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Evolutionary lineage of *Spermophilus superciliosus* - *S. fulvus* (Rodentia, Sciuridae) in the quaternary of the Dnieper area: An ability of a biostratigraphical implication



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ABSTRACT

An extinct ground squirrel species *Spermophilus superciliosus* was studied with respect to its occlusal morphology, patterns of bunodonty, size and proportions of M³ to clarify spatial and temporal aspects of its interspecific variation and abilities of a biostratigraphical implication of its fossils. This species is well-recognizible and shares with *S. fulvus* a specific (fulvoid) pattern of the occlusal morphology. At the same time, *S. superciliosus* demonstrates significant intraspecific variation, which, in general, supports the recognition of previously described subspecies (*S. superciliosus palaeodesnensis* and *S. superciliosus fulvoides*). Distinctive features of *S. superciliosus palaeodesnensis* can be explained by adaptation to feeding on tough, high-abrasive food (grass). This subspecies turns out to be a morphologically well-recognizable and ecologically peculiar representative of the Late Pleistocene fauna of the Northern Dnieper Left Bank area. Previously established morphological differentiation of *S. superciliosus fulvoides* also finds confirmation in the present study; however, morphological, palaeogeographical and stratigraphical limits of *S. s. fulvoides* should be clarified. "*S. s. fulvoides*" may contain three different subspecies to describe.

Despite of the significant variability and a long time of existence, definite trends in *S. superciliosus* evolution are absent, so, neither occurrence frequencies of the studied occlusal characters, nor the patterns of bunodonty can be used as biostratigraphical indices. Instead, subspecies of *S. superciliosus* turn out to be well-recognizable. These subspecies will be of some biostratigraphical potential, especially after obtaining more detailed picture of intraspecific variation.

Spatial distribution of ground squirrel taxa (both species and subspecies) is much more affected by geographical barriers, than those of most of the rodents. It makes the Pleistocene ground squirrels an eminently suitable subject for palaeogeographical reconstructions.

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1. Introduction

Spermophilus superciliosus, a large extinct ground squirrel, is known to have appeared in the late Middle Pleistocene of Poland (Socha, 2014), Crimea (Gromov et al., 1965), the Dnieper area (Popova, 2008a) and the Middle Transurals (Pogodina, 2006). This species was an ancestor of *S. fulvus* (Gromov et al, 1965), which is one of the few convincing phylogenetic events for fossil *Spermophilus*. *Spermophilus superciliosus* is also an exception among the other ground squirrels in the considered area from the standpoint of specific diagnostics. Middle and Late Pleistocene ground squirrels are commonly cited in faunal lists as *Spermophilus* sp.; this prudence is

all the more reasonable because *S. suslicus* s. lato was recently subdivided into two species on the basis of their karyotypes (*Spermophilus odessanus*, with 36 chromosomes, and *S. suslicus* s. stricto, with 34 chromosomes) (Zagorodniuk and Fedorchenko, 1995). Although multivariate analysis has shown that *S. suslicus* and *S. odessanus* distinctly differ in their cranial characteristics (Filipchuk et al., 2005), specific identification of their fossil remains still presents an insoluble problem because the usual fragmentariness of the fossil material prevents application of the discriminatory models mentioned. Identification of other species now inhabiting the Ukrainian area (*S. pygmaeus* and *S. citellus*) has not been much more successful (see a review by Krokhmal and Rekovets (2010); devoted to the Pleistocene small mammal localities of Ukraine). This situation implies the necessity of a new approach to the diagnostics of ground squirrel remains (Popova, 2008b). *S. superciliosus* is a

suitable taxon to test whether this approach really works. This species has always been found to be well-identified, because of its larger size, and the results obtained by the new method of specific identification are easily cross-validated.

S. superciliosus was larger by a factor of ~1.3, in accordance with Hutchinson's rule, to avoid competition (Hutchinson, 1959) with the previously mentioned sympatric ground squirrels (*S. pygmaeus*, *S. suslicus* and *S. odessanus*). This is evidence of a significant resemblance between the species' niches.

The first appearance of *S. superciliosus* in the second half of the Saalian glaciation suggests a climatic influence on the speciation event. Body size increase must be a winning strategy under such conditions, and this case is parallel to recent northern *S. undulatus* and *S. parry*, which are large. The relative primitiveness of the tooth morphology was emphasized by Gromov et al. (1965) for *S. superciliosus* and its descendant, *S. fulvus*. This implies that the representatives of the lineage were generalists in their feeding strategy. Broadening of their trophic niche gave them the resistance to severe, and especially important, unstable climates. When *S. superciliosus* coexisted with other *Spermophilus* species, it dominated during cool epochs and became relatively rare during warming events (Black and Kowalsky, 1974).

Another argument in favour of the periglacial adaptations of S. superciliosus is its presence on both sides of the Dnieper. This river seems to be an insurmountable barrier for recent Spermophilus species in the Dnieper area. Two of these species (S. pygmaeus and S. suslicus) live on the left bank, and one species inhabits the right bank (S. odessanus). This situation, with the single exception described (Rekovets, 1979, 1985, Popova, 2015), has been inherited from the Late Pleistocene. Thus, the range of S. superciliosus is unusual and requires an explanation. Pidoplichko (1931), who found the first remains of the species on the Dnieper right bank, identified them as S. rufescens (a synonym of S. major) because S. superciliosus was unknown in the Ukrainian Pleistocene at that time. These findings were explained by Riznitchenko's Dnieper inrush (Riznichenko, 1932) at the end of the Late Pleistocene: the fossils of the "russet ground squirrel" (recently eastern, trans-Volga species) on the right bank of the Dnieper should be understood as being part of the left bank population that was isolated on the Dnieper right bank as a result of the river channel change (Pidoplichko, 1932). However, the number of S. superciliosus localities on the right bank later increased; meanwhile I. G. Pidoplichko formed his specific anti-glacial views mostly based on palaeofaunistic and palaeozoogeographic data. In this context, the presence of S. superciliosus on both sides of the Dnieper became an important piece of evidence against the Quaternary glaciations for Pidoplichko (1951): S. superciliosus had to get around the Dnieper upper reaches from the north, which he consequently supposed were ice-free areas. In any case, the range of S. superciliosus expanded to the north further than that of any other European ground squirrels.

A vast natural range of *S. superciliosus* (from Crimea to the Middle Urals and from southern England and Denmark to the Right Bank of the Volga) does not conflict with the idea of generally periglacial adaptations for the species. To the contrary, this is in good accordance with the palaeozoogeography of the tundrosteppe hyperzone, where such extensive species ranges were common.

The data create a strong impression that *S. superciliosus* was a typical tundro-steppe species that was closely connected to the respective ecosystems and became extinct along with them. In fact, remains of the species have been found in the Crimea Mesolithic (Gromov et al., 1965), in the early Holocene of Germany (Heinrich, 1969), and in the Late Holocene of the Dnieper area (Popova, 2015). In Ukraine, this large desert-steppe ground

squirrel was mentioned as living even during the 1920s (Pidoplichko, 1951).

Thus, we have a time span of approximately 0.2 MY BP in which to trace S. superciliosus evolution. Great climatic changes and significant multidirectional ecosystem reorganizations were taking place during that time. The species is easily identified, and its ecological preferences seem quite clear; moreover, a living descendant of S. superciliosus (S. fulvus) is available. S. fulvus seems to be ecologically very similar to S. superciliosus, and another recent close relative (S. major) is distinctly different. Against the blank background of other fossil ground squirrels (a poorly explored group, which retained archaic dental features throughout its evolution) (Agajanian, 2006), S. superciliosus appears to be the most promising species for elucidating the scale and direction of interspecific variations of the dental system, for the study of the regional or environmental influences associated with this variability and for testing new approaches to the species identification and biostratigraphic implications. These are the aims of this study.

2. Material and methods

Khalepia (the *S. superciliosus* sample size is 12 specimens, mostly isolated lower cheek teeth, and only two upper molars, M¹ (very worn) and M³). The material was obtained from the alluvium of the so-called periglacial terrace (Hnidyn series in later works) of the Skvirka River (Fig. 1). The alluvium is exposed in the Dnieper cliff, near the Khalepia village in the Kyiv region. The section and adjacent area were studied and described by Matoshko (1999). The alluvium of the Hnidyn series is believed to be formed as a result of the melting of the Dnieper Ice Tongue between 240 and 140 ka (Matoshko et al., 2004). The fauna from this locality was collected by Popova (2004b) and Krokhmal et al. (2009)

Novgorod-Siverskyi site (19 isolated cheek teeth). This is part of the type series of *S. superciliosus palaeodesnensis* (Rekovets, 1979). The locality is situated in the northeastern suburb of the town of Novgorod-Siverskyi, Tchernigiv region (Fig. 1). It is an abandoned building-stone quarry. The bones came mostly from fillings in karst niches, where they had been deposited as the prey of owls. The geological setting and taphonomy of the locality are characterized by Gromov et al. (1965) and Rekovets (1985). The latter work also includes a full list of the fauna and age estimation (Late Weischelian).

Mezhyrich palaeolithic site (thirteen isolated teeth and one upper tooth row without M³). The site is situated in Mezhyritch village, Tcherkassky region, above the confluence of the Ros' and Rosava rivers (Fig. 1). A fan of a large gully formed an elevated surface above the level of the second terrace, creating a suitable plot for human settlement. Small mammal fauna were collected from the occupation layer, which has a radiocarbon date of 14.5 ka BP (Sinitsyn et al., 1997). The latest summary of small mammal data from the site is presented in Rekovets et al. (2014).

Kostianiets. A skull and a jaw of two different individuals were obtained from the Holocene krotovina level in the slope-wash silts and sandy silts crowning the Quaternary sequence in the southern wall of the Kostianets sand pit (a northern suburb of the town of Kaniv, Cherkassy region. The geological setting and taphonomy of the locality are characterized in Popova (2015)).

In addition, materials collected by I. Pidoplichko from the krotovinas of Yerki (Cherkassy region) and Borodaevka (Dniepropetrovsk region) (two lower jaws with an incomplete tooth row) were available. Pidoplichko (1932) considered them to be of Holocene age. In this paper, these remains have been included in the Kostianets sample, to which they are close in location, age and

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