The Carpathians and Lower Danube as a barrier for the dispersal of steppe rodents in the Pleistocene and Holocene: Ground squirrels as a case study

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1 Introduction

The role of Carpathians as a driver of biodiversity is especially high for the steppe fauna, on the first place, for hibernating small mammals. For mole-rats, jerboas, ground squirrels, with their limited abilities to crossing geographical barriers, the Carpathians together with the lower flow of the Danube and Prut rivers and the forest zone north to the mountains are a part of an "Iron Curtain", effectively dividing the steppe ecosystems of the Eastern and the Western Europe and thus increasing their spatial heterogeneity.
Pleistocene environment provided more opportunities of faunal exchange compared to the present day, due to the strongly increased area of open landscapes. For ground squirrels, *Spermophilus*, however, the Carpathian-Low Danube barrier was a formidable challenge even during the Pleistocene. Starting from their first appearance in Europe 2.5 MY ago, ground squirrels of the Eastern and Western Europe always belong to different species. The only exception consists of larger ground squirrels of the subgenus Colobotis, which was represented by the only species *S.* (C.) *superciliosus* throughout their huge range, but by several well-defined subspecies. Here we will not consider this subgenus.

2 Carpathian-Low Danube barrier: the way around

Pleistocene ground squirrel species of Subcarpathia (Ukraine, Moldova) are closely related to that of the area north to the Carpathians. Namely, there were closely related sister-species pairs: *S. praecox* and *S. polonicus* in the Early Pleistocene (Popova et al., 2021); *S. odessanus* (=36-chromosome *S. suslicus* west to the Dnipro (Zagorodniuk et al., 2008)) and extinct *S. citelloides* in the Middle and Late Pleistocene (Kowalski, 2001). This suggests the Middle and Upper Dniester valley to have provided a steppe corridor between the Northern Black Sea area and uplands of southern Poland, where the landscape allowed open habitats to exist during cold epochs of the Pleistocene (Popova et al., 2021). On the other hand, the species level of the differentiation between Central European and Subcarpathian ground squirrels is evidence that this corridor must have been opened only for short time, under certain conditions. For the last time such event took place when the Lublin isolate of *S. odessanus* appeared. The event must be very recent because there are no Holocene findings of *S. odessanus* in Poland (Kowalski, 2001) and must have been a result of agricultural changes of landscape, which caused both the increase of suitable open areas and food resources for ground squirrels.

3 Carpathian-Low Danube barrier: the possibility of the breakthrough?

Circumstances of the occurrence of the European ground squirrel *S. citellus* east from the Carpathians, on the first sight, look similar to that for Polish *S. odessanus*: there were no evidence of *S. citellus* in any of the Holocene or Pleistocene localities (Krokhmal and Rekovets, 2010); its appearance is believed to be very recent (Gromov and Erbaeva, 1995).
Primarily (during the Pleistocene), *S. citellus*, an ancient, to some extent archaic and rather termophilous species, was restricted to southern Europe. Early Holocene warming allowed the spread of *S. citellus* northward, where this species replaced *S. citelloides* in the southern part of the range of this latter, while the northern part of the *S. citelloides* range turned out to be occupied by forests, unsuitable for ground squirrels. As a result, *S. citelloides* went extinct and *S. citellus* stayed the only ground squirrels of Western Europe. Later on (c. 5 ky) (Ramos-Lara et al., 2014), the agricultural transformation of landscape caused the expansion of the species further to the north, as far as Germany and Southern Poland. However, *S. citellus* had been unable to cross the Carpathian-Low Danube barrier for a long time. What is important, that, in contrast to *S. odessanus*, *S. citellus* definitely did not use the Dniester corridor. The recent Polish population of *S. citellus* (now extinct) were restricted to Silesia and a large distance separated it from Subcarpathia.
Thus, the appearance of *S. citellus* in Subcarpathia seems to be triggered by a factor other than the above triggers of expansion. The Early Holocene warming, which was the cause of expansion for *S. citellus* from its primary Pleistocene range, does not correspond in time. Landscape changes (both climatic, Pleistocene, and agricultural, Late Holocene), which favoured the faunal exchange through the Dniester corridor, do not fit spatially (no spatial connection with populations that could have been ancestral). Agricultural transformation of landscapes, which caused further (Late Holocene) expansion of *S. citellus* north (virtually, in the forest zone) cannot be excluded to play a role here, but looks unlikely as a main trigger. A rare random event is the most likely explanation.
New palaeontological data may shed more light on certain drivers of the faunal exchanges.

4 Results

Ground squirrel fossils of from three localities of the Dniester area were studied: 1) Tadirka Cave, Khmelnytskyi oblast', Early Holocene (Ridush, 2022); 2) Zeleniv, Chernivtsi Oblast', Last Glacial Maximum (Ridush et al., 2021; Popiuk, Ridush, 2022); 3) Korman' 9, Chernivtsi Oblast', Epigravettian site, 22 cal BP (Kulakowska et al., 2021).
Ground squirrels are represented by *S. odessanus* only in each locality. In such a way, our new data support the barrier role of the Carpathians and the Low Danube for the dispersal of ground squirrel species and, generally, the history of occurrence of ground squirrel species in Subcarpathia outlined above.

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