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Taxonomic analysis of the formation of the Recent small mammal fauna in the southern part of eastern Europe

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Abstract. The historic development of Arvicolidae and other small mammals in the Pleistocene is reviewed. The temporal sequence of taxa and their migrations are discussed. The time of origin of the Recent species is investigated. Mammal associations of the Late Pleistocene are the basis for the formation of the Recent communities. The peculiar role of the eastern European periglacial faunas in this process is noted.

Key words: small mammals, taxonomic analysis, East Europe.

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I. INTRODUCTION

Problems regarding the development of the mammal fauna have up till now been studied mainly from the zoogeographical and ecological points of view, while less attention has been paid to taxonomic aspects. Taxonomic analysis has seldom been applied to the study of the history of the mammal fauna, especially at the species level. Such analysis is hindered by a number of problems, discrimination of the Recent species from their predecessors being the most complicated among them. This discrimination is almost impossible when direct evolutionary transformation has occurred.

Other problems are associated with the migration of taxa and ecological groups, sometimes even of whole faunas. Such migrations are conditioned by the transformation of landscapes and climate. The most significant transformations occurred in the Late Pleistocene, the time of the glacial maximum in the Palearctic region. The mammal fauna of this period can be considered as the foundation of the Recent fauna. The identification of centers of origin and dispersal routes of the taxa is important in this connection.

A third group of problems is associated with incompleteness of the fossil record and with our insufficient knowledge of Recent faunas, especially in so far as zoogeographical aspects are concerned. The latter seem to be very important, because problems of the formation of the mammal fauna are associated with landscape and climatic zonation.

III. THE FORMATION OF RECENT SMALL MAMMAL FAUNA IN EASTERN EUROPE

Reliable records of Insectivora are known from the southern part of eastern Europe since the Early Pleistocene (Villanyian and Biharian faunas). It is not possible to determine the time of

appearance of the Recent species more precisely. However, there are sufficient grounds for supposition that the Recent species of *Erinaceus, Hemiechinus, Talpa, Sorex, Suncus, Crocidura,* and *Neomys* have existed in the region since the Late Pleistocene.

The genus *Desmana* was represented in the Pleistocene by at least four species: *D. meridionalis* TOPACHEVSKY & PASHKOV, 1990, *D. nogaica* TOPACHEVSKY & PASHKOV, 1990, *D. gureevi* TOPACHEVSKY & PASHKOV, 1990, and *D. palaeoborysthenica* TOPACHEVSKY, 1959. The recent species *D. moschata* L., 1758 appeared at the end of this period (TOPACHEVSKY & PASHKOV 1990).

Species of Lagomorpha are better known. According to TOPACHEVSKY, the genus *Lepus* appeared at the end of the Eopleistocene, represented by a species not yet identified but closely related to *L. europaeus* PALLAS, 1778. The species *L. tanaiticus* GUREEV, 1964 (now extinct) inhabited the periglacial zone in the Late Pleistocene. At that time *L. europaeus* was present in southern Europe. The Recent species *L. timidus* L.,1758 and *L. europaeus* probably appeared in the course of the formation of the middle Biharian fauna.

The genus *Ochotona* appeared in the early Eopleistocene and was then represented by forms related to *O. polonica* SYCH, 1980 and *O. lazari* KRETZOI, 1941. The latter is the most probable ancestor of *O. pusilla* PALLAS, 1768, which is known from the faunas of the late Biharian. In the late Pleistocene, the extinct species *O. spelaeus* OWEN, 1846 was present in Europe. This species was a component of the periglacial faunas (REKOVETS 1990).

The high species diversity of Marmotinae peculiar to the Miocene and Pliocene decreased in the Quaternary, when the genera *Spermophilus* and *Marmota* were present. According to GROMOV, the origin of the Recent species of the "*suslicus-citellus*" group (it is not possible to distinguish them as fossils) is subsequent to the Dnieper glaciation (the level of the Swanscombe and Taubach faunas). *S. citelloides* KORMOS, 1916 and, probably, *S. primigenius* KORMOS, 1934 are the ancestral species. The extinct species *S. severskensis* GROMOV, 1965 was surely a component specific to the periglacial faunas. *S. nogaici* TOPACHEVSKY, 1957 (Early Pleistocene) belongs to the subgenus *Urocitellus*. At the beginning of the Late Pleistocene, *S. pygmaeus* PALLAS, 1778 appeared in the southern part of eastern Europe, being represented by the subspecies *S. p. gromovi* REKOVETS, 1979, which has clear phylogenetic affinities with *S. primigenius*. The latter is the most probable ancestor of *S. p. brauneri* MARTINO, 1916. *S. suslicus abbreviatus* is also recorded in the Late Pleistocene of the region. It is probably ancestral to *S. s. suslicus* GUELDENSTAEDT, 1770.

Remains of the subgenus *Clobotis* are known from the Early Pleistocene, although the species has not yet been determined. In the Late Pleistocene of Europe, *S. superciliosus* KAUP, 1839 is recorded. It is represented by *S. s. palaeodesnensis* REKOVETS, 1979 in the eastern part of the area (periglacial faunas) and by *S. s. fulvoides* GROMOV, 1961 in the southern part of Ukraine. Their phylogenetic affinities with Recent species of the subgenus are not definitely determined. The group probably has an Asiatic origin.

Remains of *Marmota* are extremely rare. This genus probably migrated from the east and is represented by the Recent form *M. bobac* MULLER, 1774.

Rare remains of *Hystrix* have been found in Pliocene and Early Pleistocene faunas in the Odessa catacombs and in Tarkhankut (Crimea). This genus also occurs in western Europe and the Caucasus.

The genus *Castor* appeared in the Early Pleistocene in the form of the species *C. tamanensis* VERESHCHAGIN, 1951. *C. fiber* L., 1758 is also present in the Pleistocene. The phylogenetic relationships between these species are not clear.

The history of the Gliridae in the southern part of eastern Europe remains poorly known because of the generally inadequate material. A few records of *Glis* (beginning of the Early Pleistocene) and *Myomimus* (Early Pleistocene) are known. These groups dominate in sites on the Russian plain and in western Europe and may shed new light on the history of the Recent species.

The Recent species *Sicista betulina* PALLAS, 1778 and *S. subtilis* PALLAS, 1773 are known from the Early Pleistocene. *S. vinogradovi* TOPACHEVSKY, 1965 and *S. praeloriger* KORMOS, 1930 are their most probable ancestors. Remains of *Sicista* are absent in the periglacial faunas, except at the Mezhirich site.

Allactaga major KERR, 1792 appeared in the Early Pleistocene. *A. ucrainica* GROMOV & SCHEVTSCHENKO, 1961 is the most probable ancestor of this species. In the Late Pleistocene, *A. gromovi* TERZEA, 1974 and *A. major severskensis* REKOVETS, 1973 were present. These species are now both extinct.

The genus *Alactagulus* is known from the end of the Early Pleistocene. It is rather rare in Pleistocene deposits. These remains have been identified as *A.* cf. *acontion*. Revision of this group is necessary, because these remains are currently referred to the genus *Pygerethmus*. *Pliopygerethmus brachidens* was abundant in the studied region at the beginning of the Early Pleistocene and is the ancestor of *Pygerethmus*. Remains of *Plioscirtopoda stepanovi* TOPACHEVSKY & SKORIK, 1971 have also been recorded. This genus is the direct ancestor of the recent *Scirtopoda*. The time of origin of *S. telum* LICHTENSTEIN, 1823 is not known precisely. Remains of this species are rather abundant in the Late Pleistocene of Crimea (GROMOV 1961).

The evolution of the extant Spalacidae took place exclusively in the northeastern Paratethys region. The Recent species appeared in the Early Pleistocene. *S. minor* TOPACHEVSKY, 1959 is the probable ancestor of *S. graecus* NEHRING, 1898. In the Early Pleistocene, a form related to *S. arenarius* RESHETNIK, 1939 appeared. *S. polonicus* MÉHELY, 1909 and *S. microphtalmus* GÜLDENSTAEDT, 1770 appeared at the end of the Middle Pleistocene. The Pleistocene range of *Nannospalax leucodon* NORMANN, 1840 was in a continuous state of change. Today, this species occurs in the studied region as a secondary immigrant. Species of the genus *Spalax* are absent from the periglacial faunas.

The family Muridae provides the most complex problems. The Recent taxa are not sufficiently studied and many species groups are currently over-split. Extinct groups are practically unstudied, despite abundant remains from Miocene, Pliocene and Pleistocene deposits. Most of them are labelled *Apodemus* sp. The group "*jeanteti-dominans*" is the most probable ancestral form of *Sylvaemus silvaticus* L., 1758 and is also similar to *Apodemus flavicollis* MELCHIOR, 1854.

The genus *Mus* is known from the Middle Pleistocene. The species distinctness of the remains is not confirmed. Remains of the genus *Micromys* are known from the Pliocene, but the origin of the Recent species has not been determined.

The Cricetidae, as well as the Muridae, contribute to the background of the Miocene and Pliocene faunas, when they are represented by other groups than at present. Some *Cricetus* may be phylogenetically related to *Allocricetus* (TOPACHEVSKY & SKORIK 1992). The latter were widely represented in Europe in the Pliocene and Early Pleistocene. The oldest remains of *Cricetus* are from the Eopleistocene (Taman faunas) when the genus was represented by a species related to *C. nannus* SCHAUB, 1930. This species was later replaced by *C. praeglacialis* SCHAUB, 1930, which was the direct ancestor of *C. cricetus* L., 1758. The first record of Cricetulus is from the beginning of the Early Pleistocene, while the origin of the Recent *C. migratorius* PALLAS, 1785 is unclear. The smaller subspecies *C. m. parvus* REKOVETS, 1985 existed in the periglacial faunas. It was probably an ancestor of the Recent *C. m. bellicosus* CHARLEMAGNE, 1916 (REKOVETS 1985).

The Arvicolidae is the best studied small mammal group. The genus *Ellobius* appeared in the Early Pleistocene (it was probably present in the early Biharian fauna). Its phylogeny is well studied. *E. melitopoliensis* TOPACHEVSKY, 1973 existed at the end of the Early Pleistocene and might be an ancestral form of the Recent *E. talpinus*. The latter was represented in the Early Pleistocene by *E. t. tschernojaricus* ALEXANDROVA, 1976 and in the Late Pleistocene by *E. t.*

palaeoucrainicus REKOVETS, 1985, which is the probable ancestral subspecies of the Recent *E. t. tanaiticus* ZUBKO, 1940.

The evolution of the subgenus *Afganomys* took place further east than the present study region (TOPACHEVSKY & REKOVETS 1982).

The genus *Clethrionomys* appeared in the Late Pliocene with the species *C. sokolovi* TOPACHEVSKY, 1965. The latter transformed into the Recent *C. glareolus* SCHREBER, 1780 in the Late Pleistocene.

The genus *Lagurus* appeared at end of the Early or the beginning of the Middle Pleistocene with the species *L. transiens* JÁNOSSY, 1962, which later evolved into *L. lagurus* PALLAS, 1773. In the Pleistocene, *Lagurus* was represented by *L. l. pleistocenicus* ALEXANDROVA, 1965 and *L. l. major* ZAZHIGIN & REKOVETS, 1985. The latter subspecies was a component of the periglacial faunas. The phylogeny of the genus is well documented (REKOVETS 1994).

The genus *Eolagurus* appeared at the end of the Early Pleistocene (the beginning of the late Biharian) as a result of migration from the east. A second migration of *Eolagurus*, represented by *E. luteus* EVERSMANN, 1840, to eastern Europe took place at the beginning of the Middle Pleistocene. It is interesting that this species was a typical representative of periglacial faunas (the subspecies *E. l. antecedens* REKOVETS, 1978, now extinct).

The appearance of *Arvicola* in the southern part of eastern Europe at the beginning of the Middle Pleistocene was also the result of migration. Transformation of *Mimomys* to *Arvicola* took place in the Early Pleistocene in the central parts of Europe and western Siberia. This transformation took the following path: *A. cantiana* HINTON, 1910 – *A. chosaricus* ALEXANDROVA, 1976 – *A. terrestris* L., 1758. The Recent species appeared at the end of the Middle Pleistocene. Its evolution was characterized by some changes in the occlusal surface of the teeth (MARKOVA 1981).

The genus *Microtus* is represented in the studied region by the subgeneric groups *Stenocranius*, *Terricola*, *Pallasiinus*, *Agricola*, and *Microtus*. The ancestral group is the genus *Allophaiomys*. The transformation from *Allophaiomys* to *Microtus* took place at the end of the Early Pleistocene. This issue was the subject of a detailed discussion at the International Paleotheriological Symposium in honor of Prof. K. KOWALSKI (Kraków, May 1994). It has not been definitely resolved and requires further discussion.

The subgenus *Stenocranius* definitely originated at the beginning of the late Biharian from the "*hintoni-gregaloides* group". However, the transformation of *M. gregaloides* HINTON, 1923 into *M. gregalis* PALLAS, 1779 did not take place in the southern part of eastern Europe, but further north. In the south the Recent species appeared several times as a result of migrations. In the Würm faunas it was here represented by the extinct subspecies *S. g. kriogenicus* REKOVETS, 1978 (REKOVETS 1985, 1994).

Representatives of the genus *Terricola* appeared at the beginning of the Middle Pleistocene, simultaneously with the subgenus *Microtus*. The phylogenetic affinity between *M.* (*Terricola*) *arvalidens* KRETZOI, 1958 and the recent *M. subterraneus* SALYS-LONGSCHAMPS, 1836 is not sufficiently established. The appearance of *M.* (*Terricola*) *subterraneus* in eastern Europe is not definitely documented. Remains of the species are recorded at the end of the Middle Pleistocene in the northern parts of Europe.

The Early Pleistocene species *M. nivaloides* F. MAJOR, 1902 was at that time evolving into *M. arvalis* PALLAS, 1779. *M. quentheri* DANFORD & ALSTON, 1880 probably had a similar origin. *Terricola* and *M. arvalis* were not represented in the periglacial faunas.

The subgenus *Pallasiinus* appeared at the end of the Early Pleistocene, represented by *M. protoeconomus* REKOVETS, 1994, and then evolved into *M. nivalinus* HINTON, 1923. The extinct subspecies *M. oeconomus major* REKOVETS, 1978 was present in the periglacial faunas.

Middle Pleistocene records of *Agricola* are rare. The taxonomy of this subgenus has not yet been studied. The fossil species is probably related to the recent *M. agrestis* L., 1761. It was absent from the perigracial faunas.

III. CONCLUSIONS

The following conclusions can be reached from the review presented above.

In the Early Pleistocene of the southern part of eastern Europe, the formation of the Recent fauna involved taxa at the generic and, partly, the specific level. It was a crucial period in the evolution of the mammal fauna. The Recent species were formed at the end of the Early to the Middle Pleistocene (Tiraspol and Singil faunas or Templomyhegy-Mauer phase). In the Late Pleistocene, some peculiar subspecific taxa were represented (especially among Arvicolidae); only a few recent species evolved at that time (*Dicrostonyx torquatus* PALLAS, 1779).

The occurrence of migrating taxa (e. g., *Eolagurus*, *Arvicola*, some Spalacidae) was peculiar to the process of formation of the Recent fauna. Such periodic migrations were conditioned by the cold periods of the Pleistocene.

Periglacial (mixed or tundra-steppe) faunas are characteristic of the central and parts of the southern regions of eastern Europe. These faunas were not ancestral to the recent micromammal faunas of the studied region. Some taxa became extinct (e. g., *Ochotona spelaeus*, *Lepus tanaiticus*, *Spermophilus severskensis*, *S. superciliosus*). The distribution of some others (e. g., *Lagurus*, *Eolagurus*, *Marmota*, *Allactaga*, *Cricetulus*) was reduced in areal extent to the south and east. It is clear that the recent micromammal fauna of the central and parts of the southern region of eastern Europe included species that migrated from the southeast. Therefore, this fauna is of allochtonous origin. At the the same time, the recent micromammal fauna of the southern part of eastern Europe was formed on the foundation of the Late Pleistocene fauna and is therefore autochtonous.

The recent micromammal fauna was formed by temporal transformation of the taxa (e. g., Lagurini, *Allophaiomys*, *Microtus*), as well as by migration. The Pliocene fauna was a basis for the fauna formation in the Early Pleistocene at the generic level. The development of the Recent species took place in the Early Pleistocene.

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