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The lowermost Pleistocene rodent and soricid (Mammalia) fauna from Beremend 14 locality (South Hungary) and its biostratigraphical and palaeoecological implications

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Abstract – The limestone quarry of Beremend yielded the classical Late Pliocene and Early Pleistocene vertebrate faunas studied for more than a century. The Beremend 14 site was discovered in the 1970s by Dénes Jánossy. Twenty four small mammal species and twenty seven elements of herpetofauna were identified from its rich vertebrate material. Based on the taxonomical study of small mammals, we suppose that the stratigraphic position of the site is the Early Pleistocene MN 17 Zone. The palaeoecological analysis of the fauna suggests warm, dry climate and open, probably wooded grassland vegetation surroundings of the site with smaller open water surface. With 47 figures and 14 tables.

Key words – biostratigraphy, Early Pleistocene, Hungary, palaeoecology, small mammals

INTRODUCTION

The Szőlő Hill of Beremend is located approximately 9 km south from the range of Villány Hills and municipality Villány, in South Hungary. Altitude of the flat, loess covered, limestone hill is 174 m. The limestone quarry of Beremend yielded the classical vertebrate faunas studied for more than a century by Petényi, Kretzoi, Krolopp, and Jánossy (see in Jánossy 1986). Numerous karst cavities containing Pliocene-Pleistocene mammalian faunas were explored from the Lower Cretaceous limestone. According to Kretzoi (1969) and Kretzoi & Pécsi (1982) the sites of Beremend represent Late Pliocene Beremendian Biochronological Phase. However, according to Krolopp (1990), this phase overlaps with the beginning of the Early Pleistocene (Early Villanyian).

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Bone remains were first presented from Beremend by Petényi (1864). Since then, 26 sites have been described from the quarry (Kretzoi 1956; Jánossy 1986; Kordos 1991; Pongrácz 1999; Császár & Kordos 2004) (Fig. 1). Beremend 14 site discovered in the 1970s, is northeast from the Beremend Crystal Cave. Unfortunately, we have not got other information from this site, because it has been destroyed, probably it was a karst fissure with red clay infill-

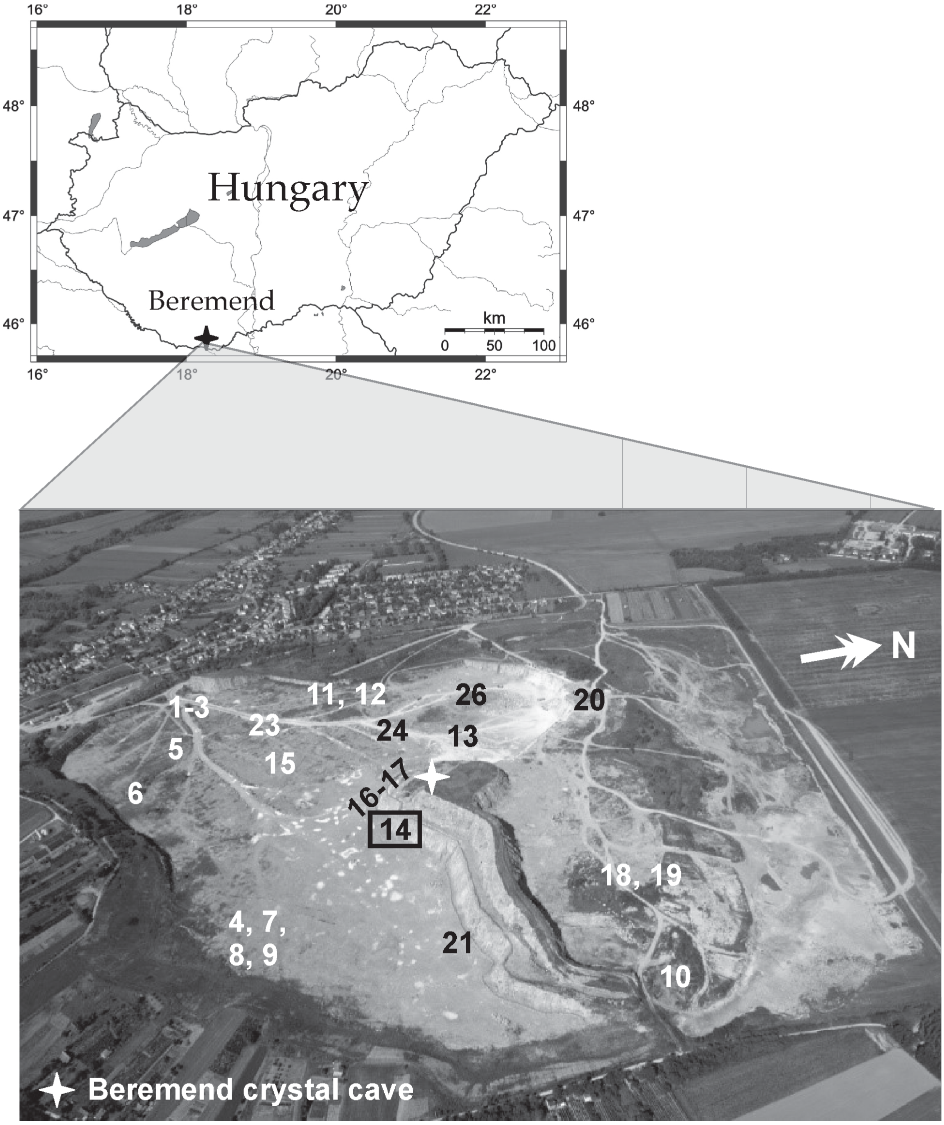


Fig. 1. Location of the Beremend 14 site (Villány Hills, South Hungary)

ing. This paper presents the soricid and rodent fauna, and its biostratigraphical as well as palaeoecological implications.

The presented fossils were unearthed from previously screen-washed deposits, which were probably collected by Dénes Jánossy in 1977. The unprocessed, scattered material is stored in the Department of Palaeontology and Geology of the Hungarian Natural History Museum, Budapest. Due to sorting and processing of this material (VER 2016.3568., 2016.3569., 2016.3570., 2016.3571., 2016.3572., 2016.3573., 2016.3574.), rich fauna was found. We have identified the fossils as follows:

Triturus cristatus (Laurenti, 1768)
Lissotriton vulgaris (Linnaeus, 1758)
Salamandridae indet.
Bombina variegata Linnaeus, 1758
Pelobates fuscus (Laurenti, 1768)
Bufo bufo (Linnaeus, 1758)
Bufotes viridis Laurenti, 1768
Bufo sp.
Hyla arborea (Linnaeus, 1758)
Rana temporaria Linnaeus, 1758
Rana sp.
Anura indet.
Lacertidae indet.
Anguidae indet.
Sauria indet.
Sauria indet. coprolite
Hierophis viridiflavus Lacépède, 1789
Hierophis gemonensis (Laurenti, 1768)
Coronella austriaca Laurenti, 1768
Elaphe quatuorlineata Szyndlar, 1984
Elaphe paralongissima (Lacépède, 1789)
Zamenis longissimus Laurenti, 1768
Natrix natrix (Linnaeus, 1758)
Natrix tessellata (Laurenti, 1768)
Natrix sp.
Telescopus fallax (Fleischmann, 1831)
Colubridae indet.
Carnivora indet.
Chiroptera indet.
Erinaceomorpha indet.
Talpidae indet.

Crocidura kornfeldi Kormos, 1934
Sorex minutus Linnaeus, 1766
Sorex runtonensis Hinton, 1911
Sorex (Drepanosorex) savini Hinton, 1911
Beremendia fissidens (Petényi, 1864)
Petenyia hungarica Kormos, 1934
Asoriculus gibberodon (Petényi, 1864)
Spermophilus primigenius (Kormos, 1934)
Glis minor Kowalski, 1956
Estramomys aff. *simplex* Jánossy, 1969
Sicista praeloriger Kormos, 1930
Prospalax cf. *priscus* (Nehring, 1897)
Allocricetus ehiki Schaub, 1930
Cricetus nanus (Schaub, 1930)
Dolomys milleri Nehring, 1898
Villanyia exilis Kretzoi, 1956
Mimomys reidi Hinton, 1910
Mimomys pusillus (Méhely, 1914)
Pitymimomys pitymyoides (Jánossy et van der Meulen, 1975)
Borsodia newtoni (F. Major, 1902)
Allophaiomys deucalion Kretzoi, 1969
Lagurodon arankae (Kretzoi, 1954)
Apodemus dominans Kretzoi, 1959
Micromys praeminutus Kretzoi, 1959

SYSTEMATIC PALAEONTOLOGY

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

Eight Soricidae species were determined in the Beremend 14 fossil assemblage (Table 1). *Crocidura kornfeldi* Kormos, 1934 is ranged to subfamily Crocidurinae, while other six forms: *Sorex minutus* Linnaeus, 1766; *Sorex* (*Drepanosorex*) *savini* Hinton, 1911; *Sorex runtonensis* Hinton, 1911; *Beremendia fissidens* (Petényi, 1864); *Petenyia hungarica* Kormos, 1934, and *Asoriculus gibberodon* (Petényi, 1864) belong to subfamily Soricinae. One form could not be exactly determined, because it shows both Crocidurinae and Soricinae characters, so it was defined as Soricidae gen. et sp. indet.

Table 1. The specific remains of the Beremend 14 Soricidae fauna

Species	Remain		Teeth		MNI	
	n	%	n	%	n	%
Crocidura kornfeldi	101	17.06	158	30.56	13	21.67
Sorex minutus	9	1.52	7	1.35	3	5.00
Sorex savini	9	1.52	11	2.13	4	6.67
Sorex runtonensis	15	2.53	26	5.03	5	8.33
Beremendia fissidens	435	73.48	292	56.48	28	46.67
Petenyia hungarica	7	1.18	10	1.93	2	3.33
Asoriculus gibberodon	12	2.03	10	1.93	4	6.67
Soricidae gen. et sp. indet.	4	0.68	3	0.58	1	1.67
Total	592	100.00	517	100.00	60	100.00

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, n = number of specimens, min. = minimum, max. = maximum, sd. = standard deviation, MNI = minimum number of individuals. Calculation of MNI is based on the number of identical, ipsilateral teeth. Morphological terms are used after Reumer (1984). Measurements are given in mm.

Remarks – In the relative groups of the shrews several Erinaceomorpha and Talpidae species with more than 250 specimens occurred in the Beremend 14 sample, but they are not discussed in this paper.

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

Crocidura kornfeldi Kormos, 1934
(Fig. 2)

Material – 14 left mandible fragments with 3 I_1, 4 A_1, 9 A_2, 10 M_1, 10 M_2, 5 M_3; 12 right mandible fragments with 1 I_1, 3 A_1, 4 A_2, 5 M_1, 4 M_2, 1 M_3; 1 skull fragment with left A^1, A^3, M^1-M^3 and right A^1-A^3, P^4, M^1-M^2; 15 left maxillary fragments with 2 I^1, 1 A^1, 1 A^2, 1 A^3, 5 P^4, 9 M^1, 7 M^2; 8 right maxillary fragments with 1 I^1, 3 A^1, 3 A^2, 2 A^3, 4 P^4, 5 M^1, 4 M^2; Isolated teeth: 7 left and 12 right I_1, 2 left and 5 right M_1 or M_2, 2 right M_3, 5 left and 5 right I^1, 1 left and 1 right A^1, 2 right P^4, 4 left and 2 right M^1, 1 left and 2 right M^2.

Measurements – Table 2.

Description – Dental formula is 143/123. The dental elements are not pigmented. The coronoid process is blunt and low. The coronoid spicule is small,

Table 2. Measurements of *Crocidura kornfeldi* teeth (Beremend 14)

		n	min.	mean	max.	sd.
M^1	LL	10	1.28	1.42	4.48	0.06
	BL	10	1.46	1.53	1.60	0.04
	AW	10	1.65	1.74	1.80	0.05
	PW	10	1.92	2.05	2.18	0.08
M^2	LL	10	1.12	1.21	1.28	0.05
	BL	10	1.16	1.24	1.32	0.05
	AW	10	1.88	1.96	2.04	0.05
	PW	10	1.56	1.62	1.76	0.07
M_1	L	10	1.40	1.58	1.72	0.10
	W	10	0.98	1.04	1.18	0.10
M_2	L	10	1.38	1.52	1.64	0.10
	W	10	0.86	0.92	0.96	0.04

situated high and indistinct. The external temporal fossa is long, narrow and indistinct. The internal temporal fossa is reaching to halfway up the coronoid process, and a subfossa is present above it. I^1 apex is pointed and the talon also has a little, sharp cone. The cingulum along the posterior buccal margin is narrow but well-pronounced, usually it is undulate. The first upper antemolar is elongated, the two posterior ones are considerably smaller. A^3 is somewhat smaller than A^2. The parastyle of P^4 is protruding and separated from the paracone by a deep valley. The protocone is small. A small hypocone is visible on the cingulum-like ridge running along the lingual margin of the tooth. The posterior margins of P^4 and M^1 are much concave. Both of the upper molars are relatively broad and short. The M^1 AW is far smaller than the PW. The shape of M^2 is trapezoidal, its anterior part is far wider than the posterior one. The parastyle on M^2 is long and curved, while the metastyle is short and straight. M^3 protocone, paracone, and hypocone are about equal in size. I_1 is slightly bicuspulate. The buccal cingulum is narrow but pronounced. A_1 is anteroposteriorly quite elongate, but low, A_2 is much higher. M_1-M_2 buccal cingula are narrow but well-pronounced. It is undulate in all specimens, but it is less undulate on M_2 than on M_1. M_3 talonid is reduced to a single cuspid.

Remarks – There are two similar *Crocidura* species reported from the Early Pleistocene of Europe: *C. kornfeldi* Kormos, 1934 and *C. obtusa* Kretzoi, 1938. Botka & Mészáros (2015) distinguished these two forms by the characteristics of the mandible. Based on the shape of the coronoid process and the indistinct coronoid spicule we ranged the Beremend 14 *Crocidura* remains to *C. kornfeldi.*

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

Sorex minutus Linnaeus, 1766
(Fig. 3)

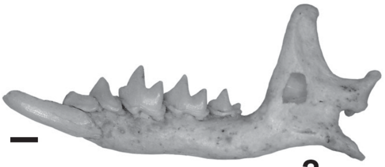
Material – 1 incomplete right mandible with A_2 fragment and M_1-M_2 (M_1: L = 1.24, W = 0.66; M_2: L = 1.01, W = 0.60); 2 left and 2 right edentulous mandible fragments; 1 left I^1 fragment; 1 right A^1; 1 right M^1 (LL = 1.28, BL = 1.28, AW = 1.36, PW = 1.52); 1 right M^2 (LL = 1.12, BL = 1.14, AW = 1.40, PW = 1.29).

Description – Very small-sized *Sorex* form with light orange pigmentation on the tip of the teeth. M^1-M^2 are subquadrate, with specifically concave posterior emargination. The buccal cingulum is well-developed but narrow, and usually undulated on the lower molars. The anterior edge of the coronoid process is concave, the apex bends slightly towards anterior direction. The external temporal fossa is developed as a longitudinal groove. The coronoid spicule is present. The internal temporal fossa is high and triangular, continuing to the tip of the coronoid process.

Sorex runtonensis Hinton, 1911
(Fig. 4)

Material – 1 left corpus mandibulae with condyle; 1 left mandible fragment with I_1 and A_2-M_3 (M_1: L = 1.34, W = 0.76; M_2: L = 1.16, W = 0.68); 1 left mandible fragment with M_1-M_3 (M_1: L = 1.50, W = 0.80; M_2: L = 1.30, W = 0.78); 1 left mandible fragment with M_1-M_2 (M_1: L = 1.56, W = 0.84; M_2: L = 1.32, W = 0.80); 1 incomplete left mandible with I_1 fragment and A_2-M_2 (M_1: L = 1.48, W = 0.80; M_2: L = 1.32, W = 0.76); 1 left mandible fragment with A_2-M_2 (M_1: L = 1.54, W = 0.84; M_2: L = 1.36, W = 0.76); 1 right I_1 (L = 3.04, H = 0.78); 2 left P^4 (LL = 1.08, BL = 1.40, W = 1.68; LL = 0.96, BL = 1.56, W = 1.62); 1 left M^1 (LL = 1.45, BL = 1.44, AW = 1.56, PW = 1.73); 3 right M^1 (LL = 1.32, BL = 1.33, AW = 1.44, PW = 1.52; LL = 1.44, BL = 1.44, AW = 1.48, PW = 1.64; LL = 1.40, BL = 1.36, AW = 1.52, PW = 1.66); 1 right M^1 and 1 right M^2 fragments.

Description – The teeth are pigmented with orange to red colour. The pentagonal P^4 has a well-developed parastyle and protocone. The protocone is placed in the central part of the anterior side of the tooth. The subquadrate M^1 has well-developed hypocone and indistinct metaloph. The posterior emargination of P^4 and M^1 is moderately developed. The coronoid process is tall and leans forwards; its anterior margin is concave. The deep external temporal fossa of coronoid process runs along the posterior border of the process. The coronoid spicule is well-developed. The internal temporal fossa is high and triangular. I_1 is tricuspulate. M_1 is bigger than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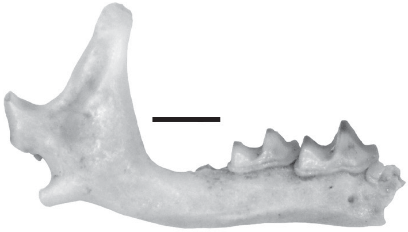
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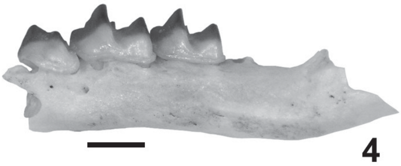
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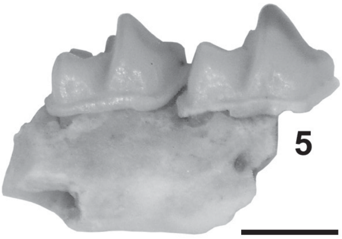
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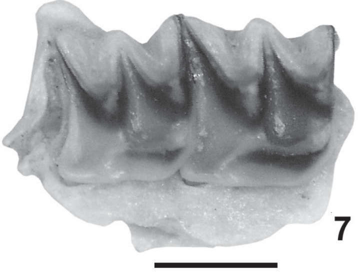
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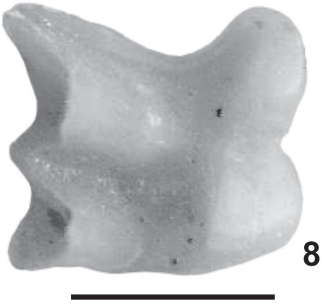
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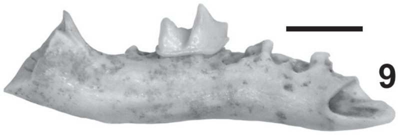
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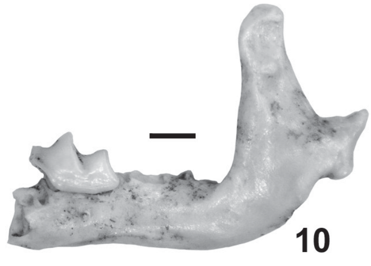
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Fig. 2. *Crocidura kornfeldi* Kormos, 1934; complete left mandible, buccal view (VER 2016.3572.1.). – **Fig. 3.** *Sorex minutus* Linnaeus, 1766; incomplete right mandible with A_2 fragment and M_1-M_2, buccal view (VER 2016.3572.2.). – **Fig. 4.** *Sorex runtonensis* Hinton, 1911; left mandible fragment with A_2 and M_1-M_2, buccal view (VER 2016.3572.3.). – **Fig. 5.** *Sorex* (*Drepanosorex*) *savini* Hinton, 1911; right mandible fragment with M_1-M_2, buccal view (VER 2016.3572.4.). – **Fig. 6.** *Beremendia fissidens* (Petényi, 1864); complete right mandible, buccal view (VER 2016.3572.5.). – **Fig. 7.** *Petenyia hungarica* Kormos, 1934; right maxillary fragment with M^1-M^2, occlusal view (VER 2016.3572.6.). – **Figs 8–9.** *Asoriculus gibberodon* (Petényi, 1864). – **8.** Left M_1, occlusal view (VER 2016.3572.7.). – **9.** Right mandible fragment with M_2, buccal view (VER 2016.3572.8.). – **Fig. 10.** Soricidae gen et sp. indet.; left mandible fragment with M_1, buccal view (VER 2016.3572.9.). Scale bars = 1 mm

M_2. M_1 buccal cingulum is undulate while it is straight in M_2 and M_3. The molars are characterized by high entoconid crests. M_3 is unreduced with basined talonid.

Sorex (*Drepanosorex*) *savini* Hinton, 1911
(Fig. 5)

Material – 2 right mandible fragment with M_1-M_2 (M_1: L = 1.50, W = 0.88; M_2: L = 1.44, W = 0.80; M_1: L = 1.52, W = 0.94; M_2: L = 1.48, W = 0.84); 1 left I_1 (L = 3.20, H = 0.82); 2 right M_1 (L = 1.60, W = 0.92; L = 1.58, W = 0.86); 1 left M_2 (L = 1.44, W = 0.88); 1 right M_2 (L = 1.32, W = 0.68); 1 left M^1 fragment; 1 right M^1 (LL = 1.44, BL = 1.48, AW = 1.64, PW = 1.72).

Description – Large-sized shrew with light-orange pigmentation on the teeth. M^1 is square, its metaloph is present. I_1 is tricuspulate. M_1 is bigger and more elongated than M_2. Buccal cingulum is not undulate on the lower molars. The entoconid crests are high on M_1-M_2.

Remarks – Two *Sorex* (*Drepanosorex*) species are known from the European Lower Pleistocene. *Sorex savini* was described by Hinton (1911) from West Runton, England. In the Betfia (also known as Püspökfürdő, Romania) material Kormos (1930) distinguished another species for a similar form as *S. margaritodon*. Thence several shrew remains were mentioned from different localities as *S.* (*D.*) *margaritodon* or *S.* (*D.*) *savini*. The taxonomical details are shown in another article of the current issue of the present journal (Botka & Mészáros 2016). After those studies, *Sorex* (*Drepanosorex*) *margaritodon* Kormos, 1930 is regarded here as a synonym of *Sorex* (*Drepanosorex*) *savini* Hinton, 1911, so the Beremend 14 specimens are systematized as *S.* (*D.*) *savini*, which is the earlier name, so the valid one.

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

Beremendia fissidens (Petényi, 1864)
(Fig. 6)

Material – 14 left more or less complete mandibles (containing also coronoid process and condyle), with 7 I_1, 7 A_1, 8 A_2, 11 M_1, 12 M_2, 9 M_3; 14 right one, with 8 I_1, 4 A_1, 7 A_2, 13 M_1, 12 M_2, 10 M_3; 11 left mandible fragments with 2 I_1, 2 A_1, 2 A_2, 2 M_1, 3 M_2; 10 left mandible fragments with 3 I_1, 1 A_1, 2 A_2, 7 M_1, 5 M_2, 1 M_3; 3 left more or less complete skulls; left teeth: 3 I^1, 3 A^1, 3 A^2, 2 A^3, 3 P^4, 3 M^1, 2 M^2, 1 M^3; right teeth: 3 I^1, 1 A^1, 1 A^2, 2 A^3, 1 A^4, 3 P^4, 3 M^1, 3 M^2, 2 M^3; 8 left maxillary fragments with 6 P^4, 4 M^1, 4 M^2, 2 M^3; 12 right maxillary fragments with 1 I^1, 2 A^1, 3 P^4, 8 M^1, 4 M^2, 1 M^3; isolated teeth: 19 left and 14 right I_1, 13 left and 8 right M_1, 6 left and 7 right M_2, 7 left and 6 right M_3, 15 left and 14 right I^1, 10 left and 8 right P^4, 5 left and 4 right M^1, 9 left and 6 right M^2, 1 left and 2 right M^3, 48 antemolars.

Measurements – Table 3.

Description – Dental formula is 153/123. The teeth are intensively stained dark red. The I^1 is fissident with a bifid apex. Four upper antemolars are present. A^1 and A^2 are of about equal size, A^3 is smaller and A^4 is even smaller, it is quite reduced. The posterior emargination is moderate on the P^4, M^1 and M^2. The lingual part of the P^4 crown is very low. The occlusal outline of the M^1 is square with rounded corners, M_2 is trapezoidal. The M^3 is relatively small and triangular. The I_1 is grooved, acuspulate, the apex curves upwards. The A_1 is unicuspid, the A_2 is bicuspid. The M_1 and M_2 trigonid basins are deep and broad, entoconid crests are present. The M_3 is reduced but its talonid is basined. The mandibular body is robust, strongly built, slightly leans laterally. The ascending ramus is anteroposteriorly broad and leans strongly medially. The coronoid process is narrow, short, stout and leans anteriorly in lateral view. The coronoid spicule is thin, poorly developed and nearly vertical. The condyloid process is characteristic. The upper articular facet is narrow and cylinder-shaped. The interarticular area is broad. The lower facet leans strongly anteriorly and it is not visible in buccal view. The angular process is very short. The internal temporal fossa is small, deep and pocketed, its shape is often round.

Remarks – There are two *Beremendia* species known from the European fossil assemblages. According to Botka & Mészáros (2015) the larger *B. fissidens* and the smaller *B. minor* are well distinguished by the size of the upper and the lower molars. On the basis of these measurements the Beremend 14 form seems to belong to the bigger species, so it was determined as *B. fissidens* (see Table 2 and Botka & Mészáros 2015, Tables 1–2).

Table 3. Measurements of *Beremendia fissidens* teeth (Beremend 14)

		n	min.	mean	max.	sd.
M^1	LL	4	2.42	2.52	2.62	0.09
	BL	4	2.48	2.64	2.76	0.12
	AW	4	2.60	2.68	2.88	0.13
	PW	4	2.76	2.83	2.92	0.08
M^2	LL	4	1.88	2.03	2.20	0.14
	BL	4	1.96	2.11	2.16	0.09
	AW	4	2.69	2.74	2.84	0.07
	PW	4	2.00	2.27	2.36	0.18
M_1	L	7	2.80	2.85	3.00	0.08
	W	7	1.60	1.67	1.72	0.04
M_2	L	7	2.26	2.34	2.40	0.06
	W	7	1.36	1.44	1.56	0.06

Genus *Petenyia* Kormos, 1934

Petenyia hungarica Kormos, 1934
(Fig. 7)

Material – 1 left mandible fragment with M_2-M_3 (M_2: L = 1.24, W = 0.84; M_3: L = 1.04, W = 0.60); 1 left mandible fragment with M_3 (L = 1.14, W = 0.64); 1 right mandible fragment with M_1 (L = 1.39, W = 0.80); 1 left M_1 (L = 1.36, W = 0.80); 1 left maxillary fragment with P^4 and broken M^1 (LL = 0.84, BL = 1.48, W = 1.40); 1 right maxillary fragment with M^1-M^2 (M^1: LL = 1.40, BL = 1.44, AW = 1.41, PW = 1.49; M^2: LL = 1.24, BL = 1.16, AW = 1.49, PW = 1.36); 1 right M^1 fragment.

Description – The teeth have dark red (sometimes nearly black) pigmentation. P^4, M^1 and M^2 have nearly straight posterior margin. P^4 is triangular, its parastyle is well-developed and as a rule, connected to the paracone by a high parastylar crest. Hardly any posterior emargination is present on M^1-M^2. Paracone and metacone are much better developed than the protocone, the hypocone is not developed. Protocone and hypocone are separated. In occlusal view the lower molars are relatively wide and short. The entoconid crest is high. The wide re-entrant valley opens low, directly above the broad buccal cingulum. M_3 has a well-developed buccal cingulum, its talonid is reduced to a single hypoconid. The tip of the coronoid process of the mandible is broad, slightly divergent with a strongly undulating outline. The posterior margin is straight. The coronoid spicule is very large and strongly pronounced; it divides the external temporal fossa into two almost equal parts. The internal temporal fossa is high and triangular; it extends to the tip of the coronoid.

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

Asoriculus gibberodon (Petényi, 1864)
(Figs 8–9)

Material – 1 left mandible fragment with M_1-M_3 (M_1: L = 1.54, W = 0.81; M_2: L = 1.34, W = 0.76; M_3: L = 1.06, W = 0.60); 1 left mandible fragment with M_2 (L = 1.32, W = 0.76); 1 right mandible fragment with M_2 (L = 1.32, W = 0.80); 1 left and 3 right edentulous mandible fragments; 1 left M^1 (LL = 1.40, BL = 1.36, AW = 1.52, PW = 1.60); 1 right I_1 (I_1: L = 3.04, H = 0.76); 1 left M_1 (L = 1.42, W = 0.76); 1 fragmentary left I^1; 1 fragmentary right M^2.

Description – Pigmentation is hardly-visible: only the very tips of some teeth have a light orange colour. I^1 is fissident. M^1 protocone and hypocone are separated by a wide valley, the metastyle protrudes. The anterior margin bends beside the protocone. The lower incisor is short and bicuspulate. M_1-M_2 cingula are developed on both lingual and buccal sides, the buccal one is slightly undulate, particularly in M_1. The buccal re-entrant valley opens directly above the cingulum. The lingual cingulum in M_3 is weak but well-visible; the talonid is not reduced but basined. The anterior margin of the coronoid process is usually slightly concave. The internal temporal fossa is relatively small and narrow. The upper condylar facet is narrow, long and cylinder-shaped. The lower facet is strongly elongated lingually and pointing downwards. The interarticular area is notched lingually and hence quite narrow and elongate.

Soricidae gen. et sp. indet.
(Fig. 10)

Material – 1 left mandible fragment with M_1 ($L = 1.76$, $W = 0.84$); 1 edentulous right mandible fragment; 1 left I^1 ($L = 1.92$, $H = 1.40$); 1 right I^1 ($L = 1.84$, $H = 0.36$).

Description – Medium-sized Soricidae form. The coronoid process of the mandible is *Neomys*-like: the external temporal fossa is divided by a strong coronoid spicule. Otherwise, this species is different from Neomini shrews in its unpigmented teeth and *Crocidura*-like condyle. The M_1 buccal cingulum is as weak as at crocidurines, but – opposite of them – it is not undulated. Upper incisors are not fissident, they are very similar to *C. kornfeldi* I^1 yielded by this site, but they are somewhat bigger than the *Crocidura* teeth.

Order Rodentia Bowdich, 1821

Seventeen rodents were determined in the Beremend 14 fossil assemblage, which can be classified into 7 families (Sciuridae, Gliridae, Eomyidae, Dipodidae, Spalacidae, Cricetidae and Muridae) (Table 4). Most of the species (mainly voles) belong to family Cricetidae, whereas the other families include only 1–2 species.

Family Sciuridae Gray, 1821
Genus *Spermophilus* Cuvier, 1825

Spermophilus primigenius (Kormos, 1934)
(Figs 11–12)

Material – Isolated teeth: 1 right M_2; 1 right M_3; 1 left M_3; 2 left P^4; 1 left M^2; 2 right M^2.

Description – The premolar is relatively small, front is narrower than rear (like *Sciurus*) and consisting of four cusps. On the labial side it is protoconid and

Table 4. Rodent remains (Beremend 14)

Species	Remain		MNI	
	n	%	n	%
Spermophilus primigenius	8	1.04	2	0.63
Glis minor	3	0.39	1	0.31
Estramomys aff. *simplex*	2	0.26	1	0.31
Sicista praeloriger	2	0.26	1	0.31
Prospalax cf. *priscus*	6	0.78	2	0.63
Allocricetus ehiki	55	7.13	13	4.08
Cricetus nanus	163	21.14	45	14.11
Dolomys milleri	1	0.13	1	0.31
Villanyia exilis	1	0.13	1	0.31
Mimomys reidi	130	16.86	65	20.38
Mimomys pusillus	76	9.86	30	9.40
Pitymimomys pitymyoides	28	3.63	11	3.45
Borsodia newtoni	126	16.34	63	19.75
Allophaiomys deucalion	4	0.52	2	0.63
Lagurodon arankae	134	17.38	71	22.26
Apodemus dominans	13	1.69	4	1.25
Micromys praeminutus	19	2.46	6	1.88
Total	771	100.00	319	100.00

hypoconid, on the lingual side is metaconid and entoconid. The anterior incisal tip is the longest. Between this and the protoconid a slight trace of the anterior inner cusp (paraconid) can be seen. A tiny accessory cusp is observed between metaconid and entoconid. The molars are large and broad, M_1 and M_2 are rhombic and consisting of the above-mentioned four main elements. The paraconid is weakly indicated on both teeth, between the meta- and entoconid, on the other hand, there are two clearly perceptible intermediate cusps. On the last molar (M_3), only one can be observed, but it is more developed. The premolar has two roots in all cases, whereas the molars have four roots.

Family Gliridae Muirhead, 1819

Genus *Glis* Birsson, 1762

Glis minor Kowalski, 1956

(Figs 13–14)

Material – Isolated teeth: 1 left P_4; 1 left M_1 (L = 1.63, W = 1.63); 1 right M^1 (L = 1.66, W = 1.73).

Description – ***M***^{1}: The tooth has rounded square shape and seven ridges. The first and third main ridges (anteroloph and protoloph) are isolated; there is a small, isolated ridge (anterior extra ridge) between the latter two. The fourth ridge is isolated (anterior centraloph), whereas the fifth and seventh ridges (metaloph and posteroloph) are joined on the palatinal side. Between the latter two ridges, there is a small, isolated ridge (posterior extra ridge).

P$_4$: Triangular tooth, with five ridges. The first and the second ridges (anterolophid and metalophid) are joined on both sides. The third ridge (mesolophid) is isolated, whereas the fourth and fifth ridges (posterior extra ridge and posterolophid) are joined on the labial side.

M$_1$: Anteriorly elongated, narrowed tooth, with seven ridges. The first, second and third ridges (anterolophid, anterior extra ridge and metalophid) are joined on the labial side. The fourth ridge (centralophid) is short and isolated. The fifth, sixth and seventh ridges (mesolophid, posterior extra ridge, and posterolophid) are joined on the labial side.

Family Eomyidae Winge, 1887
Genus *Estramomys* Jánossy, 1969

Estramomys aff. *simplex* Jánossy, 1969
(Fig. 15)

Material – Isolated teeth: 1 right M$_1$ (L = 0.93, W = 0.96); 1 left M$_2$ (L = 0.8, W = 1.00).

Description – Roundish, lengthwise slightly compressed, brachyodont tooth with four roots. The paraconid and the protoconid-metaconid folds are in contact with each other on the occlusal surface.

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

Sicista praeloriger Kormos, 1930
(Fig. 16)

Material – Isolated teeth: 1 right M$_1$ (L = 1.20, W = 0.93); 1 left M$_3$.

Description – The molar is two-rooted. The occlusal outline is rounded. The protoconid and the hypoconid are the highest cusps. The anteroconid, metaconid and entoconid are also well-developed. The mesolophid is low but clearly visible. The posterolophid is low and tenuous. The entoconid exhibits two spurs near the base, both directed away from the hypolophulid, one pointing to the mesolophid, and the other to the posterolophid.

Family Spalacidae Gray, 1821
Genus *Prospalax* Méhely, 1908

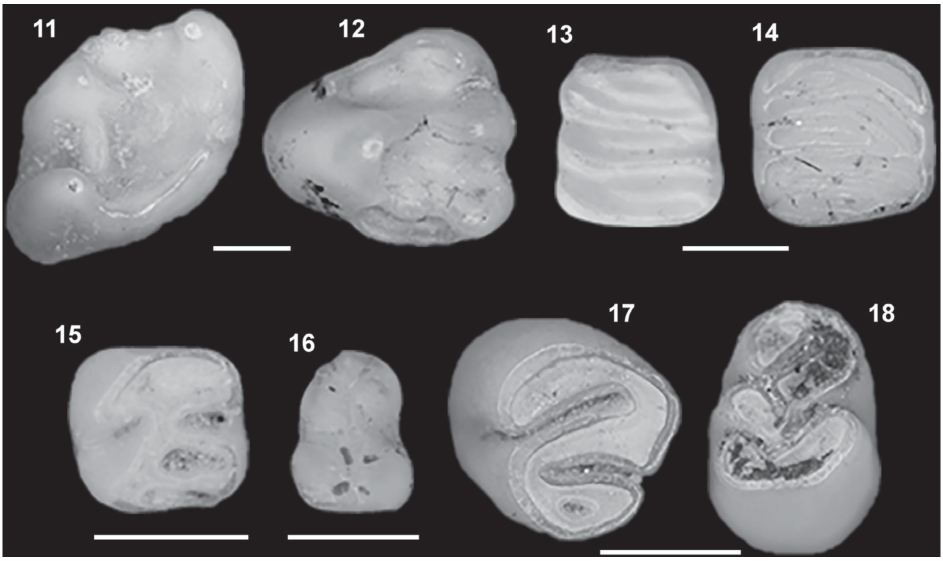
Prospalax cf. *priscus* (Nehring, 1897)
(Figs 17–18)

Material – Isolated teeth: 1 left M$_1$; 2 left M$_2$; 1 right M$_2$; 1 right M$_3$; 1 M^x

Description – Cylindrical, hypsodont molars with two roots. Both in the lingual and labial sides there are enamel folds on the occlusal surface.

Family Cricetidae Fischer von Waldheim, 1817
Subfamily Cricetinae Fischer von Waldheim, 1817

The method of taking measurements of the hamster teeth is after Daams & Freudenthal (1988, Fig. 1). Morphological nomenclature is after Daams & Freudenthal (1988, Fig. 2), some special morphological elements are after Cuenca-Bescos (2003, Fig. 1). Abbreviations: L = maximal antero-posterior length of the occlusal surface, W = maximal linguo-labial width of the occlusal surface. Measurements are given in mm.



Figs 11–12. *Spermophilus primigenius* (Kormos, 1934). – **11.** Left M$_3$ (VER 2016.3573.1.). – **12.** Left M^2 (VER 2016.3573.2.). – **Figs 13–14.** *Glis minor* Kowalski, 1956. – **13.** Left M$_1$ (VER 2016.3573.3.). – **14.** Right M^1 (VER 2016.3573.4.). – **Fig. 15.** *Estramomys* aff. *simplex* Jánossy, 1969; right M$_1$ (VER 2016.3573.5.). – **Fig. 16.** *Sicista praeloriger* Kormos, 1930; right M$_1$ (VER 2016.3573.6.). – **Figs 17–18.** *Prospalax* cf. *priscus* (Nehring, 1897). – **17.** Right M$_3$ (VER 2016.3573.7.). – **18.** M^x (VER 2016.3573.8.). All occlusal views, scale bars = 1 mm

Genus *Allocricetus* Schaub, 1930

Allocricetus ehiki Schaub, 1930
(Figs 19–24)

Material – 55 molars.

Measurements – Table 5.

Description – The molars show the general characters of the modern hamsters: the cones/ conids are definitely higher than the lophs/lophids.

M^1: Anterostyle is found in 4/11. Parastyle is not developed as cuspula, only cingulum is found. Protolophule 1 is developed in 8/11. Short remnant mesoloph is rare: 1/11. Entostyle is completely missing. It has three or four roots.

M^2: It has rectangular outline. The labial anteroloph is slightly longer and stronger than the lingual one. Protolophule 1 is constant. Remnant mesoloph is completely missing. It has four roots.

M^3: It has subtriangular outline. The posterior portion (hypocone, metacone) is narrower than the anterior one (protocone, paracone). The labial anteroloph is definitely better developed than the lingual one. Protolophule 1 is constant. In the centre of the occlusal surface central ring and remnant mesoloph are missing. It has three roots.

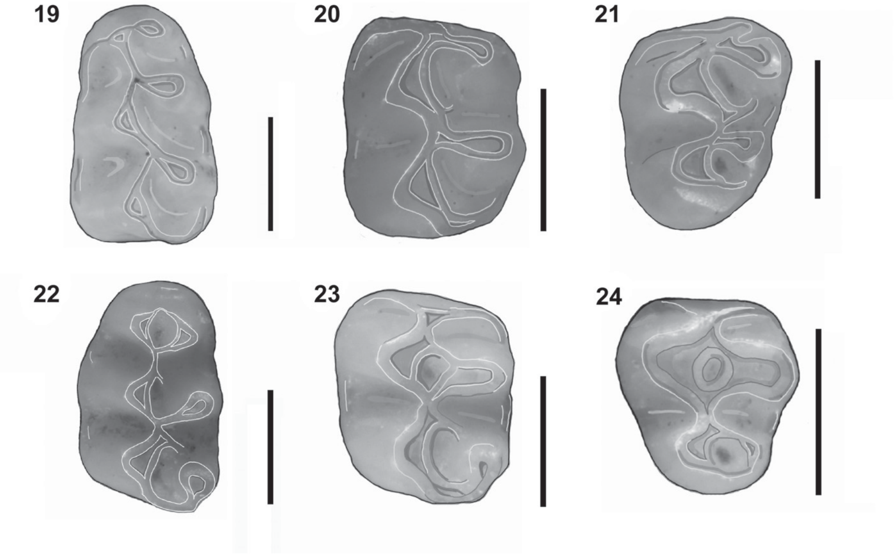
M_1: Mesial surface is smooth and concave without anterostylid. Anteroconid consists of two equally developed cuspulas. The anterolophulid connects the labial anteroconid cuspula and the protoconid. Mesoconid and mesolophid are not developed. It has two roots.

M_2: It has rectangular outline. Lingual anterolophulid is missing (4/13), short (6/13), or middle developed (3/13). Mesolophid is rare (3/13). It is short, and reaches the posterior basis of the metaconid. Mesoconid is not developed. It has two roots.

M_3: It has subtriangular outline, the entoconid is reduced. Lingual anterolophid is missing (4/7) or short (3/7). Mesolophid is missing (3/7), or short (4/7). It does not reach the posterior surface of the metaconid (2/7), or reaches the posterior surface of the metaconid (2/7). Central ring is missing. It has two roots.

Remarks – Some plesiomorph characters (remnant mesolophs/mesolophids, undivided or 3-parted anteroconids) of the *A. ehiki* populations of Villány 3 and Osztramos 3 (Hír 1993) are not found among the molars of Beremend 14.

Allocricetus cf. *ehiki* or other large-sized *Allocricetus* species first appeared in the Late Miocene of Anatolia and Greece: *Allocricetus aylasevimae*, Çorakyerler, Turkey (MN 10–11) by Ünay *et al.* (2006); *Allocricetus* sp., Kavurca, Turkey (MN 13) by Rummel (1998); *Allocricetus* cf. *ehiki*, Maramena, Greece (MN 13) by Daxner-Höck (1995).



Figs 19–24. *Allocricetus ehiki* Schaub, 1930. – **19.** Left M_1 (VER 2016.3574.1.). – **20.** Left M_2 (VER 2016.3574.2.). – **21.** Right M_3 (reversed) (VER 2016.3574.3.). – **22.** Left M^1 (VER 2016.3574.4.). – **23.** Left M^2 (VER 2016.3574.5.). – **24.** Right M^3 (reversed) (VER 2016.3574.6.). Scale bars = 1 mm

In the Carpathian Basin this species appeared in Villány 3 and occurred up to the Middle Pleistocene. Last occurrence was found in the level 8 in the sequence of Tarkő (Hír 1997).

Table 5. Dimensions of *Allocricetus ehiki* molars (Beremend 14)

		n	min.	mean	max.	sd.
M^1	L	11	2.00	2.12	2.28	0.10
	W	11	1.23	1.33	1.50	0.10
M^2	L	10	1.55	1.69	1.78	0.10
	W	10	1.20	1.41	1.55	0.12
M^3	L	1		1.25		
	W	1		1.15		
M_1	L	13	1.83	2.01	2.15	0.10
	W	13	1.08	1.22	1.30	0.08
M_2	L	13	1.50	1.61	1.83	0.10
	W	13	1.20	1.28	1.38	0.06
M_3	L	7	1.40	1.48	1.55	0.07
	W	7	1.13	1.19	1.25	0.06

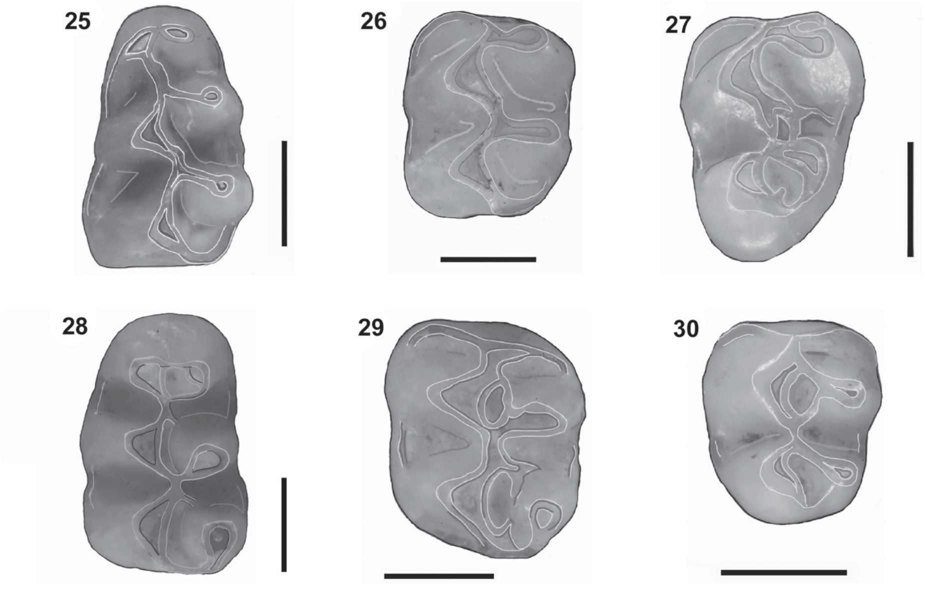
Cricetus nanus (Schaub, 1930)
(Figs 25–30)

Material – 8 maxillae with complete tooth rows, 21 maxillae with incomplete tooth rows, 10 mandibulae with complete tooth rows, 13 mandibulae with incomplete tooth rows, 24 M^1, 24 M^2, 23 M^3, 18 M_1, 10 M_2, 12 M_3.

Measurements – Tables 6 and 7.

Description – ***M^1***: The mesial surface is smooth, anterostyle is rare: 7/45. The relatively wide anterocone consists of two equally developed cones, which are as well-developed as the other main cones of M^1: proto-, para-, hypo- and metacones. Parastyle is not developed as cuspula, only low developed cingulum is found. Protolophule 1 is nearly constant: 41/45. Short remnant mesoloph is found only in 1/45, which is developed on the anterior surface of the metacone. There are four roots and one tiny root under the paracone.

M^2: It shows rectangular outline. The labial anteroloph is slightly stronger than the lingual one. Protolophule 1 is constant. Short remnant mesoloph is rare: 7/44, which is developed on the anterior surface of the metacone. It has four roots.



Figs 25–30. *Cricetus nanus* (Schaub, 1930). – **25.** Left M_1 (VER 2016.3574.7.). – **26.** Left M_2 (VER 2016.3574.8.). – **27.** Left M_3 (VER 2016.3574.9.). – **28.** Left M^1 (VER 2016.3574.10.). – **29.** Left M^2 (VER 2016.3574.11.). – **30.** Left M^3 (VER 2016.3574.12.). Scale bars = 1 mm

Table 6. Length of *Cricetus nanus* upper and lower tooth rows (Beremend 14)

C. nanus upper tooth rows	n	min.	mean	max.	sd.
L M^1-M^2-M^3	8	5.6	5.85	6.15	0.16
C. nanus lower tooth rows	n	min.	mean	max.	sd.
L M^1-M^2-M^3	10	5.05	5.84	6.05	0.30

***M*^{3}**: It shows subtriangular outline, the hypocone and the metacone are reduced. Some morphological elements defined by Hír (1998, fig. 28) are rare: central ring: 4/44, remnant mesoloph: 8/44. There are three roots.

***M*$_1$**: It has elongated trapezoidal outline. The anteroconid region is narrower than the width across the hypoconid and the entoconid. The anteroconid consists of two equally developed cuspulas. Those are smaller than the other main cusps (proto-, meta-, hypo- and entoconid) of the M_1. The anterolophulid connects the labial cuspula of the anteroconid and the protoconid. Y-like anterolophulid (which has two, equally developed anterior branches running to the two cuspulas of the anteroconid) was found only in one case. Additional morphological elements (anterostylid, mesolophid, mesoconid, lingual anterolophulid) are completely missing. It has two roots.

***M*$_2$**: It has rectangular outline. Lingual anterocingulum is missing: 10/30, short: 10/30, middle developed: 8/30, or long: 2/30. Short mesolophid is rare (2/30), which reaches the posterior basis of the metaconid. There is no mesoconid, but central ring is developed in one case. It has two roots.

***M*$_3$**: It shows subtriangular outline, the entoconid is reduced. Lingual antrocingulum is missing: 7/31, short: 7/31, middle developed: 13/31, or long:

Table 7. Dimensions of *Cricetus nanus* molars (Beremend 14)

		n	min.	mean	max.	sd.
M^1	L	45	2.33	2.50	2.75	0.09
	W	45	1.48	1.63	1.75	0.08
M^2	L	44	1.85	1.98	2.15	0.08
	W	44	1.58	1.68	1.78	0.06
M^3	L	37	1.33	1.60	1.75	0.13
	W	37	1.20	1.43	1.70	0.11
M_1	L	41	2.23	2.32	2.53	0.06
	W	41	1.28	1.39	1.53	0.06
M_2	L	30	1.80	1.90	2.05	0.07
	W	30	1.38	1.55	1.65	0.06
M_3	L	31	1.68	1.92	2.18	0.12
	W	30	1.35	1.47	1.65	0.08

4/31. Mesolophid is missing: 8/31, it is short, does not reach the posterior basis of the metaconid: 2/31. It reaches the posterior basis of the metaconid: 21/31. A central ring is missing: 11/31, or developed: 20/31. Two roots.

Remarks – Originally this hamster was described as a subspecies, *Cricetus cricetus nanus* (Schaub, 1930). But on the basis of the metrical and morphological characters and also their stratigraphical range Hír regarded this taxon as a distinct species: *Cricetus nanus* (Hír 1994, 1997).

Related to the other *C. nanus* populations studied by Hír (1994) the material of Beremend 14 is special because of the relatively small dimensions and the more frequent mesolophids and central rings in the morphology of M_3. These characters suggest that the larger hamster from Beremend 14 can be an early representative of *C. nanus* (Figs 31–32).

The flourishing of the species is experienced in the typical *Allophaiomys* faunas without progressive *Microtus* and *Pitymys* species (Poland: Zabia; Bohemia: Chlum 6; Slovakia: Kolinany 3, Vcelare 3b/1, Vcelare 4a/5, Vcelare 4a/7, Vcelare 4e, Vcelare 5, Vcelare 6; Hungary: Osztramos 2, Osztamos 8, Osztramos 14; Romania: Betfia 2, Betfia 10; Russia: Akkulaevo 2, Akkulaevo 3) (Hír 1994). Later the presence of *C. nanus* with reduced abundance was verified in the fauna of the Somssich Hill 2 (Hír 1998). The last occurrence of *C. nanus* was found in the 12th level of the Tarkő Rock-shelter (Hír 1994).

Up to the present we had no data on the ancestors and the origin of this hamster.

Subfamily Arvicolinae Gray, 1821

Abbreviations used in the voles M_1 descriptions: L = length of occlusal surface, A = anteroconid length, W = width of occlusal surface, B = the shortest distance between BRA3 and LRA4, C = the shortest distance between BRA3 and LRA3, Asd = anterosinuid height, Hsd = hyposinuid height, Hsld = hyposinulid height, A/L = A × 100/L, B/W = B × 100/W, C/W = C × 100/W (Fig. 33). Morphological terms are used after Rekovets & Nadachowski (1995) and Tesakov (2004). Measurements are given in mm.

Genus *Dolomys* Nehring, 1898

Dolomys milleri Nehring, 1898

(Fig. 34)

Material – 1 right M_1 (L = 3.72, A = 1.80, W = 1.44, Hsd = 0.68, Hsld = 0.40, A/L = 48.38).

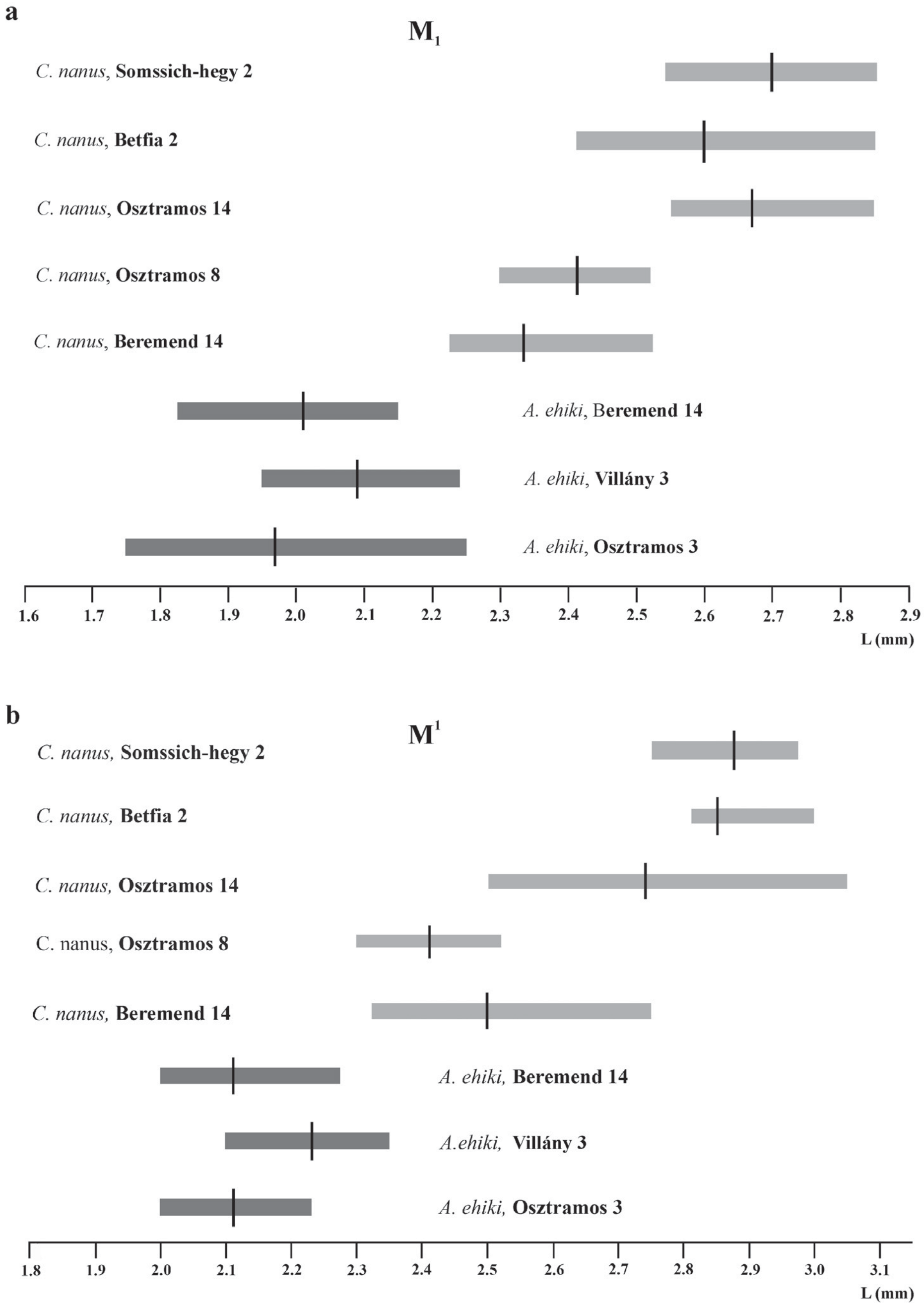


Fig. 31. A comparison of the min.-mean-max. ranges of M_1 length (a) and M^1 length (b) of some *Allocricetus ehiki* and *Cricetus nanus* populations

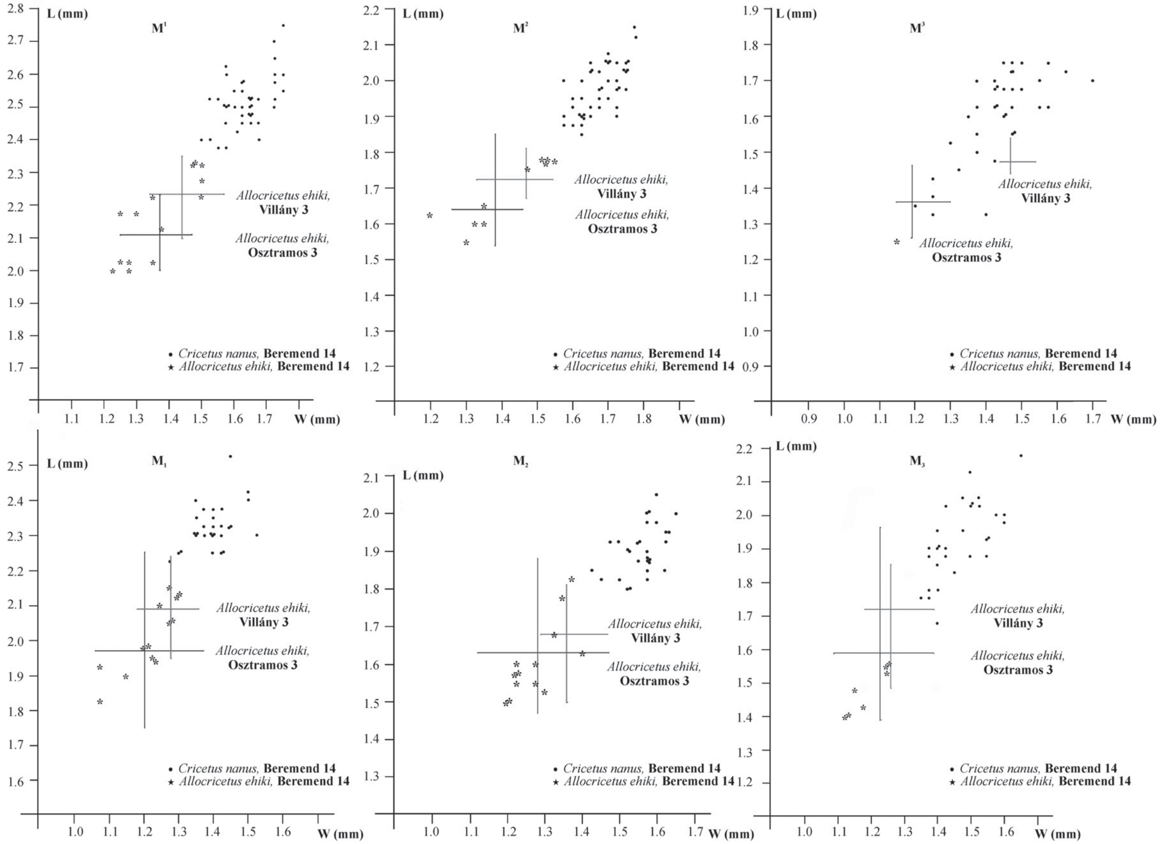


Fig. 32. Scatter diagrams of the Cricetinae molars from Beremend 14 related to the ranges and mean values of the *Allocricetus ehiki* materials from Villány 3 and Osztramos 3

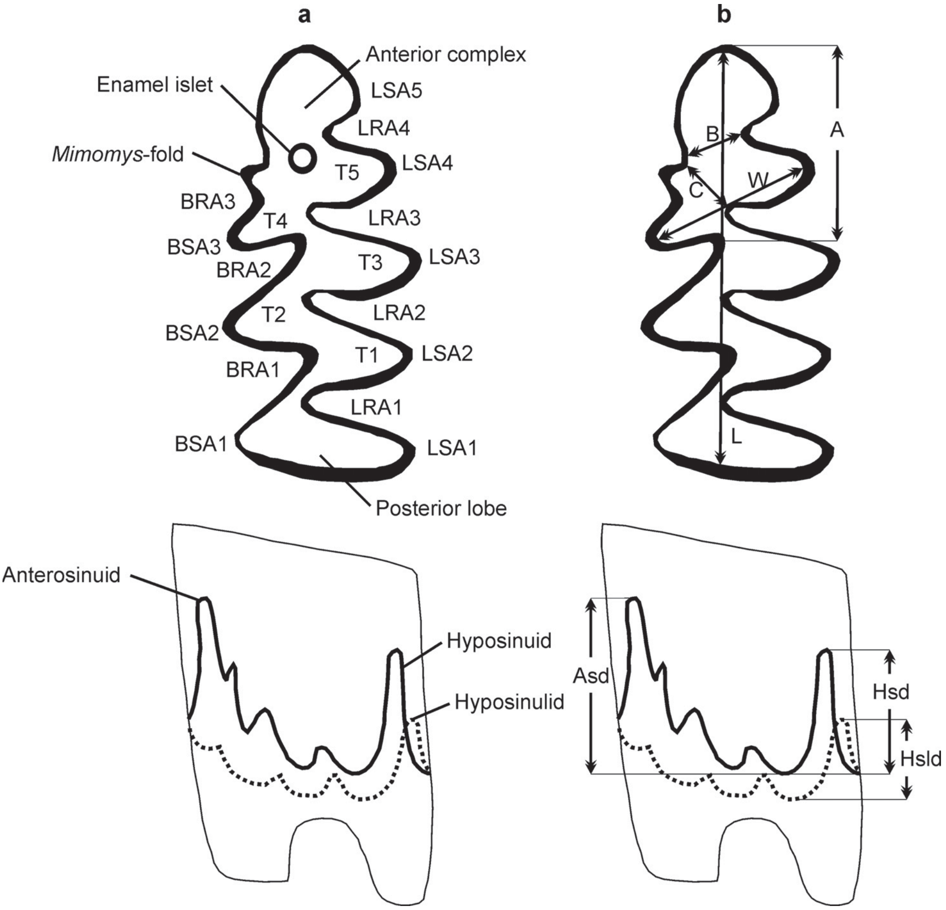


Fig. 33. a. Terminology used in the description of vole M_1. BRA = buccal re-entrant angle, BSA = buccal salient angle, LRA = lingual re-entrant angle, LSA = lingual salient angle, T = triangle. **b.** Measuring methods for vole M_1. For explanation see text

Description – Large, rooted tooth with pointed triangles. Cementum is missing. Its enamel shows *Mimomys*-like or negative enamel differentiation (thicker trailing enamel edges than their complementary leading edges).

Genus *Villanyia* Kretzoi, 1956

Villanyia exilis Kretzoi, 1956
(Fig. 35)

Material – 1 left M_1 (L = 2.30, A = 0.93, W = 0.96, Asd = 1.50, Hsd = 1.07, Hsld = 0.43, A/L = 40.43).

Description – Small tooth without cementum, *Mimomys*-fold or enamel islet. Its enamel shows *Microtus*-like or positive enamel differentiation (thicker leading enamel edges than their complementary trailing edges).

Genus *Mimomys* F. Mayor, 1902

Mimomys reidi Hinton, 1910
(Fig. 36)

Material – Isolated teeth: 65 right M_1; 65 left M_1.

Measurements – Table 8.

Description – In most cases, teeth have cementum, *Mimomys*-fold and enamel islet. Their enamel shows *Mimomys*-like or negative enamel differentiation.

Table 8. Measurements of *Mimomys reidi* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	125	2.27	2.87	3.33	0.16
A	57	0.90	1.07	1.37	0.11
W	109	0.63	1.19	1.40	0.11
Asd	6	2.73	2.92	3.33	0.21
Hsd	6	2.00	2.44	2.67	0.28
Hsld	57	1.33	1.71	2.10	0.19
A/L	57	31.76	38.13	48.72	3.89

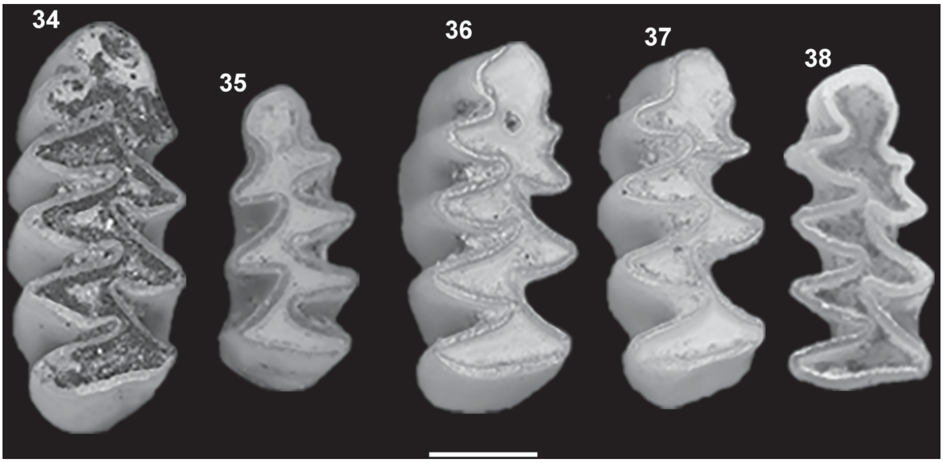


Fig. 34. *Dolomys milleri* Nehring, 1898; right M_1 (VER 2016.3573.9.). – **Fig. 35.** *Villanyia exilis* Kretzoi, 1956; left M_1 (VER 2016.3573.10.). – **Fig. 36.** *Mimomys reidi* Hinton, 1910; right M_1 (VER 2016.3573.11.). – **Fig. 37.** *Mimomys pusillus* (Méhely, 1914); right M_1 (VER 2016.3573.12.). – **Fig. 38.** *Pitymimomys pitymyoides* (Jánossy et van der Meulen, 1975); right M_1 (VER 2016.3573.13.). All occlusal views, scale bar = 1 mm

Mimomys pusillus (Méhely, 1914)
(Fig. 37)

Material – Isolated teeth: 46 right M_1; 30 left M_1.

Measurements – Table 9.

Description – In most cases, teeth have cementum and *Mimomys*-fold. Their enamel shows *Mimomys*-like or negative enamel differentiation.

Table 9. Measurements of *Mimomys pusillus* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	41	2.40	2.63	2.77	0.08
A	41	0.87	0.99	1.27	0.07
W	40	0.97	1.07	1.17	0.06
Asd	2	2.63	2.90	3.17	0.38
Hsd	2	2.23	2.28	2.33	0.07
Hsld	21	1.17	1.83	2.13	0.23
A/L	41	33.33	37.64	45.78	2.28

Genus *Pitymimomys* Tesakov, 1998

Pitymimomys pitymyoides (Jánossy et van der Meulen, 1975)
(Fig. 38)

Material – Isolated teeth: 11 right M_1; 17 left M_1.

Measurements – Table 10.

Description – Middle-sized teeth with *Mimomys*-fold. Broad communications are present between triangles at the occlusal surface. The enamel thickness is nearly always uniform.

Table 10. Measurements of *Pitymimomys pitymyoides* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	19	2.33	2.53	2.73	0.12
A	19	0.83	1.02	1.20	0.08
W	19	0.97	1.05	1.20	0.06
Asd	2	3.00	3.17	3.33	0.24
Hsd	3	2.60	2.72	2.83	0.12
Hsld	4	2.07	2.48	2.90	0.38
A/L	19	35.71	40.36	45.00	2.62

Genus *Borsodia* Jánossy et van der Meulen, 1975

Borsodia newtoni (F. Major, 1902)
(Fig. 39)

Material – 1 right mandible with M_{1-3}; 2 right mandible fragments with M_1; 1 left mandible fragment with M_1; 2 left mandible fragments with M_{1-2}; Isolated teeth: 60 right M_1; 60 left M_1.

Measurements – Table 11.

Description – Middle-sized, rooted teeth without cementum. Their enamel shows *Microtus*-like or positive enamel differentiation.

Table 11. Measurements of *Borsodia newtoni* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	33	2.23	2.50	2.77	0.13
A	33	0.83	1.04	1.23	0.09
W	33	0.90	1.05	1.20	0.07
Asd	6	1.83	2.29	2.80	0.35
Hsd	5	1.97	2.10	2.23	0.11
Hsld	26	1.13	1.53	2.00	0.25
A/L	33	36.36	41.54	46.84	2.84

Genus *Allophaiomys* Kormos, 1932

Allophaiomys deucalion Kretzoi, 1969
(Fig. 40)

Material – 1 left mandible fragment with M_1; Isolated teeth: 2 right M_1; 1 left M_1.

Measurements – Table 12.

Table 12. Measurements of *Allophaiomys deucalion* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	4	2.27	2.48	2.70	0.19
A	4	1.03	1.08	1.20	0.08
W	4	0.93	0.98	1.03	0.05
B	4	0.23	0.33	0.40	0.07
C	4	0.27	0.28	0.30	0.02
A/L	4	41.56	43.66	45.59	1.74
B/W	4	25.00	33.24	40.00	6.34
C/W	4	26.67	28.21	29.03	1.05

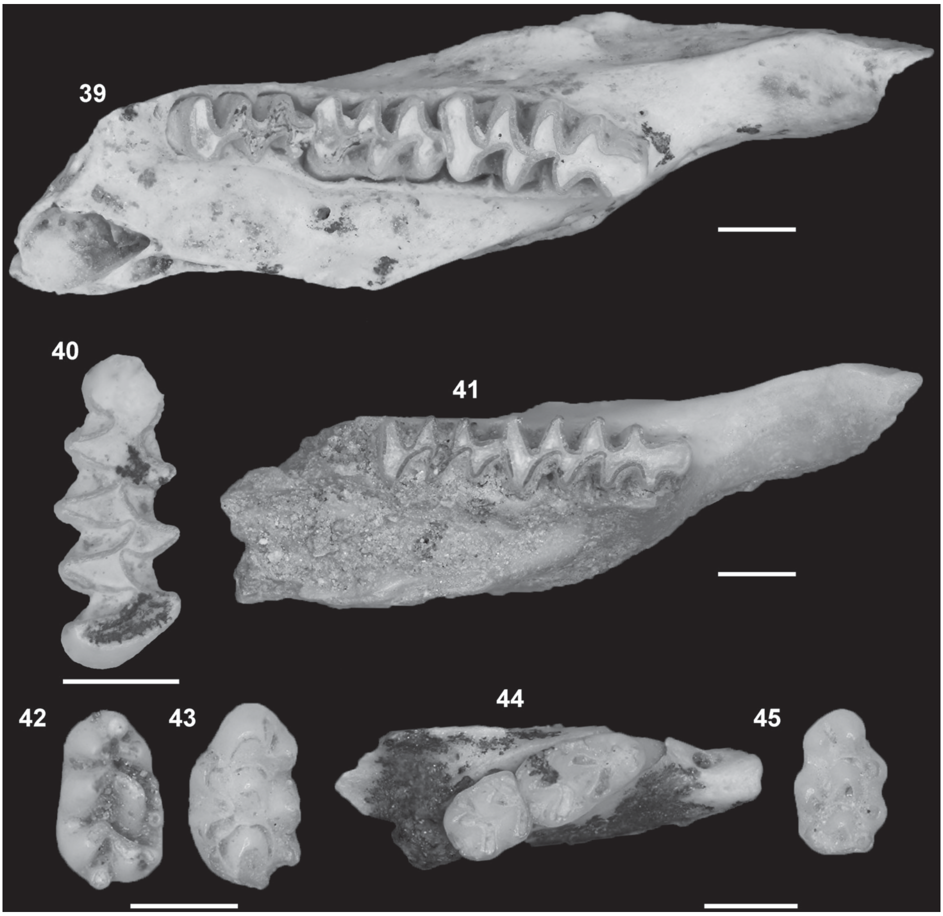


Fig. 39. *Borsodia newtoni* (F. Major, 1902); right mandible with M_{1-3} (VER 2016.3573.14.). – **Fig. 40.** *Allophaiomys deucalion* Kretzoi, 1969; right M_1 (VER 2016.3573.15.). – **Fig. 41.** *Lagurodon arankae* (Kretzoi, 1954); right mandible fragment with M_{1-2} (VER 2016.3573.16.). – **Figs 42–43.** *Apodemus dominans* Kretzoi, 1959. – **42.** Right M_1 (VER 2016.3573.17.). – **43.** Left M^1 (VER 2016.3573.18.). – **Figs 44–45.** *Micromys praeminutus* Kretzoi, 1959. – **44.** Left mandible fragment with M_{1-2} (VER 2016.3573.19.). – **45.** Right M^1 (VER 2016.3573.20.). All occlusal views, scale bars = 1 mm

Description – Middle-sized, rootless teeth with cementum. Their enamel shows *Microtus*-like or positive enamel differentiation.

Genus *Lagurodon* Kretzoi, 1956

Lagurodon arankae (Kretzoi, 1954)

(Fig. 41)

Material – 1 right mandible fragment with M_{1-2}; 1 right mandible fragment with M_1; 6 left mandible fragments with M_{1-2}; Isolated teeth: 61 right M_1; 65 left M_1.

Measurements – Table 13.

Description – Small-sized, hypsodont, rootless teeth without cementum. The enamel thickness is nearly always uniform.

Table 13. Measurements of *Lagurodon arankae* M_1 (Beremend 14)

	n	min.	mean	max.	sd.
L	4	2.27	2.48	2.70	0.19
A	4	1.03	1.08	1.20	0.08
W	4	0.93	0.98	1.03	0.05
B	4	0.23	0.33	0.40	0.07
C	4	0.27	0.28	0.30	0.02
A/L	4	41.56	43.66	45.59	1.74
B/W	4	25.00	33.24	40.00	6.34
C/W	4	26.67	28.21	29.03	1.05

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1829

Apodemus dominans Kretzoi, 1959

(Figs 42–43)

Material – Isolated teeth: 4 right M_1; 2 left M_1; 1 right M_2; 1 right M_3; 1 right M^1; 2 left M^1; 1 right M^2; 1 left M^2.

Measurements – Table 14.

Description – Late Pliocene mouse, which belongs to the *Apodemus sylvaticus* group.

Table 14. Measurements of Muridae material (Beremend 14)

Apodemus dominans		n	min.	mean	max.	sd.
M_1	L	4	1.64	1.73	1.88	0.11
	W	4	1.00	1.04	1.12	0.06
M^1	L	3	1.88	1.96	2.00	0.07
	W	3	1.16	1.21	1.24	0.05
Micromys praeminutus		n	min.	mean	max.	sd.
M_1	L	9	1.32	1.43	1.48	0.06
	W	9	0.72	0.80	0.88	0.05
M^1	L	6	1.44	1.49	1.52	0.03
	W	6	0.92	0.97	1.04	0.04

Genus *Micromys* Dehne, 1841

Micromys praeminutus Kretzoi, 1959
(Figs 44–45)

Material – 1 left mandible fragment with M_1; 1 left mandible fragment with M_{1-2}; Isolated teeth: 4 right M_1; 4 left M_1; 1 right M_2; 1 left M_2; 3 right M^1; 3 left M^1; 1 right M^2.

Measurements – Table 14.

Description – Very small-sized mouse. The additional cusps are missing in its molars, although an enamel rib replacing them, which is similar to *Apodemus*.

BIOSTRATIGRAPHY

The previous studies, mainly related to the Late Pliocene Beremend 26 site, found that the filling up of karstic cavities was episodic, it linked sheet washes. As a result, infillings represent a longer interval, at least 200 kyr (Marsi & Koloszár 2004).

Many long-lived species are present in the Beremend 14 shrews. *Sorex runtonensis* is one of the most abundant representatives of its genus in the European Pleistocene. Its oldest record dates from the MN 17 zone, the youngest ones are known from several Late Pleistocene localities (Osipova *et al.* 2006). *Sorex minutus* 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. *Beremendia fissidens* is also reported from the MN 14 Zone to the Tarkőian Phase of the Middle Pleistocene in Europe (Botka & Mészáros 2014).

Contrarily, some of the shrews are used to determine the age of the locality. *Petenyia hungarica* shows a long stratigraphic range from the Miocene/Pliocene boundary (MN 13/14 Zone) to the end of the Early Pleistocene (Rzebik-Kowalska 2000). The first occurrence of *Asoriculus gibberodon* in Hungary is reported by Mészáros (1998) from the Late Miocene MN 12 Zone and it occurs to the end of the Early Pleistocene (Rzebik-Kowalska 2000). The first report on *Crocidura kornfeldi* in the European mainland is from the boundary of the MN 16 and MN 17 Zone from Greece. It disappeared from the continent in the Middle Pleistocene (Botka & Mészáros 2015). *Sorex* (*Drepanosorex*) *savini* is reported from the Early Pleistocene MN 17 Zone until the Late Biharian Stage of the Middle Pleistocene (Botka & Mészáros 2016). The simultaneous occurrence of these four species determines the age of Beremend 14 locality to be neither older nor younger than the Early Pleistocene.

Some modifications can be made within this period by the significant attendance of *Asoriculus* in the fauna. Despite of its sporadic occurrence to the end of the Early Pleistocene (Jánossy 1986), the sure presence of *Asoriculus gibberodon* in Hungary is reported only to the end of the MN 17 Zone (Reumer 1984).

On the basis of simultaneous occurrences of rodents, mainly the short-ranged voles, the age of Beremend 14 site was further refined. Naturally, there are many long-lived rodent species also present in the fauna. *Spermophilus primigenius* was a frequent species from the MN 17 Zone to Middle Pleistocene mainly in Central Europe (Jánossy 1986; Reumer & Hoek Ostende 2003). *Glis minor* appears in the Early Pliocene MN 14 Zone (Lindsay *et al.* 2013), but is also present in the late Early Pleistocene (Striczky & Pazonyi 2014). *Apodemus dominans* is also a long-lived species, it appeared in the latest Turolian MN 13 Zone and disappeared at the end of the Pliocene (Wang & Flynn 2013). The other mouse species, *Micromys praeminutus*, is reported from the Early Pliocene MN 15 Zone to the Middle Pleistocene MQ 2 Zone (Jánossy 1986; Horáček *et al.* 2013). *Sicista praeloriger* appears in the Late Pliocene MN 16 Zone (Beremend 15; Jánossy 1987), and survives until the end of the MQ 1 Zone (Lindsay *et al.* 2013). *Prospalax priscus* as well appears in the MN 16A Zone and disappears in the MQ 1 Zone, at the end of the *Mimomys savini/Mimomys pusillus* Biozone (Jánossy 1986; Lindsay *et al.* 2013). *Allocricetus* cf. *ehiki* appeared in the Late Miocene (MN 10–11) in the Eastern Mediterranean, but in Central Europe it is known only from the Late Pliocene up to the Middle Pleistocene.

Ranges of other rodents are much shorter. Some rodents are typical Late Pliocene species: *Dolomys milleri* (MN 15B-MN 17) (Lindsay *et al.* 2013) and *Estramomys simplex* (MN 16A – end of MN 17) (Fejfar & Horáček 1983; Jánossy 1986; Lindsay *et al.* 2013), other ones appear at the end of the MN 17 Zone: *Villanyia exilis* (Jánossy 1986), *Allophaiomys deucalion*, *Lagurodon arankae* (Tesakov 2004), *Cricetus nanus*. However, some of the voles (*Borsodia newtoni*, *Mimomys reidi*, *Pitymimomys pitymyoides*) lived solely in the MN 17 Zone (Jánossy 1986; Tesakov 2004). Thus we suppose that the stratigraphic position of the site is the MN 17 Zone (Fig. 46).

PALAEOECOLOGY

Based on the previous clay mineral studies, filling up of the Beremend 26 site occurred in humid, warm Mediterranean or subtropical climate (Marsi & Koloszár 2004). However, some younger, Early Pleistocene, red clay infillings were also found in the Beremend quarry, which are composed of clay minerals suggesting semiarid climate (Dezső *et al.* 2007).

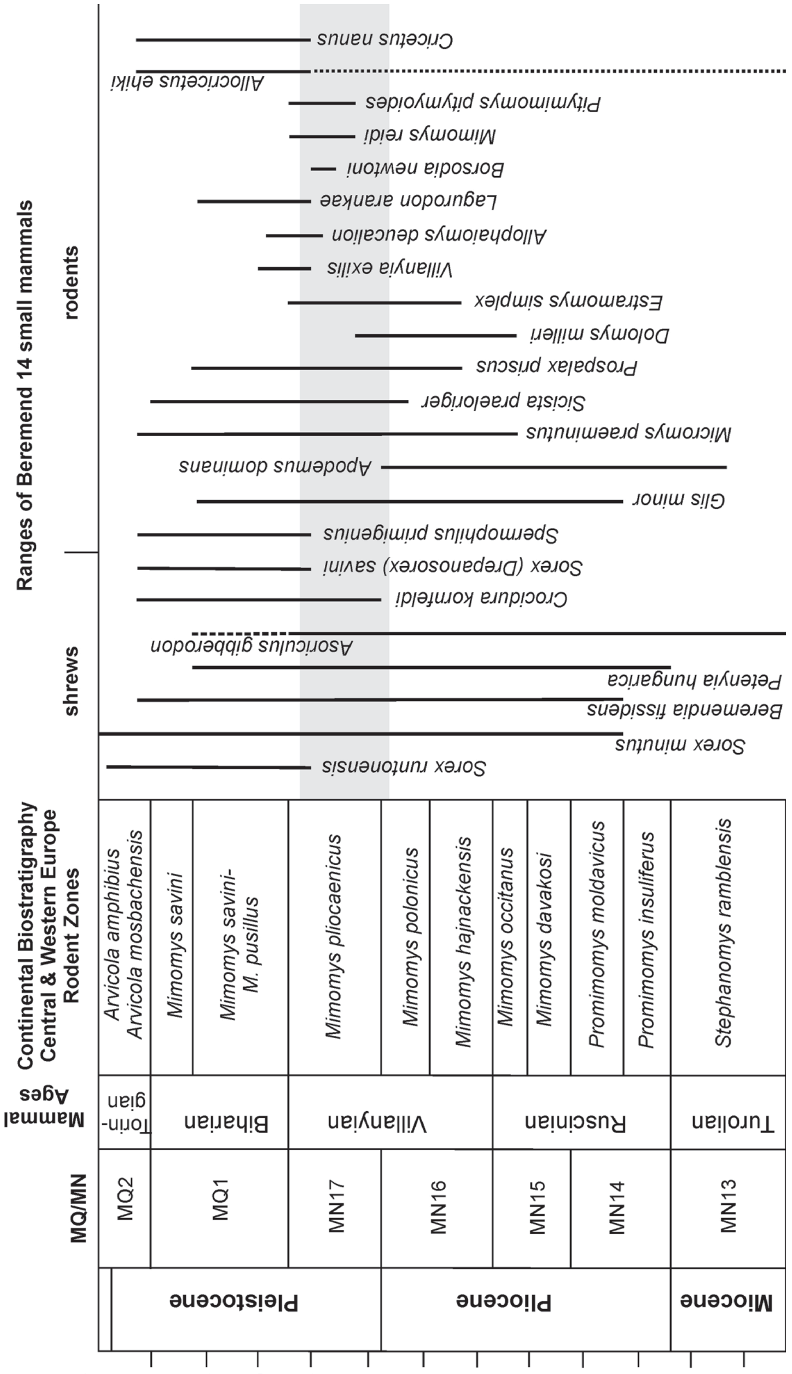


Fig. 46. Ranges of Beremend 14 small mammals (after McGowran & Denbigh 2008; Tesakov 2004).

The ecological compound of the Soricidae fauna is varied. *Crocidura* prefers warm climate and dry terrains, with more or less open grasslands. *Sorex runtonensis* is also an indicator of arid and relatively open environments (Osipova *et al.* 2006). *Sorex minutus* and *Asoriculus gibberodon* indicate a humid environment with a good covering of vegetation (Reumer 1984; Rzebik-Kowalska 1995). The presence of open water is marked by *Sorex* (*Drepanosorex*) *savini* (Reumer 1984; Maul & Parfitt 2010). *Beremendia* and *Petenyia* are typified by Reumer (1984) as opportunist and ubiquitous genera. Conversely, Botka & Mészáros (2014) raised that the occurrence of *Beremendia* is connected with open water in most of the paleobiotopes. Since it is unproved *Beremendia* is ranged to the "water-indicator or opportunist" group in our ecotype reconstruction (Fig. 47).

The ecological composition of the shrew fauna shows a significant rate of water-preferring (and "possibly riparian") forms, which indicates an open water surface, perhaps with a good vegetation cover. It is supported by the presence of some forest shrews, too. At the same time we suppose the dominance of open grassland ecotypes in the wider surroundings because of the great number of the steppe indicators (*Sorex runtonensis* and *Crocidura kornfeldi*).

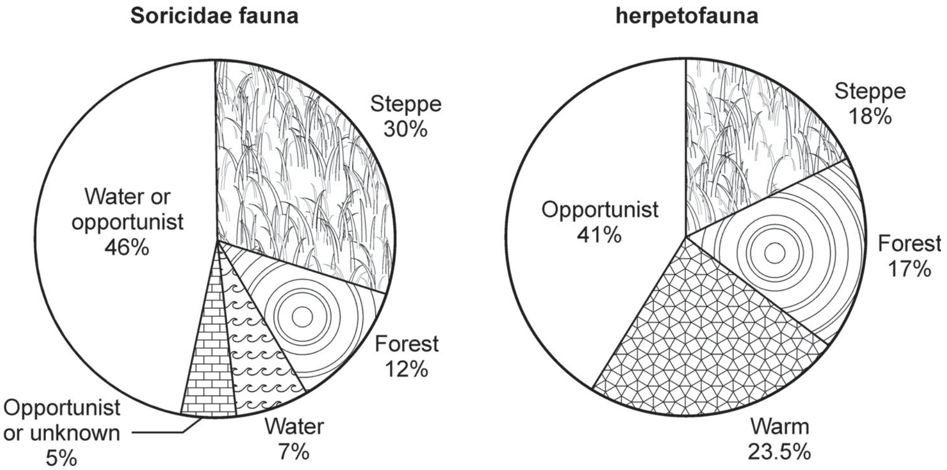


Fig. 47. Ecological composition of the Soricidae and the herpetofauna (% of MNI). Shrews – steppe forms: *Crocidura kornfeldi* and *Sorex runtonensis*; forest species: *Sorex minutus* and *Asoriculus gibberodon*; open water indicator: *Sorex* (*Drepanosorex*) *savini*; opportunist or unknown: *Petenyia hungarica* and Soricidae gen. et sp. indet.; water indicator or opportunist: *Beremendia fissidens*. Herpetofauna – steppe forms: *Pelobates fuscus*, *Bufo bufo*, *B. viridis*, *Bufo* sp.; forest species: *Hyla arborea*, Anguidae indet., *Coronella austriaca*, *Zamenis longissimus*; warm indicator species: *Coluber viridiflavus*, *C. gemonensis*, *Elaphe quatuorlineata*, *Telescopus fallax*; opportunist: *Bombina variegata*, *Rana temporaria*, *Rana* sp., *Natrix natrix*, *N. tessalata*, *Natrix* sp.

Hamsters and some voles (*Mimomys reidi*, *Borsodia newtoni*, *Lagurodon arankae*) are dominant among rodents. Unfortunately, ecological needs of these extinct voles are unknown, but the dominance of hamsters suggests open habitat, probably grassland. This conclusion is also justified by the insignificant dormice and mice material.

The herpetofauna and its ecological composition show a similar picture as shrews. The ratio of the water indicator species (*Triturus cristatus*, *Lissotriton vulgaris*) is negligible, however, opportunistic forms show high ratio (41%). Proportion of the forms preferring open habitat and forest species is equal (17–18%), but the warm indicator species (*Coluber viridiflavus*, *C. gemonensis*, *Elaphe quatuorlineata*, *Telescopus fallax*) appear in significant amounts (23.5%) in the herpetofauna (Fig. 47).

The palaeoecological analysis suggests warm, dry climate and open, probably wooded grassland vegetation in the surroundings of the site with smaller open water surface. Our results confirm the previous concepts (Dezső *et al.* 2007; Pazonyi 2006, 2011) about the Early Pleistocene climate and vegetation in the region.

*

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