

Preliminary report on the Early Pleistocene vertebrate sites of Beremend Crystal Cave (Beremend 16, South Hungary) and on their palaeoecological importance

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Abstract – Formerly, the Early Pleistocene vertebrate material collected independently from 15 different sampling sites of Beremend Crystal Cave were merged together and treated as a whole, under the name of Beremend 16. However, the thorough analysis of the fauna of each separate sampling site revealed considerable taxonomic, palaeoecological and stratigraphic differences, which render the aforementioned unification unjustified. Diverse and sparse assemblages were recognized based on the fossil richness and taxonomic composition of the samples. Some of the assemblages contain only bats, whereas others consist of further small mammals besides the bats as well as herpetofaunal elements. The compositional dissimilarities suggest taphonomical or age differences comparing the sites. Based on our environmental reconstruction, a water body varying in size was always present in the vicinity of the cave during the studied time period, which was surrounded by an open or a more closed vegetation depending on the slight climatic changes. Our stratigraphic analysis showed that most of the sites can be dated between 1.5 and 1.2 Ma. In the case of two sites, it was possible to make a more precise age estimation (1.2 Ma) based on the appearance of the white-toothed shrew, *Crocidura obtusa*. With 4 figures and 4 tables.

Key words – Beremend, Early Pleistocene, palaeoecology, small vertebrates, stratigraphy

INTRODUCTION

Szőlő Hill of Beremend is located approximately 9 km south of the Villány Hills and municipality Villány, in South Hungary. The altitude of this flat, loess-covered limestone hill was 174 m before the mining activity. The limestone quarry of Beremend has yielded classic palaeovertebrate faunas, which were studied for more than a century by Salamon J. Petényi, Miklós Kretzoi, and Dénes Jánossy,

meanwhile the mollusc faunas were studied by Endre Krolopp (see JÁNOSSY 1986). During that time, quarrying unearthened fossil-bearing caves and cavities in the Late Cretaceous limestone, which resulted in rescue excavations (KRETZOI 1956; JÁNOSSY 1986; KORDOS 1991; PONGRÁCZ 1999; CSÁSZÁR & KORDOS 2004). According to KRETZOI (1969) and KRETZOI & PÉCSI (1982), these sites represent the Late Pliocene Beremendian Biochronological Phase; however, according to KROLOPP (1990), their age most likely spans up to the beginning of the Early Pleistocene (Early Villanyian Biochronological Phase).

Vertebrate remains were described first from Szőlő Hill by PETÉNYI (1864). At the beginning of the twentieth century, Tivadar Kormos, Lajos Méhely and later Jenő Noszky collected palaeovertebrate material from various sites on the hill (JÁNOSSY 1996). During subsequent studies, 26 fossil-bearing cavities were discovered in the quarry (KRETZOI 1956; JÁNOSSY 1986; KORDOS 1991; PONGRÁCZ 1999; CSÁSZÁR & KORDOS 2004) (PAZONYI *et al.* 2016, Fig. 1). Most recently, new material was collected, and a scientific revision was based on the newly found and previously collected remains (PAZONYI *et al.* 2016; SZENTESI 2016; TREMBECZKI *et al.* 2018).

Beremend Crystal Cave was discovered at the end of 1984 by Mihály Magusits; the exploration in the same and the following year demonstrated that it forms a part of a larger system (TAKÁCS-BOLNER 1986). According to recent studies, Beremend Crystal Cave is a typical hydrothermal cave system, which was formed as a result of mixing corrosion. It has several levels and a labyrinth-type network of passages characterized by sudden size changes. It is exceptionally rich in minerals, spherical cavities and other morphologies, which were created by hydrothermal processes (VIGASSY *et al.* 2010). Vertebrate finds from the cave were mentioned first by TAKÁCS-BOLNER (1986), but collecting and scientific studies have only been done later by JÁNOSSY (1992, 1996) and György Topál (JÁNOSSY & TOPÁL 1985; JÁNOSSY *et al.* 1987; JÁNOSSY 1996). JÁNOSSY (1992, 1996) discussed all material from Beremend Crystal Cave as a whole as Beremend 16, and all that were found outside, above the entrance as Beremend 17. He also considered that the material within the cave was infiltrated from the fissure fillings which can be found outside (JÁNOSSY *et al.* 1987). Later studies suggested that considerable differences can be observed when comparing the vertebrate assemblages of the individual sampling sites (SZENTESI 2016; TREMBECZKI *et al.* 2018), thus the unification of the assemblages of Beremend 16 (and possibly 17) is not justified.

The aims of the current study are to compare the taxonomic composition of each sampling site within the cave with each other (addressing also the abundance of each species within an assemblage) and to draw palaeoecological and stratigraphic conclusions based on the small mammals and herpetofaunal elements.

MATERIAL AND METHODS

Dénes Jánossy and György Topál collected fossils from Beremend Crystal Cave altogether six times between 1985 and 1987. Their excavations yielded 20 small vertebrate-rich red clay samples (Fig. 1). The material was discussed by them as a whole, under the name of Beremend 16. Fortunately though, the original numbering of the sampling sites is still noted besides the material stored within the collections of the Department of Palaeontology and Geology at the Hungarian Natural History Museum, and their field report has also been archived. These documents, on the one hand, reveal that not all of the numbers represent individual sampling sites. There were places where they went collecting repeatedly, giving a new number to each new sample during every occasion (Fig. 1). On the other hand, the documentation reveals that György Topál recognized notable ecological differences comparing the assemblages of different sampling sites (JÁNOSSY *et al.* 1987). Based on this information, we were able to recognize 15 individual sampling sites and study their material separately. The small mam-



Fig. 1. Cross-section of Beremend Crystal Cave (Beremend 16) with the location of the fossil sites (numbers of the original samples are indicated) (JÁNOSSY *et al.* 1987)

mals and the herpetofaunal elements were revised here, whereas the large mammals were only mentioned on the basis of the original field report (JÁNOSSY *et al.* 1987; Table 1).

In this article, when mentioning an individual sampling site within the cave, we always indicate all numbers that represent samples collected from the same place, such as 2/15/16. However, in order to avoid confusion and long site names, we will not mention that these were all described as Beremend 16 before, thus the full citation in the latter case should look like as Beremend 16/2, Beremend 16/15 and Beremend 16/16.

During the taxonomic analysis, we determined all elements from the formerly only partially studied herpetofauna from Beremend Crystal Cave. Furthermore, with the addition of newly found specimens that were recovered from the previously collected, but unpicked sediment samples, we revised the entire small mammal fauna. By specifying minimum number of individuals (MNI) for each taxon in each site (Table 1), a palaeoecological analysis became possible.

The determination of the climate tolerance of most bat species was based on their current distribution (BIHARI *et al.* 2007), as most species are still extant, apart from four. These ecological characteristics are presumed at Pliocene and Pleistocene sites (POPOV 2004; GUNNELL *et al.* 2011; TRAVNICKOVA 2016).

Eptesicus nilssoni and *Myotis dasycneme* are considered to be cold preferring species, because they live mainly in northern Eurasia. To the south, they occur along the latitudes of Central Europe (Table 2).

All species of the genus *Rhinolophus* prefer warm climate; they are most frequent today in the Mediterranean Region and Africa. Their occurrence extends north up to the Carpathian Basin. *Miniopterus schreibersi* is found in many warm regions of the world, with central France, southern Germany, and Slovakia as the northern border of its habitat in Europe. *Myotis blythi* is a typical species of southern Europe, Asia Minor, and the Middle East.

Many species have a broad temperature tolerance. *Plecotus abeli* is extinct, but its descendant, *Plecotus auritus* occurs from North Africa to latitude 64° N in Europe (WOŁOSZYN 1987). Recent *Myotis mystacinus*, *M. nattereri*, *M. daubentoni*, *M. brandti*, and *M. bechstein* species also have the same distribution.

M. praeivius and *M. steiningeri* are extinct, and the occurrence of the recent *Myotis schaubi* is reported only in some areas of the Middle East, thus their ecological tolerances are hardly known.

Most bats are less indicative of climate than the typical ecotope which is definitely required by them. *Myotis blythi* and *Miniopterus schreibersi* are the inhabitants only of open grasslands. Regardless of the surrounding vegetation, *Myotis daubentoni* and *M. dasycneme* occur along larger water bodies. *Eptesicus nilssoni*, *Myotis nattereri*, *M. bechstein*, *M. brandti*, *M. mystacinus*, and *Rhinolophus euryale*

Table 1. The summarized vertebrate fauna of Beremend Crystal Cave (Beremend 16)

taxa	Localities of Beremend 16															
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20	
Pisces																
Cyprinidae indet.								1								
Amphibia and Reptilia																
<i>Salamandra salamandra</i>									1						1	
<i>Triturus cristatus</i>								7		1			1		1	
<i>Lissotriton vulgaris</i>								11		1			1		1	
Salamandridae indet.										2					1	
<i>Bombina variegata</i>							1	16		2				1		
<i>Bombina</i> sp.					1											2
cf. <i>Latonia</i> sp.									1							
<i>Pliobatrachus langhae</i>	2								1							
<i>Pelobates fuscus</i>					1		1	7		3			1		1	
<i>Bufo bufo</i>		1						4		3						
<i>Bufo viridis</i>	3		1	1				137		38			1		1	
Bufonidae indet.	1									1			1		1	
<i>Hyla arborea</i>							1	27		10			1			
<i>Rana temporaria</i>								12		4			1			
<i>Rana</i> cf. <i>dalmatina</i>										1			2			
<i>Pelophylax esculentus</i> group	2		1	1			1	27		12			6		8	
Ranidae indet.	1			1			1	13		4			1			
Anura indet.	3			1	1		1	2	31	9			1		2	

Table 1 (continued)

taxa	Localities of Beremend 16										19	20	
	1	2/15/16	3	4	5	6	7	8	9	10			11/18
Testudines indet.								1					
<i>Lacerta cf. viridis</i>								13					
Lacertidae indet.	1			1	1	1	1	10		3	1	2	2
Sauria indet.	1			1				3		1			
<i>Hierophis cf. viridiflavus</i>	1		1				1	1		1		1	1
<i>Hierophis gemonensis</i>								1				1	
<i>Coronella cf. austriaca</i>								1					
<i>Elaphe cf. paralongissima</i>	1							1		1		1	
<i>Elaphe cf. quatuorlineata</i>								1		1			
<i>Zamenis longissimus</i>	3		1	1	1	1	1	6		1		2	1
<i>Natrix natrix</i>	1	1	1					4		2		1	1
<i>Natrix tessellata</i>	2	1	1	1	1	1	1	10		2		1	1
<i>Natrix</i> sp.		1	1	1	1	1	1	1	1	1			
<i>Telescopus cf. fallax</i>								1					
Colubridae indet.	3		1	1	1	1	1	8		1	1	1	3
<i>Vipera cf. ursinii</i>								1					
<i>Vipera cf. berus</i>								1					
<i>Vipera</i> sp.	1				1			1	1	1			
Euliporyphla													
<i>Desmana thermalis</i>								1					
<i>Crocidaura obtusa</i>	1							2					

Table 1 (continued)

taxa	Localities of Beremend 16															
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20	
<i>Crocidura</i> sp.	1								33		1				5	
<i>Sorex minutus</i>	1			4					3		1			1		
<i>Sorex runtonensis</i>				8			4	6	2		2			1	3	
<i>Sorex (Drepanosorex) savini</i>	1			7			3	2	2		2			1	1	
<i>Petenyia hungarica</i>									1		1					
<i>Asoriculus gibberodon</i>	1		1						2		1					
<i>Beremendia fissidens</i>	2		1	1	1		1	5	1		1				1	
Chiroptera																
<i>Myotis brandti</i>	1	5	1	1	1		4	1	1	3	5	1		3	2	
<i>Myotis nattereri</i>		14	9	1	1		14	1	1	11	13	3	2	22	14	
<i>Myotis schaubi</i>		8	3	1	1	1	5	1	2	1	8	5	2	15	9	
<i>Myotis blythi</i>	2	13	1	1	1	1	3	1	1	1	17	1		23	12	
<i>Myotis daubentoni</i>											3			1		
<i>Myotis steingeri</i>		3	1				2	1	1	3	3	1	1	2	1	
<i>Myotis dasycneme</i>							1							1	1	
<i>Myotis bechsteini</i>											1					
<i>Myotis praeuius</i>	2															
<i>Myotis mystacinus</i>														1		
<i>Plecotus abeli</i>		2									2				1	
<i>Eptesicus nilssoni</i>							1								1	
<i>Miniopterus schreibersi</i>		1		1	1			1	1	1	1	2		3	1	

Table 1 (continued)

taxa	Localities of Beremend 16															
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20	
<i>Rhinolophus mehelyi</i>	3	24	3		2						5	12	1		1	
<i>Rhinolophus macrorhinus</i>		4	1								2	5	2		1	
<i>Rhinolophus euryale</i>														1	1	
Lagomorpha and Rodentia																
<i>Hypolagus beremendensis</i>							1	1	1	1	1			1	1	
<i>Hystrix</i> sp.								1						1		
<i>Spermophilus primigenius</i>	1							3	3					1		
<i>Sicista</i> sp.								2	2		1					
<i>Apodemus sylvaticus</i>	1							8	8	1	1				1	
<i>Apodemus uralensis/sylvaticus</i>								2								
<i>Cricetus nanus</i>								2	5					1		
<i>Mimomys savini</i>	1				14			1	14	1			1		1	
<i>Mimomys pusillus</i>	1							1	5	1				1	1	
<i>Lagurodon arankae</i>	2				12		1	3	191	13				2	4	
<i>Microtus (Allophatomys) pliocaenicus</i>	1				41		1	12	18	4				2	3	
Carnivora																
<i>Mustela palerminae</i>								1	1	1					1	
<i>Pannonictis</i> sp.								1				1		1		
<i>Canis</i> cf. <i>etruscus</i>															1	

Table 1 (continued)

taxa	Localities of Beremend 16														
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20
<i>Canis (cf. Xenocyon) sp.</i>											1				
<i>Vulpes praeglacialis</i>											1				
<i>Vulpes sp.</i>											1		1		
<i>Homotherium crenatidens</i>							1				5		1		
<i>Leo sp.</i>											1				
<i>Hyaena sp.</i>											1?				
<i>Ursus sp.</i>											1		1	1	1
Artiodactyla and Perissodactyla															
<i>Megalovis sp.</i>							1				5		1	1	1
<i>Ovis sp.</i>											1		1	1	
<i>Antelope sp.</i>											2		1	1	1
<i>Nemorhoedus sp.</i>							1				5		1	1	1
<i>Ovibos sp.</i>											1				
<i>Leptobos sp.</i>														1	
<i>Cervus sp. (middle-sized)</i>											1				
<i>Equus (Allohippus) sp.</i>											1				
Proboscidea															
<i>Mammuthus meridionalis</i>															1

Table 2. Climatic and environmental preferences of the small vertebrates recovered from Beremend Crystal Cave (Beremend 16) (ARNOLD & OVENDEN 2002; EGGERT 2002; THIRION *et al.* 2002; DUGUET & MELKI 2003; DENOËL 2004; POPOV 2004; BLAIN & VILLA 2006; BÖHME *et al.* 2006; BIHARI *et al.* 2007; GUNNELL *et al.* 2011; ŽAGAR *et al.* 2011; CARISIO *et al.* 2014; MIRÓ *et al.* 2016; TRAVNICKOVA 2016)

Species	Climate	Vegetation/Ecotope
<i>Salamandra salamandra</i>	widespread	closed
<i>Triturus cristatus</i>	widespread	closed
<i>Lissotriton vulgaris</i>	widespread	closed
<i>Bombina variegata</i>	widespread	water
<i>Pliobatrachus langhae</i>	unknown	water
<i>Pelobates fuscus</i>	widespread	open
<i>Bufo bufo</i>	widespread	open
<i>Bufotes viridis</i>	widespread	open
<i>Hyla arborea</i>	widespread	closed
<i>Rana temporaria</i>	widespread	closed
<i>Rana cf. dalmatina</i>	widespread	closed
<i>Pelophylax esculentus</i> group	warm	water
<i>Lacerta cf. viridis</i>	warm	open
<i>Hierophis cf. viridiflavus</i>	warm	closed
<i>Hierophys gemonensis</i>	warm	open
<i>Coronella cf. austriaca</i>	widespread	opportunist
<i>Elaphe cf. paralongissima</i>	warm	unknown
<i>Elaphe cf. quatuorlineata</i>	warm	closed
<i>Zamenis longissimus</i>	warm	closed
<i>Natrix natrix</i>	widespread	water
<i>Natrix tessellata</i>	warm	water
<i>Telescopus cf. fallax</i>	warm	open
<i>Vipera cf. ursinii</i>	warm	open
<i>Vipera cf. berus</i>	widespread	closed
<i>Desmana thermalis</i>	warm	water
<i>Crocidura</i> sp.	warm	open
<i>Sorex minutus</i>	cold	closed
<i>Sorex runtonensis</i>	cold	open
<i>Sorex (Drepanosorex) savini</i>	unknown	water
<i>Petenya hungarica</i>	widespread	opportunist
<i>Asoriculus gibberodon</i>	widespread	open

Table 2 (continued)

Species	Climate	Vegetation/Ecotope
<i>Beremendia fissidens</i>	widespread	water
<i>Myotis brandti</i>	widespread	forest
<i>Myotis nattereri</i>	widespread	forest
<i>Myotis schaubi</i>	unknown	unknown
<i>Myotis blythi</i>	warm	open
<i>Myotis daubentoni</i>	widespread	water
<i>Myotis steiningeri</i>	unknown	unknown
<i>Myotis dasycneme</i>	cold	water
<i>Myotis bechsteini</i>	widespread	forest
<i>Myotis praevius</i>	unknown	unknown
<i>Myotis mystacinus</i>	widespread	forest
<i>Plecotus abeli</i>	unknown	forest
<i>Eptesicus nilssoni</i>	cold	forest
<i>Miniopterus schreibersi</i>	warm	open
<i>Rhinolophus mehelyi</i>	warm	opportunist
<i>Rhinolophus macrorhinus</i>	warm	opportunist
<i>Rhinolophus euryale</i>	warm	forest
<i>Hypolagus beremendensis</i>	unknown	open
<i>Hystrix</i> sp.	unknown	open
<i>Spermophilus primigenius</i>	unknown	open
<i>Sicista</i> sp.	unknown	open
<i>Apodemus sylvaticus</i>	widespread	opportunist
<i>Apodemus uralensis/sylvaticus</i>	widespread	open
<i>Cricetus nanus</i>	unknown	open
<i>Mimomys savini</i>	unknown	water
<i>Mimomys pusillus</i>	unknown	unknown
<i>Lagurodon arankae</i>	unknown	open
<i>Microtus (Allophaiomys) pliocaenicus</i>	unknown	unknown

are closed forest dwelling species. Their occurrence is often related to the proximity of water, but they are definitely attached to forests. *Plecotus abeli* may be the same indicator based on the occurrence of its living relatives. *Rhinolophus mehelyi* and *R. macrorhinus* are found in European karst areas and occur in grassy and wooded areas as well in warm climate (Table 2).

In the Soricomorpha assemblage, *Sorex minutus* and *Asoriculus gibberodon* indicate humid, wooded or bushy environment (REUMER 1984, RZEBIK-KOWALSKA 2003). All the *Crocidura* species prefer warm climate, dry terrains, and open grasslands. *Sorex runtonensis* is an indicator of markedly cold and more or less open environment (OSIPOVA *et al.* 2006). The presence of river or lakeside is marked by *Desmana thermalis* (RÜMKE 1985), *Sorex (Drepanosorex) savini* (REUMER 1984, MAUL & PARFITT 2010), and *Beremendia fissidens* (BOTKA & MÉSZÁROS 2014). *Petenyia* is typified by REUMER (1984) as opportunist and ubiquitous genus (Table 2).

RESULTS

Taxonomic results

The analysis of the fauna from each individual sampling site revealed remarkable differences regarding the fossil richness and taxonomic composition of the assemblages (Table 1), thus it is desirable to compare the relative abundances of species and larger taxa in each of the sites with the others.

Regarding the fossil richness, there are sites with a sparse assemblage, with fewer than 10 MNI, like sites 4, 6, and 13/14. The material from such sites was excluded from the palaeoecological analysis. There are sites with an MNI between 10 and 50 (sites 1, 3, 7, 8, 10, and 12/17), which provided a basis for a more reliable interpretation. Finally, there are sites with a rich assemblage (sites 2/15/16, 5, 9, 11/18, 19, and 20), which allowed us to draw firm palaeoecological conclusions.

Regarding the faunal composition, there are sites with only bat remains (sites 6 and 13/14), but the MNI in these assemblages is extremely low (Table 1). There are sites, where bats and herpetofaunal elements are present (sites 2/15/16, 4, 10, and 12/17), and there are sites, where other small mammals are also present besides the members of the two aforementioned groups (sites 1, 3, 5, 7, 8, 9, 11/18, 19, and 20).

Marked differences can be recognized regarding the relative abundance of individual species when comparing the different sampling sites. There is no dominant species among the herpetofaunal elements in the case of most samples (sites 1, 2/15/16, 3, 4, 5, 6, 7, 8, 10, 12/17, and 13/14). The green toad (*Bufo viridis*) is dominant in site 9 and 11/18, whereas remains belonging to the *Pelophylax esculantus* group are the most frequent in site 19 and 20. Comparing all samples, the most salamandrids (especially *Lissotriton vulgaris*) can be found in the assemblage from site 9. Apart from the latter, only a few salamandrids were found from sites 11/18, 19, and 20. Turtles were only found in the assemblage from site 9.

The most lacertid lizards were recovered also from site 9. Only a few of them were found from sites 1, 5, 8, 12/17, 19, and 20. Among snakes, colubrids are relatively frequent, whereas vipers are rare. Members of the latter group were only found from sites 1, 5, 8, 9, and 11/18. The most frequent snakes in the assemblages are the dice snake (*Natrix tessellata*, especially from site 9) and the Aesculapian snake (*Zamenis longissimus*), but the grass snake (*Natrix natrix*) is relatively frequent as well.

No dominant small mammal species is present in the assemblages from sites 1 and 20. Most of the white-toothed shrews (Crocidae) were recovered from the latter two sites. However, the relative abundances of genera *Crocidae*, *Beremendia*, and *Lagurodon* are balanced in the case of site 1, slightly more *Crocidae* and *Lagurodon*, as well as *Sorex runtonensis* and *Microtus (Allophaiomys)* were found from site 20. The taxonomic composition of the two sites is similar, besides the already mentioned genera and species, both assemblages contain *Sorex (Drepanosorex) savini*, *Apodemus sylvaticus*, *Mimomys savini*, and *Mimomys pusillus*. There is no dominant bat in the assemblage recovered from site 1, but *Myotis* species dominate together in the case of site 20.

The relative abundance of *Lagurodon* and *Microtus (Allophaiomys)* is equal in the case of site 19, where, in addition, all three *Sorex* species and grassland dwelling small mammals including hares, voles, and hamsters are present in the same assemblage. The composition of the bat fauna of site 19 is very similar to that of site 20.

Sites 5 and 8 are characterised by the dominance of *Microtus (Allophaiomys)*, which was found together with relatively frequent *Sorex* and *Beremendia* remains. A notable abundance of *Mimomys savini* is present in the assemblage from site 5, whereas more hares and hamsters were found in the case of site 8. Only a few bats were found from these sites.

Lagurodon arankae is the dominant small mammal in the assemblages from sites 9 and 11/18. In addition, *Crocidae* is a relatively frequent remain from site 9, likewise, *Sorex runtonensis* and *Sorex (Drepanosorex) savini* from site 11/18. Both of the latter assemblages contain *Sicista* and *Apodemus sylvaticus*. The bat fauna of site 9 is sparse. Besides the dominance of *Myotis* species, the presence of water preferring forms with Mediterranean *Rhynolophus* and *Miniopterus* is notable in the assemblage from site 11/18.

Sites 2/15/16 and 12/17 are dominated by warm preferring *Rhynolophus* bats, but a considerable amount of both grassland and forest *Myotis* species was also found. The dominance of the forest dwelling *Myotis* species is clear in the bat fauna of sites 3, 7, and 10.

Among shrews a *Crocidae* form was identified in sites 9 and 20, which could not be referred to any valid names. Nowadays, three *Crocidae* species

are recognized from the European Early Pleistocene: *Crocidura zorzii* Pasa, 1942; *Crocidura kornfeldi* Kormos, 1934, and *Crocidura obtusa* Kretzoi, 1938 (ROFES & CUENCA-BESCÓS 2011). *C. zorzii* is bigger than the specimens found in Beremend Crystal Cave. BOTKA & MÉSZÁROS (2015) showed that *C. kornfeldi* and *C. obtusa* can be distinguished mainly on the basis of the mandibular coronoid process. MÉSZÁROS *et al.* (2019) confirmed this by redefining *C. obtusa* species. The structure of the coronoid process of specimens from sites 9 and 20 differs from both above mentioned shrews. Therefore, this form should be described as a new species. Unfortunately, the species level identification of jawless *Crocidura* remains is problematic, so they are mentioned here under the name, *Crocidura* sp. as well. We believe that no trouble is caused by using this contracted nomenclature in the conclusions, because the stratigraphic ranges of either the new species or the indeterminable specimens are similarly useless. Otherwise, the specific ecological characters of genus *Crocidura* allow us using these forms together in the palaeoecological reconstruction.

Palaeoecological results

The species richness of the herpetofauna is different comparing the individual sites. Three sites (6, 13/14, and 2/15/16) did not contain herpetofaunal elements at all. The heliophilous animals (e.g., *Bufo viridis* and *Lacerta viridis*) are frequent (57%) in the studied samples, but the water preferring species (e.g., *Pelophylax esculentus* group and *Natrix tessellata*) are not rare either (31%). This latter group primarily appears in sites 5, 9, 11/18, and 20. The burrowing green toad (which is more active at night) is the most frequent in the case of sites 9 and 11/18 comparing all assemblages. The relative abundance of both forest dwelling animals (e.g., *Rana dalmatina* and *Zamenis longissimus*) and opportunists (e.g., *Rana temporaria* and *Coronella austriaca*) is 6% in the case of these two sites. The forest dwelling *Rana dalmatina* appears only in the assemblages from sites 11/18 and 19, whereas most of the remains of *Zamenis longissimus* was found from site 9. Opportunist taxa are not frequent; *Rana temporaria* is present in the assemblages from sites 11/18 and 19, whereas *Coronella austriaca* only appears in the case of site 9.

The above mentioned data suggest that the history of the herpetofauna can be divided into several stages, which can be correlated with the changes recognized in the case of the chiropteran assemblages (see below). However, it can be concluded that a permanent water body was near the Beremend Crystal Cave during the Early Pleistocene, but its size may have changed during the studied period due to changing climate. The periodic appearance of opportunist taxa may be related to these changes.

Among shrews of the Beremend Crystal Cave, the dominance of the warm grassland indicator *Crocidura* is conspicuous in site 9. *Asoriculus gibberodon* and *Sorex minutus*, which prefer closed forests and scrubland environment, occur in several sites, but much less frequently. Their relative abundance is similar to that of aquatic insectivores (*D. thermalis*, *S. (D.) savini* and *Beremendia*). *S. runtonensis*, living in cold steppe areas, is hardly present in the assemblage, compared to its abundance in other Early Pleistocene localities.

Most of the Beremend 16 bat species prefer warm climate. We found only few species that are especially cold tolerant in some of the sites. Most of them are inhabitants of more or less closed forests or scrubby areas, while indicators of open vegetation are less frequent. Many of them like to hunt over larger water surfaces. The bat fauna refers to a mosaic ecotype along a larger body of water in a moderately warm climate.

Among lagomorphs and rodents from the locality, only a few are indicative of the environment. But most of these indicate an open grassland environment (*Hypolagus beremendensis*, *Hystrix* sp., *Spermophilus primigenius*, *Sicista* sp., *Apodemus uralensis*, *Cricetus nanus*). Among arviculids, only the ancient water vole, *Mimomys savini* and a lagurid, *Lagurodon arankae* can be used as an environmental indicator.

Taking into account the entire small vertebrate fauna of the assemblages and the environmental preferences of the taxa (Table 2), a palaeoclimatic and vegetational reconstruction could be made for almost all sites within the Beremend Crystal Cave. In order to draw such conclusions, the number (Tables 3–4) and relative abundance (Figs 2–3) of the environmental indicator taxa were considered. Those sites, where the MNI was lower than 10, were excluded from the palaeoecological analysis (sites 4, 6, 13/14). Based on this analysis, the following environments can be differentiated:

1. Cold, dry climate, open vegetation with a close proximity of a relatively large water body (sites 5 and 8). Although the richness of these sites (22–26 species) is sufficient, it has to be taken into consideration that most of the taxa are widespread, thus especially the climatic reconstruction might not be reliable.
2. Temperate, dry climate, grassland with slightly more closed patches. The size of the water body was probably somewhat smaller than above (sites 1, 11/18, 19, and 20). These assemblages are rich, with more than 30 species. A lot of the recovered taxa are indicative of the environment and the climate, thus these conclusions are reliable.
3. Temperate, dry climate with primarily closed vegetation. Most likely, only a small water body was present in the vicinity (sites 3, 7, and 10). The species

Table 3. Number of climatic indicator species grouped in larger taxa and their total number given for each site of the Beremend Crystal Cave (Beremend 16)

taxa	Localities of Beremend 16															
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20	
Amphibia and Reptilia																
Warm	5	1	3	2	3	3	1	3	9	5				6	3	
Cold																
Wide or unknown tolerance	10	3	3	3	10	3	3	9	23	1	21	2		14	12	
Eulipotyphla																
Warm	2								3	1				2	1	
Cold	1				2			1	2	2					1	
Wide or unknown tolerance	3		2		2		2	2	4	4				1	2	
Chiroptera																
Warm	2	4	3		3	1	1		2	1	4	4	2	3	5	
Cold								2	1					1	2	
Wide or unknown tolerance	2	5	4	2	3	1	4		4	3	7	4	3	6	5	
Lagomorpha and Rodentia																
Warm																
Cold																
Wide or unknown tolerance	6				3		3	6	12		7			7	6	
Sum																
Warm	9	5	6	2	6	1	2	3	14	1	10	4	2	11	9	
Cold	1				2		2	2	2		2			1	3	
Wide or unknown tolerance	21	8	9	5	18	1	10	17	43	4	39	6	3	28	25	

Table 4. Number of environmental indicator species grouped in larger taxa and their total number given for each site of the Beremend Crystal Cave (Beremend 16)

taxa	Localities of Beremend 16															
	1	2/15/16	3	4	5	6	7	8	9	10	11/18	12/17	13/14	19	20	
Amphibia and Reptilia																
Open	1	1		1	2			1	7		3			3	2	
Closed	2		2		1			3	9		9			7	4	
Water	4	2	2	2	2		1	2	5		4			4	3	
Opportunist or unknown	8	1	2	2	8		3	6	11	1	10	2		6	6	
Eulipotyphla																
Open	2				1			1	3		2			1	2	
Closed	2		1		1				2		2			1		
Water	2				2		2	3	3		2			1	2	
Opportunist			1						1		1					
Chiroptera																
Open	1	2	1		2	1	1		2	1	2	2		2	2	
Closed	1	3	2	2	2		3		2	2	4	2	1	4	5	
Water							1				1			2	1	
Opportunist or unknown	2	3	4		2	1	2	1	2	1	4	4	4	2	4	
Lagomorpha and Rodentia																
Open	2				1		2	3	7		3			5	2	
Closed																
Water	1				1			1	1		1				1	
Opportunist or unknown	3				1		1	2	4		3			2	3	
Sum																
Open	6	3	1	1	6	1	3	5	19	1	10	2	0	11	8	
Closed	5	3	5	2	4	0	3	3	13	2	15	2	1	12	9	
Water	7	2	2	2	5	0	2	5	9	0	8	0	0	7	7	
Opportunist or unknown	13	4	7	2	11	1	6	9	18	2	18	6	4	10	13	

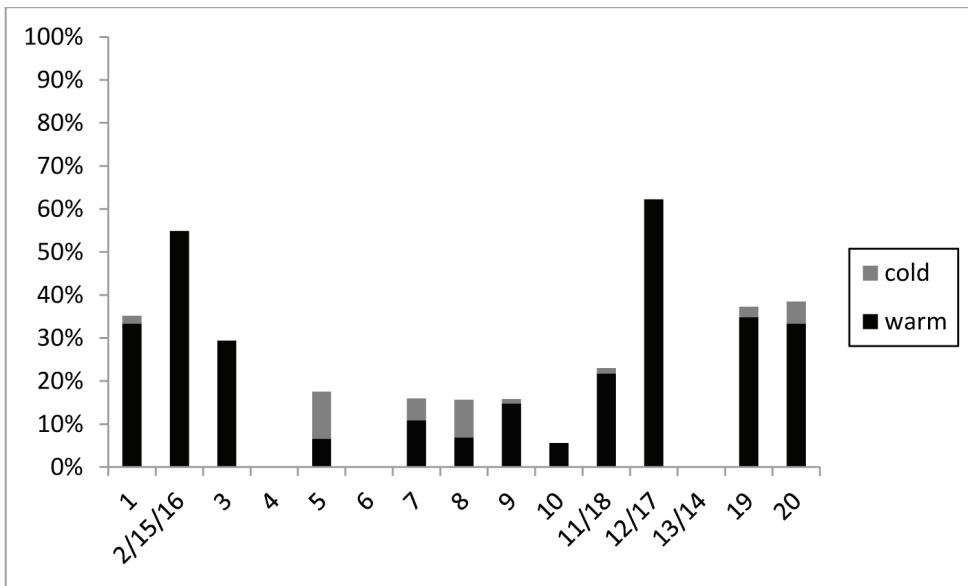


Fig. 2. Relative abundance of the climatic indicator taxa compared to the entire recovered assemblage of each site

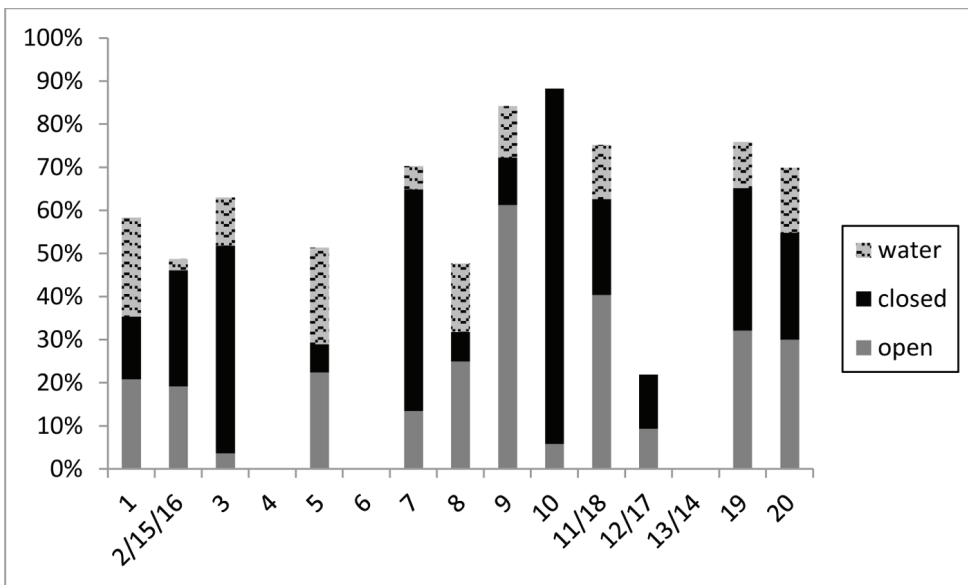


Fig. 3. Relative abundance of the environmental indicator taxa compared to the entire recovered assemblage of each site

richness is low, climatic indicator taxa are sparse, thus these conclusions are less reliable than above.

4. Temperate, dry climate, open vegetation with a medium-sized water body (site 9). Extremely rich assemblage with more than 50 species, however, the number of climatic indicator taxa is low, thus these conclusions might not be reliable.
5. Warm, dry climate with the dominance of more closed vegetation. The water body was probably small (sites 2/15/16 and 12/17). The species richness is low, although climatic indicator taxa are abundant, environmental indicators are sparse, thus the environmental reconstruction might not be reliable.

Stratigraphic results

Most of the Eulipotyphla species of Beremend Crystal Cave are too long-ranged for using them in a stratigraphic investigation. *Sorex minutus* appeared in the Early Pliocene MN 14 zone and is still living (RZEBIK-KOWALSKA 1991). Similarly, the oldest record of *Sorex runtonensis* can be dated back to the Late Pliocene, whereas the youngest ones are known from several Late Pleistocene localities (OSIPOVA *et al.* 2006). *Beremendia fissidens* is also reported from the MN 14 zone up to the Tarkóian Phase of the Middle Pleistocene in Europe (BOTKA & MÉSZÁROS 2014). *Desmana thermalis* emerged at the beginning of the Early Pleistocene (MN 17 zone) and disappeared at the end of the Late Pleistocene (RÜMKE 1985) (Fig. 4).

Based on some of the shrew remains, however, we can conclude that the sites are not younger than the end of the Early Pleistocene. The stratigraphic range of *Petenya hungarica* spans from the Miocene/Pliocene boundary (MN13/14 zone) up to the end of the Early Pleistocene (RZEBIK-KOWALSKA 2000) (Fig. 4). The first occurrence of *Asoriculus gibberodon* in Hungary is reported by MÉSZÁROS (1998) from the Late Miocene MN 12 zone, and it disappears only at the end of the Early Pleistocene (RZEBIK-KOWALSKA 2000). The Early Pleistocene age of the sites is supported by the occurrence of *Sorex (Drepanosorex) savini*, which is reported from the Early Pleistocene MN 17 zone until the Late Biharian Stage of the Middle Pleistocene (BOTKA & MÉSZÁROS 2016).

Crocidura obtusa seems to be the most useful shrew for making stratigraphic conclusions, because it was present in Central Europe from the late Early Pleistocene (1.2 Ma) to the earliest Late Pleistocene (BOTKA & MÉSZÁROS 2015). Therefore, on the basis of its occurrence, we can determine the age of some sites as the second half of the Biharian Age.

The Pleistocene chiropteran assemblages are less useful for drawing stratigraphic conclusions than for presuming ecological conditions, because their

elements hardly changed since the Pliocene. The bat species identified from Beremend Crystal Cave support the conclusions drawn from other fauna elements (WOŁOSZYN 1987; TOPÁL 1989; TRAVNICKOVA 2016).

The genera *Myotis*, *Rhinolophus*, *Eptesicus*, *Miniopterus*, and *Plecotus* have been present since the Miocene or the Early Pliocene. Among the species, *M. bechstein*, *M. blythii*, *M. daubentoni*, *M. emarginatus*, *M. mystacinus*, and *M. nattereri* appeared in MN 15, while *M. brandti*, *M. dasycneme*, and *M. schaubi* emerged in MN 17. Based on their presence, the fauna cannot be older than the Early Pleistocene.

There are three species in the fauna that occur only in the Biharian Age in the Carpathian Basin: *Eptesicus nilssoni*, *Miniopterus schreibersi*, and *Plecotus abeli*. These species suggest that sites 2/15/16, 5, 7, 9, 11/18, 12/17, 19, and 20 are from the second part of the Early Pleistocene.

The only short-ranged form from the locality is the group identified by György Topál as *M. "praeivus" ssp.* at site 1, which species is reported from the MN 16–17 zones. This would be difficult to interpret considering the stratigraphic view formed on the basis of the overall fauna. But in our opinion, until finding further morphological evidence for a grounded separation of this species from the Early Pleistocene *M. praeivus*, this temporary solution would help to avoid unnecessary confusion related to the range of the latter taxon.

In the age determination of the sites where small mammals were found, rodents and large mammals play an important role as well. Among rodents, voles (*Mimomys savini*, *M. pusillus*, *Microtus (Allophaiomys) pliocaenicus*, *Lagurodon arankae*) clearly indicate an Early Pleistocene age. *Lagurodon arankae* appeared 2.0 Ma, *M. pusillus* and *M. savini* emerged 1.8 Ma, whereas the first *Microtus (Allophaiomys) pliocaenicus* remains can be dated back to only much later, to 1.5 Ma (MAUL & MARKOVA 2007; TESAKOV 2004). Their co-occurrence indicates that the sites are younger than 1.5 Ma (Fig. 4). These voles (apart from *M. savini*) disappeared around the Early/Middle Pleistocene boundary. Therefore, those sites, where *M. (A.) pliocaenicus* was found (sites 1, 5, 7, 8, 9, 11/18, 19, and 20), can be dated between 1.5 Ma and 0.78 Ma. Because neither *Microtus (Terricola)* nor *Prolagurus* remains were found at the sites, the members of which genera appeared around 1.1 Ma and 1.2 Ma, respectively (MAUL & MARKOVA 2007; TESAKOV 2004), the age of the sites is probably older than these dates.

Among large mammals, *Homotherium crenatidens* appeared 1.35 Ma (DIEDRICH & MCFARLANE 2017), thus those sites where fossils of this particular species were found (sites 7, 11/18 and 19), are probably younger than this date (Fig. 4).

In conclusion, the age of the sites within the Beremend Crystal Cave can be correlated with the late Early Pleistocene. The sites can be dated back between

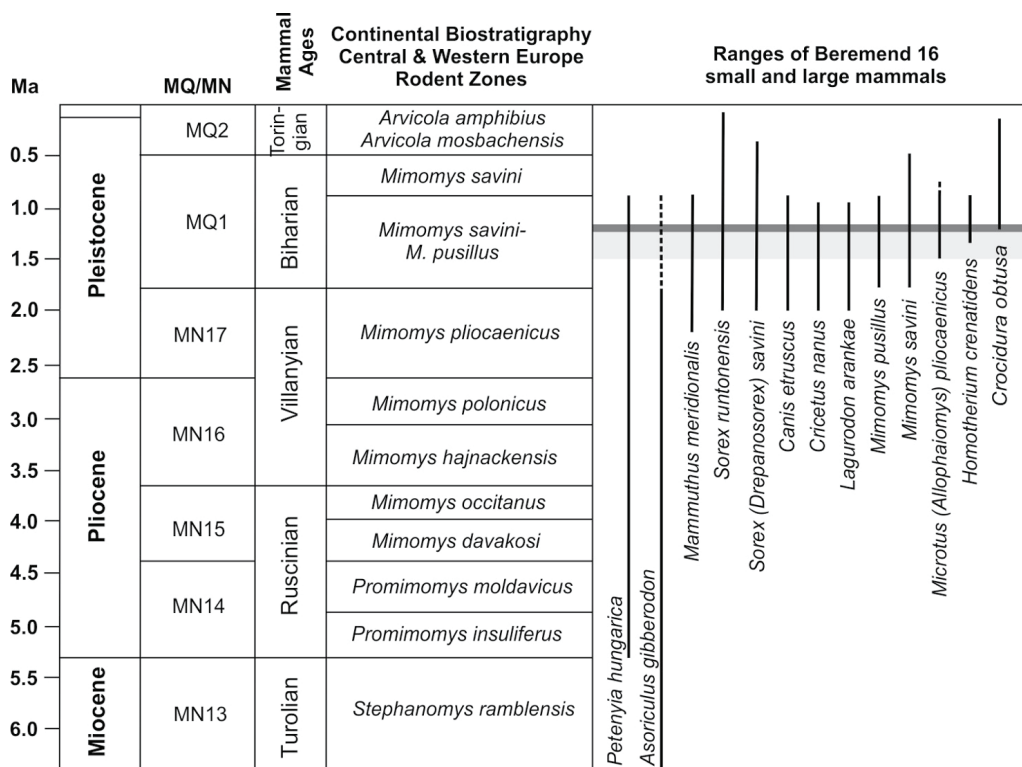


Fig. 4. Stratigraphically important small and large mammal taxa of Beremend Crystal Cave (Beremend 16). The most probable age of the older sites is indicated by a light grey zone, whereas age of the younger sites is marked with dark grey (after MCGOWRAN & DENBIGH 2008; TESAKOV 2004)

1.5 Ma and 1.2 Ma. Within this time period, older and younger sites can be separated based on the ranges of the mammals in their fauna. The material of the older sites can be dated between 1.5–1.2 Ma (sites 5, 8, and 20) and 1.35–1.2 Ma (sites 7, 11/18, and 19). The material of the younger sites (1 and 9) accumulated approximately 1.2 Ma, as indicated by the presence of *Crocidura obtusa*, which just appeared around that date (Fig. 4).

CONCLUSIONS

Based on our thorough taxonomic, palaeoecological and stratigraphic analysis of the samples collected from 15 different sites within the Beremend Crystal Cave, it can be concluded that these assemblages cannot be unified and interpreted as a whole, because of several considerable differences that were pointed out here regarding their faunal content, their age, and the former environment they represent.

Diverse and sparse assemblages were recognized based on the fossil richness and taxonomic composition of the samples from each site. Some of these assemblages contain only bats, whereas others contain other small mammals and herpetofaunal elements as well. These dissimilarities exist probably due to taphonomical or age differences.

Apart from the appearance of *Crocidura obtusa*, no relevant evolutionary or faunistical event can be identified in the assemblages, thus it can be assumed that the age difference between the sites is minor. According to the results of the detailed stratigraphic analysis, which was based on the ranges of the mammal taxa found within the assemblages, the sites can be divided into an older and a younger group. The material of the older sites can be dated between 1.5–1.2 Ma (sites 5, 8, and 20) and 1.35–1.2 Ma (sites 7, 11/18, and 19), whereas the material of the younger sites (1 and 9) accumulated approximately 1.2 Ma, as indicated by the presence of *Crocidura obtusa*.

The palaeoecological study of the small vertebrate fauna showed that the material of the different sites accumulated under distinct palaeoenvironmental conditions, which also confirms that not all of the sites are contemporaneous. It can also be concluded that a water body varying in size was in the close proximity of the cave during the entire studied time period. The lake was surrounded by open or sometimes more closed vegetation depending on the changes of the erstwhile climate.

Based on the assemblages older than 1.2 Ma, the following three environments were recognized:

1. Cold and dry climate, open vegetation with the close proximity of a relatively large water body (1.5–1.2 Ma). Most likely a grassland, which was present during the accumulation of the fossils at sites 5 and 8.
2. Temperate and dry climate, primarily open vegetation and the close proximity of a relatively large water body (1.35–1.2 Ma). These suggest a grassland environment with woodland patches. These conditions were present during the accumulation of the fossils at sites 11/18, 19, and 20.
3. Temperate and dry climate, primarily closed vegetation with only a small water body in the vicinity (1.35–1.2 Ma). This woodland environment was reconstructed based on the material of sites 3 and 7. Site 10, which has an uncertain age and contains only bats and herpetofaunal elements, is also indicative of a warm environment with closed vegetation, thus it was tentatively assigned here.

Based on the assemblages of the younger sites, which have an age of approximately 1.2 Ma, the following two environments were recognized:

1. Temperate and dry climate, open vegetation with only a small water body in the vicinity. Site 9 belongs to this group, in which grassland dwelling species are dominant.
2. Temperate and dry climate, primarily open vegetation with woodland patches. Site 1 belongs to this group, of which environment is essentially identical to that of group 2 in the case of the older sites.

Among the 12 assemblages that were included in the stratigraphic and palaeoecological analyses, two (sites 2/15/16 and 12/17) contained only bats and herpetofaunal elements, thus their age and the environment, in which they were formed, are uncertain. These assemblages are characterised by low species number, however, warm preferring taxa are dominant and the relative abundance of taxa indicative of a closed vegetation is slightly higher than the relative abundance of those which preferred open environments. These most likely suggest a grassland environment with woodland patches for these sites.

*

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