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Beremendia (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Southern Hungary) and their taxonomic, biostratigraphical, palaeoecological and palaeobiogeographical relations

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Abstract – *Beremendia fissidens* and *B. minor* remains of the late Early Pleistocene vertebrate fauna of the Somssich Hill 2 locality are described. *B. minor* is reported here as a new element in the site. This record emended the stratigraphic range of this species to the Early Biharian Stage, Nagyharsányhegy Phase (ca. 900 ka). The detailed morphological and morphometrical studies gave a chance to make a new differential diagnosis between the two forms. Both of them might have been characterized by special nutrition strategy (poisoning snails and other small animals by their grooved lower incisor and storing them in their pits) and they could have lived in forest- and bush-covered lake-, or riversides. The European stratigraphical and palaeobiogeographical occurrences of the genus are summarized on the basis of published literature. With 30 figures and 3 tables.

Key words – *Beremendia fissidens*, *Beremendia minor*, Early Pleistocene, Soricidae, Somssich Hill, Villány Hills, Hungary

INTRODUCTION

The Somssich Hill 2 site is one of the most important Pleistocene vertebrate localities of Hungary. It was discovered by Dénes Jánossy and György Topál in 1975. The excavation led by them between 1975 and 1985 yielded rich Pleistocene fauna, of which preliminary list is given by Jánossy (1986). The molluscan fauna of the locality was elaborated by Krolopp (2000), and some mammal groups were also described by János Hír (cricetids) and Dénes Jánossy (lemmings and arvicolids) (Hír 1998; Jánossy 1983, 1990). Most of the Somssich Hill 2 material is under elaboration in the Department of Palaeontology and Geology of Hungarian Natural History Museum, by the cooperative research group of the Hungarian Academy of Sciences, the Hungarian Natural History Museum and the Eötvös Loránd University (OTKA K104506; project leader: Piroska Pazonyi). Up to now mainly preliminary reports were published on the results of this work

(Botka & Mészáros 2014; Mészáros *et al.* 2013; Pazonyi *et al.* 2013*a*, *b*; Pazonyi & Virág 2013*a*, *b*; Szentesi 2013, 2014*a*).

A great number of soricid fossils were found in the Somssich Hill material. Seven shrew species were mentioned by Botka & Mészáros (2014), and two of them (*Beremendia fissidens*, *B. minor*) are discussed here in detail.

LOCALITY

The Somssich Hill 2 site is located ca. 500 m west of Villány, on the top of the Somssich Hill (today known as Villány Hill) in Southern Hungary, Villány Hills (GPS coordinates: N 45° 52' 26.66", E 18° 26' 32.71"; EOVX = 58998, EOVY = 603025) (Fig. 1).

The locality is a sediment-filled karst fissure in the Jurassic limestone of the Villány Hills. Fifty layers were separated within the excavated infilling sediment (each layers are 20–30 cm in thickness). The sediment was loess-like yellow aleurite in the upper layers, but became red and more clayey down from the layer 28 (Kordos 1991). The cave was excavated in depth of ca. 9.5 m (Jánossy 1999).

MATERIAL AND METHODS

The fossil material of the locality is stored in the Department of Palaeontology and Geology of the Hungarian Natural History Museum, Budapest. Several shrew species were identified in the material collected by Dénes Jánossy (Botka & Mészáros 2014). The fossil bones are poorly preserved, most of them are fragmentary, the complete mandibles and maxillae are relatively rare. The *Beremendia* shrews are well distinguished from the other shrew species of the locality by the large-sized elements (skull elements, teeth and humeri).

The fifty layers yielded 169 *B. fissidens* and 11 *B. minor* remains (minimum number of individuals: 61, and 8, respectively). At the determination of the minimum number of individuals all the bone elements and teeth were taken into consideration. During the anatomical description and measurements of specimens the method presented by Reumer (1984) was followed.

The measurements were made by a calibrated eyepiece micrometer of a Nikon SMZ800 microscope and were given in mm. The R 3.1.1. software was used for making the morphometrical analyses. The SEM photos were taken by a Hitachi S-2600N Variable Pressure Scanning Electron Microscope (VPSEM).

The abbreviations in the description and the measurements are used as follows: 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.

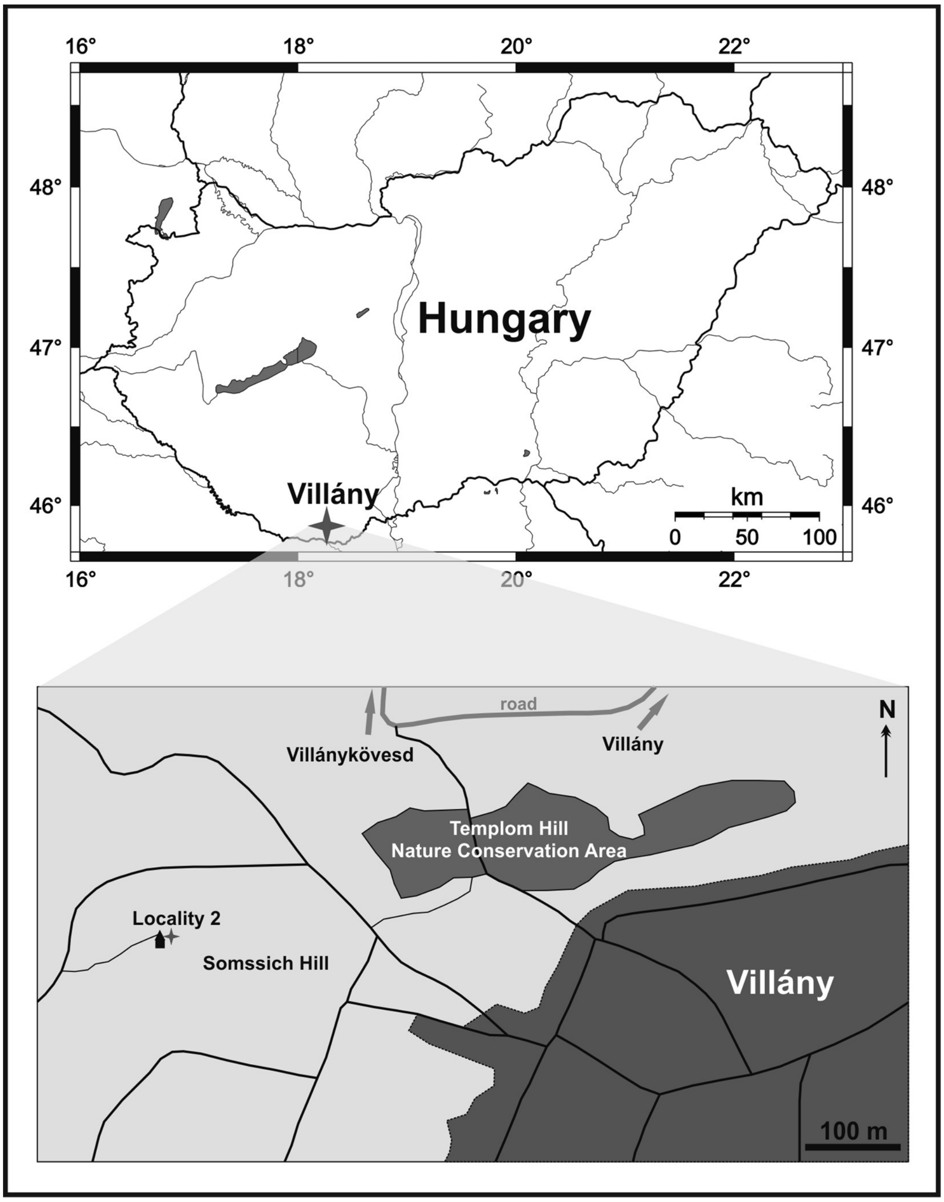


Fig. 1. The geographical situation of Somssich Hill 2 locality (after PAZONYI *et al.* 2013*a*)

SYSTEMATIC DESCRIPTION

Phylum Vertebrata Linnaeus, 1758
Classis Mammalia Linnaeus, 1758
Order Eulipotyphla Waddell *et al.*, 1999
Family Soricidae Fischer von Waldheim, 1817
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Beremendiini Reumer, 1984
Genus *Beremendia* Kormos, 1934

Upper incisor strongly fissident; teeth heavily pigmented; Blarinini-like condyle with broad interarticular area and anteriorly placed lower facet; lower incisor acuspulate; entoconid crests are present (Reumer 1984).

This is the only monogeneric tribe (Beremendiini) among the Soricinae, comprising only the extinct genus *Beremendia*. Separation of this tribe from the other tribes is based on the intermediate position of its morphology between the Soriculini (bifid I^1 and presence of entoconid crests) and the Blarinini (structure of the condyle and intense dark red pigmentation) (Reumer 1984).

Beremendia fissidens (Petényi, 1864)
(Figs 2–12, 16)

1864 *Crossopus fissidens* n. gen. n. sp. – Petényi, pp. 60–70, pl. I, fig. 5.
1911 *Neomys fissidens* (Petényi) – Kormos, pp. 156–158, pl. VII, figs 1–3.
1930 *Neomys* (?) *fissidens* (Petényi) – Heller, pp. 254–258, text-figs 2–4, pl. XV, figs 1–3.
1930 *Beremendia fissidens* n. gen. (Petényi) – Kormos, pp. 43–44, 57.
1934 *Beremendia fissidens* (Petényi) – Kormos, pp. 299–301, fig. 33.
1936 *Beremendia fissidens* (Petényi) – Heller, pp. 107–108, pl. VII, figs 1–2.
1949 *Beremendia fissidens* (Petényi) – Friant, pp. 256–257, fig. 17.
1958 *Beremendia fissidens* (Petényi) – Kowalski, pp. 13–14, fig. 4.
1959 *Beremendia fissidens* (Petényi) – Sulimski, pp. 152–154, tab. 7, text-fig. 4: 1a-f, pl. III, fig. 7.
1966 *Beremendia fissidens* (Petényi) – Fejfar, figs 4f-j, 5f-h, 10d, h.
1967 *Beremendia fissidens* (Petényi) – Repenning, pp. 50–51, fig. 35.
1976 *Beremendia fissidens* (Petényi) – Freudenthal *et al.*, pl. I. figs 7–8.
1976 *Beremendia fissidens* (Petényi) – Rzebik-Kowalska, pp. 360–368, tabs I–III, X, figs 1–11, 21, 23, 25, 28–29, 33–35.
1979 *Nectogalinia altaica* n. gen. n. sp. – Gureev, p. 458, fig. 235.
1984 *Beremendia fissidens* (Petényi) – Reumer, pp. 131–138, text-fig. 16, pl. 32, figs 1–13, pl. 33, figs 1–6, pl. 34, figs 1–4, pl. 35, figs 1–2.
1996 *Beremendia fissidens* (Petényi) – Dahlmann & Storch, p. 185, tab. 3.
2002 *Beremendia fissidens* (Petényi) – Aguilar *et al.*, p. 24, pl. II, figs 11–14.
2003 *Beremendia fissidens* (Petényi) – Popov, pp. 60–62, tab. V, figs 7–8.
2004 *Beremendia fissidens* (Petényi) – Suárez & Mein, pp. 122–123, fig. 8c-e.
2006 *Beremendia fissidens* (Petényi) – Harrison *et al.*, pp. 121–124, figs 1a-c, 3c, 4a-b.
2007 *Beremendia* cf. *fissidens* (Petényi) – Čermák *et al.*, fig. 3a, c.

2007 *Beremendia fissidens* (Petényi) – Cuenca-Bescós & Rofes, pp. 113–115, fig. 3a.
2007 *Beremendia fissidens* (Petényi) – Horáček *et al.*, pp. 459–460, pl. 2, figs 3–4.
2009 *Beremendia fissidens* (Petényi) – Rofes & Cuenca-Bescós, pp. 24–30, tab. 1, figs 3–5.
2010 *Beremendia fissidens* (Petényi) – Furió *et al.*, pp. 929–936, figs 2–8.
2012 *Beremendia fissidens* (Petényi) – Hellmund & Ziegler, p. 81, pl. 1, fig. 3.
2013 *Beremendia fissidens* (Petényi) – Cuenca-Bescós *et al.*, fig. 4d.
2013 *Beremendia fissidens* (Petényi) – Rzebik-Kowalska, pp. 25–28, tabs 30–32, fig. 5: 7.
2014 *Beremendia fissidens* (Petényi) – Bennàsar *et al.*, tab. 2, figs 3–4.
in press *Beremendia fissidens* (Petényi) – Botka & Mészáros, tabs 1–2, pl. I, figs 1–7.

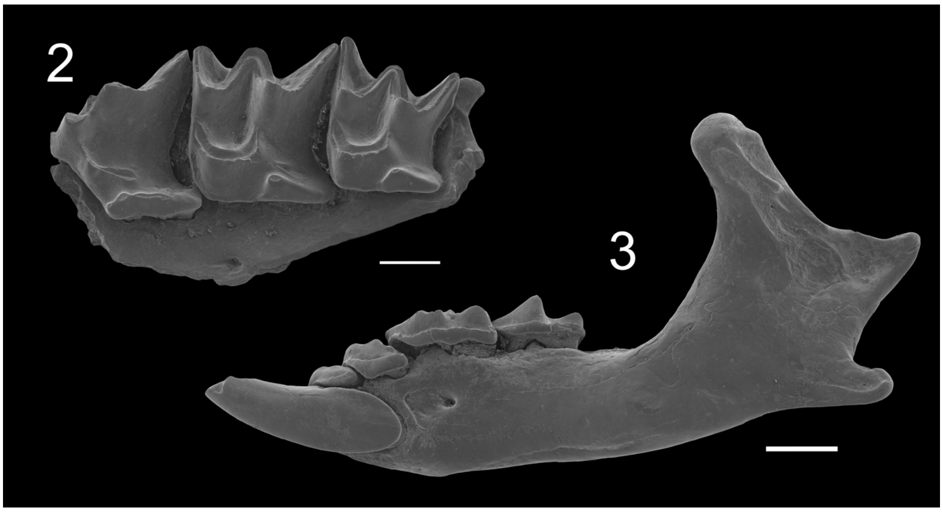
Type material – *Crossopus fissidens* Petényi, 1864: Hungarian Natural History Museum, Department of Palaeontology and Geology, inventory number V 61.1585. Syntypes: 1 skull fragment, 2 left and 2 right maxillae, 13 left and 15 right mandibles, 1 condyle and 8 I_1.

Type locality – Beremend limestone quarry (locality 2), Villány Hills, Hungary, Upper Pliocene (Villányian Stage, Beremend Phase, MN 16).

Studied material – Somssich Hill 2 locality: 13 left maxillary fragments, 11 right maxillary fragments, 9 left mandibles, 6 right mandibles, 20 left mandible fragments, 18 right mandible fragments, 8 left I^1, 13 right I^1, 5 left P^4, 6 right P^4, 5 left M^1, 4 right M^1, 3 left M^2, 2 right M^2, 10 left I_1, 5 right I_1, 1 left A_1, 1 left A_2, 8 left M_1, 6 right M_1, 3 left M_2, 7 right M_2, 1 right M_3 and 4 humeri.

Measurements – Table 1.

Dental formula – 153/123 or 143/123 (A^4 is missing from a few specimens).



Figs 2–3. *Beremendia fissidens* (Petényi, 1864), Somssich Hill 2. 2 = left maxillary fragment with P^4-M^2, layer 14, occlusal view, scale bar: 1 mm, 3 = left mandible with I_1-M_2, layer 30, buccal view, scale bar: 2 mm

Table 1. Measurements of *Beremendia fissidens* teeth from Somssich Hill 2 (for the abbreviations see "Material and methods")

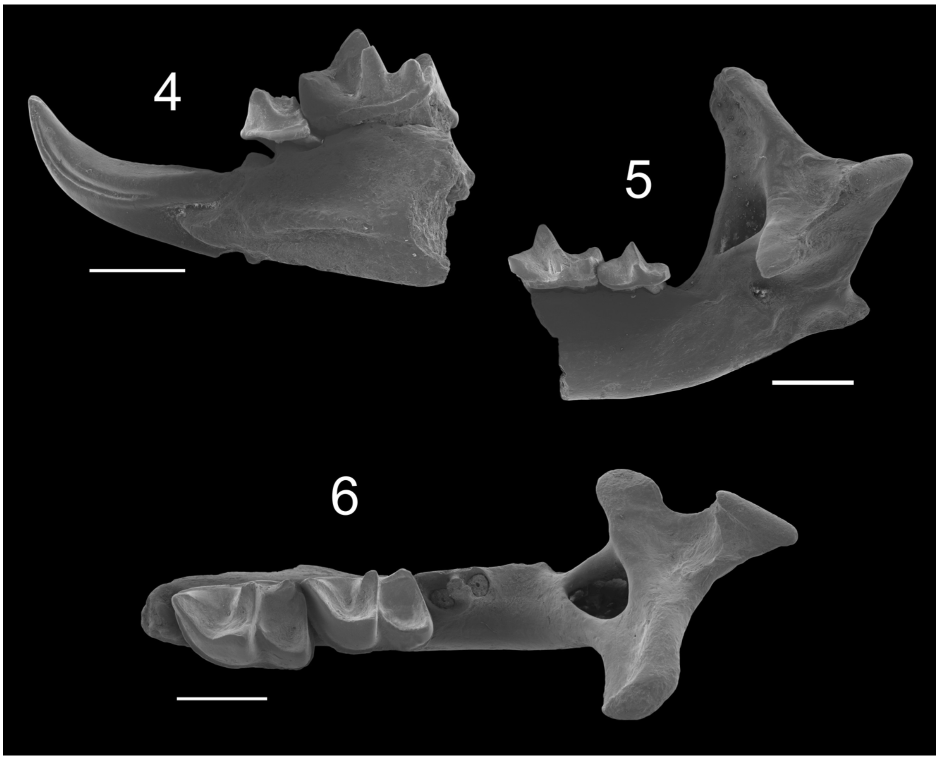
		n (pcs)	min. (mm)	mean (mm)	max. (mm)	SD (mm)
I^1	L	9	3.33	3.62	4.20	0.2687
	H	9	2.10	2.31	2.50	0.1422
P^1	BL	17	2.47	2.79	2.93	0.1167
	LL	17	1.40	1.55	1.80	0.1202
	W	17	2.40	2.58	2.77	0.1185
M^1	LL	18	2.20	2.35	2.57	0.1004
	BL	18	2.20	2.46	2.70	0.1565
	AW	18	2.33	2.57	2.73	0.1091
	PW	17	2.33	2.58	2.80	0.1214
M^2	LL	7	1.53	1.78	2.00	0.1665
	BL	7	1.80	2.00	2.20	0.1540
	AW	7	2.27	2.45	2.67	0.1359
	PW	7	1.67	1.88	2.00	0.1258
I_1	L	4	5.93	6.33	6.60	0.2961
	H	4	1.47	1.77	2.00	0.2211
M_1	L	20	2.67	2.85	3.00	0.1110
	W	20	1.47	1.61	1.73	0.0873
M_2	L	24	1.93	2.30	2.47	0.1302
	W	24	1.33	1.44	1.63	0.0764
M_3	L	14	1.50	1.62	1.73	0.0834
	W	14	0.83	0.95	1.13	0.0834

Original diagnosis – The original diagnosis of Petényi (in old Hungarian language) highlighted the bifid upper incisor, the acuspulate lower incisor and the relative position of the incisors and antemolars as specific morphological characters. The new species was described as „*Crossopus*" *fissidens* and was classified to the group of the red-toothed water shrews (after Petényi 1864).

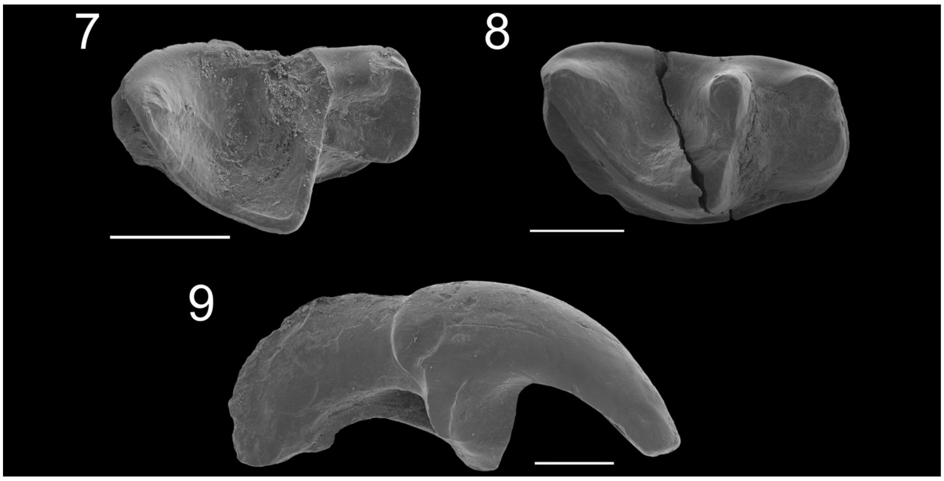
Emended diagnosis – Teeth intensively stained dark red. I^1 is strongly fissident with a bifid apex. Four upper antemolars are present. A^1 and A^2 are of about equal size, A^3 is smaller and A^4 is smaller again. A^4 is reduced, hidden and not visible in buccal view or is lacking. The posterior emargination is moderate on P^4, M^1 and M^2. The parastyle of the M^1 is moderately developed. M^3 is relatively small. I_1 is grooved, acuspulate, the apex curves upwards. A_2 is bicuspid and has a posterolingual basin. M_3 is reduced. The ramus is strong and robust. The coronoid process is stout, anterolaterally curved; the angle of the curve may vary. The angular process is short and flat. The external pterygoid fossa is definitely or less deeply pocketed. The upper facet is narrow; its shape may vary from elliptic to oval. The interarticular area is broad with a lingual margin. The lower facet leans strongly anteriorly and it is not visible in buccal view. The internal temporal fossa is small, deep and pocketed (after Reumer 1984).

Anatomical description – Some detailed anatomical descriptions were already published on *B. fissidens* (Rzebik-Kowalska 1976; Reumer 1984; Rofes & Cuenca-Bescós 2009; Botka & Mészáros in press). Therefore, only the most important morphological characters and the differential diagnosis between the two discussed forms are presented in this article.

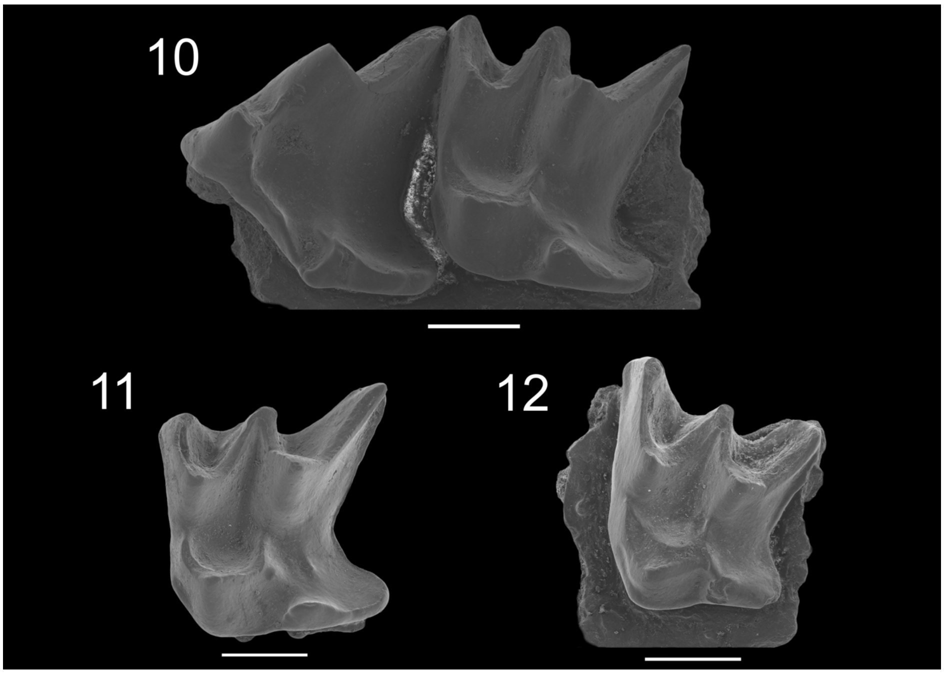
Mandible – The mandibular body is robust, strongly built, slightly leans laterally. The symphysis terminates below the posterior root of M_1. The ascending ramus is anteroposteriorly broad and leans strongly medially. The coronoid process is narrow, short, stout and leans anteriorly in lateral view. The coronoid



Figs 4–6. *Beremendia fissidens* (Petényi, 1864), Somssich Hill 2, scale bar: 2 mm. 4 = right mandible fragment with I_1, A_2 and M_1, layer 13, lingual view, 5 = right mandible fragment with M_2-M_3, layer 28, lingual view, 6 = left mandible fragment with M_1-M_2, layer 32, occlusal view



Figs 7–9. *Beremendia fissidens* (Petényi, 1864), Somssich Hill 2, scale bar: 1 mm. 7 = left M_3, layer 32, occlusal view, 8 = left M_3, layer 5, occlusal view, 9 = left I^1, layer 11, buccal view



Figs 10–12. *Beremendia fissidens* (Petényi, 1864), Somssich Hill 2, scale bar: 1 mm. 10 = left maxillary fragment with P^4-M^1, layer 32, occlusal view, 11 = right M^1, layer 28, occlusal view, 12 = left maxillary fragment with M^2, layer 31, occlusal view

spicule is thin, poorly developed and nearly vertical. The condyloid process is characteristic. The angular process is very short (Figs 3–6).

Dentition – I^1 is fissident with a bifid apex. The lingual part of P^4 crown is very low. The occlusal outline is nearly triangular but it can be variable. The occlusal outline of M^1 is square with rounded corners. By comparison, M^2 has a more developed parastyle which protrudes buccally beyond the mesostyle and the metastyle. M^3 was not found in the studied material. The crown and the root of I_1 are equally stout and elongated. The crown of the lower incisor is grooved and acuspulate. M_1 and M_2 have trapezoidal outlines in occlusal view; the trigonid basins are deep and broad. M_3 is reduced but its talonid is basined (Figs 2, 6–12, 16).

Differential diagnosis (according to present study on the material of the Somssich Hill 2 and Osztramos 7 localities): *B. fissidens* differs from *B. minor* not only in size but there are also some different morphological characters. These are the following: I^1 – the angle between the ventral part of the apex and the anterior margin of the talon is different; I_1 – *B. fissidens* has a less pointed apex and has a less curved lower incisor; M_3 – *B. fissidens* has a low entoconid, a straight hypolophid and the posterior margin of the talonid is angular. Contrarily, *B. minor* has a high entoconid, a rounded hypolophid and the posterior margin of the talonid is round (Figs 7–8, 15).

Remarks – According to our observations *B. fissidens* specimens from Osztramos 7 site (MN 16) have four upper antemolars being situated in one line. *B. fissidens* remains from Somssich Hill 2 locality (late Early Pleistocene) have four upper antemolars as well but the fourth is situated more lingually, hidden beside P^4. Four antemolars are not characteristic at all for *Beremendia* species, for example the East Asian *B. jiangnanensis* Jin *et al.,* 2009 usually has three upper antemolars (Jin *et al.* 2009). Reduction of the number of the upper antemolars could be an evolutional trend in the tribe.

Beremendia minor Rzebik-Kowalska, 1976
(Figs 13–15)

1962 *Beremendia fissidens* (Petényi) – Dehm, pp. 25–26, pl. 3, figs 10–13.
1964 *Beremendia* sp. – Fejfar, pp. 33–34.
1976 *Beremendia minor* n. sp. – Rzebik-Kowalska, pp. 369–371, tabs IV–V, figs 12–16, 17a, 18c.
1984 *Beremendia minor* Rzebik-Kowalska – Reumer, p. 101, text-fig. 16, pl. 32, figs 14–15, pl. 33, figs 7–9, pl. 35, figs 3–6.
1996 *Beremendia minor* Rzebik-Kowalska – Dahlmann & Storch, p. 185.
2009 *Beremendia minor* Rzebik-Kowalska – Rofes & Cuenca-Bescos, pp. 30–32, fig. 5.
2013 *Beremendia minor* Rzebik-Kowalska – Rzebik-Kowalska, pp. 26, 28.

Type material – Holotype: right mandible fragment with P^4-M^3 and skull processes except angular process (ZZSiD, No. MF/1513). I^1, left and right maxillary fragment with M^1 and M^2, left mandible fragment with M_1 and skull processes except the angular process, and 9 right mandible fragments, partly with skull processes except the angular process and all together providing a full set of the lower teeth except I_1 (Rzebik-Kowalska 1976).

Type locality – Rębielice Królewskie 1A, Poland, Upper Pliocene (MN 16, Lower Villafranchian Stage).

Studied material – Somssich Hill 2 locality: 1 right maxillary fragment, 1 left mandible fragment, 5 right mandible fragments, 1 right P^4, 1 left M^1, 1 right I_1 and 1 right M_2.

Measurements – Table 2.

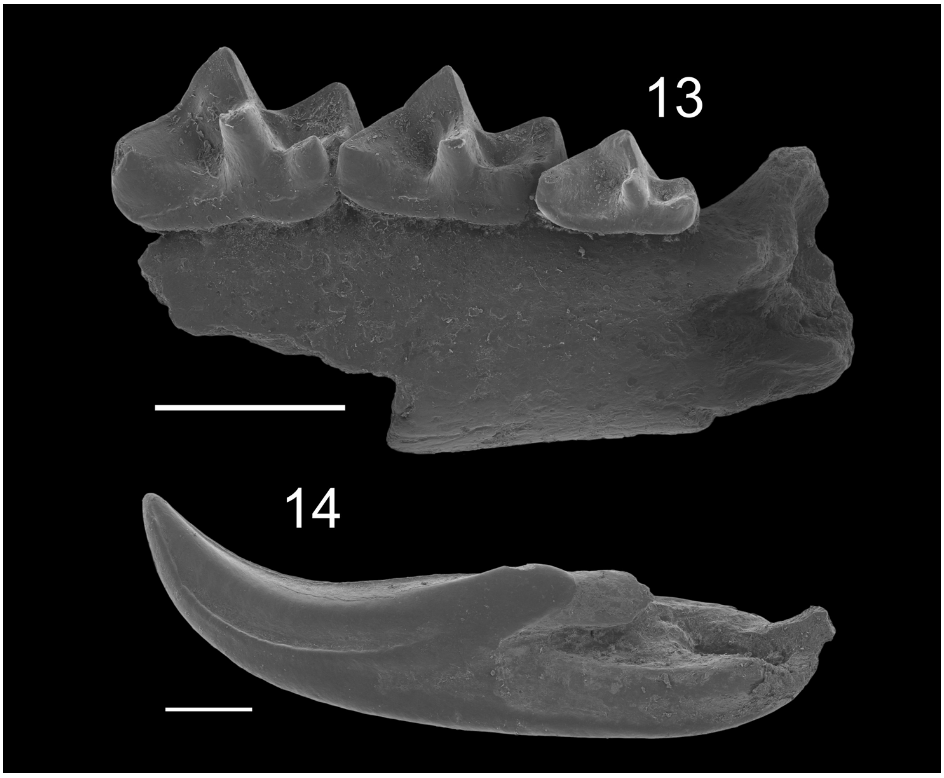
Dental formula – 153/123.

Original diagnosis – The morphological structure of *B. minor* is an exact counterpart of the structure of *B. fissidens*, in connection with which its classification in the genus *Beremendia* does not rouse doubt. However, the dimensions of this species are much smaller than those of the members of *B. fissidens* from the same locality and the smallest specimens from the Pliocene locality at Węże I. As the difference in size is conspicuous, the dimensions of the two forms do not overlap, and they occur in the same locality, the small form has been included in a separate species (after Rzebik-Kowalska 1976).

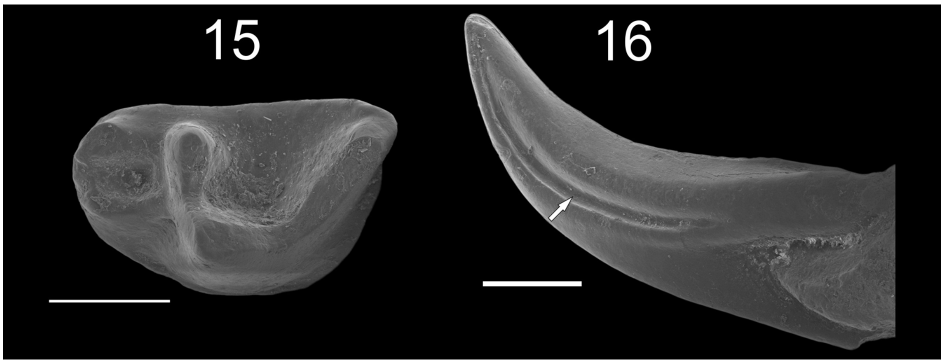
Emended diagnosis – According to Reumer (1984) *B. minor* is morphologically identical to *B. fissidens*. The two species differ only in size, *B. minor* is considerably smaller than *B. fissidens*.

Table 2. Measurements of *Beremendia minor* teeth from Somssich Hill 2 (for the abbreviations see "Material and methods")

		n (pcs)	min. (mm)	mean (mm)	max. (mm)	SD (mm)
M^1	LL	1	–	1.87	–	–
	BL	1	–	2.00	–	–
	AW	1	–	2.07	–	–
	PW	1	–	1.87	–	–
M^2	LL	1	–	1.47	–	–
I_1	L	1	–	5.93	–	–
	H	1	–	2.13	–	–
M_1	L	3	2.33	2.44	2.60	0.1388
	W	3	1.13	1.31	1.40	0.1540
M_2	L	6	1.80	1.90	2.07	0.1022
	W	6	1.07	1.16	1.33	0.1089
M_3	L	2	1.33	1.33	1.33	0.0024
	W	2	0.80	0.84	0.87	0.0495



Figs 13–14. *Beremendia minor* Rzebik-Kowalska, 1976, Somssich Hill 2. 13 = right mandible fragment with M_1-M_3, layer 35, lingual view, scale bar: 2 mm, 14 = right I_1, layer 14, medial view, scale bar: 1 mm



Figs 15–16. *Beremendia fissidens* (Petényi, 1864) and *Beremendia minor* Rzebik-Kowalska, 1976, Somssich Hill 2, scale bar: 0.5 mm. 15 = *B. minor* right M_3, layer 35, occlusal view, 16 = *B. fissidens* right I_1, layer 13, medial view, the venom groove is marked by the white arrow

Anatomical description – The dimensions of the species are significantly smaller than those of *B. fissidens* (not only the dental elements but also the size of the mental foramen, its anterior basin and the parameters of the symphysis fossa). I^1 – The angle of I^1 is smaller between the ventral part of the apex and the anterior margin of the talon. I_1 – It has a more pointed apex and a more curved lower incisor. M_3 – *B. minor* has a high entoconid, a rounded hypolophid and the posterior margin of the talonid is round (Figs 13–15).

Remarks – The occurrence of the small form of *Beremendia* is also mentioned by FEJFAR (1964) from Hajnačka (Slovakia), which corresponds in age with Rębielice Królewskie. FEJFAR described them as *Beremendia* sp. According to RZEBIK-KOWALSKA (1976) *Beremendia fissidens* remains from Schernfeld (Austria) (DEHM 1962) and the *Beremendia* sp. from Hajnačka (FEJFAR 1964) seems to be as small as *B. minor* in dimensions. The measurements of the small form of *Beremendia* from the Somssich Hill 2 locality compounds with the aforementioned remains (DEHM 1962; FEJFAR 1964).

CONCLUSIONS

Taxonomy

The bigger *B. fissidens* and the smaller *B. minor* are well distinguished by the size of the upper and lower molars (Figs 17–20). The separation is supported by the morphometrical analysis made on the M_2 length and width of the two forms.

We used *P*-values of the Shapiro-Wilk normality test to demonstrate the separation of the two *Beremendia* species (SHAPIRO & WILK 1965; RAZALI & WAH

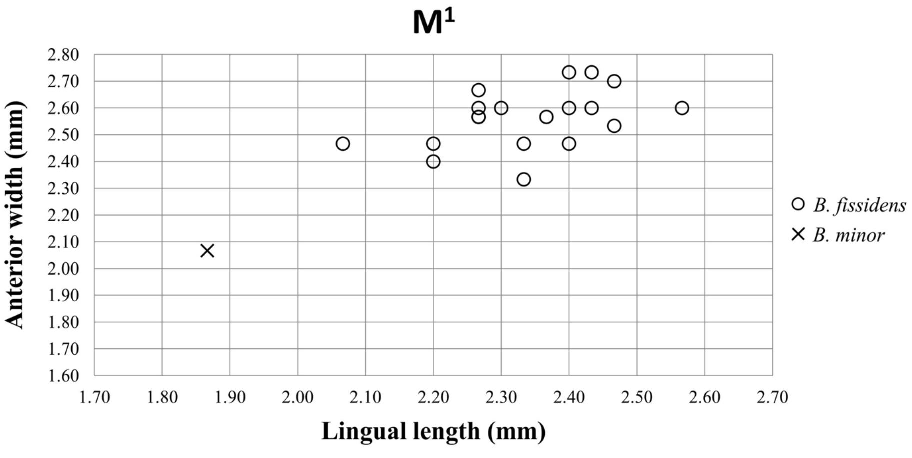


Fig. 17. Measurements of the M^1 teeth of *B. fissidens* and *B. minor* specimens

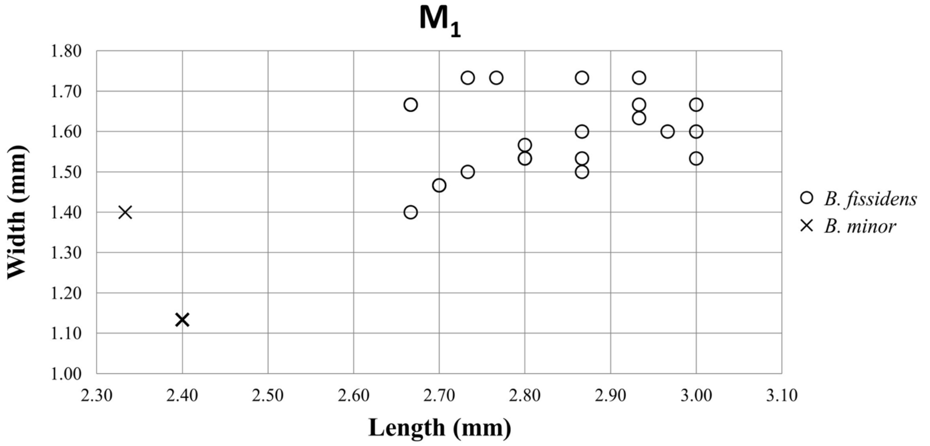


Fig. 18. Measurements of the M_1 teeth of *B. fissidens* and *B. minor* specimens

2011). *P*-value above 0.05 shows a normal distribution which indicates the presence of only one species (in case of 95% confidence interval) (Goodman 2008). In the case of the common set of the measurement data of *B. fissidens* and *B. minor* do not show normal distribution, indicating the presence of different species (*P*-value of length: 0.0026, *P*-value of width: 0.0017). Contrarily, *P*-value of length is 0.0581, *P*-value of width is 0.1017 at *B. fissidens*, while *P*-value of length is 0.1165, *P*-value of width is 0.0460 at *B. minor* (because of the few data it is plausible). The measurements of the two different species show normal distribution if we divide them.

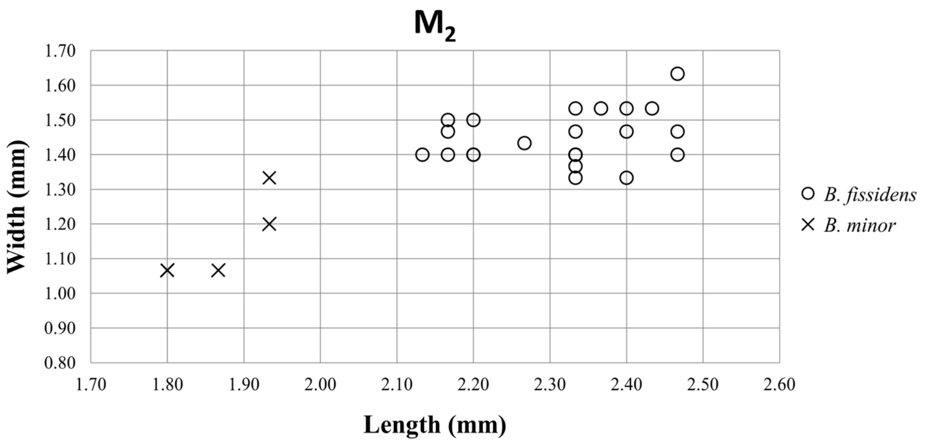


Fig. 19. Measurements of the M_2 teeth of *B. fissidens* and *B. minor* specimens

The linear correlation (Fig. 21), the box plots (Fig. 22), the regression lines (Fig. 23) and the confidence ellipses (Fig. 24) show that the measurement data of Somssich Hill 2 *B. fissidens* and *B. minor* specimens constitute two significantly different sets (confidence interval 95%).

Making a comparison between the Hungarian *Beremendia* specimens and the older Polish ones (after Fejfar 1964 and Rzebik-Kowalska 1976) shows that the detachment of the two forms became more expressive to the end of the Early Pleistocene (Fig. 25). The difference was caused by the size growth of *B. fissidens* while the measurements of *B. minor* did not develop significantly. This divergent progression could be the main evolutionary trend after the specific separation.

Some details in the dental morphology (the form of the upper and lower incisors), the size of the mental foramen and its anterior basin, the parameters of the sympysis fossa also prove them to be different taxa.

The main differential characters are present on M_3 talonid, which were similarly found not only here, but on the specimens of the North Hungarian Pliocene Osztramos 7 (MN 16) site as well.

Sum up, the main differential characters between *B. fissidens* and *B. minor* specimens from the Somssich Hill 2 locality are as follows: *B. fissidens* is bigger (mainly in the length of the lower molars). It has basined M_3 talonid with straight posterior margin (hypolophid) and the entoconid is lower than that one of the smaller species. Contrarily, *B. minor* has a more reduced, not basined M_3 talonid with rounded posterior margin and with high entoconid (Figs 7–8, 13, 15, 17–25).

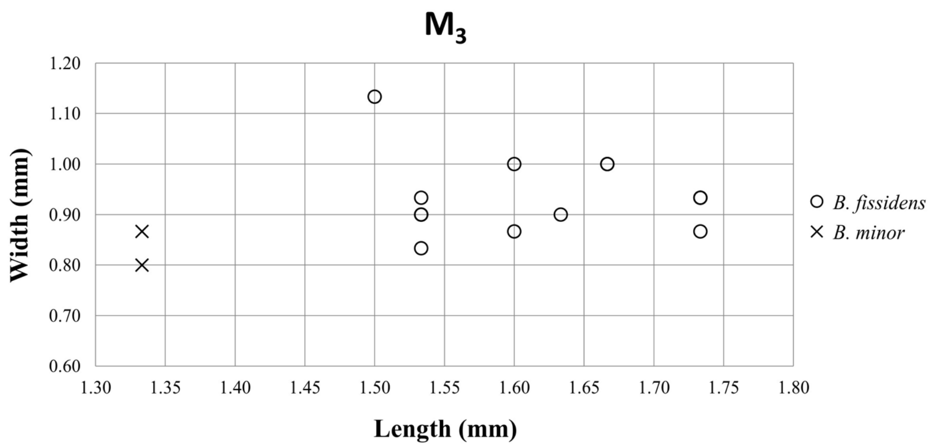


Fig. 20. Measurements of the M_3 teeth of *B. fissidens* and *B. minor* specimens

Biostratigraphy

The estimated age of Somssich Hill 2 locality is approximately 800–900 ka (*Mimomys savini-M. pusillus* biozone by Kordos 1994) on the basis of the vole fauna (Pazonyi *et al.* 2013*a*, *b*; Pazonyi & Virág 2013*a*, *b*) (Fig. 26). The identified shrew and dormouse fauna (*Sorex, Crocidura, Beremendia, Glis, Muscardinus* and *Dryomimus* species) confirmed this hypothesis (Botka & Striczky 2014; Botka & Mészáros 2014).

B. fissidens is present from the MN14 zone (Osztramos 1, Podlesice, Zalesiaki 1B and Zamkowa Dolna Cave B) to the Tarkő Phase (ca. 350 ka) of the Middle Pleistocene (Tarkő) in Europe (Reumer 1984; Stefaniak *et al.* 2009; Jánossy 1986) (Figs 27–29). The presence of *B. minor* in the studied material was surprising because this species was only found at Pliocene localities e.g. Rębielice Królewskie 1A (MN16), Osztramos 1 (MN14), Osztramos 7 (MN16), Hajnačka (MN16), Ivanovce (MN15) and Gundersheim-Findling (MN15) (Rzebik-Ko-

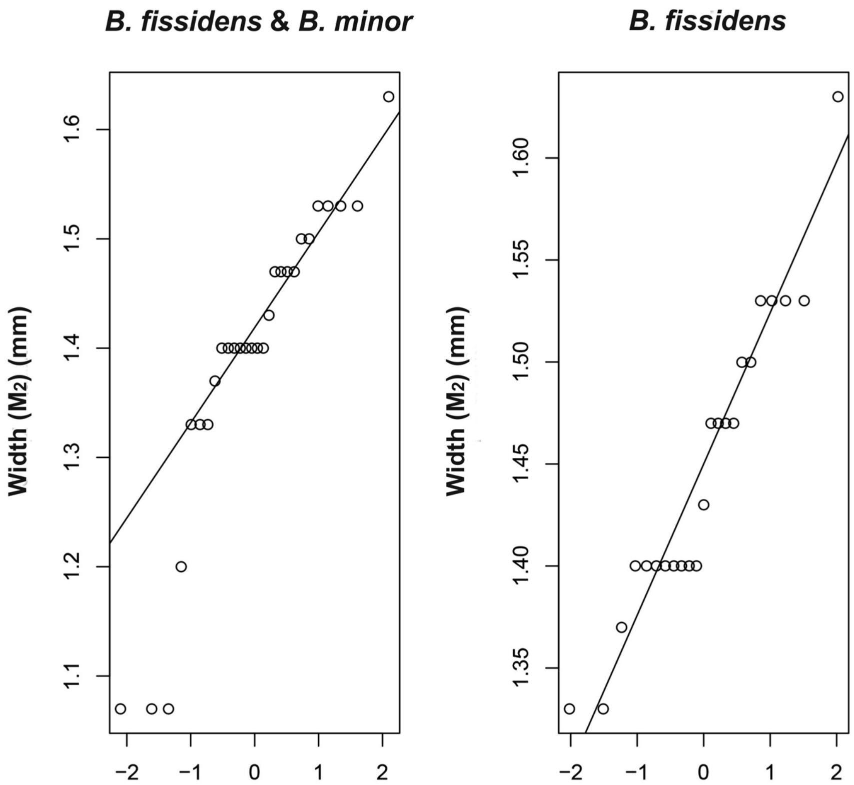


Fig. 21. Linear correlation of the Somssich Hill 2 *Beremendia* M_2 measurements (confidence interval 95%)

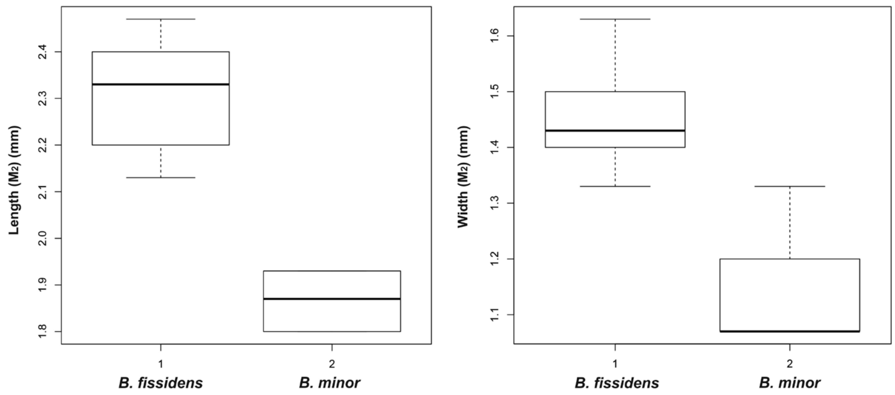


Fig. 22. Box plot of the separation of the Somssich Hill 2 *Beremendia* M_2 measurements (confidence interval 95%)

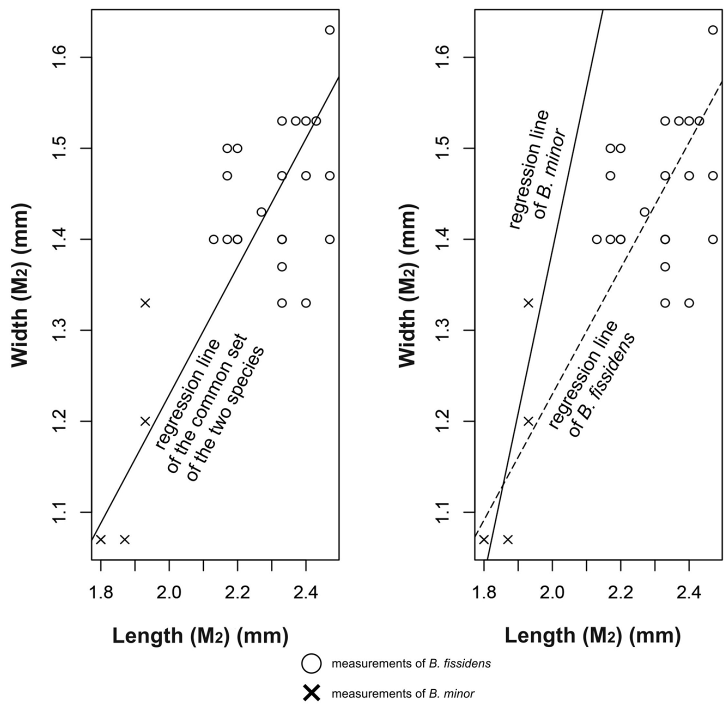


Fig. 23. Regression lines of the Somssich Hill 2 *B. fissidens* and *B. minor* M_2 measurements. The linear equations: y (the common set of the two *Beremendia* species) = 0.5678x + 0.1254, y (*B. fissidens*) = 0.1770x + 1.0377, y (*B. minor*) = 1.4752x – 1.6047

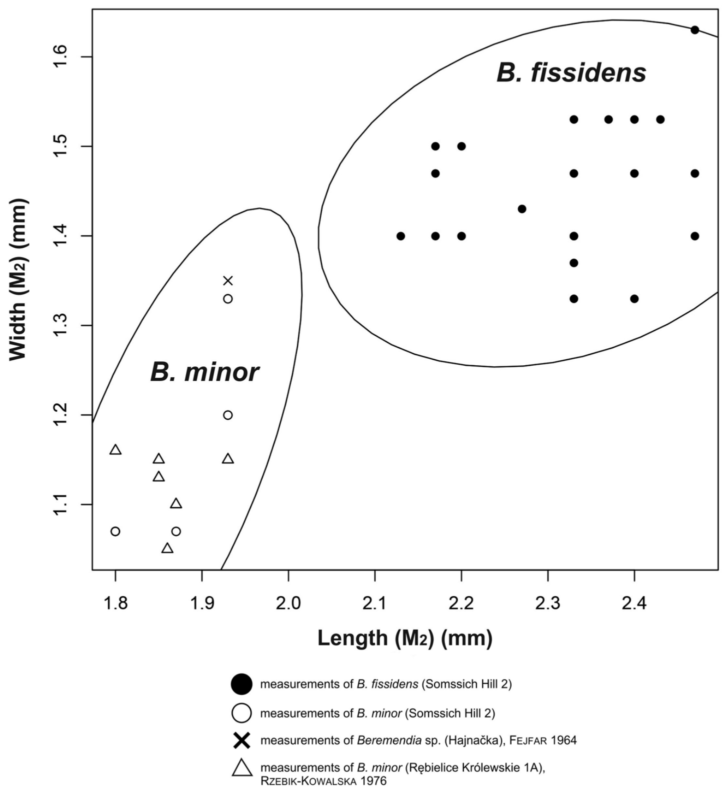


Fig. 24. Confidence ellipses of the Somssich Hill 2 *B. fissidens* and *B. minor* M_2 measurements (confidence interval 95%)

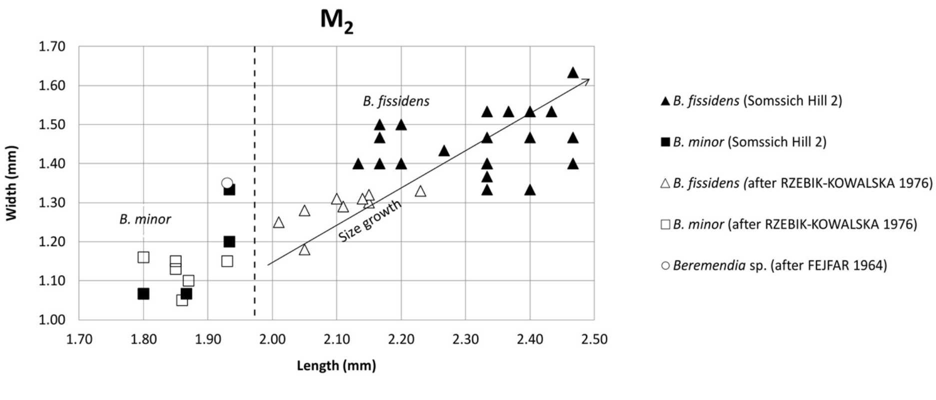


Fig. 25. Comparison between the Hungarian *Beremendia* specimens and the older Polish ones

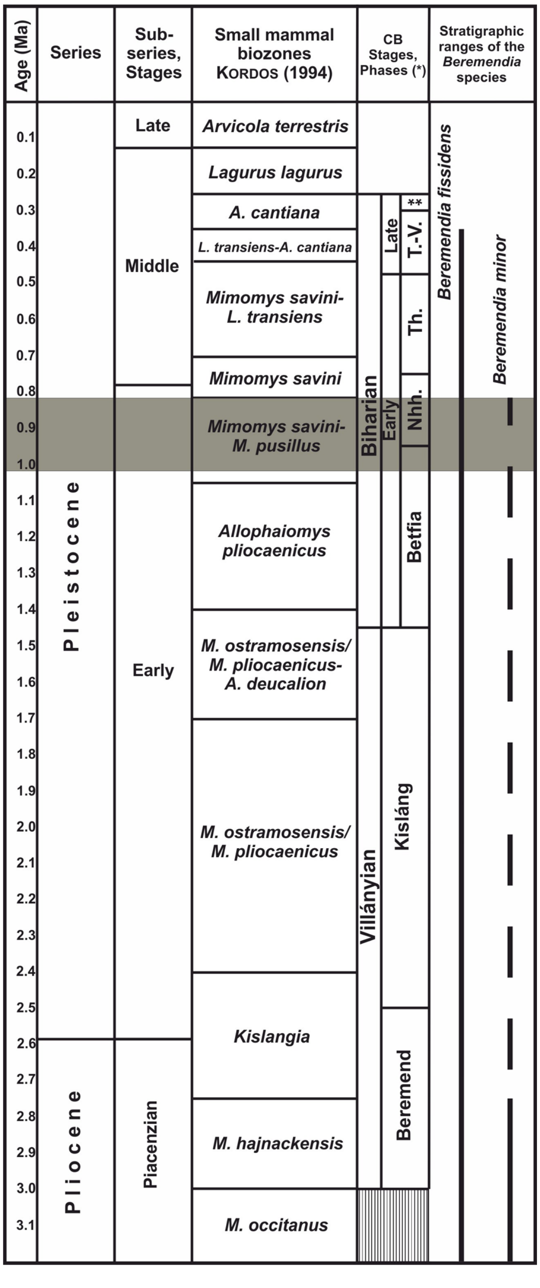


Fig. 26. Stratigraphical position of the Somssich Hill 2 locality (after Kordos 1994, Kretzoi 1969, Kretzoi & Pécsi 1982, Pazonyi *et al.* 2013a), with the stratigraphical range of the studied species (CB = Carpathian Basin, * = after Kretzoi 1969, Kretzoi & Pécsi 1982, Nhh. = Nagyharsányhegy Phase, Th. = Templomhegy Phase, T.-V. = Tarkő-Vértesszőlős Phase and ** = Uppony Phase)

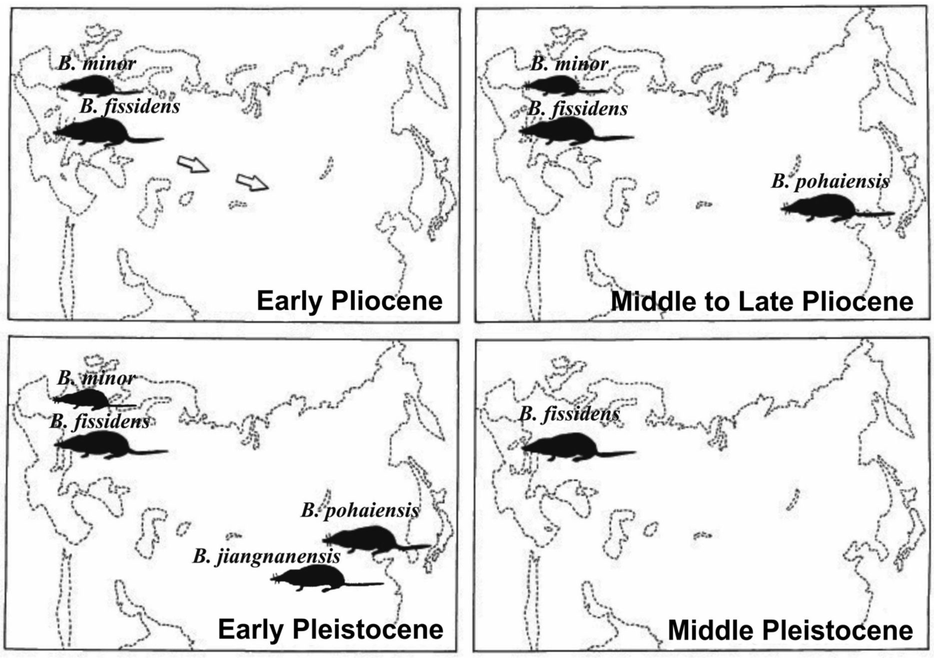


Fig. 27. Distribution of the genus *Beremendia* in Eurasia during the Plio-Pleistocene (modified after Jin & Kawamura 1996)

COUNTRY	FAD (First Appearance Datum)	LAD (Last Appearance Datum)
Poland	Early Pliocene (MN 14)	Middle Pleistocene
Hungary	Early Pliocene (MN 14)	Middle Pleistocene
Switzerland	Middle Pliocene (MN 15)	Middle Pliocene (MN 15)
Austria	Middle Pliocene (MN 15)	Late Pliocene (MN 16)
Slovenia	Middle Pliocene (MN 15)	Early Pleistocene (MN 17)
Greece	Middle Pliocene (MN 15)	Early Pleistocene (QM 01)
Slovakia	Middle Pliocene (MN 15)	Early Pleistocene (QM 01)
Czech Republic	Middle Pliocene (MN 15)	Early Pleistocene (QM 01)
Germany	Middle Pliocene (MN 15)	Middle Pleistocene
Romania	Middle Pliocene (MN 15)	Middle Pleistocene
Spain	Late Pliocene (MN 16)	Early Pleistocene (QM 01)
Italy	Late Pliocene (MN 16)	Middle Pleistocene
the Netherlands	Early Pleistocene (MN 17)	Early Pleistocene (MN 17)
Bulgaria	Early Pleistocene (MN 17)	Early Pleistocene (MN 17)
England	Early Pleistocene (MN 17)	Middle Pleistocene
France	Early Pleistocene (MN 17)	Middle Pleistocene
Croatia	Early Pleistocene (QM 01)	Early Pleistocene (QM 01)
Georgia	Early Pleistocene (QM 01)	Early Pleistocene (QM 01)
Ukraine	Early Pleistocene (QM 01)	Middle Pleistocene
Russia	Early Pleistocene (QM 01)	Middle Pleistocene

Fig. 28. First (FAD) and last (LAD) appearance data of the genus *Beremendia* in the European countries

walska 1976, 2013; Reumer 1984; Fejfar 1964; Dahlmann & Storch 1996) by this time. According to Rzebik-Kowalska (2013) it is likely that for some reason *B. minor* is rarely found in fossil materials because it is similar to some other more frequent taxa e.g. *Paenelimnoecus* or *Neomys*.

According to our data, *B. minor* is present in the Early Pleistocene of Hungary; therefore, the stratigraphical range of this species could have been extended (with ca. further 2 million years) (Fig. 26).

Palaeoecology

Today *B. fissidens* is said in the references to had been venomous. This hypothesis is induced by its specially adapted, first lower incisor on which there is a well-marked "venom groove" running along the medial side of its crown (Fig. 16).

Furió *et al.* (2010) analyzed the anatomical characters of *Beremendia*. Examining its dental characters, they do reassess the venomous nature of the

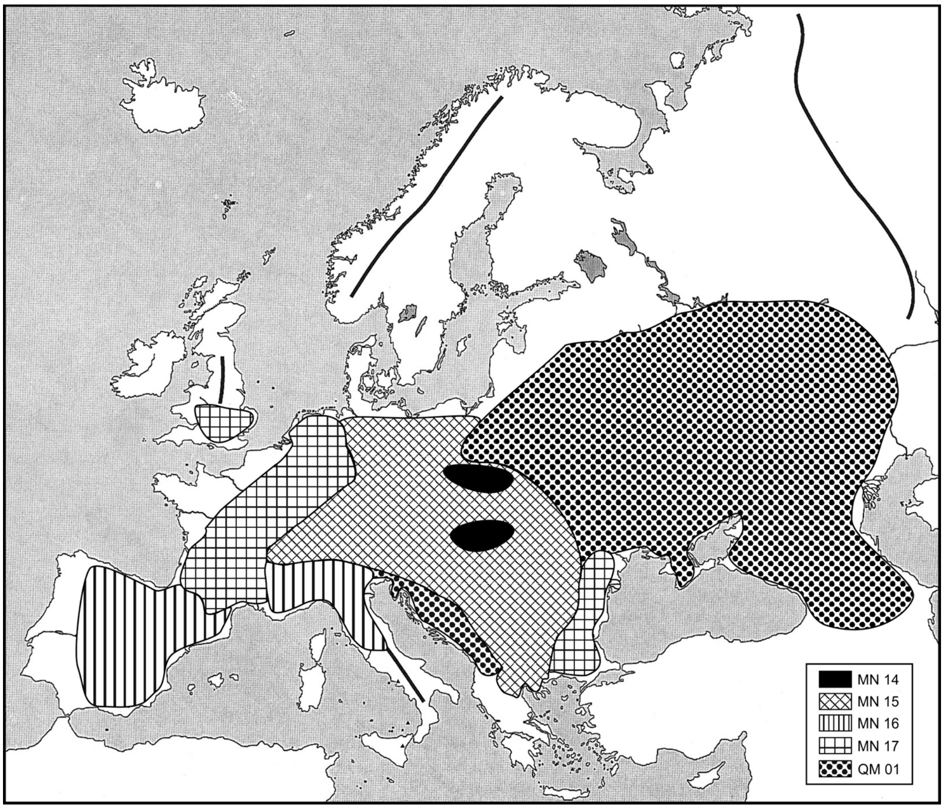


Fig. 29. Occurrence of the genus *Beremendia* in Europe on the basis of the FADs. The marked areas show the maximal distribution of the genus in the given time interval

species included in this genus and they deduce that the diet of *Beremendia* was highly specialized in coleopterans and gastropods. According to them, the use of venom in shrews feeding on non-struggling prey can be reliably explained as a mechanism to subdue the prey without killing them before the real time of consumption. The induction of victims into a comatose-state permits their hoarding for a longer time in a better state of preservation than if they were dead, thus diminishing the risk of starvation (LIGABUE-BRAUN *et al.* 2012). Such strategy provides important benefits to their users under unpredictable conditions, because the effects of environmental unpredictability are consequently reduced.

BENNÁSAR *et al.* (2014) have found taphonomical evidences that *B. fissidens* may have had the capacity to bite prey larger than itself (small mammals, e.g. moles). The addition of small vertebrates to complement a diet based on insects and snails could have been a way of responding to the needs of the high metabolic rate characteristic of the giant shrews.

The stratigraphic range of the genus *Beremendia* in Europe

	PLIOCENE			PLEISTOCENE			REFERENCES
	MN 14	MN 15	MN 16	MN 17	Early	Middle	AUTHORS (publication year)
Romania:							**RZEBIK-KOWALSKA (2005b)**
Dranič-0		X					RZEBIK-KOWALSKA (2002)
Podari 2			X				RZEBIK-KOWALSKA (2002)
Slatina 2				X			RADULESCU & SAMSON (2001)
Izvoru 2					X		RZEBIK-KOWALSKA (2002)
Braşov					X		RADULESCU & KISGYÖRGY (1970)
Ursilor Cave (Chiscau)					X	X	TERZEA (1983)
Betfia 2,5,7,9,10,11,13					X	X	TERZEA (1973), RZEBIK-KOWALSKA (2000)
Gesprengberg Cave						X	TERZEA (1983)
Greece:							**DOUKAS (2005)**
Ptolemais lignite mines		X					VAN DE WEERD (1979)
Tourkobounia 1			X				REUMER & DOUKAS (1985)
Voulgarakis					X		KOUFOS (2001)
Marathoussa					X		KOUFOS (2001)
Switzerland:							**ENGESSER (2005)**
Vue-des-Alpes		X					BOLLIGER *et al.* (1993)
Slovakia:							**FEJFAR & SABOL (2005)**
Ivanovce		X					FEJFAR & SABOL (2004)
Hosťovce 2		X	X				CERMAK *et al.* (2007, 2008)
Hajnačka			X				FEJFAR (1964), FEJFAR & SABOL (2004)
Plešivec 1			X				FEJFAR & HORACEK (1983)
Kolíňany 1,2,3					X		HORACEK & LOZEK (1988)
Včelare 3,4,5,6					X		HORACEK (1985)
Gombasek 1,2					X		KRETZOI (1941)
the Netherlands:							**REUMER (2005)**
Brielle 1				X			VAN DER MEULEN & ZAGWIJN (1974)
Oosterschelde				X			REUMER *et al.* (2005)
Tegelen				X			FREUDENTHAL *et al.* (1976), REUMER (1984)
Zuurland				X			REUMER & HORDIJK (1999)
Bulgaria:							**RZEBIK-KOWALSKA & POPOV (2005)**
Varshets				X			POPOV (2003)

Fig. 30a. Summary about the stratigraphical range of the genus *Beremendia* in Europe. References contain the most important publications about the localities (Romania, Greece, Switzerland, Slovakia, the Netherlands and Bulgaria)

B. fissidens is reported from ecotypes nearby open water bodies (lakes or rivers) by several authors (e.g. Cuenca-Bescós *et al.* 2005; Furió *et al.* 2010; Agustí *et al.* 2011; Garcia *et al.* 2014). Its adaptation to watersides is supported

The stratigraphic range of the genus *Beremendia* in Europe							
	PLIOCENE			**PLEISTOCENE**			**REFERENCES**
	MN 14	**MN 15**	**MN 16**	**MN 17**	**Early**	**Middle**	**AUTHORS (publication year)**
Poland:							**RZEBIK-KOWALSKA (2005a)**
Podlesice	X						KOWALSKI (1990), RZEBIK-KOWALSKA (1994, 2005a)
Zalesiaki 1A,1B	X				X	X	RZEBIK-KOWALSKA (1976, 1994)
Zamkowa Dolna Cave A,B,C	X			X	X		RZEBIK-KOWALSKA (1976, 1994, 2009), KOWALSKI (1990), STEFANIAK *et al.* (2009)
Węże 1,2		X	X				SULIMSKI (1959, 1962), RZEBIK-KOWALSKA (1994)
Rębielice Królewskie 1A,2			X			X	RZEBIK-KOWALSKA (1976, 1994)
Przymilowice 1B,2B,3A,3B				X	X		RZEBIK-KOWALSKA (1994, 2005a, 2009)
Kadzielnia 1				X	X		KOWALSKI (1958), RZEBIK-KOWALSKA (1976, 1994)
Kielniki 3A, 3B				X	X		KOWALSKI (1990), RZEBIK-KOWALSKA (1976, 1994, 2005a, 2009)
Kamyk					X		KOWALSKI (1960)
Żabia Cave A,B					X		BOSÁK *et al.* (1982), RZEBIK-KOWALSKA (1994, 2009, 2013)
Kozi Grzbiet 2						X	RZEBIK-KOWALSKA (1976), STEFANIAK *et al.* (2009)
Spain:							**VAN DEN HOEK OSTENDE & FURIO (2005)**
Barranco del Monte 1			X				LAPLANA CONESA *et al.* (2004)
Moreda 1			X				RUIZ-BUSTOS & SESÉ (1985)
Orrios 3			X				ADROVER (1986)
Valdeganga 2			X				MEIN *et al.* (1978)
Almenara-Casablanca 1				X			AGUSTI *et al.* (2011)
Sima del Elefante					X		ROFES & CUENCA-BESCOS (2009), CUENCA-BESCOS *et al.* (2010, 2013)
Gran Dolina (Atapuerca)					X		ANTONANZAS & CUENCA-BESCOS (2002)
Austria:							**ZIEGLER & DAXNER-HÖCK (2005)**
Deutsch-Altenburg 2A,2C,4B,9,14,20,21,26,30A		X					FRANK & RABEDER (1997)
Stranzendorf		X	X				FRANK & RABEDER (1997)
Germany:							**ZIEGLER *et al.* (2005)**
Gundersheim-Findling		X					HELLER (1936), DAHLMANN & STORCH (1996), DAHLMANN (2001)
Wölfersheim		X					TOBIEN (1977), DAHLMANN (2001)
Sondershausen		X					HELLMUND & ZIEGLER (2012)
Hambach 11			X				MÖRS *et al.* (1998)
Gundersheim fissure fillings			X	X	X		HELLER (1936), DAHLMANN & STORCH (1996)
Neuleiningen 11				X			MAUL (1996)
Deinsdorf				X			HELLER (1963)
Schernfeld					X		DEHM (1962), CARLS & RABEDER (1988)
Weißenburg 7					X		KOENIGSWALD (1971)
Sackdillinger Cave					X		HELLER (1930, 1956)
Hohensülzen					X	X	TOBIEN (1980)
Georgia:							
Dmanisi					X		FURIO *et al.* (2010)
England:							
East Runton (Norfolk)				X	X		STUART (1980), HARRISON *et al.* (2006), HARRISON & PARFITT (2009)
Sugworth						X	STUART (1980)
Italy:							
Cascina Arondelli (Piedmont)			X				KOTSAKIS *et al.* (2003)
Rivoli Veronese				X			FANFANI & MASINI (1997)
Monte La Mesa (Verona)					X		MARCHETTI *et al.* (2000)
Soave Cava Sud (Verona)					X	X	MARCOLINI *et al.* (2013)
Monte Peglia						X	MAUL *et al.* (1998)

Fig. 30b. Summary about the stratigraphical range of the genus *Beremendia* in Europe. References contain the most important publications about the localities (Poland, Spain, Austria, Germany, Georgia, England and Italy)

here by simultaneous occurrence with water-preferring amphibians and reptiles in the Somssich Hill 2 assemblage (Szentesi 2013, 2014*a*, *b*). On the other hand, the rodent fauna (e.g. the abundance of the dormice) of the studied site indicates the presence of closed vegetation.

The layer-by-layer occurrences of the two studied *Beremendia* species in the Somssich Hill 2 section do not show significant differences between the preferences of the two forms (Table 3). That is why both of them can be considered here as the indicators of gallery forests or bushy vegetation on the side of a lake or a river.

The stratigraphic range of the genus *Beremendia* in Europe

	PLIOCENE			PLEISTOCENE			REFERENCES
	MN 14	MN 15	MN 16	MN 17	Early	Middle	AUTHORS (publication year)
Czech Republic:							**FEJFAR & SABOL (2005)**
Měňany 3		X	X				CERMAK *et al.* (2007, 2008)
Vitošov		X	X				CERMAK *et al.* (2007, 2008)
Ctiněves 1				X			FEJFAR & HORACEK (1983)
Mokra 1					X		FEJFAR & HORACEK (1983)
Chlum 6					X		FEJFAR & HORACEK (1983)
Holštejn					X		MUSIL (1966), FEJFAR & HORACEK (1983)
Stránská skála					X		RZEBIK-KOWALSKA (1972)
Hungary:							
Osztramos 1,2,3,4,7,8,14	X		X	X	X	X	JÁNOSSY (1973, 1978), JÁNOSSY & KORDOS (1977), REUMER (1984), JÁNOSSY (1986)
Csarnóta 1,2,4		X		X			KRETZOI (1956, 1959), REUMER (1984)
Beremend 1,2,3,4,5,8,9,11,15			X	X	X		PETÉNYI (1864), KRETZOI (1956), JÁNOSSY (1986), PAZONYI (2006)
Villány 1,2,3,5,6,7,8,11				X	X	X	KORMOS (1934), KRETZOI (1956), REUMER (1984), JÁNOSSY (1986), PAZONYI (2006)
Dunaalmás 4				X	X		JÁNOSSY (1986)
Nagyharsányhegy 2,3,4,5				X	X		KRETZOI (1956), JÁNOSSY (1986)
Újlak Hill					X		JÁNOSSY (1986)
Süttő 19					X		PAZONYI *et al.* (2014)
Somssich Hill 1,2					**X**		**JÁNOSSY (1983, 1986, 1999), HÍR (1998), MÉSZÁROS *et al.* (2013), PAZONYI *et al.* (2013a, b), PAZONYI & VIRÁG (2013a, b), SZENTESI (2013, 2014a, b), BOTKA & STRICZKY (2014), BOTKA & MÉSZÁROS (2014a, b)**
Tarkő						X	JÁNOSSY (1986)
Ukraine:							
Chortkov					X		PIDOPLICKO (1956)
Gorishnya Vygnanka					X	X	MAUL (1990)
France:							
Saint-Vallier				X			SUAREZ & MEIN (2004)
Courterolles					X		BROCHET *et al.* (1983)
Valerots (Cote d'Or)					X		CHALINE *et al.* (1985)
Mas Rambault 2					X		AGUILAR *et al.* (2002)
Saint-Sauveur						X	CROCHET & MICHAUX (1981)
Slovenia:							
Črnotiče 2		X	X				HORACEK *et al.* (2007)
Račiška Pečina				X			HORACEK *et al.* (2007)
Croatia:							
Razvode					X		PAUNOVIC & JAMBRESIC (1997)
Tatinja draga					X		PAUNOVIC & JAMBRESIC (1997)
Podumci 1					X		MAUL (1990), PAUNOVIC & JAMBRESIC (1997)
Russia:							
Uryv-Pokrovka					X	X	AGADZHANYAN (2009)

Fig. 30c. Summary about the stratigraphical range of the genus *Beremendia* in Europe. References contain the most important publications about the localities (Czech Republic, Hungary, Ukraine, France, Slovenia, Croatia and Russia)

It should be noted that Botka & Mészáros (in press) gave a figure on the MNI of *B. fissidens* teeth by layers from Somssich Hill 2 site. These data were completed with some specimens, yielded by the present studies. Otherwise some teeth should have been re-determined as *B. minor*. That is why the data of Table 3 are somewhat different from Figure 4 of Botka & Mészáros (in press).

Table 3. Occurrences of *Beremendia* species in the layers of the Somssich Hill 2 locality, with the minimum number of individuals (MNI)

Layers	MNI of *B. fissidens*	MNI of *B. minor*	Layers	MNI of *B. fissidens*	MNI of *B. minor*
1	–	–	26	1	–
2	–	1	27	3	–
3	1	–	28	3	–
4	1	1	29	–	–
5	5	2	30	3	–
6	1	1	31	2	–
7	1	–	32	3	–
8	1	–	33	1	–
9	1	–	34	1	–
10	–	–	35	1	1
11	2	–	36	1	–
12	2	–	37	1	–
13	3	1	38	2	–
14	2	1	39	1	–
15	4	–	40	1	–
16	–	–	41	1	–
17	–	–	42	1	–
18	1	–	43	1	–
19	–	–	44	1	–
20	1	–	45	1	–
21	–	–	46	1	–
22	–	–	47	1	–
23	–	–	48	–	–
24	1	–	49	–	–
25	2	–	50	1	–
				61	8

Palaeobiogeography

Genus *Beremendia* was an opportunistic element in the Plio-Pleistocene faunas of Eurasia. Due to the successful strategy it became very frequent in the Early Pleistocene. The genus contains four valid species (*B. fissidens, B. minor, B. pohaiensis* (Kowalski et Li) and *B. jiangnanensis*). *B. fissidens* (Early Pliocene–Middle Pleistocene) and *B. minor* (Early Pliocene–Early Pleistocene) represented the genus in Europe, while the other two species, namely *B. pohaiensis* (Middle Pliocene–Early Pleistocene) and *B. jiangnanensis* (Early Pleistocene) were widespread in Asia (Fig. 27).

Beremendia remains are known from more than 150 localities of 20 countries from Europe. The genus had a wide distribution from the Iberian Peninsula to the Urals and from the British Isles to Central Italy and Greece (Figs 30a-c).

The first appearance of the genus was probably in Central Europe (MN14 of Poland and Hungary). The spreading of the genus started from here in the Middle Pliocene (MN15). During the Late Pliocene (MN16) the genus expanded to a south–southwest direction (Spain, Italy and certainly Southern France but in the latter area there are no evidences for the genus yet, only from MN17). In the earliest Pleistocene (MN17) we can see a northern transgression of *Beremendia* shrews to the Netherlands and Southern England. The genus reached its maximal distribution in the Early Pleistocene. From this period some localities are known in Ukraine and Russia, too (Figs 28, 30a-c).

In the Middle Pleistocene of Europe *B. fissidens* was the last representative of the genus and this species became extinct until the middle part of the Middle Pleistocene. The youngest occurrences of the genus are in Poland (Kozi Grzbiet 2 – 700 ka, Stefaniak *et al.* 2009) and in Hungary (Tarkő – 350 ka, Jánossy 1986) as well (Figs 27–30a-c).

*

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