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Periglacial micromammal faunas from the Late Pleistocene of Ukraine

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Abstract. This paper presents a reconstruction of environmental conditions in the Late Pleistocene of Ukraine based on the qualitative and quantitative composition of the small mammal fauna, the study of morphological features of extinct species (mostly molar teeth of Arvicolidae) and the distribution of different ecological groups. Questions regarding the adaptations and origin of the Recent small mammal fauna are discussed.

Key words: Ukraine, Moldova, Late Pleistocene, Recent, micromammals, Rodentia, palaeoenvironment.

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The south-western part of Eastern Europe is a region rich in remains of the Pleistocene fauna. Here are concentrated well known localities associated with the ancient alluvium (Pivikha, Matveyevka, Gun'ki) or with ancient human settlements (Novgorod-Seversky, Mezin, Tshulatov, Pushkari, Mezhyrich). The former locality type is dominant in the Early and Middle Pleistocene and the latter in the Late Pleistocene, especially the maximal (Valdai) cold period. Glacial faunas of this time are often called mixed, since they are associated with the marginal glacier zone. Over the area studied these faunas are qualitatively and quantitatively heterogeneous, displaying regional peculiarities and different habitat distributions (MARKOVA 1982).

In our opinion the periglacial (or mixed) fauna is a natural, historically formed species association, developed under the influence of a decrease in temperature and including autochtonous as well as immigrant species. These were self-regulated functional palaeobiocoenoses with special matter-energy pathways (REKOVETS 1985).

Late Pleistocene faunas developed on a background of general climatic and landscape change. Alternating cold and warm periods, changes in the shorelines of the Black and Azov Seas and shifts in the valleys of the larger rivers (Dnieper, Yuzhny Bug, Dniester) resulted in faunal migrations, taxic transformations and extinctions. The faunal zonation of the time is reflected in the faunas and has led to the distinction of six regions in Ukraine

and Moldova: north Ukraine, the middle and lower Dnieper areas, west Ukraine, Crimea and Moldova. The following ecological characterizations of the faunas are used: arctic, steppe, forest, hydrophilous and polyzonal (species with great ecological plasticity).

The small mammal faunas of these regions are composed of a majority of open land dwellers, mostly steppe species, which account for 35% to 55% of the total micromammal fauna (Fig. 1). The highest proportion of steppe species has been found in localities of the Crimea (56.5%) and the lowest in west Ukraine (28.6%). Five genera of steppe mammals (*Citellus, Marmota, Cricetulus, Lagurus* and *Ochotona*) have been found in all six regions of Ukraine and Moldova. Representatives of the genera *Allactaga* and *Eolagurus* are known from all regions except west Ukraine, *Spalax* everywhere except north Ukraine, and *Ellobius* everywhere except these two regions. Postglacial steppe faunas of the southern regions are enriched by certain semi-desert species, such as *Scirtopoda telum* LICHT., *Alactagulus acontion* PALL. and *Cricetulus eversmanni* BRANDT.

The number of hydrophilous species varies between 10% in Moldova and 17% in the Dniester area, polyzonal species between 11% in Novgorod-Seversky and 36% in west Ukraine and Moldova (Fig. 1). Over almost the entire territory investigated there are Late Pleistocene remains of *Arvicola terrestris* L., *Castor fiber* L. and *Microtus oeconomus* PALL. These have a wide distribution in suitable habitats. The highest proportion of hydrophilous species (17.8%) is known from alluvial localities (middle and lower Dnieper, Goryn') due to taphonomic peculiarities in the accumulation of the remains.

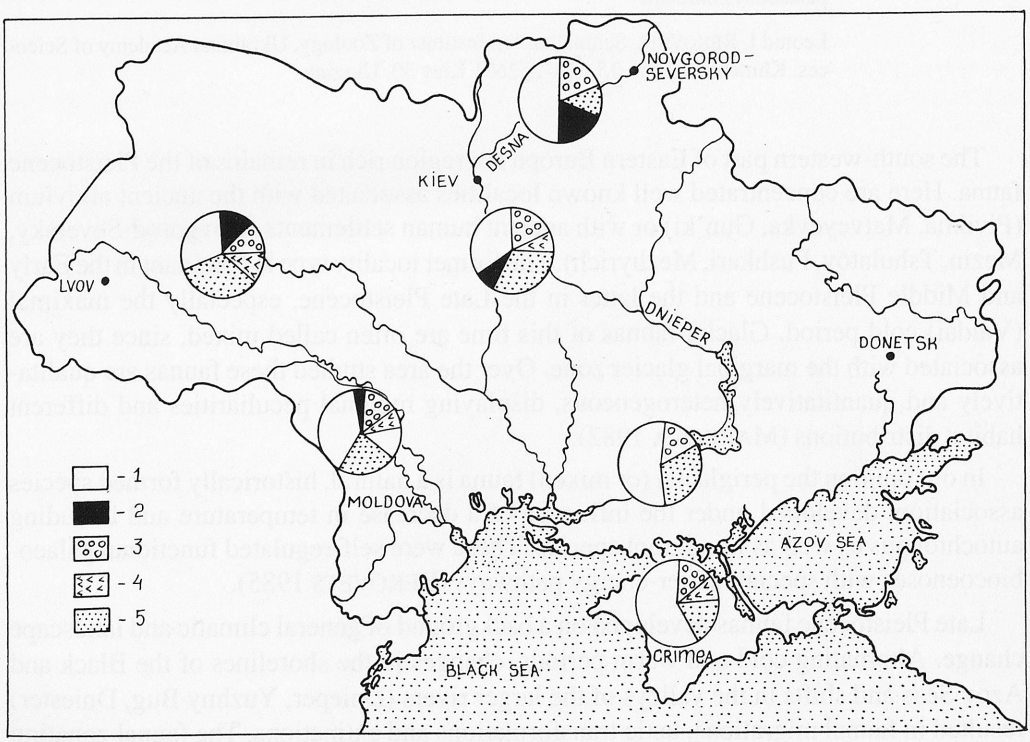

Fig. 1. The quantitative distribution of small mammal ecotypes in the Late Pleistocene of Ukraine. 1. steppe, 2. arctic, 3. hydrophilous, 4. forest, 5. polyzonal.

Polyzonal species are found to be most abundant in Moldova and west Ukraine (36%). Representatives of the genera *Lepus, Microtus* (subgenus *Stenocranius*) and *Cricetus* are also abundantly represented over the entire territory studied. Remains of *Erinaceus* and *Apodemus, Microtus arvalis* PALL. (except in north Ukraine) and *Sorex* spp. (except south Ukraine) have been found (TATARINOV 1971).

No clear tendency towards an increase in steppe species has been found along a north-south line (except Crimea). At the same time, a decrease along this line of arctic species (16% in north Ukraine, 35% in Moldova) and intrazonal species (22.2% in the north and 13% in Crimea) is well pronounced (GROMOV 1961).

Forest species are poorly represented and are absent in north Ukraine and the lower Dnieper. The most important species in this ecological community is *Clethrionomys glareolus* SCHREBER.

The ranges of arctic species, especially of *Dicrostonyx* are worthy of closer attention. The southernmost find of *D. gulielmi* SAN. is in Moldova. Rare remains of the species (0.2%) are found in the localities Brizeny I and Starye Doruitory (LOZAN 1971), as well as in recent alluvial deposits of the middle Dnieper (0.6%) and west Ukraine (5.5%). The most abundant remains are recorded in localities along the Desna river (Novgorod-Seversky, Mezin, Tshulatov) where it reaches15.9%. Another species of the arctic fauna, *Lemmus sibiricus* KER. is represented here (0.45% of remains) and is also found in west Ukraine. Representatives of this ecological group are absent in fossil micromammal faunas of the lower Dnieper and Crimea.

As a whole, the micromammal fauna of the Pleistocene of the southwestern part of Eastern Europe was a fauna indicating open steppe xerophyllic conditions, interspersed with small patches of forest and a wider development of meadow and bush habitats which mostly occurred along floodlands.

The coexistence of animals from different climatic zones of the Palaearctic is evidence for very specific physico-geographic and habitat-forming circumstances. At that time a tundra-steppe climatic regime existed over most of Ukraine (except the southern regions). This led to a complex co-occurrence of tundra, steppe and some forest landscapes as evidenced by data from a variety of animals: mammals (*Sorex arcticus, Alopex lagopus, Gulo gulo, Lynx lynx, Equus latipes, Ovibos moschatus, Rangifer tarandus*) and birds (*Lagopus lagopus*). The hypothetical existence of particular conditions in the periglacial zone is also in agreement with palynological, palaeocryological and palaeoclimatological data and is not inconsistent with palaeofaunistic conclusions.

Peculiar to any given faunistic assemblage are the animals' abilities to adapt to cold conditions. The leading factor in the evolution of small mammals is their trophic adaptation to a diet of roughage. This adaptation is connected with changes to the masticatory system, especially the molars and structure and insertions of the masticatory muscles. These transformations are reflected in the skeletal structure, affecting group evolutionary rate and individual variation and forming a basis for taxonomic analysis.

Smaller mammals of the periglacial zone of Eastern Europe differ from those of adjoining areas and closely related extant forms in their larger body size – a basic character for recognizing taxa at the subspecies level. Larger forms represented in the Novgorod-

Seversky fauna apparently were much more viable in the Late Pleistocene periglacial environment. The only exceptions are the smallest form of grey hamster (*Cricetulus migratorius* PALL.), the desert jerboa (*Allactagus jaculus* L.) and a Late Pleistocene ground squirrel, *Citellus superciliosus* KAUP (REKOVETS 1985).

The most substantial data are based on comparative morphological study of the masticatory system and molar teeth. Numerous species (e. g., *Citellus superciliosus, Eolagurus luteus* EVERSM., *Lagurus lagurus* L.) are characterised by an elongated lower diastema and more horizontal incisors in relation to the longitudinal axis of the skull. This represents a digging adaptation. The thickness of the diastemal part of the horizontal ramus indicates a thinner and less massive lower jaw.

The opposite feature, i. e., a shorter and more massive disatema is characteristic of *Citellus severskensis* GROMOV, *Marmota bobac* MULL. and most Arvicolini. These morphological characters are related to a more vertical position of the incisors and demonstrate the adaptation of these species to gnawing. The degree of development of the alveolar tubercles of the lower jaw supports these conclusions. This character is best expressed in Marmotinae and *Eolagurus*, which show adaptations to digging in dense soil, which in its turn reflects a xerophyllic environment. The development of the masseteric fossa of the lower jaw indicates mainly incisive and partly masticatory movements. This fossa is best developed in *Cricetulus migratorius, Allactaga jaculus* and *Citellus superciliosus*, with the other species differing only slightly from recent forms in this regard. Masticatory function improvement in other species must have been achieved by changes in the condylar, angular and coronoid processes and in the dentition. Almost all rodent species except *Allactaga jaculus* have a lower jaw that is wide at the base of the coronoid process. In that species this feature has been compensated for by a more vertical position and wider anterior part of the process.

Functionally similar adaptations have been demonstrated in the molars of *Citellus severskensis* with their accessory structures, stronger P^4 molarization, weak fusion of roots and strong hypoconid development. The following characters are significant: upper tooth row with strong anterior divergence, well expressed longitudinal position of cristae, nearly vertical position of P^3 root, angular process position and well developed masseteric fossa of the lower jaw in *Citellus superciliosus* (REKOVETS 1979).

Allactaga jaculus is also characterised by an apparently more advanced masticatory apparatus. It has long, broadly spaced and weakly closed roots, a massive jaw at the midpoint of the diastema, and a vertical coronoid process with strongly expressed insertion surfaces for the masticatory musculature. These adaptations to powerful masticatory movements have probably developed in this species due to particular environmental conditions.

The differentiation of the metatarsals (MT II - MT IV) is this species is also worthy of closer attention. These bones are massive in *A. jaculus*, with MT II notably stronger than MT IV and the distal processes broader. These morphological characters would seem to represent adaptations to a dryer environment (REKOVETS 1983).

The paraconid part of the M_1 in Arvicolidae is relatively complicated due to the formation of accessory enamel fields (e. g., in *Microtus gregalis*, *Microtus oeconomus*,

Lagurus lagurus, and *Dicrostonyx* spp.) or to a stronger differentiation of the enamel field of the molar teeth (e. g., in *Eolagurus luteus*, *Lemmus sibiricus*, *Arvicola terrestris*).

Some M_1 morphotypes have been identified in most of the species studied and regularities in their quantitative distribution in time traced. All Late Pleistocene species have a morphotype set identical to that of closely related extant forms. In recent species the most progressive (intricate) morphotypes are dominant and the primitive morphotypes concomitantly reduced in frequency. It should be pointed out that many widely distributed Pleistocene arvicolids (*Arvicola terrestris*, *Microtus gregalis*, *Microtus oeconomus*) of the periglacial faunas of Eastern Europe have important characters in common with recent subspecies inhabiting the northernmost regions of the Palaearctic (Figs 2-4).

The remains of rodents within the area under investigation thus show a combination of characteristics of recent tundra and steppe forms. For instance, *M. gregalis, M. oeconomus* and *A. terrestris* are close to recent northern populations in their large size, but their relative lower jaw indices and molar teeth are reminiscent of recent southern (steppe) populations. This is additional evidence for special tundra-steppe conditions in the Late Pleistocene and shows how this environment is reflected in the morphological structures of rodents and the apparent direction of the adaptations seen.

What is the postglacial climatic influence on faunistic communities and the composition of the recent mammal fauna?

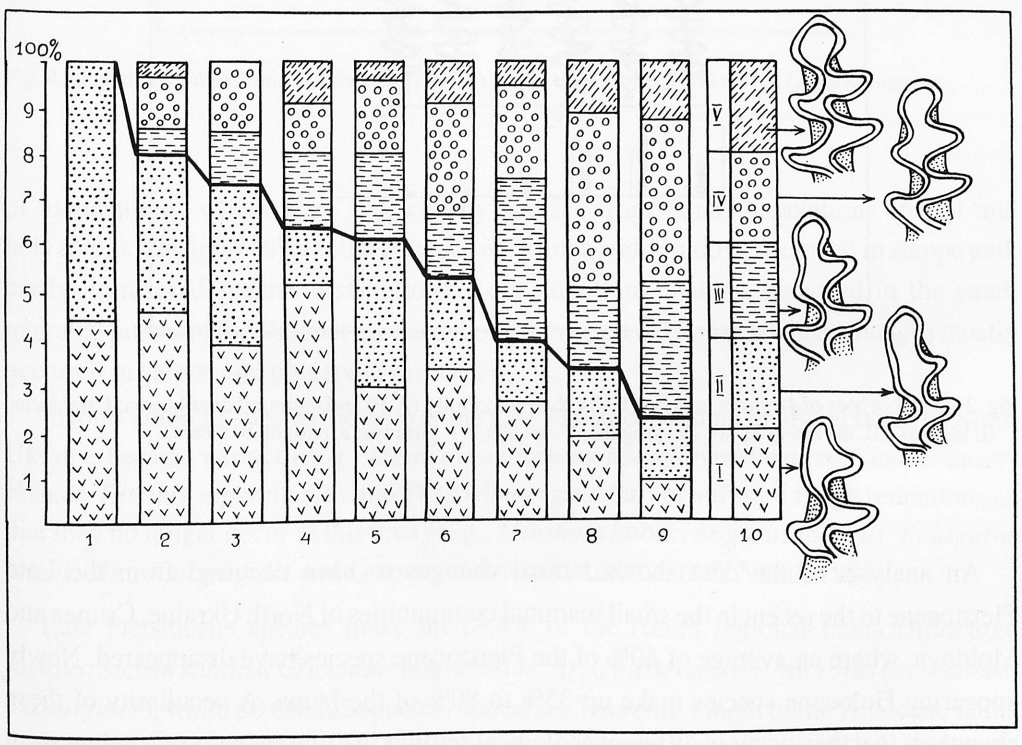

Fig. 2. Quantitative distribution of M_1 morphotypes (I-V) of *Microtus gregalis* at different Upper Pleistocene localities. 1. La Fage, 2. Pesko, 3. Dnieper alluvium, 4. Ightham, 5. Novgorod-Seversky, 6. Gencsapati, 7. Mezhyrich, 8. recent steppe, 9. recent tundra, 10. legend.

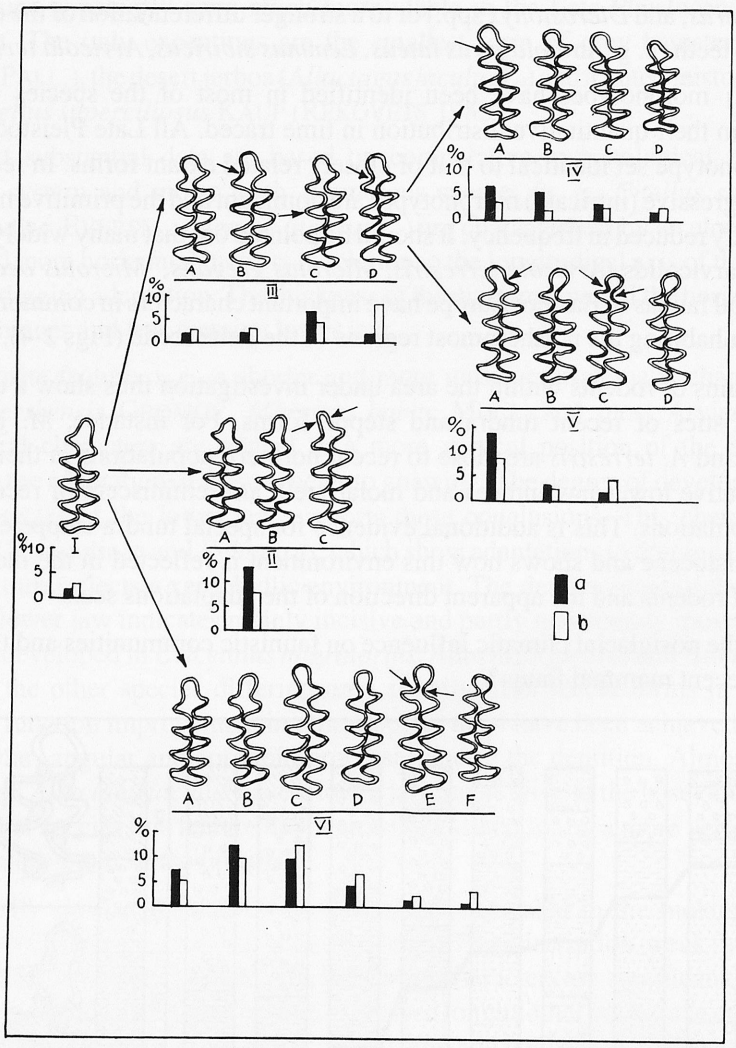

Fig. 3. Morphotypes of *Lagurus lagurus* (I-VI), their variability (A-F) and temporal distribution: I. transiens, II. lagurus, III. arvalo-gregalis, IV. gregalis, V. arvalis, VI. pitymys; a. extinct, b. recent.

An analysis of the data shows radical changes to have occurred from the Late Pleistocene to the recent in the small mammal communities of North Ukraine, Crimea and Moldova, where an average of 60% of the Pleistocene species have disappeared. Newly appearing Holocene species make up 35% to 80% of the fauna. A peculiarity of these changes is that they occur in different ecological settings in different parts of southwestern East Europe. For instance, in the northern part of Ukraine these faunistic transformations are due to partial (steppe species) or complete (arctic and polyzonal species) extinctions

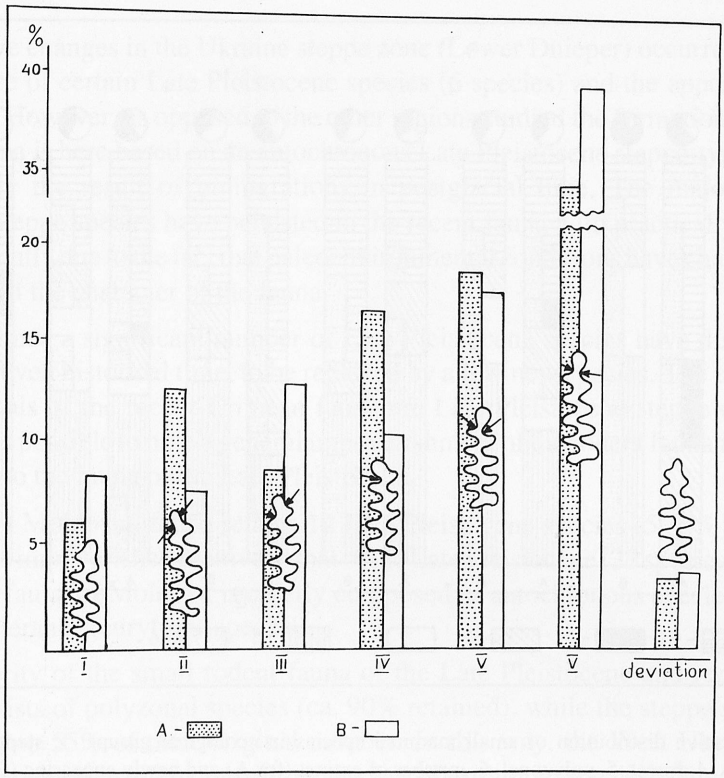

Fig. 4. Quantitative distribution of morphotypes I-VI in extinct (dotted) and recent *Lagurus lagurus*.

of associations, which were replaced by species from other associations (forest and polyzonal). The most substantial changes in Crimea and Moldova occurred in steppe and, partly, intrazonal species associations. Less important changes occurred in the small mammal faunas of the Dnieper area and the western part of Ukraine, where changes mostly occurred in steppe and polyzonal forms (Fig. 5).

In total, some 12 species (66.6%) of the Late Pleistocene small mammal fauna of North Ukraine became extinct (e. g., *Desmana moschata palaeobyrosthenica, Citellus severskensis, Citellus superciliosus* and *Dicrostonyx gulielmi*) or suffered range reductions so that they no longer occur in this area (e. g., *Marmota bobac, Lagurus lagurus, Eolagurus luteus, Microtus gregalis* and *Lemmus sibiricus*) (REKOVETS & NESIN 1993).

Late Pleistocene species make up 19.4% of the recent regional fauna (*Allactaga jaculus, Sicista subtilis, Cricetulus migratorius, Arvicola terrestris, Microtus oeconumus, Castor fiber*), while 80.6% (25 species) appeared. This enrichment of the Holocene fauna took place exclusively through forest species (genera *Clethrionomys, Glis, Dryomys, Eliomys, Muscardinus, Sicista*) and species with broad ecological tolerance, including representatives of Insectivora, Muridae and Arvicolidae.

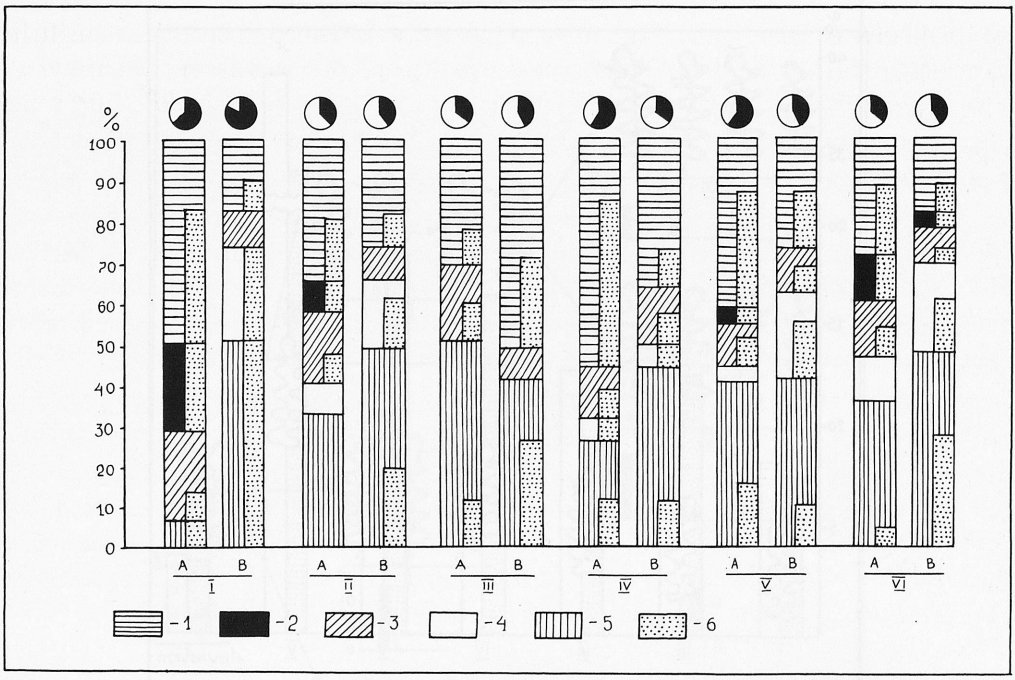

Fig. 5. Quantitative distribution of small mammal species in ecological groups: 1. steppe, 2. arctic, 3. hydrophilous, 4. forest, 5. polyzonal, 6. number of extinct (for A) and newly appearing (for B) species in the ecological groups. A. Late Pleistocene, B. Recent. The shaded sector in the figures represents the total number of extinct (for A) and newly appearing (for B) species. I. North Ukraine, II. Middle Dnieper, III. Lower Dnieper, IV. Crimea, V. Moldova, VI. West Ukraine.

These data show that the Late Pleistocene small mammal fauna of North Ukraine did not play a significant role as a source of species for the recent regional fauna, since a substantial proportion (50%) of the latter consists of polyzonal rather than steppe species. In other words, during the period from the Late Pleistocene to the recent the qualitative change in composition of the small mammal fauna took place as a result of a loss of the majority of steppe and all arctic species and an invasion of polyzonal species. The Late Pleistocene fauna consisted of 18 species and the recent one of 32 species, and the general enrichment took place through an invasion of forest and polyzonal species. These changes became possible as a response to general change to a warmer climate with newly developed meadow and forest habitats and subsequent contraction of open, steppe-like areas.

The recent small mammal fauna of the Middle Dnieper is formed from a core of autochtonous steppe and polyzonal species. These represent the main body of the recent fauna, indicating that the Late Pleistocene fauna has here not undergone any radical transformation. As a result of a general aridization and increase in mesophyllic areas a number of species became extinct and are replaced in the recent, richer fauna by forest and eurytopic species (TOPACHEVSKY 1961).

Qualitative changes in the Ukraine steppe zone (Lower Dnieper) occurred though the disappearance of certain Late Pleistocene species (6 species) and the appearance of 12 new species. However, as opposed to the other regions studied the formation of the small mammal fauna is here based on an autochtonous Late Pleistocene steppe-type fauna and is only partly the result of immigrations in postglacial time. The majority of Late Pleistocene steppe species have persisted in the recent fauna with practically no change. This is apparently due to the fact that paleoenvironmental conditions have changed so little as to not affect the character of the fauna.

In the Crimea a significant number of Late Pleistocene species have disappeared in Holocene or even historical time, to be replaced by a few new species. The core group of small mammals of the recent Crimean fauna are Late Pleistocene steppe or polyzonal forms and it is possible to note a general impoverishment of the rodent fauna in this region as compared to the fauna of the Late Pleistocene.

The recent Moldovan fauna retains 12 Late Pleistocene species (54.5%). This fauna (22 species) is impoverished relative to that of the Late Pleistocene (27 species). The recent small rodent fauna of Moldova is chiefly composed of autochtonous species with broad ecological tolerance (eurytopic species).

The majority of the small rodent fauna of the Late Pleistocene and recent of West Ukraine consists of polyzonal species (ca. 90% retained), while the steppe species have been reduced to 55% of their original number. In this way, the West Ukrainian small mammal fauna consists of an autochtonous core of eurytopic species. This recent fauna is enriched by inclusion of polyzonal, forest and some steppe species.

The small mammal fauna of North Ukraine, unlike that of other regions, is thus composed of a majority of immigrant species from remote regions and is not due to development of autochtonous faunal elements. The initial source of the recent southern Ukrainian small mammal fauna was the steppe association. The polyzonal association forms the core of the faunas in West Ukraine and Moldova, while the Middle Dnieper and Crimea faunas are formed on a core of steppe and polyzonal associations.

The total recent fauna has not been enriched or impoverished relative to that of the Late Pleistocene, as the number of species has remained almost constant. The ecological associations changed significantly, however, along with changes in landscape and climatic zones. The late Pleistocene fauna consisted of 52 species; 15 of these disappeared while 19 new species appeared.

To conclude, it should be pointed out that the climate and special tundra-steppe environment of the Late Pleistocene significantly affected the small mammal fauna, which is characterised by the following features:

1) A special qualitative and quantitative composition (tundra and steppe-zone species).
2) Specific ecological distributions and formation of associations.
3) Adaptations to the cold steppe environment, rough diet and denser soil.
4) Morphological changes, especially in the masticatory system and molars, displaying a combination of tundra (large size) and steppe (morphological adaptations) populations.

5) Major taxonomic differences between the Late Pleistocene and recent faunas lie at the subspecific level (*Desmana moschata palaeobyrosthenica, Citellus superciliosus palaeodesnensis, Allactaga jaculus severskensis, Cricetulus migratorius parvus, Eolagurus luteus antecedens, Microtus gregalis kriogenicus, Microtus oeconomus major*), with only a few distinct species (*Lepus tanaiticus, Ochotona spelaeus, Citellus severskensis, Citellus superciliosus, Dicrostonyx gulielmi*).

6) The temporal dynamics of the fauna take the form of changes in ecological communities, species extinctions, changes in taxon ranges and migrations.

7) The periglacial small mammal fauna was not an autochtonous source of ancestors to the recent fauna.

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