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A new middle Pleistocene small vertebrate fauna from the Nagyharsány Crystal Cave (Villány Hills, Southern Hungary)

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Abstract – The Nagyharsány Crystal Cave in the Villány Hills (Southern Hungary) has yielded a very rich assemblage of small vertebrate material, mainly consisting of isolated frog bones. The systematic collection involved sampling from several levels in three different sites. During the detailed taxonomic processing of the vertebrate material, a total of 78 taxa were identified. In addition to the rich herpetofauna, birds as well as small and large mammal remains were found. Preliminary palaeoecological studies have also been carried out on material from Site I. The small vertebrates of the lower levels indicate a warmer, moister, and more closed environment. Towards the top of the series, this gradually changes to a cooler, drier, more open one. The taxonomic, allometric, and palaeoecological results also allowed the stratigraphic position of the sites to be determined. We found that the material from the Nagyharsány Crystal Cave is most resembling to the material from the MIS 11 sites of the Vár Cave (Budapest). With 3 figures and 3 tables.

Key words – middle Pleistocene, MIS 11, vertebrates, palaeoecology, biostratigraphy

INTRODUCTION

Villány Hills in the south of Hungary are known to palaeontologists mainly for their very rich vertebrate sites. More than 50 localities have been discovered in this area, which are correlated with Pliocene as well as early and/or middle Pleistocene. These sites are located near four settlements, Csarnóta, Beremend, Nagyharsány, and Villány, within an area of about 25 km. The older (Pliocene) sites are near Csarnóta and on the Szőlő Hill of Beremend (several early Pleistocene sites have also been described on the latter), while early and middle Pleistocene faunas are known from the Templom and Somssich Hills near Villány and from the Szársomlyó Hill near Nagyharsány. Most of the sites were processed in the 20th century (e.g., Kormos 1937; Kretzoi 1956; Jánossy 1986; Kordos 1991; Hír 1998), but recently an increasing number of vertebrate palaeontologists have been working on these previously collected materials, discovering and publishing new fossil sites (e.g., Pazonyi *et al.* 2018*a*).

The Nagyharsány Crystal Cave is located on Szársomlyó Hill, north of Nagyharsány village (Fig. 1). It was officially discovered by Katalin Takács-Bolner and her colleagues in April 1994, although anthropogenic deposits near the entrance suggest that it may have happened earlier, probably by miners, amateur collectors, or possibly cavers (Vigassy & Leél-Őssy 2001). The cave, 550 meters long and vertically extensive, was mapped by Takács-Bolner and her colleagues and was found to contain two distinct levels. The upper part contains large chambers covered with stalactites, stalagmites, and botryoids, while the lower part is characterised by calcite layers, overlain by hot mineral calcite crust and stalactites.

The Nagyharsány Crystal Cave was formed in tectonic fissures in the lower and middle Cretaceous Nagyharsány Limestone. The main rock of this formation is 99.5% calcium carbonate. The deposits of the cave, in addition to carbonate minerals, contain quartz, sericite/illite, chlorite, smectite, ankerite and anorthosite, too. These above-mentioned minerals are derived from external materials transported to the cave by surface waters (Vigassy & Leél-Őssy 2001).

In some parts of the Nagyharsány Crystal Cave, especially at the end of the western branch, thick fine sandy clay is deposited, which is very rich in small vertebrate fossils, especially isolated frog bones. The first vertebrate remains from the cave were collected by Sándor Kraus in 1995. The next sampling took place in 1999, when Piroska Pazonyi collected a sample of the red clay accumulated at the western end of the cave (Fig. 1). According to the preliminary study by László Kordos, the small mammals recovered from this sample can be dated to the late Pleistocene or early Holocene (Vigassy & Leél-Őssy 2001). Finally, Pazonyi and her colleagues carried out a systematic collection in October 2012 in the western branch of the cave (Fig. 1).

The systematic collection involved sampling from several levels in three different sites. Most samples (I/-1 to I/6) were collected from Site I, where the clayey sediment of a roughly vertical 3 m high fissure fill was sampled in seven levels from the floor to the top of the cave. At Site II, a clayey deposit on a stalactite, a total of four samples (II/1 to II/4) were collected from different levels. Site III is very close to Pazonyi's 1999 sampling site, but while the latter is at the cave floor level (III/1 = Pazonyi's 1999 site), the newly collected material is from the slightly rising stalactite surface above it (III/2; Fig. 1).

The material from all the above-mentioned collections are discussed in this paper, but the research was mainly based on the material from the 2012 systematic collection.

MATERIAL AND METHODS

The small vertebrate remains described in this study were recovered from three different collections [Sándor Kraus (1995), Piroska Pazonyi (1999) and the systematic collection by Pazonyi and her colleagues (2012)] from the fine sandy clay (with small calcite crystals and limestone debris) sediments of the cave. In addition to these, a few sporadic finds from the cave were also collected by Pazonyi and her colleagues in 2012.

The collected material was washed through a 0.5 mm sieve in the laboratory of the Department of Palaeontology and Geology at the Hungarian Natural History Museum. The small fossils were sorted out under a stereo light microscope (Nikon SMZ 445).

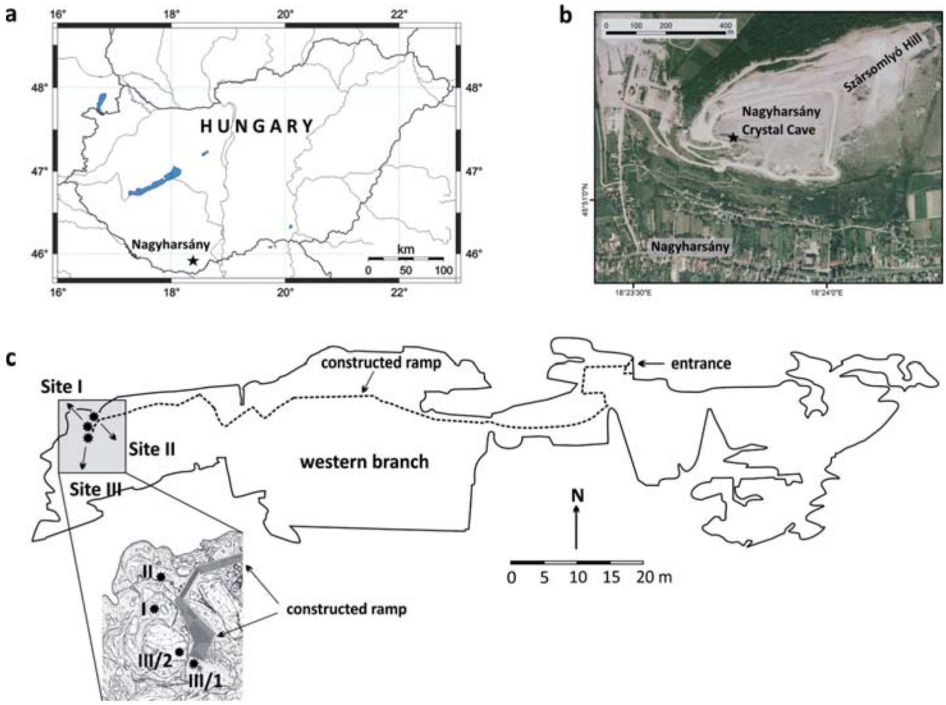

Fig. 1. Location of Nagyharsány Crystal Cave in Hungary (a), on Szársomlyó Hill (b), and the floor plan of the cave with the sites after the National Cave Register (c)

The material contained plant remains as well as bones of fish, amphibians, reptiles, birds, and mammals (Table 1). When calculating MNI (minimum number of individuals) values, all teeth and bones found at one site and determined as the same species were taken into account. We examined at least how many individuals belonging to this species had to occur here for these remains to be found in the site.

TAXONOMIC RESULTS

The fauna of the Nagyharsány Crystal Cave contains 78 vertebrate taxa. Of these, 10 amphibians, 16 reptiles, and 23 mammals were identified to species level. In terms of the number of individuals, frogs, mainly toads, make up the largest part of the material. Compared to the herpetofauna, mammals make up only a minor part of the material, but because of their stratigraphic and palaeoecological importance, we have described some species of this group in more detail. In the taxonomic descriptions, we have emphasised mainly the features relevant to the site, and in several cases, we have included information on the palaeoecology or stratigraphic features of the species in addition to the strict taxonomic features under the heading 'remarks'.

Phylum Vertebrata Linnaeus, 1758
Class Mammalia Linnaeus, 1758
Order Eulipotyphla Waddell *et al.,* 1999
Family Soricidae Fischer von Waldheim, 1817

Abbreviations used in the Soricidae descriptions: I = incisor, A = antemolar, P = premolar, M = molar, M^x = upper tooth, M_x = lower tooth, L = length, W = width, H = height, BL = buccal length, LL = lingual length, AW = anterior width, PW = posterior width. Measurements (in mm) were taken after Reumer (1984).

Subfamily Crocidurinae Milne-Edwards, 1874
Genus *Crocidura* Wagler, 1832

Crocidura obtusa Kretzoi, 1938

Material and measurements – **I/1:** left I^1 (L: 2.114, H: 1.478); right I^1 fragment; left maxillary fragment with P^4-M^2 (P^4 LL: 0.905, BL: 1.643, W: 1.462; M^1 LL: 1.347, BL: 1.358, AW: 1.458, PW: 0.809; M^2 LL: 1.147, BL: 1.152, AW: 1.645, PW: 1.426); left maxillary fragment with P^4 (LL: 1.055, BL: 1.390, W: 1.682); left maxillary fragment with M^1-M^2 (M^1 LL: 1.255, BL: 1.370, AW: 1.495, PW: 1.868;

Table 1. The vertebrate fauna of the Nagyharsány Crystal Cave sites (Sites I, II and III) and other sporadic material from the cave [Knaus 1995 and Pazonyi 2012 (*)] with the minimum number of individuals

taxa	**Sites and collections of Nagyharsány Crystal Cave**													
	Site I							**Site II**				**Site III**		**Knaus**
	I/-1	**I/1**	**I/2**	**I/3**	**I/4**	**I/5**	**I/6**	**II/1**	**II/2**	**II/3**	**II/4**	**III/1**	**III/2**	**1995/***
Plant related fossils														
Celtis sp.				*										
microcodiums		48	3										1	
Pisces														
Pisces indet.			1		1									
Amphibia and Reptilia														
Triturus cristatus	1		1	1	1	1						2	1	
Lissotriton vulgaris		3	1		1							1	1	2
Salamandridae indet.	*	*		*	*	*	*					*	*	*
Bombina variegata	3		3	4		4	1			1			3	6
Bombina sp.	*	*	*	*	*	*	*	*	*			*	*	*
Latonia cf. *gigantea*	1				3	14	5							
cf. *Latonia* sp.				*								*	*	
Alytidae indet.	*		*		*		*	*						
Pelobates fuscus	5	1	1	1	1	1	1	1	1			1	1	2
Bufo bufo	43	34	28	54	14	24	27	13	1	3		9	47	39
Bufotes viridis	921	538	692	863	279	560	778	304	44	111	4	277	817	292
Bufonidae indet.	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Hyla arborea	3	46	22	35	2	78	10	8	3	2		16	55	7
Rana temporaria	1	1	3	3	1	2	4	2		1		2	2	1
Rana cf. *dalmatina*												1		
Pelophylax esculentus group			2	3		1	1						1	5
Ranidae indet.	*	*	*	*			*			*		*	*	
Anura indet.	*	*	*	*	*		*	*	*	*	*	*	*	*
Emys orbicularis			1											
Testudines indet.	*	*			*							*	*	
Podarcis cf. *muralis*				1										
Lacerta cf. *viridis*	1	1	2	2	1							1	1	2
Lacerta sp.														*
Lacertidae indet.	*	*	*	*		*						*	*	
Anguis fragilis		1	1											
Anguidae indet.		*	*	*										
Sauria indet.		*						*				*	*	*
Scolecophidia indet.		1	1	1		1		1				1	1	
Hierophis cf. *viridiflavus*	1	1	2	2	1	1	1					1	1	1
Hierophis gemonensis	1	1								1			1	
Coronella cf. *austriaca*	1		2									1		1
Elaphe cf. *paralongissima*				2										
Elaphe cf. *quatuorlineata*														1
Zamenis longissimus	3	1		2	1	1		1				2	1	1
Natrix natrix	1	1		1	1	1		1		1		1	1	2
Natrix tesselata	3	1		4	1		1	1				1	4	2

Table 1 (continued)

taxa	**Sites and collections of Nagyharsány Crystal Cave**													
	Site I							**Site II**				**Site III**		**Knaus**
	I/-1	**I/1**	**I/2**	**I/3**	**I/4**	**I/5**	**I/6**	**II/1**	**II/2**	**II/3**	**II/4**	**III/1**	**III/2**	**1995/***
Natrix sp.	*	*	*	*	*	*	*	*	*			*	*	*
cf. *Telescopus fallax*		1		1			1						1	
Colubridae indet.	*	*	*	*	*	*	*	*	*	*		*	*	*
Vipera cf. *ammodytes*						1							1	1
Vipera berus			1	1									1	1
Vipera cf. *ursinii*	2					1								
Vipera sp.	*	*	*	*	*	*	*					*	*	*
Aves														
Passeriformes sp. indet.				1	1								1	
Fringillidae sp. indet.					1									
Mammalia														
Rhinolophus sp.				1								1		
Myotis cf. *nattereri/dasycneme*	1	1											1	
Myotis sp. (small)	1		1	1		1			1			1	1	
Talpa sp.													1	
Crocidura obtusa		3	1										2	
Crocidura sp.		1		1		1								
Sorex minutus	1				1									
Sorex araneus	1	1		1		1	1		1				2	
Beremendia fissidens			1											
Asoriculus gibberodon		1												
Ochotona sp.	1							1				1	1	
Spalax sp.				1	1	1							1	1
Spermophilus citelloides	1	1	1	1		1	1	1	1			1	1	
Glis sackdillingensis	1	1	1	1		1							1	
Sicista praeloriger		1	1	1									1	
Sicista sp.						1								
Cricetus praeglacialis		2	1	3		2						2	1	
Allocricetus bursae		1		1	1									
Microtus (*Agricola*) *agrestis*														
Lasiopodomys (*Stenocranius*) *gregalis*		1	1	2		1			1			1	2	
Microtus (*Microtus*) *arvalis*	1	2	3	2	1	1	1	1				2	5	
Microtus (*Alexandromys*) *oeconomus*				1										
Microtus (*Terricola*) sp.		1												
Lagurus transiens		1	1	1				1	2					
Clethrionomys glareolus									1					
Apodemus sylvaticus	1	6	4	3	1	1	1	1	2			1	2	
Mus sp.	1		1	2		1	1	1				2	2	
Mustela nivalis						1		1					1	
Martes martes														1
Meles meles														1*
Sus scrofa	1													

M^2 LL: 1.110, BL: 1.168, AW: 1.671, PW: 1.510); left maxillary fragment with M^3 (L: 1.155, W: 0.544); left P^4 fragment; right ramus mandibulae; right I_1 fragment; right M_1 (L: 1.194, W: 0.815); right M_1 fragment.

I/2: right mandible with M_1-M_2 (M_1 L: 1.416, W: 0.983; M_2 L: 1.388, W: 0.824), right mandible fragment; left I^1 (L: 1.802, H: 1.202); left M_2 (L: 1.280, W: 0.829).

III/2: right mandible fragment with M_2-M_3 (M_2 L: 1.404, W: 1.766; M_3 L: 1.107, W: 0.530); left edentulous mandible; left M_2 (L: 1.230, W: 0.859); right maxilla fragment with P^4-M^1 (P^4 L: 1.818, AW: 1.359, PW: 1.591); right P^4 (L: 1.627, AW: 1.545, PW: 1.638); right maxilla fragment M^1-M^2 (M^1 LL: 1.408, BL: 1.536, AW: 1.536, PW: 1.919; M^2 LL: 1.208, BL: 1.216, AW: 1.745, PW: 1.515); right mandible fragment with M_2-M_3 (M_2 L: 1.293, W: 0.895; M_3 L: 1.090, W: 0.694); right mandible fragment with digested M_1-M_2.

Remarks – The characteristic structure of the teeth and the lack of pigmentation make it certain that this shrew can be classified as *Crocidura*. The relatively small size precludes it from being one of the species still living in the Carpathian Basin nowadays. These dimensions are characteristic of the earliest *Crocidura* species (*C. obtusa* and *C. kornfeldi*) in Central Europe. These two early species cannot be distinguished from each other by size. However, MÉSZÁROS *et al.* (2020) listed some distinct morphological characters, including the shape of the spiculum coronoideum. A fragment of the jaw of this tiny *Crocidura* was found from the material of Nagyharsány Hill, on which the distinct coronoid spicule can be clearly seen. On the basis of this characteristic, we can classify this form as *Crocidura obtusa,* which was present in Central Europe from the early Pleistocene (ca. 1.2 Ma) to the earliest late Pleistocene (ca. 130–115 ka) (MÉSZÁROS *et al.* 2020).

Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Soricini Fischer von Waldheim, 1817
Sorex Linnaeus, 1758

Sorex minutus Linnaeus, 1766

Material and measurements – **I/-1:** right M^1 (LL: 1.037, BL: 1.128, AW: 1.261, PW: 1.129).

I/4: left I^1 (L: 1.225, H: 0.743); left A^1 (L: 1.060, H: 0.585).

Remarks – *Sorex minutus* is one of the longest-lived shrew species. It appears in the early Pliocene MN 14 Zone (RZEBIK-KOWALSKA 1991), it is present in the Hungarian fossil fauna to the uppermost Pleistocene (MÉSZÁROS 1999) and is still living.

Sorex araneus Linnaeus, 1758

Material and measurements – **I/-1:** left I^1 (L: 1.968, H: 1.218); right A^1 (L: 1.228, H: 0.900); right A^2 (L: 1.192, H: 0.868); left A_1 (L: 1.434, H: 0.953).

I/1: right M^3 (L: 0.702, W: 1.230).

I/3: left A_1 (L: 1.333, H: 0.978); left A_2 (L: 1.196, H: 0.802); left upper molar fragment.

I/5: right M^1 (LL: 1.624, BL: 1.554, AW: 1.472, PW: 1.645).

I/6: left I^1 fragment; right M^1 (LL: 1.700, BL: 1.746, AW: 1.804, PW: 1.843); right M^2 (LL: 1.485, BL: 1.512, AW: 1.626, PW: 1.261); left A^4 fragment.

II/2: left mandible with I_1, A_2, M_1 and M_2 (I_2 L: 1.992, H: 0.539; A_2 L: 0.692, H: 0.491; M_1 L: 1.815, W: 0.988, M_2 L: 1.566, W: 0.832).

III/2: right I_1 fragment (H: 1.207); left M_2 (L: 1.503, W: 0.892); left edentulous mandible fragment; left mandible fragment with lower antemolar fragment; left lower molar fragment; humerus fragment; femur fragment.

Remarks – This species clearly shows *Sorex* characteristics, however, the detailed determination is difficult because of the fragmentation of the findings. Therefore, we had to identify this species based on dimensions.

The shrew species presented here is clearly larger than *S. minutus*. According to Rzebik-Kowalska & Pereswiet-Soltan (2018), three larger *Sorex* species occurred simultaneously during the Pleistocene. Of these, *S. subaraneus* and *S. runtonensis* are smaller than the form found here, so we defined them as *Sorex araneus*.

The oldest remains of *S. araneus* were found in the early Pleistocene European localities. It occurred during the middle and late Pleistocene and nowadays lives in Eurasia occupying a large territory including almost all of Europe and continental Asia north of the steppe zone (Rzebik-Kowalska & Pereswiet-Soltan 2018).

Tribe Beremendiini Reumer, 1984
Genus *Beremendia* Kormos, 1934

Beremendia fissidens (Petényi, 1864)

Material – **I/2:** left M_1 fragment.

Remarks – Only a trigonal fragment of this large-sized shrew is present in the Nagyharsány Hill material. However, the red pigmentation on the tips, the relatively large size to other shrews, and the robust shape of the trigonid make it clear that it can only be *Beremendia fissidens*. This species occurred from the Pliocene MN 14 zone to the Tarkő phase of the middle Pleistocene in Europe (Botka & Mészáros 2014).

Tribe Neomyini Matschie, 1909
Genus *Asoriculus* Kretzoi, 1959

Asoriculus gibberodon (Petényi, 1864)

Material and measurements – **I/2:** left I^1 (L: 1.486, H: 1.107); left M_1 (L: 1.223, W: 0.790); right A_1 (L: 1.120, H: 0.646); right A_2 (L: 1.150, H: 0.676).

Remarks – *Asoriculus gibberodon* is a long-lived species. It was present undoubtedly in Europe from the late Miocene, MN 12 zone (Mészáros 1998) to the early Biharian (Rzebik-Kowalska 2013). This species seems to have a slightly older stratigraphic range than the other species in this locality. However, it was also found at some younger sites, which was explained by sediment redepositing (Pazonyi *et al.* 2018*a*). On the other hand, new occurrences raise the possibility of extending the stratigraphic range of the species.

Order Rodentia Bowdich, 1821

In the fossil collection of the Nagyharsány Crystal Cave, 17 rodents have been identified, which can be classified into 6 families (Sciuridae, Gliridae, Dipodidae, Spalacidae, Cricetidae, and Muridae). Most of the species (mainly voles) belong to the family Cricetidae, while the other families include only 1 or 2 species.

Abbreviations used in the rodent descriptions: P = premolar, M = molar, M^x = upper tooth, M_x = lower tooth, L = length, A = length of the anteroconid-complex, W = width, La = width of T4, Li = width of T5, La/Li = ratio of width of T4 to T5 (La/Li*100), A/L = ratio of anteroconid-complex to total tooth length (A/L*100), SDQ = enamel differentiation quotient. Measurements (in mm) and calculation of ratios were taken after Heinrich (1978), Pazonyi *et al.* (2018*b*), and Luzi *et al.* (2019).

Family Gliridae Muirhead, 1819
Genus *Glis* Birsson, 1762

Glis sackdillingensis Heller, 1930

Material and measurements – **I/-1:** right M^1 (L: 1.75, W: 2); right M^2 (L: 1.8, W: 1.85); left M^3.

I/1: right M^3.

I/2: right M_2.

I/3: right M^3.

I/5: left P^4; left M^1 (L: 1.75, W: 1.95).

III/2: right M_1 (L: 1.9, W: 1.85).

Remarks – The morphological difference between *G. glis* and *G. sackdillingensis* is mainly visible in the upper teeth. In first and second upper molars of *G. glis*, the metaloph and posteroloph are isolated, while in *G. sackdillingensis* they are connected on the palatal side. In the third upper molar the posterior centraloph is connected to the sixth extra ridge on the palatal side in *G. glis*, while this is not observed in *G. sackdillingensis*.

As well represented by Striczky & Pazonyi (2014), the size of the first upper and lower molars in *G. sackdillingensis* corresponds with the geological age of the remains. Comparing the size of the teeth recovered from the Nagyharsány Crystal Cave with previous data, it can be seen that both M^1 and M_1 are quite large, roughly the size of the recent *G. glis*. According to Jánossy (1970), the increase in size coincided with the formation of the upper layers of Tarkő Rock shelter and some Vár Cave (Budapest) sites (e.g., Fortuna Street 25, Országház Street 16). For all tooth types, the size of the dormice teeth in the Nagyharsány Crystal Cave is closest to the upper values of the material from layers 2–15 of the Tarkő Rock shelter, suggesting that the material may be contemporary with these sites.

Family Dipodidae Fischer von Waldheim, 1817
Genus *Sicista* Gray, 1827

Sicista praeloriger Kormos, 1930

Material – **I/1:** right M^3; left M_3 sin.
I/2: left M_2.
I/3: right M^1.
III/2: right M^1.
Remarks – Remains are identical to the type material of *S. praeloriger* in both size and morphology. On the first upper molar, the mesoloph is less developed and the size is larger than in *S. subtilis*. The separation of the two species is important mainly from a stratigraphic point of view. The last occurrence of *S. praeloriger* in the Carpathian Basin is a site (Fortuna Street 25) of the Vár Cave, Budapest (Jánossy 1986).

Sicista sp. [cf. *subtilis* (Pallas, 1773)]

Material – **I/5:** right M_2; right M^1.
Remarks – The morphology of both *Sicista* teeth recovered from level I/5 differs from the material of the other sites, and they most closely resemble *S. subtilis* teeth. While the width of the first upper molar of *S. praeloriger* is nearly constant throughout the tooth, the posterior part of M^1 of *S. subtilis* (and the

tooth from layer I/5) is narrower than the anterior part. In addition, the mesoloph is more developed than in *S. praeloriger*. Similar differences can be observed for M_2: the tooth is narrower and the labial side is more strongly constricted than in *S. praeloriger*.

Teeth with similar morphology were found in another site (Fortuna Street 16–18) of the Vár Cave, Budapest (Jánossy 1986; Kordos 2004).

Family Cricetidae Rochebrune, 1883
Subfamily Cricetinae Murray, 1886
Genus *Cricetus* Leske, 1779

Cricetus praeglacialis (Schaub, 1930)

Material and measurements – **I/1:** left M^1 (L: 3.5, W: 2.22); right M^2 (L: 2.9, W: 2.32); right M^2 (L: 2.85, W: 2.30).

I/2: right M_1 fragment, right M^1 (L: 3.17, W: 2.15).

I/3 left M_2 (L: 2.67, W: 2.1); left M^1 (L: 3.12, W: 2.07); right M^2 (L: 2.62, W: 2.37); right M^2 (L: 2.95, W: 2.37); right M^1 (L: 3.3, W: 2.1); right M_1 fragment, 2 left M_1 fragment.

I/5: right M_2 (L: 2.70, W: 2.30); right M_2 (L: 2.77, W: 2.10); left M_3 (L: 2.80, W: 2.10); right M^1 (L: 3.12, W: 2.07); left M_1 fragment.

III/1: 1 complete lower tooth row (L: 8.2); left M_1 (L: 3.25, W: 1.8); left M_2 (L: 2.82, W: 2.27); right M_2 (L: 2.75, W: 2.07); right M_3 (L: 3.0, W: 2.20); left M_3 (L: 2.92, W: 2.27); left M_3 (L: 2.95, W: 2.25).

III/2: right M^1 (L: 3.32, W: 2.1); left M^1 (L: 3.5, W: 2.22).

Remarks – The hamster material in the Nagyharsány Crystal Cave is far below the statistical amount, but the size of the finds is close to that of *C. praeglacialis*. In the original description, this hamster species was positioned as a subspecies. In the Hungarian literature, Jánossy (1979, 1986) classified Pleistocene hamsters with similar dimensions to recent *C. cricetus* as *C. c. praeglacialis* or *C. praeglacialis*. In his earlier works, Hír (1997*a*, *b*) preferred the species level: *C. praeglacialis*. This taxon is considered to be the most likely direct ancestor of the modern European hamster, *C. cricetus* (Hír 1997*a*, *b*).

The largest population of *C. praeglacialis* is known from Villány 8 (Kretzoi 1956; Jánossy 1979, 1986; Hír 1997*b*). The average sizes in this material are slightly larger than the sizes of the recent *C. cricetus*, but definitely smaller than the sizes of the “giant hamsters”, *C. runtonensis* and *C. major* (Hír 1997*c*, 1998). The cricetid finds from Tarkő 1, Vértesszőlős, Vár Cave (MIS 12–11), and Süttő (MIS 5) sites were classified by Hír (1997*a*, *b*, 2002) as *C. praeglacialis*.

Genus *Allocricetus* Schaub, 1930

Allocricetus bursae Schaub, 1930

Material and measurements – **I/1:** left M_1 (L: 1.82, W: 1.15).
I/3: right M_1 (L: 1.88, W: 1.16); right M^2 (L: 1.55, W: 1.39).
I/4: left M^1 (L: 2.1; W: 1.33).

Remarks – The *Allocricetus* material of the Nagyharsány Crystal Cave is very poor. The identification is based on measurements and on the detailed study of the Hungarian *Allocricetus* populations (Hír 1989, 1995). The first occurrence of *Allocricetus bursae* in the Carpathian Basin is in the *Allophaiomys* faunas of Betfia 9 and Osztramos 8, while its latest occurrence is in layer 5 of the Lambrecht Kálmán Cave (Jánossy 1964, 1979, 1986).

The finds of the hamster in the Nagyharsány Crystal Cave are not suitable for detailed biochronological conclusions. The co-occurrence of *C. praeglacialis* and *A. bursae* is possible from the early Pleistocene *Mimomys savini* faunas (Templomhegy phase, MIS 19–15) to the late Pleistocene Varbo phase (MIS 5c-a).

Subfamily Arvicolinae Gray, 1821
Tribe Arvicolini Gray, 1821
Genus *Arvicola* Lacépède, 1799

Arvicola sp. [ex gr. *amphibious* (Linnaeus, 1758)]

Material and measurements – **I/-1:** left M_1 fragment.
I/1: left M^3.
III/2: right M_1 (L: 3.92, A: 1.66, A/L: 42.51, SDQ: 88.17); right mandible fragment with M_1-M_2 (M_1 L: 3.77, A: 1.52, A/L: 40.27, SDQ: 87.68).

Remarks – The ratios (A/L, SDQ) are controversial, and do not allow a clear identification of the first lower molars. The A/L value (41.39) is close to that of *A. mosbachensis* (42.1; Berto *et al.* 2021) and significantly lower than that of *A. amphibius* (51.4; Berto *et al.* 2021). In contrast, the mean SDQ value (87.92) of the material is clearly indicative of *A. amphibius*. The boundary between the two species (*A. mosbachensis* and *A. amphibius*) is drawn at 100 based on SDQ (Heinrich 1978), but the transition was not abrupt but gradual during MIS 6 and 5 (Maul & Markova 2007; Maul *et al.* 2000). However, the steadily increasing trend in SDQ was broken during the Saalian (MIS 6–10) period, when some *amphibius*-like *Arvicola* populations with advanced enamel differentiation appeared in the central northern region of Europe (Koenigswald & Kolfschoten 1996; Masini *et al.* 2020). The teeth from the Nagyharsány Crystal Cave are very similar to these pre-Eemian *Arvicola* ex gr. *amphibius* specimens.

Similar aged *amphibius*-like *Arvicola* teeth in the Carpathian Basin were also recovered from the material of the Uppony I Rock shelter (Northern Hungary; Jánossy 1969), but in this study, the *Arvicola* material from the Nagyharsány Crystal Cave was also compared with some older (MIS 11) *Arvicola* cf. *mosbachensis* teeth from the Fortuna Street 25 site (Budapest, Vár Cave) (Table 2). The mean A/L values of the two sites [40.23 (Fortuna Street 25) and 41.39 (Nagyharsány Crystal Cave)] are close, and the mean SDQ value of the material from the Fortuna Street 25 site (115.38 ≥ SDQ ≥ 86.53, mean value: 101.48) is much lower than expected. This suggests that the *amphibius*-like *Arvicola* may have appeared in the area earlier than it was previously thought.

Table 2. Comparison of the *Arvicola* material from Fortuna Street 25 (Vár Cave, Budapest) and the Nagyharsány Crystal Cave by length of the lower first molar (L), length of the anteroconid-complex (A), ratio of anteroconid-complex to total tooth length (A/L) and enamel differentiation quotient (SDQ)

Fortuna Street 25 (Vár Cave, Budapest)				
taxa	**L**	**A**	**A/L**	**SDQ**
Arvicola cf. *mosbachensis*	3.46	1.47	42.64	108.80
Arvicola cf. *mosbachensis*	3.47	1.27	36.53	86.53
Arvicola cf. *mosbachensis*	3.51	1.44	41.19	100.18
Arvicola cf. *mosbachensis*	3.51	1.33	37.86	96.54
Arvicola cf. *mosbachensis*	3.41	1.46	42.91	115.38
mean value	**3.47**	**1.39**	**40.23**	**101.48**
standard deviation	0.04	0.09	2.88	11.14
Nagyharsány Crystal Cave (III/2)				
taxa	**L**	**A**	**A/L**	**SDQ**
Arvicola sp. (ex gr. *amphibius*)	3.77	1.52	40.27	87.68
Arvicola sp. (ex gr. *amphibius*)	3.92	1.67	42.51	88.17
mean value	**3.85**	**1.56**	**41.39**	**87.93**
standard deviation	0.11	0.11	1.58	0.35

Genus *Lasiopodomys* Lataste, 1887
Subgenus *Stenocranius* Katschenko, 1901

Lasiopodomys (*Stenocranius*) *gregalis* (Pallas, 1779)

Material and measurements – **I/1:** left M_1 (L: 2.80, A: 1.54, W: 1.00, A/L: 55.10).

I/2: right M_1 (L: 2.83, A: 1.57, W: 1.03, A/L: 55.56).

I/3: right M_1 (L: 2.63, A: 1.43, W: 1.00, A/L: 54.35); right M_1 fragment (A: 1.71, W: 1.00).

I/5: left M_1 (L: 2.80, A: 1.49, W: 0.97, A/L: 53.06).

II/2: left M_1 (L: 2.66, A: 1.43, W: 1.03, A/L: 53.76).

III/1: right M_1 (L: 2.49, A: 1.29, W: 0.97, A/L: 51.72).

III/2: left M_1 (L: 2.54, A: 1.31, W: 0.97, A/L: 51.69); left M_1 (L: 2.74, A: 1.43, W: 1.03, A/L: 52.08); right M_1 (L: 2.63, A: 1.43, W: 0.97, A/L: 54.35).

Remarks – The first lower molars of *L. gregalis* found in the Nagyharsány Crystal Cave are very similar in both morphology and size to the recent *L. gregalis* (Table 3). This species appeared in the Carpathian Basin at the beginning of the early Toringian (around MIS 12), the earliest specimens were found in the Tarkő Rock shelter and Vértesszőlős II sites (Jánossy 1986). Later, it occurred in large quantities mainly during cold periods (Saalian, Weichselian), which can be explained by palaeoecological reasons. Currently, the narrow-headed vole is distributed across the tundra region of Northern Europe and Asia, and as separate populations on the steppes. Their typical habitat is grassy plains, semi-deserts, open grassy areas in forests, and alpine meadows.

Table 3. Comparison of recent *Lasiopodomys* (*Stenocranius*) *gregalis* and material from the Nagyharsány Crystal Cave by length and width of the lower first molar (L and W), length of the anteroconid-complex (A), ratio of anteroconid-complex to total tooth length (A/L)

recent material	**L**	**A**	**W**	**A/L**
Lasiopodomys (*Stenocranius*) *gregalis*	2.43	1.34	1.00	55.29
Lasiopodomys (*Stenocranius*) *gregalis*	2.49	1.37	1.00	55.17
Lasiopodomys (*Stenocranius*) *gregalis*	2.60	1.40	1.00	53.85
Lasiopodomys (*Stenocranius*) *gregalis*	2.60	1.43	1.00	54.95
Lasiopodomys (*Stenocranius*) *gregalis*	2.60	1.49	1.06	57.14
Lasiopodomys (*Stenocranius*) *gregalis*	2.74	1.49	1.06	54.17
Lasiopodomys (*Stenocranius*) *gregalis*	2.74	1.57	1.06	57.29
mean value of recent species	**2.60**	**1.44**	**1.02**	**55.41**
standard deviation	0.12	0.08	0.03	1.34
mean value of Nagyharsány Crystal Cave material	**2.68**	**1.46**	**1.00**	**53.52**
standard deviation	0.12	0.09	0.03	1.46

Genus *Microtus* Schrank, 1798
Subgenus *Agricola* Blasius, 1857

Microtus (*Agricola*) *agrestis* (Linnaeus, 1761)

Material and measurements – **I/5:** right M_1 (L: 3.34, A: 1.8, W: 1.23, A/L: 53.85, La/Li: 65.38).

I/6: left M_1 (L: 2.91, A: 1.66, W: 1.03, A/L: 56.86, La/Li: 59.09).

II/1: right M_1 (L: 2.86, A: 1.60, W: 1.00, A/L: 56.00, La/Li: 59.09).

III/1: right mandible with M_1-M_2 (M_1 L: 2.77, A: 1.46, W: 1.06, A/L: 52.58, La/Li: 65.22); left M_1 fragment (A: 1.54, W: 0.89, La/Li: 63.16).

Subgenus: *Microtus* Schrank, 1798

Microtus (*Microtus*) *arvalis* (Pallas, 1778)

Material and measurements – **I/-1:** right M_1 fragment (A: 1.46, W: 0.97, La/Li: 83.33).

I/1: left M_1 fragment; left M_1 fragment (A: 1.46, W: 1.06).

I/2: right M_1 (L: 2.54, A: 1.34, W: 0.97, A/L: 52.81, La/Li: 70); right M_1 (L: 2.77, A: 1.46, W: 1.03, A/L: 52.58, La/Li: 66.67); right M_1 (L: 2.71, A: 1.51, W: 1.00, A/L: 55.79, La/Li: 66.67); left M_1 fragment.

I/3: right M_1 (L: 2.91, A: 1.60, W: 1.14, A/L: 54.90, La/Li: 90); left M_1 (L: 2.94, A: 1.66, W: 1.14, A/L: 56.31, La/Li: 85); left M_1 (L: 3.23, A: 1.74, W: 1.26, A/L: 53.98, La/Li: 72).

I/4: left juvenile M_1.

I/5: left M_1 fragment (A: 1.43, W: 0.86, La/Li: 70).

I/6: right M_1 (L: 2.77, A: 1.54, W: 1.03, A/L: 55.67, La/Li: 71.43).

II/1: left M_1 slightly fragmented (L: 2.63, A: 1.40, W: 0.97, A/L: 53.26).

III/1: right M_1 fragment (A: 1.46, W: 1.03); right M_1 fragment.

III/2: right M_1 fragment (A: 1.51, W: 1.03, La/Li: 75); right M_1 fragment (A: 1.51, W: 1.14, La/Li: 100); right M_1 (L: 3.09, A: 1.66, W: 1.17, A/L: 53.70, La/Li: 81.82); right M_1 (L: 2.91, A: 1.69, W: 1.06, A/L: 57.84, La/Li: 85); right M_1 (L: 2.91, A: 1.57, W: 1.14, A/L: 53.92, La/Li: 85.71); left M_1 (L: 2.86, A: 1.43, W: 1.14, A/L: 50, La/Li: 81.82); 2 left M_1 fragment.

Remarks – Separation of *M. agrestis* and *M. arvalis* on the basis of the first lower molars' morphology is very difficult, both because of the high intraspecific variation of both species and high morphological overlap between the two species based on the geometric morphometric analysis of hundreds of recent specimens (Pazonyi *et al.* 2018*b*). For this reason, we decided to use the La/Li ratio to separate the two species. Following some previous studies (e.g., Luzi *et al.* 2019; Berto *et al.* 2021), in the case of a La/Li index < 65 the specimen was assigned to *M. agrestis* whereas by larger values of the index, *M. arvalis* was defined. A slight size difference was also found between the two species, with *M. agrestis* being slightly larger (average length 2.97 mm), while the average length of *M. arvalis* M_1 is 2.82 mm.

Based on the A/L values of the whole *Microtus* material (*Microtus arvalis-agrestis* group; average A/L: 54.38), the age of the Nagyharsány Crystal Cave is closest to Visogliano A1 (Italy, MIS 11) site (average A/L: 54.01; Maul *et al.* 1998). The L value shows the same, the average M_1 length in the Nagyharsány Crystal Cave is 2.87 mm, while in the Visogliano A2 (Italy, MIS 11) it is 2.89 mm (Maul *et al.* 1998). This age is not contradicted by the value of the La/Li index but it does not exclude the possibility of a younger age (Berto *et al.* 2021).

Tribe Lagurini Kretzoi, 1955
Genus *Lagurus* Gloger, 1841

Lagurus transiens Jánossy, 1962

Material – **I/1:** right juvenile M_1 fragment.
I/2: right M_1.
I/3: right M_1 fragment.
II/1: right M_1.
II/2: 2 left M_1; right M_1.
Remarks – A common feature of first lower molars is that the transition between T4 and T5 is more or less confluent, and a *Pitymys*-type rhombus is observed in about half of the specimens. The anterior cap of the molars is primitive, often shorter and straighter than the recent form (*L. lagurus*), in which it is often labially shifted.

L. transiens is a stratigraphically important species with a short range. It is known from only a few middle Pleistocene sites in the Carpathian Basin (Tarkő Rock shelter, Vár Cave), which date to MIS 12–11 (Jánossy 1986; Kordos 2004).

PALAEOECOLOGICAL AND TAPHONOMICAL RESULTS

Microcodiums were found in only three samples: I/1, I/2, and III/1. Most specimens (48 pcs) are known from sample I/1, while only a few specimens were unearthed from the other two samples mentioned previously. Microcodiums are a problematic calcific micro feature of many calcretes and calcareous palaeosols in Cretaceous and Tertiary continental and marine deposits of the peri-Tethyan area. The studies of the features of microcodiums proved that these are of biogenic origin exhibiting perfectly preserved structural details of plant root tissues (e.g., Košir 2004). Consequently, these deposits are most likely originated from a vegetated environment. They were formed in the root zone by infiltrating the cave through the rock fissures.

Among the vertebrate fossils from the cave, frogs are the most common, but this material consists mainly of isolated bones, such as ilia and especially limb bones. Other bones, even of the most common green toads, are much rarer. Other amphibian and reptilian fossils are rare and mostly fragmentary, except for most Scolecophidia vertebrae, as they are very small (up to 1.6 mm). A partial green toad skeleton is known (Szentesi 2014) from the Nagyharsány Crystal Cave, containing the frontoparietals, prootic capsules, and vertebral column, but this is a unique find from the cave. Considering the presence of microcodiums, these data suggest that most of the vertebrate fossils entered the cave through the root zone and along fissures in the rocks.

Insectivore and rodent fossils are also relatively common in the material, although far fewer than amphibian bones. These finds are mostly isolated teeth, with some jaw and jaw fragments present, with few in situ teeth. Among the bones, only three rodents (*Cricetus praeglacialis, Apodemus sylvaticus*, *Mus* sp.) and one complete *Sorex* jaw were recovered, but two teeth of this jaw were lost. This shows that the remains of the small mammals were transported before the accumulation.

Autochtonous accumulation is most common in bat bones, as a significant proportion of the species spend long periods of time in caves. In these cases, intact skulls and jaws are present in the material, as well as numerous limb bones. In contrast, the bat specimens from the Nagyharsány Crystal Cave contain mainly isolated teeth and a few fragmentary mandibles or only maxillae, suggesting that the bats were deposited in the same way as other vertebrates. This may be because the cave entrance was too small for the bats to fly in and out. In addition, some of the species found here only retreat to the cave in winter and spend the summer daytime in the forest.

The herpetofauna and its ecological composition show the dominance of animals preferring open areas. Their proportions varied between 85.3–98.3%. The quantity of these animals is 100% in sample II/4 (stalactite), which is represented by some green toad (*Bufotes viridis*) bones. The amount of aquatic (0.8–4.6%), woodland (0.6–11.4%), and opportunist (0.3–2.9%) animals are more negligible. The largest peak of the amount of woodland animals origins from the massive presence of European tree frog (*Hyla arborea*: 11.3%) in the sample from I/5.

The most frequent animals preferring open areas are the green toads (*Bufotes viridis*), which make up the main bulk of the herpetofauna with an abundance between 80–94%. The similarly nocturnal common toad (*Bufo bufo*: 2.04–10.66%) and the burrowing spadefoot toad (*Pelobates fuscus*: 0.1–2.04%) are subordinate in the frog fauna. The amounts of other animals preferring open areas are negligible. Some reptiles can be classified here as common wall lizards (*Podarcis muralis*: 0.1% only in sample I/3) and European green lizards (*Lacerta viridis*: 0.1–0.5%), among snakes scolecophidians (0.1–0.31%), green snakes (*Hierophis viridiflavus*: 0.1–1%) and the Balkan whip snakes (*H. gemonensis*: 0.1–0.27%), European cat snakes (*Telescopus fallax*: 0.1%), and three viper species: *Vipera ammodytes* (0.1–0.27%), *V. berus* (0.1–0.27%), and *V. ursinii* (0.1–0.2 %) have been found.

The water preferring amphibian fauna is including newts (*Triturus cristatus*, 0.1–0.6% and *Lissotriton vulgaris*, 0.13–0.55%), periaquatic- (*Bombina variegata*, 0.3–1.64%) and aquatic (*Pelophylax esculentus* group, 0.1–0.31%) frogs. Reptiles from the locality also include the European pond turtle (*Emys orbicularis*, 0.1–0.13%) as well as the grass (*Natrix natrix*, 0.83%) and dice snakes (*N. tesselata*, 0.1–0.6%).

A vegetated area is suggested by the presence of the European tree and the agile frog (*Rana dalmatina*, 0.31%, only in sample III/1), among lizards the slow-worm (*Anguis fragilis*, 0.13%, only in sample I/2) and the Aesculapian snake (0.1–0.63%). Scolecophidian vertebrae have been unearthed from more samples (I/2, I/3, I/5, II/1, III/1, and III/2), but most of the remains originate from sample I/1. All scolecophidian species have fossorial or cryptozoic habits (e.g., França & Braz 2013; Shea 2015; Webb *et al.* 2001) so the remains which belong to this infraorder, possibly also suggest a forest environment close to the former depositional area.

The opportunists are also rare in the herpetofauna. Among frogs, this category includes *Latonia gigantea* (0.1–2.7%), the fossils of which are known from many different environments (e.g., Gál *et al.* 2000; Hír *et al.* 2001; Miklas 2002; Bernor *et al.* 2004; Roček 2005; Venczel & Hír 2015), and the common frog (*Rana temporaria*, 0.1–0.84%). Smooth snake (*Coronella austriaca*, 0.1–0.3%) is also an opportunist, the fossils of which are also known from the cave (in I/-1, I/2, III/1, and Kraus 1995 collection).

Among the small mammals, there are some species that indicate humid environments with dense vegetation cover and lower (*Neomys*, *Sorex,* and *Asoriculus* species) or higher (*Glis sackdillingensis*, *Arvicola* ex gr. *amphibius*, *Microtus* (*Terricola*) sp., *Apodemus sylvaticus*, *Mus* sp.) temperature. Others prefer a warm climate and dry terrains, with more or less open grasslands, such as *Crocidura* and *Rhynolophus*, or cooler climate and dry environments with grasslands or semi-deserts, such as *Spalax*, *Spermophilus*, *Cricetus*, *Allocricetus*, *Microtus arvalis/agrestis* group, *Lasiopodomys*, *Lagurus,* and *Sicista* species. *Talpa* and *Beremendia* can be ranged to the opportunist group. *Beremendia* is also an indicator of open water bodies, as is *Myotis nattereri/dasycneme*, which prefers hunting over rivers and streams running in closed forests.

In the case of Site I, where there are samples from 7 levels of the fissure, it was possible to observe ecological changes within the section. Although the number of individuals is very small and therefore the results can only be accepted with strong reservations, it is perhaps worth presenting these changes. Based on the MNI (minimum number of individuals) of the small mammals in each level, a cumulative percentage plot was constructed. Only material from levels with MNI higher than 9 was included in the analysis (levels I/-1, I/1, I/2, I/3, and I/5; Fig. 2).

It is immediately noticeable that a transition in the small mammal fauna starts at I/2 and becomes really pronounced at I/3. In the lower levels, the shrews, *S. minutus/araneus* and *C. obtusa,* dominate, but sporadic species such as *A. gibberodon* and *B. fissidens* also appear. From level I/3 these disappear completely and the proportion of shrews declines. A similar change is observed in the case of murids. The lower levels are dominated by *Apodemus sylvaticus*, which is the most abundant species (25–25%) in both I/1 and I/2. However, in the upper levels, the abundance of *Apodemus* declines, while the proportion of *Mus* sp. increases, so that the two murids are more evenly balanced.

A significant increase in the proportion of hamsters is observed towards the top of the series. As for the species of voles, only the genera *Arvicola* (water voles) and *Terricola* and the field voles (*Microtus arvalis*) are present in the lower levels, in contrast to the upper ones, where several other species of voles (*Lagurus transiens*, *Microtus agrestis*, *M. oeconomus*, *Lasiopodomys gregalis*) have been also found.

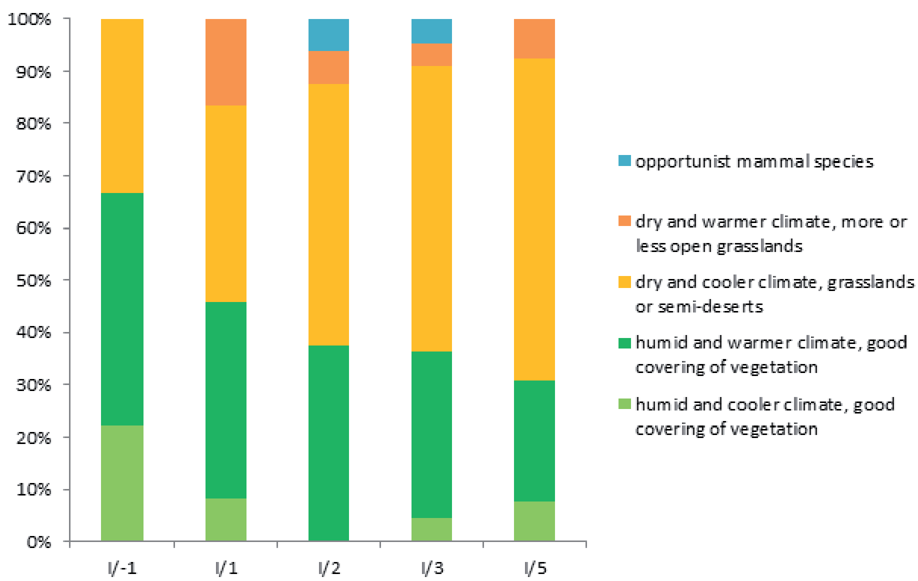

Fig. 2. Changes in the proportion of mammals with different environmental requirements in the material of Site I

The observed changes can be interpreted as a transition from a warmer, wetter, more closed environment to a cooler, drier, more open one. However, the balances of the *Mus*/*Apodemus* as well as *Crocidura*/*Sorex* ratio suggests that the vegetation was not completely open, with patches of scrub or forest certainly remaining in the area. The same is supported by the results of the herpetofauna, which may also indicate a warmer environment, as at least nine herpetological taxa are present in the fossil material. Among the frogs, the remains of *Bombina*, *Hyla arborea*, *Pelobates fuscus,* and the *Pelophylax* group suggest a warmer climate, confirmed by the remains of *Emys orbicularis*, *Lacerta viridis* as well as the typical interglacial taxon *Natrix natrix* and the thermophilic *Zamenis longissimus* (Böhme 1996, 2000, 2010). The presence of fossorial blind snakes also suggests that the sediment was deposited in a warmer environment (e.g., Dixon & Hendricks 1979, França & Braz 2013).

Unfortunately, the number of small mammal species in the samples from Site II is very low, so we were not able to carry out a similar study here, but the species composition shows similarities with II/1 and I/3, as well as II/2 and I/2. As for the two sites marked III, the number of individuals is adequate. III/2 is more similar to I/1–2 (warmer, wetter climate, more closed vegetation), while III/1 agrees well with I/3–5 (cooler, drier climate, more open vegetation).

STRATIGRAPHY

The stratigraphic position of the Nagyharsány Crystal Cave sites could be determined on the basis of ranges of the mammal species as well as the taxonomic and environmental transitions, observed in the series of Site I (Fig. 3). We also considered a number of measurements on different rodents that could help us to date the sites based on previous literature. These were the length of the lower and upper first molars of *Glis sackdillingensis* (Jánossy 1970), the measurement data (A/L, SDQ) of the *Arvicola* material from the Fortuna Street 25 site as well as the lower first molar length, A/L ratio (Maul *et al.* 1998) and La/Li ratio (Berto *et al*. 2021) for the *Microtus arvalis/agrestis* group.

According to Jánossy (1986), the middle Pleistocene can be divided into three biochronological units, the Tarkő, the Uppony, and the Solymár faunal phases. Based on the description of these phases, the material from the Nagyharsány Crystal Cave clearly belongs to the Tarkő phase (early Toringian; MIS 14–11; 550–375 ka). This is supported by the sporadic presence of early Pleistocene shrews (*Beremendia*, *Asoriculus*), along with modern shrews (e.g., *Sorex araneus*), the presence of the larger *Glis sackdillingensis*, the steppe lemming *Lagurus transiens* as well as the abundant but not dominant presence of *Microtus arvalis* in the small mammal fauna. Among the Carpathian Basin sites, this faunal phase includes the Tarkő Rock shelter material, the Vértesszőlős II site, and some of the Vár Cave faunas (Budapest – Országház Street 16, Fortuna Street 25, Fortuna Street 16–18; JÁNOSSY 1986).

In order to be able to determine the age of the sites more precisely, it was investigated whether the typical faunistic changes observed in the series of Site I (*Apodemus/Mus* shift, *Sicista praeloriger/Sicista* sp. (cf. *subtilis*) shift, *Crocidura/Sorex* ratio balancing) could also be observed in the material of other sites. We found that the material from the Nagyharsány Crystal Cave is most closely related to the material from the MIS 11 deposits of the Vár Cave. The MIS 11 age of the sites is also supported by the various measurement data (see above under

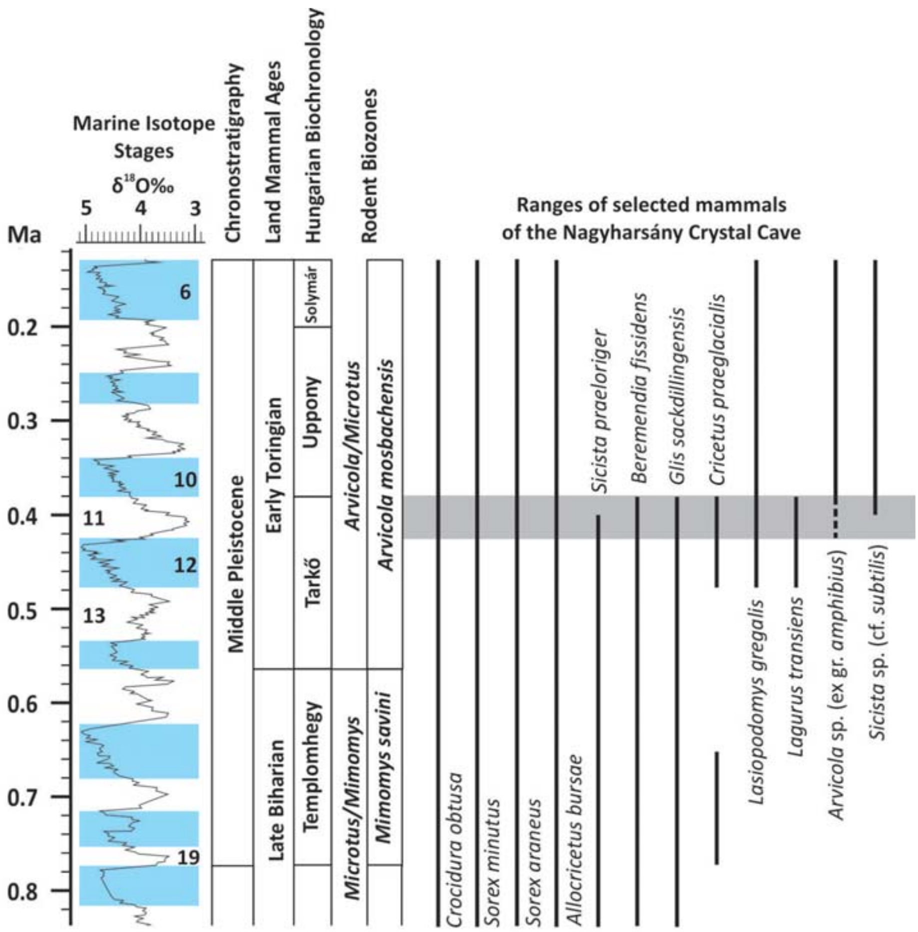

Fig. 3. Stratigraphic position of the Nagyharsány Crystal Cave sites based on some selected mammals

taxonomic results), which, e.g., based on the L and A/L values of the first lower molars belonging to the *Microtus arvalis/agrestis* group, relate the material to sites of MIS 11 age (Visogliano A1 and A2, Italy).

The main difference between the small mammals from the Vár Cave sites and from the Nagyharsány Crystal Cave is the amount of *Microtus* (*Terricola*) *arvalidens*, which is almost completely absent from the material of the latter site. The increase in the proportion of hamsters, particularly *Cricetus praeglacialis*, in the series of Site I shows the more open environment, while the same is indicated by the dominance of *Microtus arvalis* and *Microtus* (*Terricola*) *arvalidens* in the Vár Cave sites. This may be due to the environmental differences between the Villány Hills in southern Hungary and the Buda Hills in northern Hungary, which can be traced back to the early Pleistocene and persist to the present day.

The stratigraphic position of the Nagyharsány Crystal Cave material adds to our knowledge of the middle Pleistocene climate and environmental conditions of the Villány Hills. The cave material is closest in age to Nagyharsány Hill 6 (MIS 7, ca. 250 ka) faunas in the area. The Nagyharsány Hill 6 material is characterised by the predominance of species preferring a steppe environment (*Crocidura leucodon-russula* group, *Microtus arvalis*), suggesting that this fauna was deposited in a colder, drier environment compared to the Nagyharsány Crystal Cave.

CONCLUSIONS

During the detailed taxonomic processing of the vertebrate material of the Nagyharsány Crystal Cave, a total of 78 taxa were found in the study sites. The majority of the material is herpetofauna, including frogs, but also birds as well as small and large mammal remains were found.

A preliminary palaeoecological study was carried out on a series of seven samples from Site I. However, due to the small number of specimens, this only provided indicative information on the environment of the site and the former climate. Within the series, an environmental transition was observed. While the small vertebrates of the lower levels indicate a warmer, wetter, more closed environment, towards the top of the series this gradually changes to a cooler, drier, more open one. The taxonomic, allometric, and palaeoecological results also allowed the stratigraphic position of the sites to be determined. We found that the material from the Nagyharsány Crystal Cave is most closely related to the material from the MIS 11 sites of the Vár Cave (Budapest). However, the differences between the species composition of the two sites also revealed that environmental differences between the southern and northern parts of Hungary were as detectable in the middle Pleistocene as they are in the early Pleistocene and today.

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