene  $M_1$  sizes increased, and during the Holocene they turned to decrease. Morphotypes frequency was shown to change slightly, but the prevailing pattern remained the same during the whole Pleistocene period studied.

### Chapter 6. MORPHOLOGY OF BONE REMAINS OF MEGAMAMMALS.

Author describes morphology and size variability of teeth and postcranial bones in *Spelaeoartos spelaeus* Ros. et Hein., 1974; *S. rossicus* Boris., 1930; *Canis lupus* L., 1758; horse referred to *Equus* (*Equus*) L. and hare identified as *Lepus* (*Lepus*) L.

10282 remains were determined to belong to *S. spelaeus*, from one fossil population, the animals having perished mainly during dormancy. Using absolute and relative dating methods, three stages of this population existence were distinguished (initial, middle, final). The latter corresponded to the period of extinction of the species. The share of juveniles among the perished animals increased significantly from the first to the third stage, and females prevailed in the whole number.

Sex differences were only slight in the dimensions of  $dP_4^4$ ,  $P_4^4$ ,  $M_2^2$ , but the sizes of  $M_{tII}$  and  $M_{tIII}$  differed quite distinctly. Alteration in teeth sizes was not clearly trended in time (Table 48). Variability in  $dP_4^4$  in the final sample was distinctly higher than in those characterizing the early or middle stages. Variability in  $P_4^4$  and molars  $M_{1-3}^{1-2}$  was the same during the whole interval. The author thinks that increase in both the juveniles mortality and  $dP_4^4$  variability during the final period of population life could be bound up with the process of extinction.

*S. rossicus* differs from *S. spelaeus* in smaller bone dimensions and proportions of  $dP_4^4$ .

*Canis lupus* showed variation in size and proportions of  $M_1$  (Table 50); an ecomorph had been described in this species.

Two allochronic forms were distinguished among horses; they were *E. aff. latipes* Grom. (beginning of the Wurm) and *E. uralensis* Kuzm. (end of the Wurm) (Table 51).

In the genus *Lepus* (*Lepus*) during the Wurm there existed a hypsodont form, *Lepus tanaiticus* Gur., and during Holocene - the typical *L. timidus* L. At the beginning of the Wurm, *L. cf. europaeus* Pall. has been recorded, too.

## CONCLUSION

Biota history in the South Urals during the Late Pleistocene and Holocene has been studied very unequally yet. Based on pollen analyses of peatbogs, Holocene vegetation history has been studied in detail for the eastern slope altitudes of about 300-400m and for the ridge central part, altitudes of about 700 and 900-1000 m. The fauna data have been received only for the Middle and Late Holocene periods of the both slopes, altitudes about 300-500 m. Yet these fauna materials are significant for the information on the landscapes. For example, it has been shown, that in the Simsky fauna of the middle Holocene (western slope) some steppe species of the small mammals were recorded, though the pollen analyses revealed no plant communities of the steppe character.

Pollen and paleofaunistic data on the Late Pleistocene period of the biota history appear to be consistent with each other if when interpreting the data one agrees to admit that a serie of species show temporal shift of not only morphological traits but ecological characteristics, too. One is to come to such a



conclusion based on the analysis of the faunas structures and contents combined with the habitats characteristics studies. Dynamics of morphological and ecological features of the diverse species during the same time period appeared to differ significantly.

Morphological and ecogenetical differences appeared to be the most in *Dicrostonyx* species. The recent collared lemmings of Eurasia inhabit only tundras, whereas the remains of *D.cf.simplicior* dated to the first half of the Late Pleistocene were recorded in the communities of the forest-steppe type with the presence of the broad-leaved trees. Later on, during the Late Pleistocene, these territories were occupied by the significantly different communities of the so-called periglacial cold steppes, where the other lemmings, *D.guillielmi*, were recorded.

The changes of the subspecies rank have been registered in the narrow-skulled vole. In the Late Pleistocene faunas the subspecies *Microtus gregalis krigenicus* was distinguished, significantly differing from the both recent subspecies, one inhabiting tundras and the other - the steppe zone. The Pleistocene animals were the large voles, usually inhabiting cold periglacial steppes, and their first molars showed mainly the "gregaloid" and "gregaloid-microtid" patterns.

The steppe lemmings of the Late Pleistocene age were distinct for their larger sizes, too, but the morphotypes ratio in them varied less significantly than that in the narrow-skulled voles. These two species (*Lagurus lagurus* and *Microtus gregalis*) showed the same trends in size variation (Fig.54) : during the Late Pleistocene, when the climate changed toward cold and arid, the sizes in both species increased, and during the Holocene time, with the climate becoming more warm and humid, the sizes in both voles turned to increase sharply. This kind of reaction upon climatic changes may be seen in the modern type of geographical variability of both species, too.

Another type of trend has been recorded in the tundra and water voles (Fig.54). The molars morphotype characteristics in these species varied but slightly, and the interesting moment with the two forms was that the sizes in them increased both during the Late Pleistocene and Holocene, thus remaining the trend vector unchanged. This kind of sizes dynamics may be interpreted only if

to imagine the change in biotope demands in the two species. Probably the Pleistocene ancestors of the tundra and water voles were not so closely associated with humid biotopes as their Holocene descendants.

Thus, the diverse small mammals species revealed different reaction upon the cardinal paleoenvironment changes having taken place at the boundary of Pleistocene and Holocene. Owing to the different ecological and morphological adaptations small mammals gained more success than megamammals to transform from Pleistocene to Holocene.

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in the South Urals**

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