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# Evolution of small mammal communities from the south of Eastern Europe near the Plio-Pleistocene boundary

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Abstract. Small mammals of the reference sections from the south of Eastern Europe have been analyzed. An attempt is here made to investigate climatic influence on the development of small mammal communities. Faunas dating from 2.8 to 1.6 Ma were subdivided into six formal stages on the basis of the level of hypsodonty of several evolutionary lineages of arvicolids. Analysis of the structure of small mammal communities confirms the existence of a trend towards open landscapes in the region during the Late Pliocene and Early Pleistocene of southern East Europe.

Key words: Eastern Europe, Pliocene, Pleistocene, small mammals, Rodentia, faunal evolution, climate

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## I. INTRODUCTION

Systematic study of small mammal faunas of Eastern Europe began more than 30 years ago. During this time, extensive data have been collected from various stratigraphic levels of the Upper Pliocene and Lower Pleistocene. The most important contributions to our knowledge of small mammal paleontology of this area have been made by Ukrainian paleozoologists (SHEVCHENKO 1965; TOPACHEVSKY 1965; TOPACHEVSKY & SKORIK 1977; TOPACHEVSKY et al. 1979; TOPACHEVSKY & NESIN 1989, and others). A number of important studies treating isolated localities have been published by other workers (AGADJANIAN & KALUTZKAYA 1976; AGADJANIAN & GLUSHANKOVA 1986; ALEXANDROVA 1976, 1977; VANGENGEIM et al. 1990; TESAKOV 1993). Since they have been well studied, small mammal faunas enable us to consider in detail the dynamics of assemblage development near the Plio-Pleistocene boundary. It is also possible to evaluate the impact of climate on this development. The present study is based on original and literature data. The geographic position of localities analyzed or mentioned in the text is shown in Fig.1.

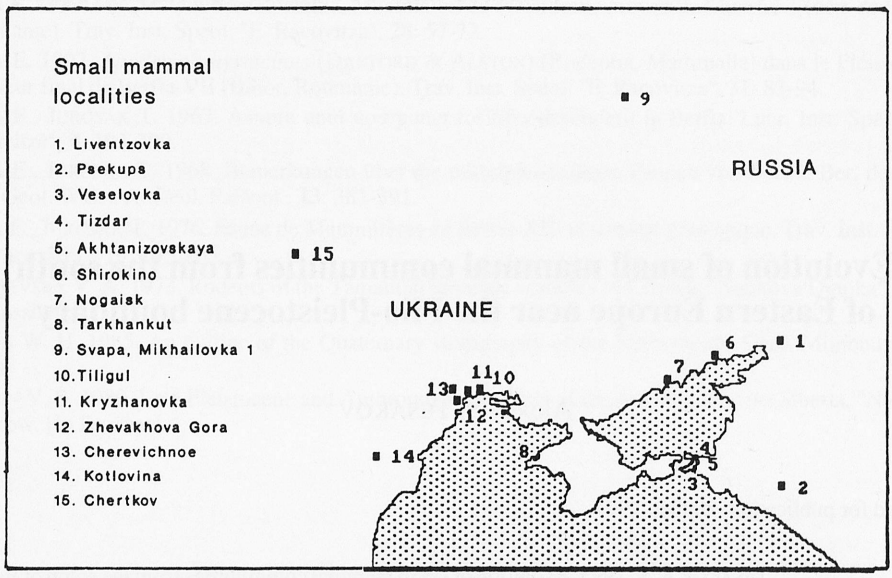


Fig. 1. Late Pliocene and Early Pleistocene small mammal localities of southern East Europe.

## II. BIOSTRATIGRAPHIC FRAMEWORK

Reliable chronological criteria are essential for any study of the development of faunal associations. For the faunas of the Khaprovian faunistic complex such a relative chronological framework is the progressing hypsodonty of the rooted voles, especially the genus *Borsodia*. In the Late Pliocene, many herbivorous rodents display intensive growth in molar height. The process reflects growing aridization and development of increasingly abrasive vegetation. The HH-index (RABEDER 1981), expressing the hypsodonty stage of a specific population by the height of the dentine tracts of the molars, is useful for the comparative analysis of different populations and for placing them in a temporal sequence. Using the criteria indicated, in combination with other geological and biostratigraphic data, I have subdivided micromammalian assemblages of the Late Pliocene and Early Pleistocene from the southern part of Eastern Europe into several developmental stages (TESAKOV 1993). I have tried to correlate these stages with the chronological and stratigraphic scales available (Fig. 2).

## III. COMPOSITION OF ARVICOLID FAUNAS

The main component of Late Pliocene – Early Pleistocene small mammal communities is arvicolids. It is therefore important to follow changes in the composition of this group. Fig. 3 illustrates the percentage of remains of different generic groups of voles throughout the time interval studied. The oldest known Villanyian arvicolid faunas of the study area are Shirokino, Veselovka, and Liventzovka 1 (TOPACHEVSKY et al. 1987; ALEXANDROVA

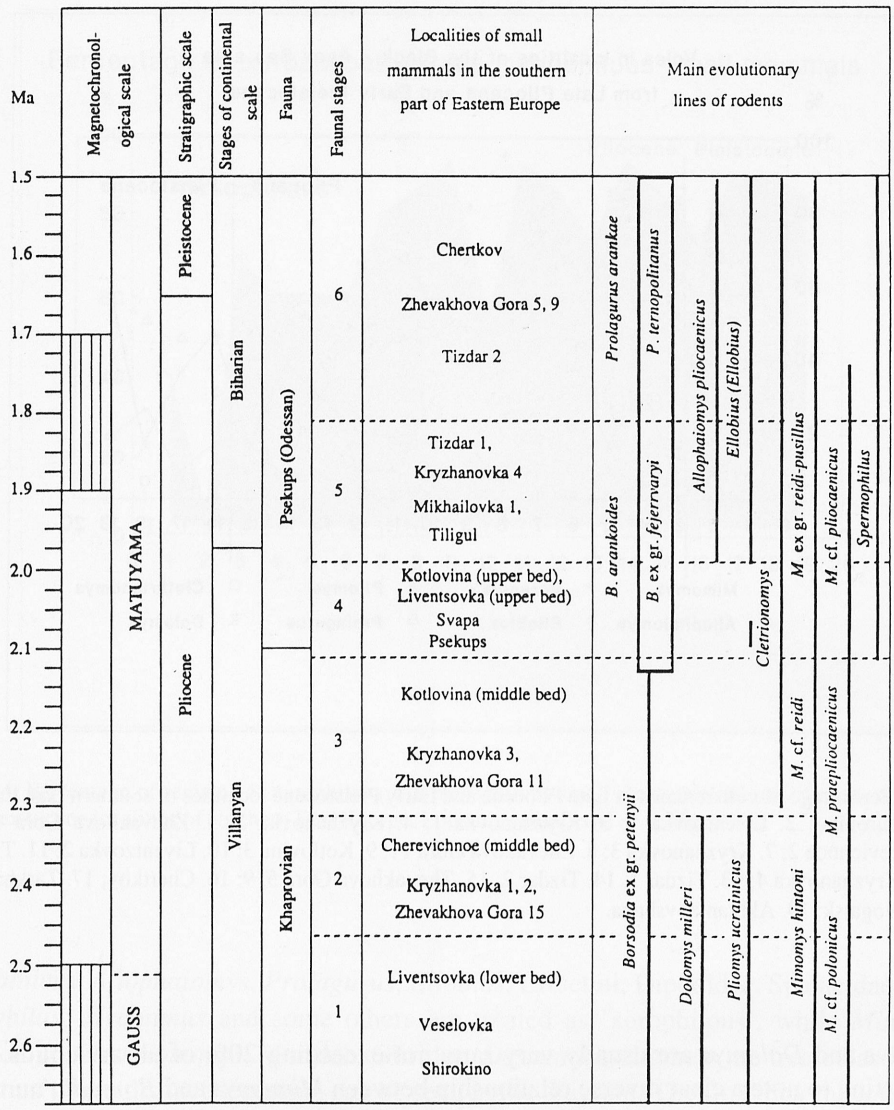


Fig. 2. Stratigraphic position of the small mammal localities.

1976; MURATOV & NEVESSKAYA 1986). These faunas were placed in the first formal stage (Fig. 2). They are characterized by a predominance of *Mimomys*, with *Borsodia* being a subdominant, and can be classified as bidominant *Mimomys-Borsodia* faunas. The predominance of *Mimomys* is interpreted as a possible indicator of relatively mesophilous conditions (TOPACHEVSKY et al. 1987).

The subsequent faunas, classified within the second, third, and fourth stages, remain bidominant, but with the *Borsodia* component prevailing and *Mimomys* as a subdominant.

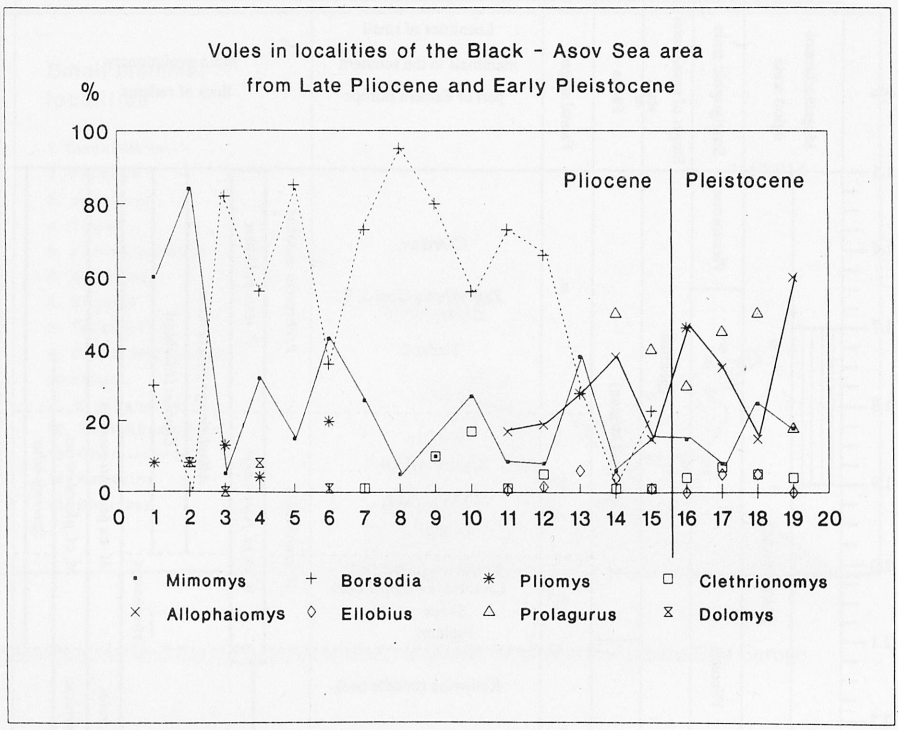


Fig. 3. Percentage of vole remains in Late Pliocene and Early Pleistocene localities of southern East Europe. 1. Shirokino; 2. Liventzovka 1; 3. Kryzhanovka 1; 4. Kryzhanovka 2; 5. Zhevakhova Gora 15; 6. Cherevichnoe 2; 7. Kryzhanovka 3; 8. Zhevakova Gora 11; 9. Kotlovina 3; 10. Liventzovka 2; 11. Tiligul; 12. Kryzhanovka 4; 13. Tizdar 1; 14. Tizdar 2; 15. Zhevakhova Gora 5, 9; 16. Chertkov; 17. Tarkhankut; 18. Nogaisk; 19. Akhtanizovskaya.

*Pliomys* and *Dolomys* are usually very rare, not exceeding 20% of all arvicolids. It is interesting to note a clear inverse relationship between *Mimomys* and *Borsodia* numbers in the Late Pliocene faunas. One of these genera usually accounts for 60% to 90% of vole remains. Faunas with these groups equally represented are rare.

The next major shift in vole associations coincides with the traditional boundary of the Khaprovian and Psekups faunistic complexes, and lies close to the Plio-Pleistocene boundary. The migrational arrival of the first rootless voles of the genus *Allophaiomys*, the phyletic transition of rooted *Borsodia* to rootless *Prolagurus*, with *Mimomys* remaining numerous, led to the appearance of the tridominant vole assemblages of the Early Pleistocene. *Clethrionomys* and *Ellobius* are less common.

## IV. MAIN TRENDS IN DIVERSITY AND ABUNDANCE

To elucidate the general trend in climatic development an analysis of xerophilous versus mesophilous small mammal remains was undertaken (Fig. 4). *Borsodia*, *Pliomys*

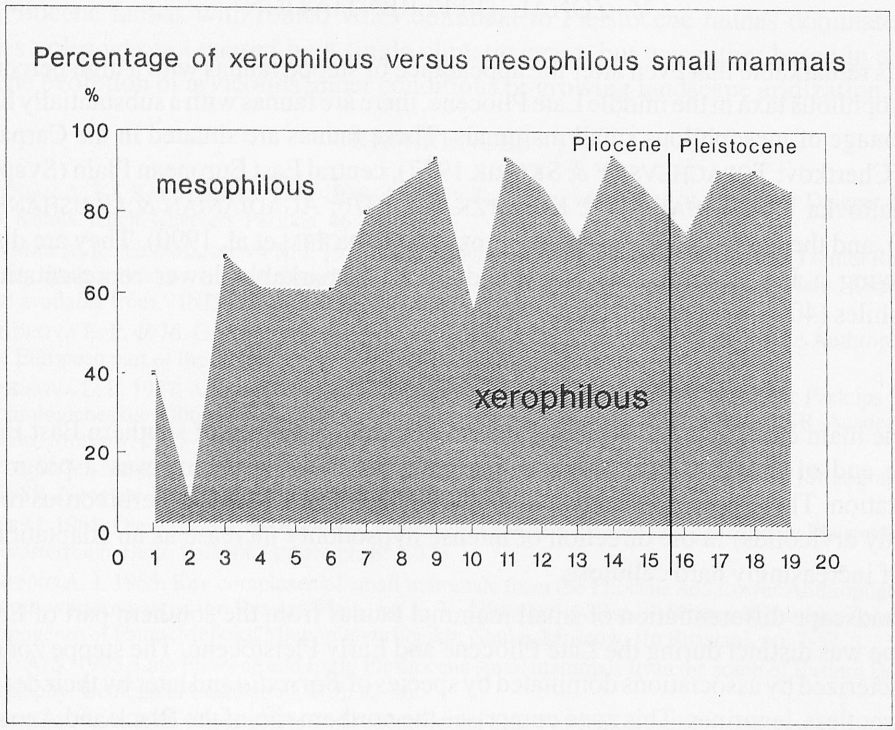


Fig. 4. Percentage of remains of xerophilous and mesophilous small mammals in Late Pliocene and Early Pleistocene localities of southern East Europe. Localities numbered as in Fig. 3.

*ukrainicus*, *Allophaiomys*, *Prolagurus*, *Ellobius*, Cricetini, Dipodidae, Spalacidae, *Spermophilus*, *Myomimus* and some others are treated as 'xerophilous', while *Mimomys*, *Dolomys*, *Clethrionomys*, Muridae, Gliridae, *Desmana* and others are treated as 'mesophilous'. Two distinct segments can be seen in the diagram. The first interval comprises faunas of the first and second formal stages. Xerophiles do not exceed 60-70% in these faunas. The second interval, comprising all remaining faunas, is distinct in that usually more than 80% of the taxa are xerophilous.

It is interesting to note that taxonomic diversity of xerophilous small mammals increases from approximately 60% of all species in the rooted vole assemblages to about 70% in *Allophaiomys* faunas, through a diversification of Dipodidae, appearance of ground squirrels and voles of the genus *Ellobius*, etc. Thus, the increase in remains of xerophilous species, the level of which is constantly high beginning with the third stage, took place earlier than the taxonomic diversification of this group. Most likely, the increase in abundance of xerophiles was the first response of the small mammal communities to the intensive desiccation of the climate and subsequent landscape aridization. Only later, in the course of ecological differentiation, did they diversify taxonomically.

## V. ZONAL DIFFERENTIATION

It is remarkable that even after the appearance of steppe faunas with a high percentage of xerophilous taxa in the middle Late Pliocene, there are faunas with a substantially higher percentage of mesophilous small mammals. These faunas are situated in the Carpathian area (Chertkov; TOPACHEVSKY & SKORIK 1977), central East European Plain (Svapa and Mikhailovka 1; AGADJANIAN & KALUTZKAYA 1976; AGADJANIAN & GLUSHANKOVA 1986), and the northern Caucasus (Psekups; VANGENGEIM et al. 1990). They are distinct in having a lower species diversity and in the remarkably lower representation of xerophiles (40-50% of specimens).

## VI. CONCLUSIONS

The main climatic trend affecting the small mammal faunas of southern East Europe at the end of the Late Pliocene and beginning of the Pleistocene was a progressive aridization. These processes caused and maintained the evolution of herbivorous rodents (mainly arvicolids) in the direction of intense hypsodonty increase as an adaptation to a diet of increasingly hard cellulose.

Landscape differentiation of small mammal faunas from the southern part of Eastern Europe was distinct during the Late Pliocene and Early Pleistocene. The steppe zone was characterized by associations dominated by species of *Borsodia* and later by their descendants, rootless lagurines. This zone comprises the northern rim of the Black and Azov Seas and the Taman' peninsula. Forest-steppe and forest conditions, characterized by assemblages dominated by *Mimomys* and *Clethrionomys*, existed in the northern Caucasus region and in the basins of the upper Dnieper and Dniester Rivers.

Taxonomic diversity of the steppe faunas increased from the Late Pliocene to the Early Pleistocene through the diversification of xerophilous elements. The number of mesophilous elements remains constant. The number of remains of smaller mammals of the open landscapes also increases with time. However, a relatively high abundance was already achieved in the middle Late Pliocene, earlier than the increase in taxonomic diversity of this ecological group. The rare forest faunas, known from central and southeastern parts of Eastern Europe, are generally characterized by a higher percentage of mesophilous forms and a lower taxonomic diversity than steppe faunas. This is most likely due to a more homogeneous natural environment with a lower mosaicity of habitats.

All associations studied are dominated by arvicolids. Three phases are present in the development of arvicolid faunas. The first is distinct in its relatively mesophilous *Mimomys-Borsodia* faunas (end of the first and beginning of the second half of the Late Pliocene). The second is characterized by xerophilous *Borsodia-Mimomys* faunas (the second half of the Late Pliocene). The third fauna is also characterized by xerophilous faunas with *Prolagurus*, *Allophaiomys*, and *Mimomys* dominant among voles (beginning of the Pleistocene). The most distinct boundary is the transition from bidominant rooted vole faunas of the Late Pliocene to tri- and polydominant faunas of largely rootless voles from the beginning of the Pleistocene. However, the commencement of a drastic restructuring of the small mammal fauna, associated with the appearance of rootless arvicolids, predates the Plio-Pleistocene boundary. Although geologically instantaneous, the change

from Pliocene faunas with rooted voles dominant to Pleistocene faunas dominated by rootless voles was not caused by a single climatic event, but was rather based in a long Pliocene evolution of arvicolids under conditions of growing landscape aridization.

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