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Microtus (Microtus) nivaloides from the Somssich Hill 2 site (southern Hungary): An Early Pleistocene forerunner of modern 'true' *Microtus* voles revealed by morphometric analyses

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ABSTRACT

Voles are among the most common and abundant rodents in Central Europe, represented by several species of *Microtus* and other genera. This group is also common in Pleistocene fossil assemblages. However, the taxonomy of fossil finds, largely based on lower first molars, is fraught with problems and opinions of various authors often diverge, hampering phylogenetic inferences and reconstruction of lineages which led to the extant species. To help solve taxonomic incongruence, we carried out morphometric analyses on the abundant late Early Pleistocene finds from the exceptionally rich site of Somssich Hill 2 (Villány Mts., southern Hungary), complemented with less numerous but also well-dated and nearly coeval material from nearby sites Villány 6 and 8, as well as Kövesvárad from northern Hungary. Landmark analysis was performed in the present paper, and in addition, cluster and discriminant analyses were applied on the conventional linear data derived from the landmark coordinates. First lower molars of well-established recent taxa from zoological museum collections were also included in the analyses, both to assess their degree in intraspecific morphological variability to inform delineation of the extinct taxa, and to compare morphologies of fossil and recent taxa to establish phylogenetic relationships. Morphometric analyses revealed that the material from Somssich Hill 2 represents a single species, *Microtus nivaloides*, whereas specimens from the somewhat younger site Villány 8 belong to *M. nivalinus*. Paleoecology of the accompanying taxa in the fossil assemblages suggests differences in their habitat: *M. nivalinus* preferred more open vegetation, whereas *M. nivaloides* was restricted to forested areas. Geometric morphometric analyses together with modern taxa defined a morphospace where the consensus shape of *M. nivaloides* is centrally located, supporting the hypothesis that it represents the ancestor of modern *Microtus* (*Microtus*) species and forms part of a lineage which led to the *M. arvalis-agrestis* group. On the other hand, morphological similarities suggest a split lineage and phylogenetic relations of late Early Pleistocene *M. nivalinus* and the recent *M. oeconomus*. The emergence of 'true' *Microtus* species stems from the radiation initiated around 1.0–0.9 Ma, an important phase in vole evolution revealed by the rich finds from Somssich Hill 2 and other sites.

1. Introduction

The karst fissure of the Somssich Hill 2 site (situated near the village of Villány, southern Hungary) is one of the richest late Early Pleistocene vertebrate localities of Central Europe. The clay-rich fissure fill yielded an exceptionally rich vertebrate assemblage which includes remains of fish, anurans (Szentesi, 2014, 2016), reptiles, birds and mammals (Jánossy, 1986, 1990). The remarkably diverse small mammalian fauna contains shrews (Botka and Mészáros, 2014), hamsters (Hír, 1998), mice (Hír, 1998), dormice (Striczky and Pazonyi, 2014) and voles (Jánossy, 1983, 1990; Pazonyi et al., 2013). The most common elements of the fauna are voles and lemmings. More than 15,000 first lower molars (m_1) were identified from the 50 layers of the fissure fill.

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Among the voles, remains of *Microtus* are the most abundant (more than 6000 lower first molars (m_1)), accompanied by *Mimomys*, *Pliomys*, and *Clethrionomys*. According to Jánossy (1990), six species of three subgenera were identified within the genus *Microtus*: the advanced *M. (Allophaiomys) pliocaenicus*, *M. (Terricola) gregaloides*, *M. (T.) arvalidens*, *M. (Microtus) arvalinus*, *M. (M.) gregalis*, *M. (M.) ratticepoides*. In addition, Jánossy (1999) mentioned *M. (M.) nivaloides* as well. Based on the co-occurrence of *M. (Allophaiomys)* and *M. (Microtus)* species, the age of the locality falls into the latest Early Pleistocene (approximately 1.0–0.9 Ma), using the chronology of Maul and Markova (2007). The assemblage is assigned to the *Mimomys savini-Mimomys pusillus* Biozone of the local biochronological system of Kordos (1994).

This interval coincides with one of the most important radiation events for the *Microtus* voles, and subsequently led to the modern diversity of this group (Rabeder, 1981). This event was most plausibly triggered by the extension of grasslands due to a progressive climate change initiated at the beginning of the Pleistocene, approximately 2.6 Ma (Kolfschoten van and Markova, 2005). However, details of the Pleistocene evolution of vole lineages are not fully understood. The key issues are the reconstruction of evolutionary lineages leading to modern vole species and constraining the age of splitting of these lineages (Van der Meulen, 1973; Rabeder, 1981; Nadachowski, 1991; Maul and Markova, 2007). Establishing the vole phylogeny is hampered by taxonomic confusion of several closely related nominal species of high morphological similarity.

In order to improve the reliability of vole taxonomy, the main aims of this work are to develop a new method which combines traditional and geometric morphometric approaches, and to demonstrate its utility in the comparison of various fossil and extant species of the genus *Microtus*. The primary focus of the present study is to prove that the morphology of the previously described four 'true' *Microtus* voles from the Somssich Hill 2 site can be interpreted as a single species, which we think is *M. nivaloides*, the oldest known *Microtus (Microtus)* species in the region. Thus we analysed all 'true' *Microtus* lower first molars that were used by Jánossy (1990, 1999). The large sample size (more than 1500 m_1) allowed us to analyse its morphological differences from and phylogenetic relationship with both voles from some nearly contemporaneous sites (Villány 6 and 8, and Kövesvárad) and modern taxa. The emergence of 'true' *Microtus* species can be regarded as the result of the radiation initiated around 1.0–0.9 Ma from a hypothetical ancestor similar to *M. nivaloides* at the Somssich Hill 2 site.

2. Geological setting and biostratigraphic framework

The studied vole material was found at four broadly contemporaneous localities in Hungary: Somssich Hill 2, Villány 6, Villány 8, and Kövesvárad. The first three localities are situated in the Villány Mountains (southern Hungary), near the village of Villány, whereas Kövesvárad is located in the Bükk Mountains (northeastern Hungary) (Fig. 1). The material was recovered from reddish brown clay or yellowish brown silt infillings of karst cavities. The karstified limestone is Middle Triassic in age at Kövesvárad and Late Jurassic at the sites of Villány 6 and 8, and Somssich Hill 2.

Somssich Hill 2 is an 8 m deep karst cavity with a surface diameter of 5 m, situated on the top of Somssich Hill, west of the village of Villány (Fig. 1). The infilling sediment is reddish brown clay at the bottom of the sequence (below 4 m), whereas it grades upwards into yellowish brown silt (Jánossy, 1990). Several interbeds of varying thickness with limestone clasts encrusted by calcite occur between depths of 2.5 and 5.0 m.

The age of Somssich Hill 2 locality is latest Early Pleistocene (approximately 1.0–0.9 Ma), equivalent of the *Mimomys savini-Mimomys pusillus* Biozone, based on the co-occurrence of advanced *Microtus (Allophaiomys)* and *Microtus (Microtus)* species together with *Mimomys savini* and *Mimomys pusillus*. Similar vole faunas have been found from Ukraine (Bolshevik 2-III, Protopopovka 2, Tikhonovka 2, Karay Dubina; Rekovets and Nadachowski, 1995) and Bulgaria (Subzone B2 of the Kozarnika Cave; Popov and Marinska, 2007) in Eastern Europe, from Poland (Zalesiaki 1; Nadachowski, 1990a) in Central Europe, as well as from Spain (the lower layers of Gran Dolina in Atapuerca; Antoñanzas and Cuenca Bescós, 2002) in Southern Europe. (Fig. 2).

Villány 6 is a north-south trending, vertical karst fissure of very large size, which is exposed in the southern wall of the limestone quarry at Templom Hill (Fig. 1). The infilling sediment is cherry-coloured terra rossa, which is penetrated by sheets of recrystallized calcareous precipitate (Kretzoi, 1956; Jánossy, 1986). Based on the occurrence of *Mimomys pusillus*, *Mimomys savini*, and the absence of *Microtus (Allophaiomys)*, the vole fauna is slightly younger than that of Somssich Hill 2, but it can also be assigned to the *Mimomys savini-Mimomys pusillus* Biozone (Kordos, 1994) (Fig. 2).

Villány 8 is a karst cavity connected to a fissure system, also exposed in the southern wall of the abandoned limestone quarry at Templom Hill, north of Villány (Fig. 1). The lower layers of the infilling sediment are reddish brown clays with calcareous interbeds, whereas upwards it grades into yellowish brown silt, similarly to the Somssich Hill 2 site (Jánossy, 1986).

Villány 8 is the stratotype section of the Templomhegy Phase within the Biharian Stage of the local biochronological system (Kretzoi and Pécsi, 1982; Jánossy, 1986). The beginning of the Templomhegy Phase is closely correlated with the Early-Middle Pleistocene boundary, and regionally marked by environmental change which led to increasing forest cover (Fig. 2). The vole fauna is slightly younger than in Villány 6, it was assigned to the *Mimomys savini* Biozone based on the absence of *Microtus (Allophaiomys)* and *Mimomys pusillus* (Kordos, 1994). Similar assemblages are known, among others, from Great Britain in Western Europe (West Runton; Maul and Parfitt, 2010) and from Poland in Central Europe (Kozi Grzbiet; Nadachowski, 1985). Those sites postdate the Matuyama-Brunhes reversal, with an approximate age between 780 and 650 ka (Maul and Parfitt, 2010).

The fossiliferous locality at Kövesvárad is a 5 m high and 3 m wide karst cavity situated east of the village of Répáshuta (Fig. 1). The vole material was recovered from the orange and reddish brown clay infilling (Jánossy, 1963, 1986). Based on the vole fauna, which is similar to that of Villány 8, the site was also assigned to the *Mimomys savini* Biozone (Kordos, 1994) (Fig. 2).

3. Material

A total of 587 teeth were selected from more than 1500 'true' *Microtus* lower first molars (m_1) from the Somssich Hill 2 site. Only those undamaged specimens were chosen, on which all of the characters discussed below were observable. From the other fossil localities included in the present study (Villány 6, Villány 8 and Kövesvárad), fewer *Microtus (Microtus)* specimens were available (26, 177 and 8 specimens, respectively). The material analysed from Villány 6 and 8 includes several specimens previously studied and reported by Van der Meulen (1973). The specimens from Somssich Hill 2 and Kövesvárad are housed in the Department of Paleontology and Geology, Hungarian Natural History Museum (HNHM), Budapest, whereas the material from Villány 6 and 8 is stored at the Department of Geological and Geophysical Collections, Geological and Geophysical Institute of Hungary (GGIH), Budapest.

First lower molars belonging to four recent species, *Microtus*

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