



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

## Sedimentological, taphonomical and palaeoecological aspects of the late early Pleistocene vertebrate fauna from the Somssich Hill 2 site (South Hungary)



*Aspects sédimentologiques, taphonomiques et paléoécologiques de la faune de vertébrés de la fin du Pléistocène inférieur du site de Somssich Hill 2 (Sud de la Hongrie)*

Piroska Pazonyi<sup>a,\*</sup>, Attila Virág<sup>a</sup>, Kinga Gere<sup>b</sup>, Gábor Botfalvai<sup>c</sup>, Krisztina Sebe<sup>d</sup>, Zoltán Szentesi<sup>c</sup>, Lukács Mészáros<sup>b</sup>, Dániel Botka<sup>b</sup>, Mihály Gasparik<sup>c</sup>, László Korecz<sup>e</sup>

<sup>a</sup> MTA-MTM-ELTE Research Group for Paleontology, POB 137, 1431 Budapest, Hungary

<sup>b</sup> Department of Palaeontology, Eötvös University, Pázmány Péter sétány 1/c, 1117 Budapest, Hungary

<sup>c</sup> Hungarian Natural History Museum, Department of Palaeontology and Geology, POB 137, 1431 Budapest, Hungary

<sup>d</sup> Department of Geology and Meteorology, University of Pécs, Ifjúság útja 6., 7624 Pécs, Hungary

<sup>e</sup> Institute of Materials and Environmental Chemistry, Research Centre for Natural Sciences, Hungarian Academy of Sciences, POB 286, 1519 Budapest, Hungary

### ARTICLE INFO

#### Article history:

Received 29 March 2017

Accepted after revision 18 June 2017

Available online 12 August 2017

Handled by Lars van den Hoek Ostende

#### Keywords:

Late early Pleistocene  
Epivillafranchian turnover  
Small vertebrates  
Sedimentology  
Taphonomy  
Palaeoecology  
ESR dating

### ABSTRACT

The Somssich Hill 2 site (Villány Mts., South Hungary) yielded one of the richest late Early Pleistocene vertebrate assemblages within the Carpathian Basin. The present paper provides a summary of all former and new taxonomical results, as well as biostratigraphical and palaeoecological conclusions, which is completed with previously unpublished sedimentological and taphonomical observations on the locality. The bulk of the fauna can be referred to the *Mimomys savini*–*Mimomys pusillus* Biozone in the Biharian (MQ1), whereas a few specimens suggest an older age, namely the *Mimomys pliocaenicus* Biozone in the late Villanyian (MN17). The bones were affected by only a short-distance aquatic transport, thus they represent a parautochthonous and relatively unaltered assemblage. Consequently, the material was considered here as a reliable base for reconstructing the direct palaeoenvironment of the cavity. The entire section was divided here to five different palaeoecological units based on the small vertebrate fauna.

© 2017 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

\* Corresponding author.

E-mail address: [pinety@gmail.com](mailto:pinety@gmail.com) (P. Pazonyi).

## R É S U M É

## Mots clés :

Pléistocène tardif  
Turnover épivillafranchien  
Petits vertébrés  
Sédimentologie  
Taphonomie  
Paléoécologie  
Datation ESR

Le site de Somssich Hill 2 (monts Villány, Sud de la Hongrie) a fourni l'un des assemblages de vertébrés les plus riches de la fin du Pléistocène inférieur, dans le bassin des Carpates. Le présent article présente un résumé de tous les résultats taxonomiques anciens et nouveaux, ainsi que les conclusions biostratigraphiques et paléoécologiques, qui sont complétés par les observations sédimentologiques et taphonomiques non publiées antérieurement sur la localité. L'ensemble de la faune peut être rapporté à la biozone à *Mimomys savini*–*Mimomys pusillus* du Biharien–MQ1), tandis que quelques spécimens suggèrent un âge plus ancien, plus exactement la biozone à *Mimomys pliocaenicus* de la fin du Villanyien (MN17). Les os n'ont été affectés que par un transport aquatique sur une courte distance, et ils représentent donc un assemblage parautochtone et relativement non altéré. Par conséquent, le matériel a été considéré ici comme un élément de base fiable pour la reconstitution du paléoenvironnement précis de la cavité. La section entière a été divisée en cinq unités paléoécologiques sur la base d'une faune de petits vertébrés.

© 2017 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

The karst cavity of the Somssich Hill 2 site (situated near the town of Villány, southern Hungary) is one of the richest late early Pleistocene vertebrate localities of central Europe (Fig. 1). It was rediscovered by Dénes Jánossy and György Topál in 1974, but was already mentioned by Kormos (1937) and Kretzoi (1956). The excavation led by them between 1975 and 1984 yielded a rich Pleistocene fauna, of which preliminary lists were given by Jánossy (1983, 1986, 1990). The continental snail fauna of the locality was described by Krolopp (2000), and some mammal groups (namely cricetids and arvicolid) were published by Jánossy (1983, 1990) and Hír (1998).

A new project (NKFI K 104506) was started in 2013 by the cooperative research group of the Hungarian Academy of Sciences, the Hungarian Natural History Museum and the Eötvös University, which aimed to review and elaborate on the taxonomy, taphonomy and palaeoecology of the material. Within the framework of this project, some articles were already published (Botka and Mészáros, 2014, 2015a, b, 2016; Striczky and Pazonyi, 2014; Szentesi, 2014, 2016), but these contain primarily taxonomical and palaeoecological conclusions. However, some questions about the locality remained unanswered up to now. The present study aimed to achieve the following goals:

- Jánossy (1986, 1990) divided the sequence into 50 “layers”, each of them 20–30 cm in thickness. However, his “layers” not always represented sedimentary strata; they were rather sampling units according to depth. In order to fill this gap, here we present a new and complex sedimentological investigation for the locality;
- according to Jánossy (1983, 1986, 1990), the site provided a typical early–middle Pleistocene fauna. However, this concept was never tested by a more exact method; therefore, this paper presents the results of an electron spin resonance (ESR) dating, accompanied by a more complex biostratigraphic interpretation of the revised fauna.

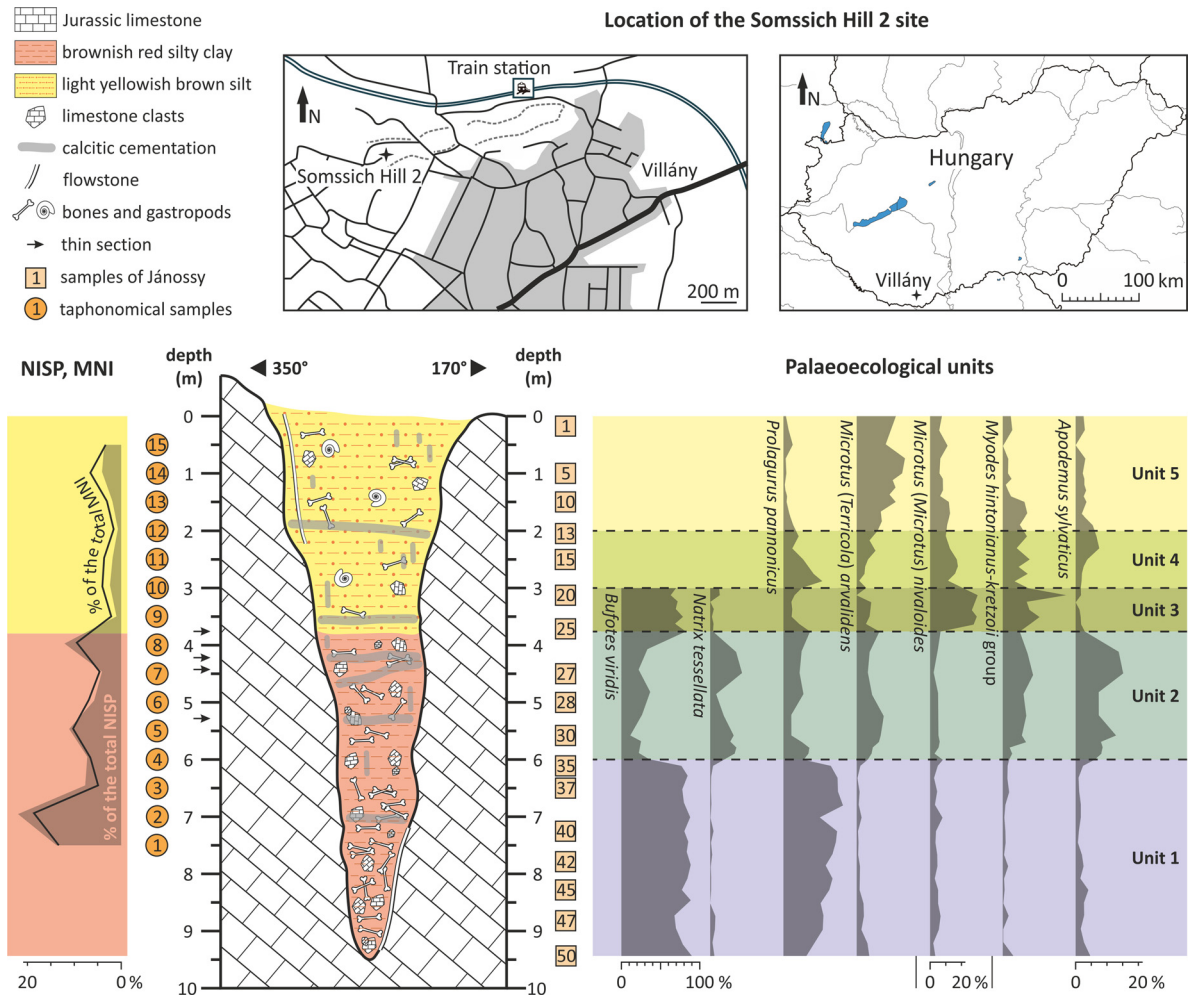
Although it is not clear how far the remains were transported from their original biocoenosis, how many distorting factors were they subjected to during the process, or how long it took for the cavity to fill up, several abundance based palaeoecological conclusions were made in the previous studies (see, e.g., Hír, 1997; Jánossy, 1983; Krolopp, 2000; Mészáros, 2015; Striczky and Pazonyi, 2014; Szentesi, 2016). Thus, it seemed necessary to perform a detailed taphonomical analysis for the site.

## 2. Material and methods

The bulk of the studied material (approximately 950,000 remains) was collected by Dénes Jánossy and is now stored in the Vertebrate Palaeontological Collection of the Hungarian Natural History Museum. The present revision revealed a remarkably diverse vertebrate fauna with 109 identified taxa (Table 1). Considering the number of bones, the material is dominated by herpetofaunal elements (around 910,000 remains), but small mammals are taxonomically the most diverse group (with 45 species). The herpetofauna is discussed in detail by Szentesi (2014, 2016). Amongst the small mammals, shrews are presented in Botka and Mészáros (2014, 2015a, b, 2016) and Mészáros (2015), whereas dormice were revised in Striczky and Pazonyi (2014).

For the sedimentological, taphonomical and ESR analyses, new sampling was carried out during the excavations in 2014 and 2015, which yielded more than 4,000 new remains. Fifteen samples of 1.0 kg were taken at depth intervals of 0.5 meters between 7.5–0.5 m in the entire section. The sediment was washed and sieved to three different size fractions (0.5–1.0 mm, 1.0–2.0 mm, > 2.0 mm). Both qualitative and quantitative observations were carried out on the found remains. The 15 new samples were correlated with the original numbering of Jánossy (1986, 1990) based on their depth and faunal composition (Fig. 1).

Electron paramagnetic resonance (EPR) spectroscopy was used for gathering information on the age of the samples. The spectra were recorded with a BRUKER EleXsys E500 spectrometer (microwave frequency 9.51 GHz,



**Fig. 1.** Geographical location and sedimentological section of the Somssich Hill 2 site. The NISP and MNI values calculated from the taphonomical sampling are indicated on the left side of the section, whereas the palaeoecological units based on the material collected by Jánosy are depicted on the right (see further discussion in the text).

**Fig. 1.** Localisation géographique et section sédimentologique du site de Somssich Hill 2. Les valeurs NISP et MNI, calculées à partir de l'échantillonnage taphonomique, sont indiquées sur la partie gauche de la section, tandis que les unités paléocologiques basées sur le matériel récolté par Jánosy figurent sur la droite (voir discussion dans le texte).

microwave power 2 mW, modulation amplitude 1 G, modulation frequency 100 kHz) in quartz EPR tubes at room temperature. Three to five arvicolid incisors were used (depending on their size) for each measurement from each new sampling unit. The ESR intensities were evaluated by an EPR simulation computer program (Rockenbauer and Korecz, 1996). The ESR ages were calculated using the following equation:  $t_{ESR} = D_e / D_{an}$ , where  $D_e$  is the equivalent dose (the apparent dose that the tooth has received since burial) and  $D_{an}$  is the annual dose rate. The intensity of the ESR signal in the sample was measured and the growth of this intensity due to added laboratory doses of gamma radiation was determined as a function. The equivalent dose was deduced by back-extrapolating the intensity curve to zero intensity (i.e. the intersection on the dose axis was interpreted as  $D_e$ ). Data points in the resulting dataset were accepted if they were within 1.5 times the interquartile range outside from the first and

third quartiles of the dataset; otherwise, they were judged as outliers. This analysis was performed by the boxplot() function of R software (R Development Core Team, 2008).

Two main taphonomical indices (NISP, MNI) were used for estimating the frequency of small mammals in the new taphonomical sampling (Supplementary Table 1). In addition, MNI values were calculated for the small mammals and herpetofaunal individuals that occur in the sample collected by Jánosy (Supplementary Table 2). These numerical descriptors are widely accepted in literature and they form the basis of further calculations (Andrews, 1990; Badgley, 1986; Grayson, 1973, 1984; Lyman, 1994, 2008).

The number of identified specimens (NISP) is an observational parameter that includes the number of taxonomically identified bones, teeth and skeletal fragments in the vertebrate assemblage (Lyman, 2008). It represents the maximum number of individuals supposing that each specimen belonged to a different animal (Badgley, 1986).

**Table 1**

Revised taxonomical list of the Somssich Hill 2 site. Superscript letters indicate deviations from the original list published by Jánossy (1990).

**Tableau 1**

Liste taxonomique révisée du site Somssich Hill 2. Les lettres en exposant indiquent les déviations observées par rapport à la liste originale publiée par Jánossy (1990).

Pisces	Aves	Sicista praeloriger Kormos, 1930	Erinaceus cf. praeglacialis Brunner, 1933
<i>Carassius</i> sp.	<i>Anser subanser</i> Jánossy, 1983	<i>Apodemus sylvaticus</i> (Linnaeus, 1758)	<i>Rhinolophus ferrumequinum</i> (Schreber, 1774)
Osteichthyes indet.	<i>Aythya</i> sp. (large species)	<i>Allocricetus bursae</i> Schaub, 1930	<i>Myotis cf. nattereri</i> (Kuhl, 1817)
<b>Amphibia</b>	Anatidae indet.	<i>Allocricetus ehiki</i> Schaub, 1930	<i>Myotis cf. brandtii</i> (Eversmann, 1845)
<i>Salamandra</i> cf. <i>salamandra</i> (Linnaeus, 1758) <sup>b</sup>	<i>Tetrao partium</i> (Kretzoi, 1962) <sup>a</sup>	<i>Cricetus nanus</i> (Schaub, 1930)	<i>Myotis dasycneme</i> Boie, 1825
<i>Triturus cristatus</i> (Laurenti, 1768) <sup>b</sup>	<i>Francolinus capeki</i> Lambrecht, 1933	<i>Cricetus runtonensis</i> Newton, 1909	<i>Plecotus cf. auritus</i> Linnaeus, 1758
<i>Lissotriton</i> cf. <i>vulgaris</i> (Linnaeus, 1758) <sup>b</sup>	<i>Coturnix</i> cf. <i>coturnix</i> Linnaeus, 1758	<i>Villanyia exilis</i> Kretzoi, 1956 <sup>b</sup>	<i>Miniopterus schreibersii</i> (Kuhl, 1817)
<i>Bombina variegata</i> (Linnaeus, 1758) <sup>b</sup>	<i>Otis</i> sp.	<i>Mimomys savini</i> Hinton, 1910	<i>Eptesicus nilssonii</i> (Keyserling and Blasius, 1839)
<i>Pelobates fuscus</i> (Laurenti, 1768) <sup>b</sup>	<i>Surnia robusta</i> Jánossy, 1977	<i>Mimomys pusillus</i> (Méhely, 1914) <sup>b</sup>	<i>Canis mosbachensis</i> Soergel, 1925
<i>Bufo bufo</i> (Linnaeus, 1758) <sup>b</sup>	<i>Athene noctua</i> cf. <i>lunellensis</i> Mourer-Chauviré, 1975	<i>Mimomys reidi</i> Hinton, 1910 <sup>b</sup>	<i>Vulpes</i> cf. <i>praecorsac</i> Kormos, 1932
<i>Bufotes viridis</i> (Laurenti, 1768) <sup>b</sup>	<i>Aquila</i> cf. <i>heliaca</i> Savigny, 1809	<i>Pitymimomys pitymyoides</i> (Jánossy and Meulen, 1975) <sup>b</sup>	<i>Meles meles</i> cf. <i>atavus</i> Kormos, 1914 <sup>a</sup>
<i>Hyla arborea</i> (Linnaeus, 1758) <sup>b</sup>	<i>Falco tinnunculus atavus</i> Jánossy, 1972	<i>Borsodia newtoni</i> (Forsyth Major, 1902) <sup>b</sup>	<i>Mustela palerminea</i> Petényi, 1864
<i>Rana temporaria</i> (Linnaeus, 1758) <sup>b</sup>	<i>Falco</i> cf. <i>vespertinus</i> Linnaeus, 1766	<i>Pliomys episcopalis-hollitzeri</i> group <sup>a</sup>	<i>Mustela praenivalis</i> Kormos, 1934
<b>Reptilia</b>	<i>Picus</i> cf. <i>viridis</i> Linnaeus, 1758	<i>Clethrionomys hintonianus-kretzoi</i> group <sup>a</sup>	<i>Lutra</i> sp.
<i>Emys</i> cf. <i>orbicularis</i> (Linnaeus, 1758)	<i>Dendrocopos submajor</i> Jánossy, 1974	<i>Lagurodon aranka</i> (Kretzoi, 1954) <sup>a</sup>	<i>Pannonictis</i> sp.
<i>Testudo lambrechtii</i> Szalai, 1934 <sup>b</sup>	<i>Galerida</i> cf. <i>cristata</i> Linnaeus, 1758	<i>Prolagurus pannonicus</i> (Kormos, 1930) <sup>a</sup>	<i>Martes foina</i> cf. <i>intermedia</i> (Severtzov, 1873) <sup>a</sup>
<i>Lacerta</i> cf. <i>viridis</i> (Laurenti, 1768) <sup>b</sup>	<i>Sitta europaea</i> -group	<i>Allophaiomys pliocaenicus</i> Kormos, 1932	<i>Felis</i> cf. <i>chaus</i> Schreber, 1777
<i>Anguis</i> sp. <sup>b</sup>	<i>Hirundo</i> cf. <i>rustica</i> Linnaeus, 1758	<i>Microtus (Terricola) arvalidens</i> (Kretzoi, 1958) <sup>a</sup>	<i>Lynx</i> sp.
<i>Pseudopus</i> cf. <i>pannonicus</i> Kormos, 1911 <sup>b</sup>	Passeriformes indet.	<i>Microtus (Terricola) hintoni</i> (Kretzoi, 1941) <sup>a</sup>	<i>Panthera onca gombaszogensis</i> (Kretzoi, 1938) <sup>a</sup>
<i>Ophisaurus</i> sp.	<b>Mammalia</b>	<i>Microtus (Microtus) nivaloides</i> Forsyth Major, 1902 <sup>a</sup>	<i>Homotherium</i> sp.
<i>Hierophis</i> cf. <i>viridiflavus</i> (Lacepède, 1789) <sup>b</sup>	<i>Macaca</i> sp.	<i>Talpa fossilis</i> Petényi, 1864	<i>Equus</i> sp.
<i>Hierophis</i> cf. <i>gemonensis</i> (Laurenti, 1768) <sup>b</sup>	<i>Lepus terraerubrae</i> Kretzoi, 1956	<i>Desmana thermalis</i> Kormos, 1930	Rhinocerotidae sp.
<i>Coronella austriaca</i> Laurenti, 1768 <sup>b</sup>	<i>Ochotona</i> sp.	<i>Crocidura kornfeldi</i> Kormos, 1934	<i>Capreolus</i> sp.
<i>Elaphe</i> cf. <i>paralongissima</i> Szyndlar, 1984 <sup>b</sup>	<i>Trogontherium</i> cf. <i>cuvieri</i> (Laugel, 1862) <sup>b</sup>	<i>Crocidura obtusa</i> Kretzoi, 1938	<i>Cervus</i> cf. <i>elaphus acoronatus</i> Beninde, 1937 <sup>a</sup>
<i>Elaphe</i> cf. <i>quatuorlineata</i> Lacepède, 1789 <sup>b</sup>	<i>Nannospalax</i> cf. <i>adventus</i> (Kretzoi, 1977) <sup>a</sup>	<i>Sorex minutus</i> Linnaeus, 1766	? <i>Alces</i> sp.
<i>Zamenis longissimus</i> (Laurenti, 1768) <sup>b</sup>	<i>Spermophilus primigenius</i> (Kormos, 1934) <sup>a</sup>	<i>Sorex runtonensis</i> Hinton, 1911	
<i>Natrix natrix</i> Linnaeus, 1758 <sup>b</sup>	<i>Sciurus whitei hungaricus</i> Jánossy, 1962 <sup>b</sup>	<i>Sorex (Drepanosorex) savini</i> Hinton, 1911 <sup>b</sup>	
<i>Natrix tessellata</i> Laurenti, 1768 <sup>b</sup>	<i>Glis sackdillingensis</i> Heller, 1930	<i>Neomys newtoni</i> Hinton, 1911 <sup>b</sup>	
<i>Telescopus</i> cf. <i>fallax</i> (Fleischmann, 1831) <sup>b</sup>	<i>Glis minor</i> (Kowalski, 1956) <sup>b</sup>	<i>Asoriculus gibberodon</i> (Petényi, 1864) <sup>b</sup>	
<i>Vipera</i> cf. <i>ammodytes</i> Linnaeus, 1758 <sup>b</sup>	<i>Muscardinus dacicus</i> Linnaeus, 1758 <sup>a</sup>	<i>Beremendia fissidens</i> (Petényi, 1864)	
<i>Vipera</i> cf. <i>berus</i> Linnaeus, 1758 <sup>b</sup>	<i>Dryomimus eliomyoides</i> Kretzoi, 1959	<i>Beremendia minor</i> Rzebik-Kowalska, 1976 <sup>b</sup>	

<sup>a</sup> Renamed taxon.<sup>b</sup> Not present in the source list.

The minimum number of elements (MNE) is a derived parameter that represents the minimum number of a particular skeletal element of an animal. The minimum number of individuals (MNI) of a given taxon is somewhat more complex. It was defined here as the greatest MNE amongst the most common skeletal elements (for example molars, femurs or mandibles) belonging to the same taxon (Badgley, 1986; Lyman, 1994, 2008). It represents the lowest possible number of animals belonging to a given taxon in the assemblage.

Besides the above-mentioned two indices, the remaining taphonomical calculations were performed only for small mammal remains from equally-sized taphonomical samples.

The relative abundances of different small mammal skeletal elements were calculated using the following equation:  $R_i = N_i / (MNI \times E_i) \times 100$ , where  $R_i$  is the relative abundance of element  $i$ ,  $N_i$  is the number of element  $i$  in the sample (i.e. the NISP), MNI is the minimum number of individuals for the taxon in question, and  $E_i$  is the exact number of element  $i$  in the skeleton (Andrews, 1990; Kos, 2003; Lyman, 1994; Matthews, 2006; Vasileiadou et al., 2007). The  $E_i$ s in the case of the teeth were calculated as a weighted mean of the average tooth number of each small mammal taxon from the taphonomical sample. Average tooth numbers for given taxa were determined based on Hillson (2005). Taxa with higher MNI contributed more to the final result than those with lower values. The resulting  $E_i$  for the teeth of small mammals was 20.

Bone modifications, such as the effects of predation, abrasion and weathering were also quantified. The most direct evidence of predatory activity is the digestion on bones and teeth (Andrews, 1990; Fernandez-Jalvo et al., 2016; Matthews, 2006). In agreement with the system developed by Andrews (1990), the small mammal remains were classified into the following four groups: no digestion marks, evidence of light, moderate or heavy digestion.

Abrasion is an indicator of the interaction between sediment particles and bones, hence it can be used indirectly for estimating the extent of transportation (Behrensmeier, 1982). Physical grinding and polishing of the fracture edges and surface of small mammal bones from the site were divided into two categories based on Korth (1979), Andrews (1990) and Fernandez-Jalvo and Andrews, 2003: unabraded and abraded bones.

Assessing the effects of weathering on the bones gives information on the duration of surface exposure before burial (Behrensmeier, 1978). Based on the presence or absence of splitting and flaking associated with cracks (Andrews, 1990), the small mammal remains were classified as unweathered or weathered bones.

In order to decide if two sub-samples were drawn from the same distribution (i.e. to show the similarities or differences of the taphonomical parameters in the lower and upper part of the cavity), non-parametric Kolmogorov-Smirnov tests were performed on the numerical data by the `ks.test()` function of R software (R Development Core Team, 2008). The null hypothesis of equality of the distributions was rejected if the  $p$ -value was lower than 0.05.

For testing the correlation of two distributions, a linear regression was fitted to the data using the least squares

method. The correlation coefficient ( $r$ ) was calculated by the `cor()` function of R software. The determination coefficient ( $r^2$ ) was used here to assess the goodness of fit.

In order to identify palaeoecological grouping within the rich material collected by Jánossy, a principal component analysis (PCA) was performed using the `princomp()` function of R software on the small mammals (apart from the bats) and the herpetofaunal elements. The MNI of the small mammal taxa (Supplementary Table 2) were normalized to percentages in each of the 50 samples using the total small mammal MNI in a given sample. The same approach was used separately in the case of the herpetofaunal elements, so that the large number of herpetofaunal remains could not hide the ecological signal derived from the abundance changes of the small mammal taxa. The final PCA was based on the combination of the resulting separately normalized datasets. Loading values of each taxa on the first three principal components were used to identify which species are responsible for the separation of the palaeoecological units. The abundance changes of the taxa with the highest loading values were visualized and then analysed using the `plot()` function of R software.

### 3. Results

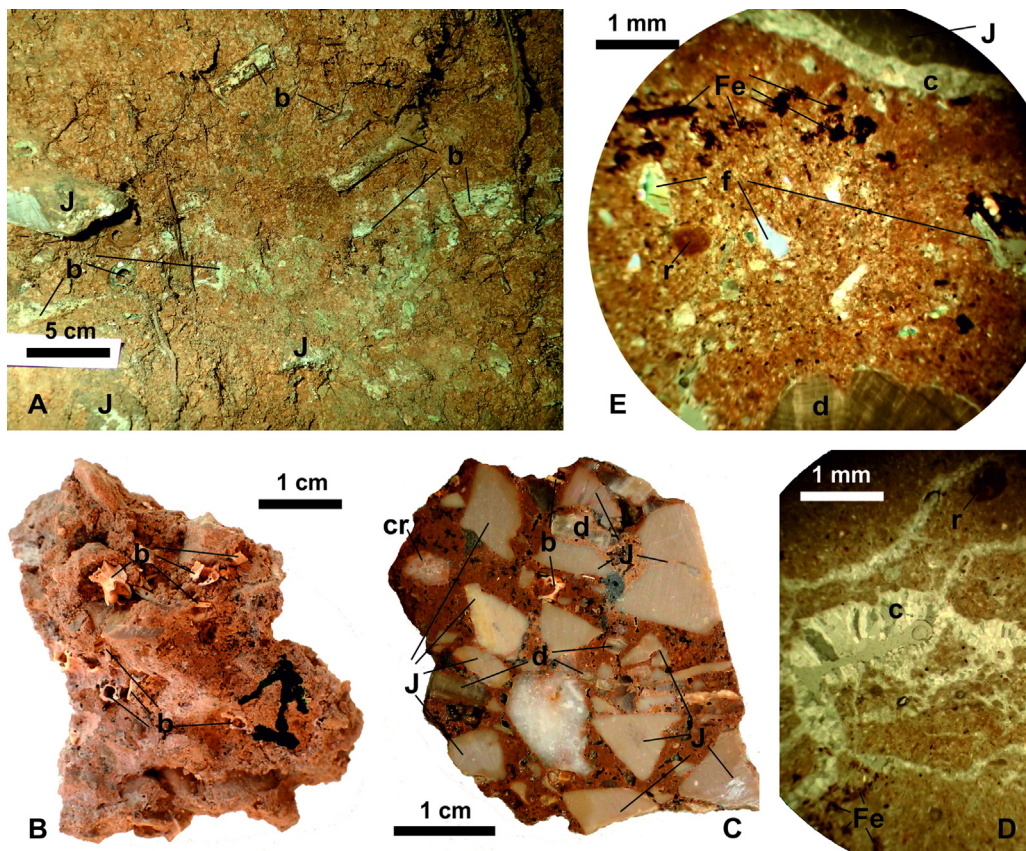
#### 3.1. Sedimentological description

The Somssich Hill 2 site is an 8 m deep, vertical, downward tapering karst cavity with a surface diameter of 5 m in the Upper Jurassic (Oxfordian) Szársomlyó Limestone Formation. Its present appearance results from the excavations of Dénes Jánossy between 1975 and 1984. The walls are made up of the fossiliferous clastic infilling sediment or by flowstone. The host limestone is nowhere visible inside the hollow. The infill of the cavity is bipartite.

Above 3.8 m depth from the surface, the sediment is light yellowish brown, porous, carbonate-cemented silt, with scattered bones, gastropod shells and limestone fragments (Fig. 2A). The amount of limestone clasts is markedly lower in the light yellowish brown silt than in the underlying breccia (see below). The silt contains a dense network of carbonate precipitations. Despite its colour, dominant grain size and carbonate content, this sediment cannot be called loess due to its gravel content and strong cementation, rather a transition between loess and slope sediments or cavity infills.

Below 3.8 m, the infill is mostly breccia with brownish red silty clay matrix, in patches gravelly clay. The breccia in the lower part is mud-supported. The clasts are vertebrate bones, teeth, and maximum 20 cm large angular-subangular fragments of the host Jurassic limestone and of laminated sparry calcite (dripstone) (Fig. 2B–C). The matrix contains numerous pores and irregular vugs, often lined with calcite crystals, and is cemented to various degrees by calcite. No bedding is visible; in some places grain size changes in indistinct, horizontal lenses or in irregular patches.

Under the microscope, both the upper and the lower sediments contain: sand-sized quartz grains, sometimes rounded or subrounded ones; rounded red clay and



**Fig. 2.** Sedimentological features of the fossiliferous deposits. Macroscopic view of A) the yellowish silt (depth 2.0 m), B) the silt-clay transition (3.8 m) and C) the breccia with red clay matrix (5.3 m; cut sample). Photomicrographs: D) heavily calcite-cemented silt with desiccation cracks lined with sparry calcite; E) matrix of the red clay-bearing breccia. b: bone; c: calcite; cr: calcrete fragment; d: driptestone clast; Fe: iron-oxide precipitation; J: Jurassic limestone clast; r: redeposited red clay (soil) fragment.

**Fig. 2.** Caractéristiques sédimentologiques des dépôts fossilifères. Vue macroscopique A) du silt jaunâtre (profondeur 2,0 m), B) de la transition silt : argile (3,8 m), C) de la brèche à matrice argileuse rouge (5,3 m ; échantillon en coupe). Microphotographies : D) silt à ciment fortement calcitique, avec fentes de dessiccation soulignées par de la calcite sparitique ; E) matrice de la brèche comportant de l'argile rouge. Légende : b : os ; c : calcite ; cr : fragment de calcrète ; d : claste de stalactite ; Fe : précipitation d'oxyde de fer ; J : claste de calcaire jurassique ; r : fragment d'argile (sol) rouge redéposé.

rare calcrete fragments; coarse sand-sized angular bone fragments; and angular driptestone clasts (Fig. 2E). Cracks and voids occur frequently, irregular or around grains, often lined or filled with calcite crystals (Fig. 2D–E). Rust-coloured patches of iron-oxide/hydroxide stain with diffuse boundaries are common. The cement is typically micritic, but can also be sparry, including fascicular optic calcite.

Carbonate precipitations occur in large amounts above 6.8 m depth. The most common type is stratiform, which occurs as few-centimetre-thick hard, cemented planes, horizontal or dipping to various directions. The second type includes vertical, cylindrical carbonate nodules with a diameter of a few cm and a length of a few dm, most common above 4.5 m. They are strongly cemented sections of the sediment, typically with diffuse, powdery boundaries. The third type, driptestone (mostly flowstone) was precipitated onto the clastic sediments. It is comprised of columnar, sparry calcite laminae, bunches of which alternate in irregular patterns with the silt or clay. This forms the wall of the lower part of the fossiliferous cavity.

### 3.2. Biostratigraphical framework and ESR dating

Based on the ranges of the most abundant arvicolid in the material collected by Jánossy (*Mimomys savini*, *M. pusillus*, *Lagurodon arankae*, *Prolagurus pannonicus*, *Allophaiomys pliocaenicus*, *Microtus arvalidensis*, *M. hintoni*, *M. nivaloides*), the fauna can be correlated with the *Mimomys savini*–*Mimomys pusillus* Biozone in the Biharian (MQ1) (Maul and Markova, 2007; Tesakov, 2004; Fig. 3). Similar vole faunas have been found in Ukraine (Bolshevik 2-III, Protopopovka 2, Tikhonovka 2, Karay Dubina; Rekovets and Nadachowski, 1995) and Bulgaria (Subzone B2 of the Kozarnika Cave; Popov and Marinova, 2007) in eastern Europe, in Poland (Zalesiaki 1; Nadachowski, 1990) in central Europe, as well as in Spain (the lower layers of Gran Dolina in Atapuerca; Antoñanzas and Cuenca Bescós, 2002) in southwestern Europe.

The large mammal material from the Somssich Hill 2 site is rather fragmentary compared to the extremely rich microvertebrate record, but it shows some features, which are characteristics of the so-called Epivillafranchian faunal turnover. The main indicators of this event are the size

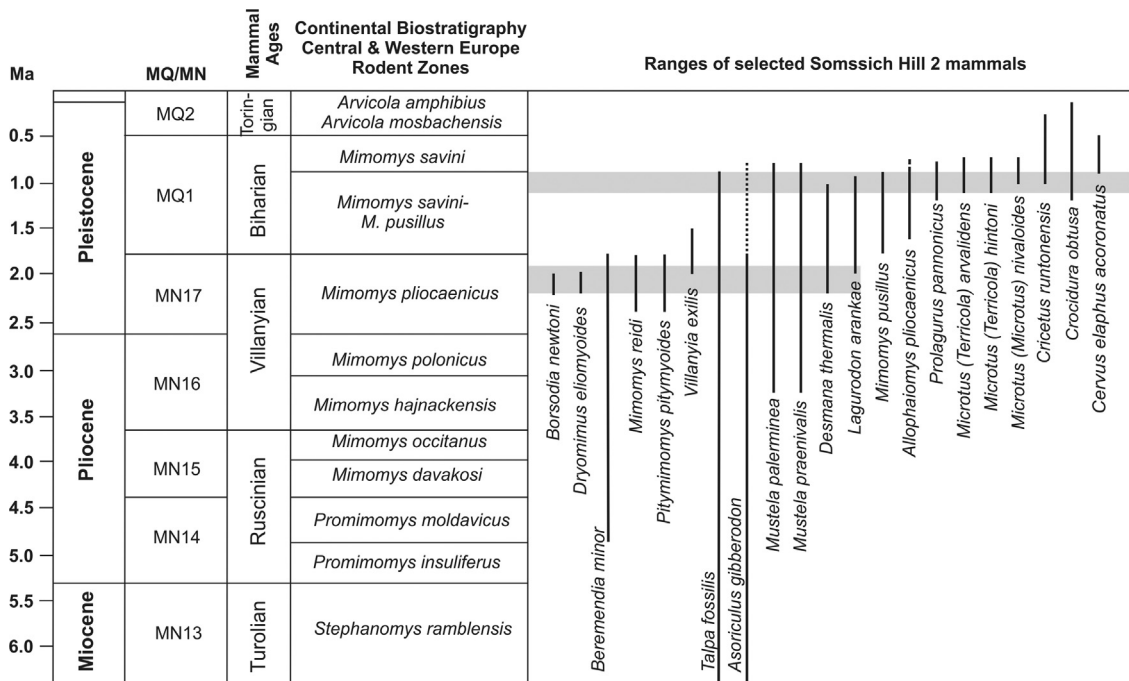


Fig. 3. Age of the Somssich Hill 2 assemblage based on the ranges of the biostratigraphically most important mammal taxa.

Fig. 3. Âge de l'assemblage de Somssich Hill 2 basé sur les biozones des plus importants taxons de mammifères.

parameters of *Mustela palerminea* and *Canis mosbachensis*, because the mandible size of the former is intermediate between the typical Villafranchian *Mustela palerminea* and the middle Pleistocene (and recent) *Mustela erminea*, whereas the size of the isolated teeth of the latter are transitional between the Villafranchian *Canis arvensis* (and *C. etruscus*) and the middle Pleistocene *Canis mosbachensis* (Gliozzi et al., 1997; Petrucci et al., 2013).

Considering the first appearance dates of *Crocidura obtusa*, *Cricetus runtonensis* and *Cervus elaphus acoronatus* (Botka and Mészáros, 2015b; Hír, 1997; Petronio et al., 2011) and the last appearance dates of *Mustela palerminea* and *M. praenivalis* (Jánossy, 1986), the co-occurrence of these taxa also supports the above-mentioned age determination (Fig. 3).

However, a few species mainly from the upper, light yellowish brown silt have ranges that suggest an older age, the *Mimomys pliocaenicus* Biozone in the late Villanyian (MN17): *Dryomimus eliomyoides* (five dormouse specimens), *Villanyia exilis*, *Mimomys reidi*, *Pitymimomys pitymyoides*, *Borsodia newtoni* (58 vole specimens), *Asoriculus gibberodon*, *Beremendia minor* (18 shrew specimens).

All of the ESR data measured here were accepted, apart from the one for sample 14 at 1.0 m depth, which was judged as an outlier. The measurements varied between 2.0 and 0.5 Ma with a large error (from  $\pm 10$  kyr to 450 kyr). The mean was 1.15 Ma with a standard deviation of 0.45 Ma and the median was 1.0 Ma (Fig. 4). The average age agrees well with the above described biostratigraphic interpretation for the bulk of the material. A linear regression was also fitted to the measurements, but due to the high variability of

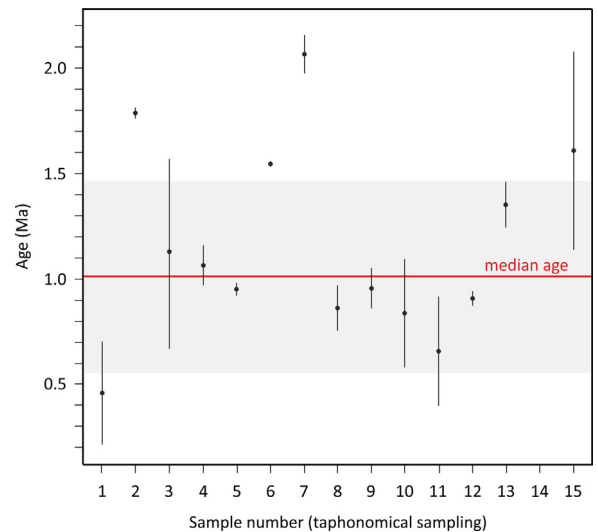


Fig. 4. The results of the ESR dating (further discussion in the text).

Fig. 4. Résultats de la datation ESR (voir discussion dans le texte).

the data, the determination coefficient was extremely low. Thus, it was not possible to assess a reliable age difference between the lower and the upper part of the sequence.

### 3.3. Taphonomical description

The total NISP of the taphonomical samples is 4534 for the small mammals, which includes cranial elements, teeth, vertebrae, and limb bones (including fragments). The

bulk of the material (84% of the total NISP) was retrieved from the lower part of the cavity (i.e. from the breccia below 3.8 m depth; Fig. 1). According to their NISP value, isolated teeth are dominant in the assemblage (74%). The second and third major groups are mandibles and vertebrae with 7 and 4%, respectively.

Based on the MNI calculation the small mammal assemblage represents at least 242 individuals (Fig. 1). In a similar way to the NISP values, 75% of the MNI was retrieved from the lower breccia, and arviculids are the most abundant group (with 55% of the total MNI). Mice contribute with approximately 14% and shrews with 12% to the total MNI, whereas the other groups are only subordinately represented (with <7%).

According to the relative abundance calculations, all of the studied skeletal elements are underrepresented compared to their expected number. Based on the MNI of small mammals, it seems that 69% of the isolated teeth and 67% of the mandibles were found at the site, thus these are the best represented elements. Maxillary fragments (30%) and femurs (32%) are approximately equally represented, whereas 10–25% of the other limb bones were found. Vertebrae are only subordinately represented with a  $R_i$  around 1% (Fig. 5A).

The NISP and the MNI have a similar distribution along the entire section based on the taphonomical samples, which means that the MNI values are higher where the number of found remains is also higher (Fig. 1; Supplementary Table 1). Fitting a linear regression on the data, the determination coefficient was 0.95. However, the average NISP/MNI ratio is 20.8 (with a standard deviation of 4.1) for the lower breccia and 12.1 for the upper silt (with a standard deviation of 3.8). A Kolmogorov-Smirnov test based on the latter parameter also rejected the null hypothesis that the samples from the lower breccia and from the upper light yellowish brown silt were drawn from the same distributions at a 0.05 alpha level. Consequently, the materials from the two different sedimentological units were treated here separately from now on.

In the lower breccia, predation marks were observed on 14% of the studied small mammal remains. Only 17% of the specimens were abraded and 8% was affected by weathering. In the upper light yellowish brown silt, 22% of the remains were digested, 23% were abraded and 20% were affected by weathering (Fig. 5B). The Kolmogorov-Smirnov tests based on these parameters rejected the null hypotheses that the samples from the lower breccia and from the upper light yellowish brown silt were drawn from the same distributions at a 0.05 alpha level.

Comparing the total arvicolid MNI based abundances of different taxa in the taphonomical samples and the material collected by Jánosy, it seems that the two distributions are similar to each other (although the taphonomical sampling had a lower resolution, thus fewer abundance peaks are visible). The two most common arviculids (*Prolagurus pannonicus* and *Microtus (Terricola)* spp.) were chosen from the taphonomical material for testing this hypothesis (Fig. 6). Linear regressions were fitted to the percent abundance of these taxa from both samplings. The determination coefficients were high (0.77 and 0.78, respectively), which supports the aforementioned similarity. According

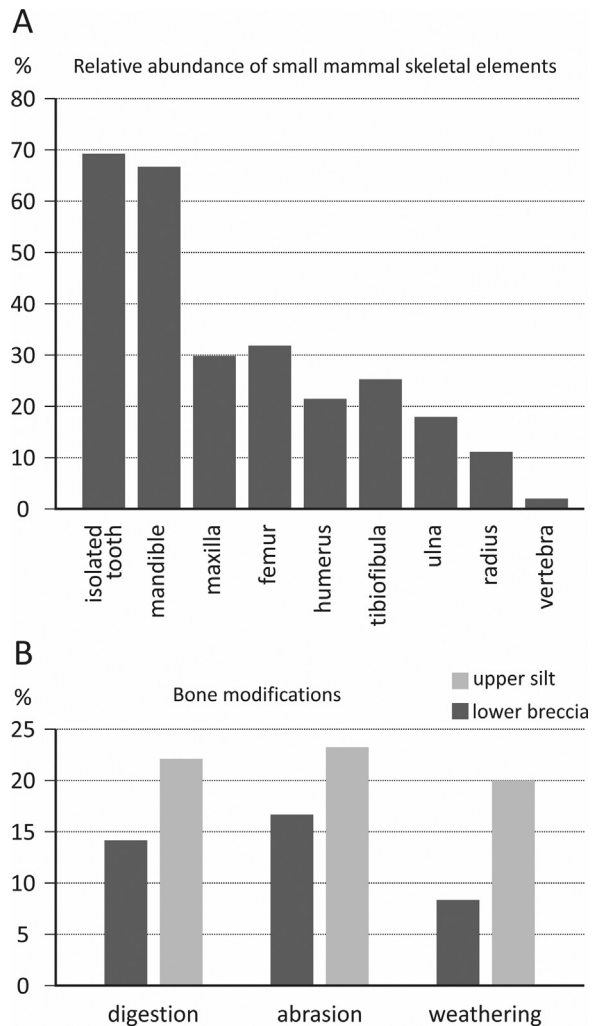


Fig. 5. Taphonomical parameters of the small mammal bones found in the 15 taphonomical samples: A) relative abundance of different skeletal elements, B) modifications observed on the bones and teeth.

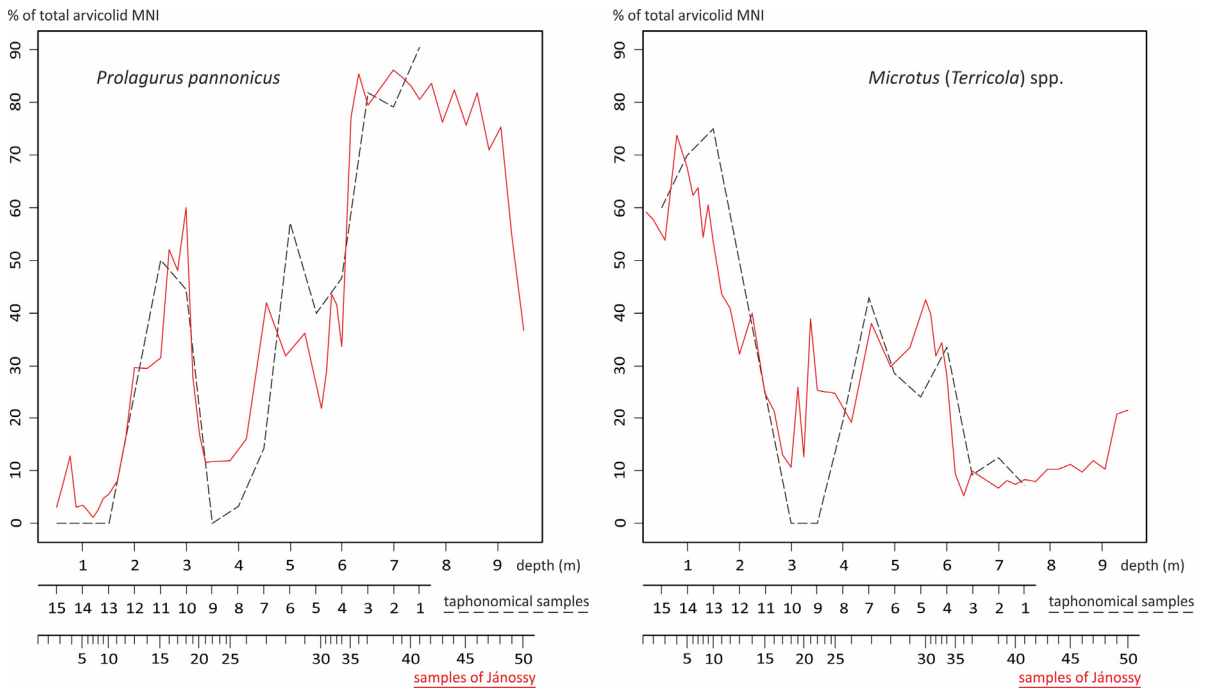
Fig. 5. Paramètres taphonomiques des os de petits mammifères trouvés dans les 15 échantillons taphonomiques : A) abondance relative de différents éléments de squelette, B) modifications observées sur les os et les dents.

to these results, the abundance based conclusions that were drawn using the material collected by Jánosy were accepted as being generally valid for the site. In addition, the paleoecological results presented in this article (see below) were based on the small mammals and the herpetofaunal elements of the original, richer collection.

### 3.4. Abundance based palaeoecological units

The principal component analysis showed that amongst the small mammals, *Prolagurus pannonicus* and *Microtus (Terricola) arvalidens* have the greatest contributions to PC1, which explained 68% of the total variance. Within the herpetofauna, *Bufo viridis* and *Natrix tessellata* explain also a great part of the variance along the same axis. PC2 and PC3 explain 12 and 6% of the total variance, respectively.





**Fig. 6.** Comparison of the total arvicolid MNI based abundances of *Prolagus pannonicus* and *Microtus (Terricola)* spp. from the 15 taphonomical samples and from the rich material collected by Jánosy.

**Fig. 6.** Comparaison des abondances totales de MN1 d'arvicolidés entre *Prolagus pannonicus* et *Microtus (Terricola)* spp. établie à partir des 15 échantillons taphonomiques et du matériel abondant récolté par Jánosy.

Besides the above-mentioned four taxa, *Microtus (Microtus) nivaloides* and the *Clethrionomys hintonianus-kretzoi* group have the highest loading values related to the latter components. Based on the abundance changes of these taxa, the entire section can be divided into five different palaeoecological units (two in the lower breccia and three in the upper silt; Fig. 1, Fig. 7).

Unit 1 – Between 9.0–6.0 m (i.e. samples 50–35 of Jánosy), *Prolagus pannonicus* and *B. viridis* are the dominant species (with 57% of the small mammal MNI and 81% of the herpetofaunal MNI, respectively). Compared to these, the other taxa are very scarcely represented in this unit.

Unit 2 – Between 6.0–3.8 m (i.e. samples 34–26 of Jánosy), *Microtus (Terricola) arvalidens* and *P. pannonicus* occur with equal abundances (each represents 22% of the small mammal MNI). Similarly, *B. viridis* and *N. tessellata* are equally important elements in the herpetofauna (each of them contributing with 26% to the herpetofaunal MNI). Comparing with the previous unit, the abundances of *P. pannonicus* and *B. viridis* decrease, whereas those of *M. (T.) arvalidens* and *N. tessellata* increase. *M. (M.) nivaloides* remains infrequent, but the abundance of *Clethrionomys* slightly increases. The upper boundary of this unit coincides with the sedimentological boundary between the lower breccia and the upper silt.

Units 3 and 4 – Between 3.8–2.0 m (i.e. samples 25–13 of Jánosy), *P. pannonicus* has a moderate abundance peak (23%), whereas *M. (T.) arvalidens* has a local minimum. However, based on *M. (M.) nivaloides* and *Clethrionomys*, this section can be divided into two different units with a boundary at 3.0 m (between samples 19 and 18 of Jánosy).

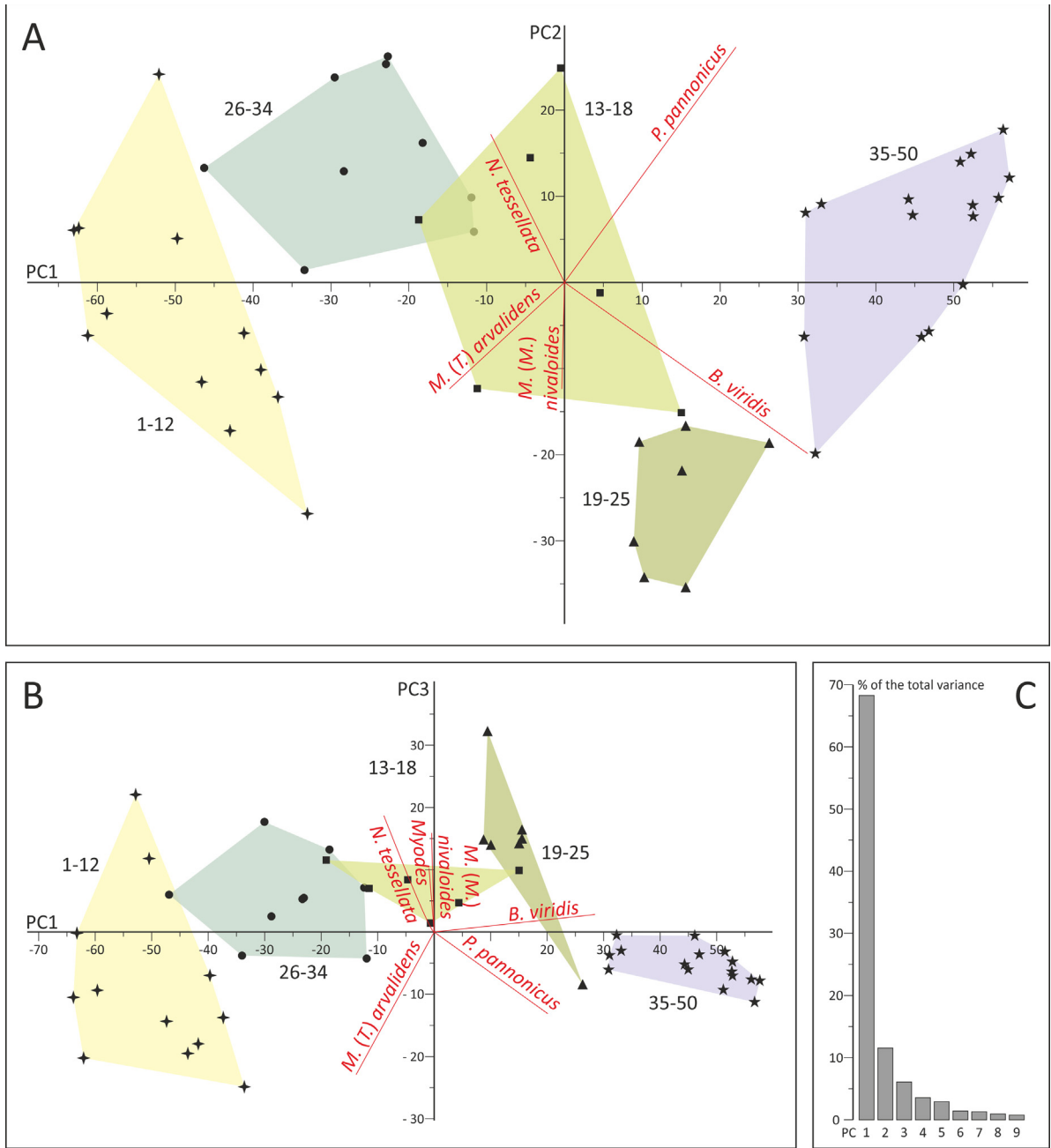
Both of the latter taxa have abundance peaks (24 and 10%) in Unit 3 between 3.8–3.0 m, whereas their importance slightly decreases (to 14% and 6%, respectively) in Unit 4 from 3.0 m to 2.0 m. Amongst the herpetofaunal elements, *B. viridis* is the dominant species (72%) in Unit 3, whereas *N. tessellata* is very scarcely represented. Unfortunately, the herpetofaunal signal becomes unreliable above 3.0 m, because the MNI for the samples drops to around 50 or below.

Unit 5 – Above 2.0 m, *M. (T.) arvalidens* becomes dominant (44%), whereas *P. pannonicus* and *Clethrionomys* are scarcely represented. The abundance of *M. (M.) nivaloides* is also decreases, but it remains slightly higher (9%) than in Units 1 and 2.

## 4. Discussion

### 4.1. Origin and transport of sediments and fossils

The red clay in the lower part of the cavity is a weathering product. It originates at least partly from outside the cavity, as shown by the lack of well-developed in situ soil micromorphological features and by the presence of rounded, redeposited and water-transported red clay and calcrete fragments (Fig. 2C, E). Dominantly angular and subangular clasts from the host limestone suggest transport from a very short distance by water (e.g. sheet wash) or by gravity processes. Sand-sized angular fossil fragments were probably moved by water, either into or within the sediment.



**Fig. 7.** PCA analysis performed on the normalized MNI values of the small mammals and the herpetofaunal elements within the rich material collected by Jánosy (further discussion in the text). A) and B) show the results, whereas C) depicts the variances explained by the first nine principal components.

**Fig. 7.** Analyses PCA réalisées sur les valeurs normalisées MNI des petits mammifères et des éléments herpétofauniques sur l’abondant matériel collecté par Jánosy (voir discussion dans le texte). A) et B) montrent les résultats, tandis que C) illustre les variances explicitées par les neuf premières composantes principales.

The bulk of the silt material may have easily been carried by the wind, supported beside the grain size by the high porosity and lack of visible water-induced sedimentary structures (like lamination; Fig. 2A, D). There is no sandy sediment in the immediate surroundings of the fossil site to be washed in by water, therefore sand-sized quartz grains also support aeolian transport. Based on the results of Viczián (2002) and Dezsó et al. (2007), the light yellow

colour of the upper silt is the result of the high calcite and minor iron mineral (dominantly goethite) content.

As the site was located on a hilltop already at the time of deposition (Sebe et al., 2015), and because their angular form indicates transport from very small distance, dripstone fragments cannot have originated from outside the cavity. Because flowstone was precipitated onto silt and clay, the most plausible explanation to the formation

of these fragments is that water flowing down the karstic cavity undermined the flowstone coatings on the silt or clay surfaces, which fell down and broke into pieces (Fig. 2C).

The strong carbonate cementation, the irregular cracks and voids lined with calcite crystals as well as the iron-oxide stains indicate alternating wetting and drying of the sediment (Stoops et al., 2010; Tucker and Wright, 1990). Ample flowstone coatings, the formation of flowstone fragments, and several cm large open voids suggest that there was vertical water flow – at least percolation – in parts of the cavity, which could generate material movement. This process could have resulted in the low NISP value above 3.8 m. It is, however, more plausible that the silt-clay matrix was washed downward in the cavity rather than the fossils themselves, thus increasing the density of bones within the sediment, especially in the lower part. Water flow must have become substantially reduced after the pervasive cementation of the deposits occurred (Fig. 1). However, the dominance curves depicted on Fig. 1 show alternating peaks of the species with different environmental preferences (see the discussion in Section 4.2). In a sequence where the material movement changed the original position of the fossils the dominance changes would not be so regular, which further strengthens the idea that the material movement was not a substantial factor.

The low percentage of abraded bones (Fig. 5B) indicates that most of the small mammal remains were not exposed to long-term or excessive physical impacts before final burial. However, this does not imply that the fossils were not accumulated by water, because microvertebrate bones can be transported in suspension for a relatively long period without notable abrasion (Behrensmeyer, 1975; Dodson, 1973). In addition, only a few bones were affected by weathering in the taphonomical samples, which suggests (according to Andrews, 1990 and Behrensmeyer, 1978) that the bulk of the material was buried within a short period after the death of the animals.

The relative abundance of different skeletal elements in an observed sample is important for assessing, e.g., the presence and extent of fluvial transport that affected the material before deposition (Andrews and Evans, 1983; Behrensmeyer, 1975; Dodson, 1973; Lyman, 1994). If material has been moved to a distal accumulation place before the final burial, there should be an increase in the relative abundance of vertebrae compared with that of jaws and teeth (Andrews and Evans, 1983; Dodson, 1973). In the case of the small mammals in the taphonomical samples, it seems that the relative abundance values (with a few vertebrae, more limb bones and many cranial elements) show a reverse distribution considering the number of elements in a complete skeleton (Fig. 5A). The high relative abundance of mandibles and teeth suggests that the place of the initial deposition could not be far from the cavity and the effects of water transport are not remarkable (Andrews and Evans, 1983; Dodson, 1973). The low abundance of small mammal vertebrae in the studied assemblage could be explained by two causes: (1) The vertebrae are more sensitive against the destructive environmental effects (such as temperature fluctuations, trampling or cave corrosion) than the other

parts of the skeleton, because they are more porous and their density is low, thus they can be rapidly degraded before or after the burial (Behrensmeyer, 1975). (2) For the same reasons, they can be transported easier than the larger, heavier and denser limb bones, thus the vertebrae of a disarticulated skeleton can be easily eliminated from the assemblage by a water current (Behrensmeyer, 1975; Dodson, 1973; Voorhies, 1969). Although both processes could have contributed to the observed low abundance, the first scenario seems more plausible, because the locality is a relatively closed karst cavity with a corrosive environment.

These taphonomic data are in good agreement with the sedimentological observations. The relatively mobile bones are rare in the small mammal assemblage, whereas the heavier and denser remains (such as teeth, mandibles and limb bones) are better represented (similarly to a lag deposit; Behrensmeyer, 1982). The low proportion of weathered and abraded bones together with the relative abundance calculations suggest that the effects of the water transport were limited and the remains were plausibly transported into the cavity from the close proximity of the site, similarly to the red clay and calcrete fragments in the sediment. Excessive water transport often results in a mixture of different assemblages, which remarkably alters the structure of the original living community and makes palaeoecological reconstruction more difficult. However, this is not the case in the Somssich Hill 2 site, because it can be interpreted as a proximal accumulation (such as Andrews and Evans, 1983).

Predation is one of the most common processes that can create remarkable bone concentrations (Andrews, 1990; Andrews and Evans, 1983; Dodson and Wexlar, 1979; Fernandez-Jalvo et al., 2016; Stoetzel et al., 2011; Sukselainen et al., 2017). The fact that predation marks found at the site could only be classified into the light digestion category (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992), suggests that the contact with the stomach acid of the predator lasted for only a short period of time (Fernandez-Jalvo et al., 2016). The digestion concentrated at the tips of rodent incisors and at the occlusal edges of the arvicolid molar crowns. It seems that most of the teeth were in situ in their alveoli at the time of digestion. These observations together with the low abundance of digested bones (Fig. 5B) are not consistent with an assemblage accumulated by mammalian predators that have a long digestion period. However, Andrews (1990) described similar taphonomical characteristics in the case of owl pellets. It seems that pellets dropped near the direct surroundings of the karstic cavity could be a factor that contributed to the accumulation of the bones.

Although herpetofaunal remains from the taphonomical material were not studied here, they are abundant in the samples collected by Jánossy. According to Szentesi (2014, 2016), the high abundance of juvenile specimens and the presence of several articulated vertebral rows in the material together with the lack of abrasion, weathering and digestion marks suggest that these elements were most likely not transported to an appreciable distance from their original habitat, but living individuals fell into the cavity probably related to their annual breeding migrations.

#### 4.2. Palaeoecological interpretation

The extreme dominance of *Prolagurus pannonicus* in Unit 1 suggests an open environment, most likely a steppe (Fig. 1). This is supported by the fact that *Cricetus runtonensis* and *Sorex runtonensis* have their highest abundances in this part of the section (11 and 19% of the MNI, respectively), because both taxa preferred open habitats. Besides, *S. runtonensis* is an indicator of cold environments according to Osipova et al. (2006).

The decreasing importance of vole lemmings in Unit 2 suggests a minor closure of the vegetation. It is also supported by an abundance peak of *Apodemus sylvaticus* (with a maximum of 15%) and the slight increase in the abundance of *Clethrionomys* (to around 6%). The abundance peak of *Natrix tessellata* within this unit suggests a semi-closed environment with an open water surface in the close proximity of the site (Amr et al., 2011; Mebert et al., 2011; Žagar et al., 2011). The decrease in the abundance of *Bufo viridis* compared to the previous unit might be related to the fact that these animals avoided the closest proximity of the nearby waterbody (Böhme et al., 2006). The fact that *Microtus (Terricola) arvalidens* becomes more abundant in this unit might be related to a slight increase in temperature (see the discussion of Unit 5 for more details).

The moderate abundance peak of *Prolagurus pannonicus* together with the local minimum of *M. (T.) arvalidens* suggest that the temperature dropped at the beginning of Unit 3. Based on the reappearance of *B. viridis* and the decline of *N. tessellata*, the above-mentioned open water surface probably disappeared from the close proximity of the site. However, the overall humidity was most likely higher than in Unit 1, because the abundance peak of *Clethrionomys* suggests at least a semi-closed vegetation. It seems that *Microtus (Microtus) nivaloides* and *Microtus (Terricola) hintoni* preferred a similar environment as the latter taxon. The environment remained similarly cold at the beginning of Unit 4, but a slightly more open vegetation returned, indicated by a slight decrease of these three taxa. The scarcity of *A. sylvaticus* in Unit 3 can be explained by the cold temperature, whereas the slight increase in its abundance suggests a minor warming event at the end of Unit 4.

The cooling at the beginning of Unit 3 was also detected by Krolopp (2000). However, based on the continental snail fauna of the upper silt, he was not able to differentiate Units 3 and 4. He reconstructed a karst shrubland for these two parts of the section. Viczián (2002) and Dezső et al. (2007) studied clay minerals of the upper 4.5 m of the section. Based on their results, the substitution of kaolinite with chlorite above 3.8 m can also be interpreted as the result of cooling.

According to Krolopp (2000), the uppermost part of the silt (Unit 5) represents a xerothermic grassland. *Crociodura*, which also prefers warm and dry climate with open vegetation (Osipova et al., 2006), is scarcely present in the entire section, but its only abundance peak coincides with this unit. The open environment is also supported by the scarcity of *Clethrionomys*, whereas the warm climate is further strengthened by the extremely rare occurrence of *P. pannonicus*. The dominant small mammal of Unit 5 is *M. (T.) arvalidens*, which also has its highest abundance

values in this part of the section. It suggests that this species could be a good indicator of warm and dry climate with open habitats.

#### 5. Conclusions

According to the detailed biostratigraphic interpretation of the revised fauna, the Somssich Hill 2 assemblage contains mainly a late early Pleistocene fauna that can be correlated with the *Mimomys savini*–*Mimomys pusillus* Biozone in the Biharian (MQ1). In addition, the rich mammal material shows some features which are characteristics of the so-called Epivillafranchian faunal turnover. The age was also confirmed by ESR dating with a resulting median of 1.0 Ma. In addition, the fauna contains a few specimens that suggest an older age, namely the *Mimomys pliocaenicus* Biozone in the late Villanyian (MN17).

The sedimentological analysis showed that the red clay in the lower breccia is a weathering product, whereas the clasts and bone fragments within the matrix were most likely affected by short-distance water transport. The material of the upper yellowish brown silt could be interpreted as resulting, at least partly, from aeolian transport. Thus, this could be one of the oldest dated loess-like sediment in the region.

The low proportion of abraded and weathered small mammal bones together with the fact that the relatively mobile elements are rare in the assemblage suggests that the remains were probably transported into the cavity from the close proximity of the site. Digestion marks are rare, and only light digestion was observed on the bones, which suggest that the material was at least partly accumulated as owl pellets. As a parautochthonous and relatively unaltered assemblage, the Somssich Hill 2 material is considered as a reliable base for reconstructing the direct palaeoenvironment of the cavity. A strong linear correlation was shown between abundance changes within the taphonomical samples and within the material collected by Jánossy. Consequently, palaeoecological units were established here based on the small mammals and herpetofaunal elements from the latter, because it yielded a considerably richer material than the taphonomical sampling.

Considering the results of a PCA analysis, the section was divided into five different palaeoecological units. Unit 1 was interpreted as a cold steppe, whereas Unit 2 was most likely a semi-closed environment with an open water surface in the close proximity of the site. The temperature dropped, but the overall humidity increased at the beginning of Unit 3, which can be characterized with the most closed vegetation within the studied section (probably a karst shrubland). Unit 4 was slightly more open and the temperature started to increase at the end of this phase. Unit 5 was probably a warm and dry grassland.

#### Funding

This project was financially supported by the National Research, Development and Innovation Office (NKFI K 104506, NKFI K 116665, NKFI PD 104937). This paper is MTA-MTM-ELTE Paleo Contribution No. 246.

## Acknowledgements

The authors are grateful to Alexey Tesakov, János Hír and Andrea Mindszenty for useful data and consultations, and to Szabolcs Leél-Össy for his essential help with the excavations. The colleagues at the Department of Palaeontology and Geology of the Hungarian Natural History Museum and at the MTA-MTM-ELTE Paleontological Research Group are also acknowledged.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2017.06.007>.

## References

- Amr, Z.S., Mebert, K., Hamidan, N., Abu Baker, M., Disi, A., 2011. Ecology and Conservation of the Dice Snake (*Natrix tessellata*) in Jordan. *Mertensiella* 18, 393–400.
- Andrews, P., 1990. Owls, caves and fossils. University of Chicago Press, Chicago, 231 p.
- Andrews, P., Evans, E.M.N., 1983. Small mammal bone accumulations produced by mammalian carnivores. *Paleontol. Soc.* 9 (3), 289–307.
- Antoñanzas, R.L., Cuenca Bescós, G., 2002. The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 186, 311–334.
- Badgley, C., 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaio* 1, 328–338.
- Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bull. Mus. Comp. Zool.* 146, 473–578.
- Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4 (2), 150–162.
- Behrensmeyer, A.K., 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* 8 (3), 211–227.
- Böhme, M., Ilg, A., Ossig, A., Küchenhoff, H., 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. *Geology* 34 (6), 425–428.
- Botka, D., Mészáros, L., 2014. *Beremendia* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Southern Hungary) and their taxonomic, biostratigraphical, palaeoecological and palaeobiogeographical relations. *Fragm. Palaeont. Hung.* 31, 83–115.
- Botka, D., Mészáros, L., 2015a. A Somssich-hegy 2-es lelőhely (Villányi-hegység) alsó-pleisztocén *Beremendia fissidens* (Mammalia, Soricidae) maradványainak taxonómiai és paleoökológiai vizsgálata. [Taxonomic and palaeoecological studies on the Lower Pleistocene *Beremendia fissidens* (Mammalia, Soricidae) remains of the Somssich Hill 2 locality (Villány Hills)]. *Földt. Közl.* 145 (1), 73–84 (in Hungarian, with English abstract).
- Botka, D., Mészáros, L., 2015b. *Crocidura* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, Southern Hungary). *Fragm. Palaeont. Hung.* 32, 67–98.
- Botka, D., Mészáros, L., 2016. *Sorex* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, Southern Hungary). *Fragm. Palaeont. Hung.* 33, 135–154.
- Dezső, J., Rauscik, B., Viczián, I., 2007. Villányi-hegységi karsztos hasadékkitöltések szemcseösszetételei és ásványtani vizsgálata. Granulometric and mineralogical analysis of karstic fissure filling sediments in the Villány Mts. (S Hungary). *Acta GGM Debrecina* 2, 151–180.
- Dodson, P., 1973. The significance of small bones in paleoecological interpretation. *Contrib. Geol. Univ. Wyo.* 12, 15–19.
- Dodson, P., Wexlar, D., 1979. Taphonomic investigations of owl pellets. *Paleobiology* 5 (3), 275–284.
- Fernandez-Jalvo, Y., Andrews, P., 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *J. Archaeol. Sci.* 19, 407–428.
- Fernandez-Jalvo, Y., Andrews, P., 2003. Experimental effects of water abrasion on bone fragments. *J. Taphon.* 1 (3), 147–163.
- Fernandez-Jalvo, Y., Andrews, P., Denys, C., Sesé, C., Stoetzel, E., Marin-Monfort, D., Pesquero, D., 2016. Taphonomy for taxonomists: Implications of predation in small mammal studies. *Quat. Sci. Rev.* 139, 138–157.
- Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D., 1997. Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Riv. Ital. Paleontol.* 103 (3), 369–388.
- Grayson, D.K., 1973. On the methodology of faunal analysis. *Am. Antiq.* 39 (4), 432–439.
- Grayson, D.K., 1984. *Quantitative Zooarchaeology: Topics in the analysis of archaeological faunas*. Academic Press, Orlando, Florida, 202 p.
- Hillson, S., 2005. *Teeth*. Cambridge University Press, Cambridge, 388 p.
- Hír, J., 1997. A short sketch of the evolution and stratigraphy of the Plio-Pleistocene cricetids (Rodentia, Mammalia) in Hungary. *Folia Hist. Nat. Mus. Matraensis* 22, 43–49.
- Hír, J., 1998. Cricetids (Rodentia, Mammalia) of the Early Pleistocene vertebrate fauna of Somssich Hill 2 (Southern Hungary, Villány Mountains). *Ann. Hist. Nat. Mus. Nat. Hung.* 90, 57–89.
- Jánossy, D., 1983. Lemming-remain from the Older Pleistocene of Southern Hungary (Villány, Somssich Hill 2). *Fragm. Palaeont. Hung.* 11, 55–60.
- Jánossy, D., 1986. *Pleistocene vertebrate faunas of Hungary*. Akadémiai Kiadó, Budapest, 208 p.
- Jánossy, D., 1990. Arvicolidis from the Lower Pleistocene sites at Beremend 15 and Somssich-hegy 2, Hungary. In: Fejfar, O., Heinrich, W.D. (Eds.), *International Symposium of Evolution, Phylogeny and Biostratigraphy of Arvicolidis*. Geological Survey, Prague, pp. 223–230.
- Kormos, T., 1937. Zur Geschichte und Geologie der oberpliozänen Knochenbreccien des Villányer Gebirges. *Matemat. Termesztudom. Ert.* 56, 1061–1110.
- Korth, W.W., 1979. Taphonomy of microvertebrate fossil assemblages. *Ann. Carnegie Mus.* 48, 235–285.
- Kos, A.M., 2003. Characterisation of post-depositional taphonomic processes in the accumulation of mammals in a pitfall cave deposit from southeastern Australia. *J. Archaeol. Sci.* 30, 781–796.
- Kretzoi, M., 1956. A Villányi-hegység alsó-pleisztocén gerinces faunái. Lower Pleistocene vertebrate faunas of Villány Hills. *Geol. Hung., Ser. Pal.* 27, 1–264 (in Hungarian).
- Krolopp, E., 2000. Alsó-pleisztocén Mollusca-fauna a Villányi-hegységből (Lower Pleistocene mollusc fauna from the Villány Mts. (Southern Hungary)). *Malakol. Tajekozt.* 18, 51–58 (in Hungarian, with English abstract).
- Lyman, R.L., 1994. *Vertebrate taphonomy*. Cambridge University Press, 524 p.
- Lyman, R.L., 2008. *Quantitative paleozoology*. Cambridge University Press, 348 p.
- Matthews, T., 2006. Taphonomic characterisation of micromammals predated by small mammalian carnivores in South Africa: application to fossil accumulations. *J. Taphon.* 4 (3), 143–161.
- Maul, L.C., Markova, A., 2007. Similarity and regional differences in Quaternary arvicolid evolution in central and eastern Europe. *Quatern. Int.* 160 (1), 81–99.
- Mebert, K., Conelli, A.E., Nembrini, M., Schmidt, B.R., 2011. Monitoring and Assessment of the Distribution of the Dice Snake in Ticino, southern Switzerland. *Mertensiella* 18, 117–130.
- Mészáros, L., 2015. Palaeoecology of the Early Pleistocene Somssich Hill 2 locality (Hungary) based on *Crocidura* and *Sorex* (Mammalia, Soricidae) occurrences. *Hantkeniana* 10, 147–152.
- Nadachowski, A., 1990. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. *Quartärpaläontologie* 8, 215–223.
- Osipova, V.A., Rzebik-Kowalska, B., Zaitsev, M.V., 2006. Intraspecific variability and phylogenetic relationships of the Pleistocene shrew *Sorex runtonensis* (Soricidae). *Acta Theriol.* 51 (2), 129–138.
- Petronio, C., Bellucci, L., Martinetto, E., Pandolfi, L., Salari, L., 2011. Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in central Italy. *Geodiversitas* 33 (3), 485–517.
- Petrucci, M., Cipullo, A., Martínez-Navarro, B., Rook, L., Sardella, R., 2013. The Late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontogr. Abt. A Palaeozool. Stratigr.* 298 (1–6), 113–145.
- Popov, V.V., Marinska, M., 2007. An almost one million year long (Early to Late Pleistocene) small mammal succession from the archaeological layers of Kozarnika Cave in northern Bulgaria. *Cour. Forsch. Inst. Senck.* 259, 79–92.

- R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rekovets, L., Nadachowski, A., 1995. Pleistocene voles (Arvicolidae) of the Ukraine. *Paleontol. Evol.* 28–29, 145–245.
- Rockenbauer, A., Korecz, L., 1996. Automatic computer simulations of ESR spectra. *Appl. Magn. Res.* 10, 29–43.
- Sebe, K., Pazonyi, P., Gasparik, M., Szujó, G.L., 2015. Uplift history of the Villány Hills (SW Hungary) based on paleontological data. *Geophys. Res. Abstr.* 17 (Paper 13518).
- Stoetzel, E., Marion, L., Nespoulet, R., El Hajraoui, M.A., Denys, C., 2011. Taphonomy and palaeoecology of the late Pleistocene to middle Holocene small mammal succession of El Harhoura 2 cave (Rabat-Témara, Morocco). *J. Hum. Evol.* 60, 1–33.
- Striczky, L., Pazonyi, P., 2014. Taxonomic study of the dormice (Gliridae, Mammalia) fauna from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, South Hungary) and its palaeoecological implications. *Fragm. Palaeont. Hung.* 31, 51–81.
- Stoops, G., Marcelino, V., Mees, F., 2010. Interpretation of Micromorphological Features of Soils and Regoliths. Elsevier, 720 p.
- Sukselainen, L., Peltonen, H., Kaakinen, A., Zhao-Qun, Z., 2017. Small mammal taphonomy of three Miocene localities from Damiao, Nei Mongol, China. *Vertebr. Palasiat.* 55 (1), 71–88.
- Szentesi, Z., 2014. Előzetes eredmények a késői kora-pleisztocén Somssich-hegy 2 (Villányi-hegység) ősgerinces-lelőhely kétéltűinek vizsgálatában. [Preliminary results on a study of amphibians of the late early Pleistocene Somssich Hill 2 palaeovertebrate locality (Villány Hills)]. *Földt. Közl.* 144 (2), 165–174 (in Hungarian with English abstract).
- Szentesi, Z., 2016. Urodeles from the lower Pleistocene Somssich Hill 2 palaeovertebrate locality (Villány Hills, Hungary). *Földt. Közl.* 146 (16), 37–46.
- Tesakov, A.S., 2004. Biostratigraphy of Middle Pliocene–Eopleistocene of eastern Europe (based on small mammals). Moscow, Nauka, 247 p. (in Russian).
- Tucker, M.E., Wright, V.P., 1990. Carbonate sedimentology. Blackwell, 482 p.
- Vasileiadou, K., Hooker, J.J., Collinson, M.E., 2007. Taphonomic evidence of a Paleogene mammalian predator–prey interaction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 243, 1–22.
- Viczián, I., 2002. Clay mineralogy of Quaternary sediments covering mountainous and hilly areas of Hungary. *Acta Geol. Hung.* 45 (3), 265–286.
- Voorhies, M.R., 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *Contrib. Geol. Univ. Wyo.* 1, 1–69.
- Žagar, A., Krofel, M., Govedič, M., Mebert, K., 2011. Distribution and Habitat Use of Dice Snakes (*Natrix tessellata*) in Slovenia. *Mertensiella* 18, 207–216.