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Late Pliocene Soricidae (Insectivora, Mammalia) from Varshets (North Bulgaria)

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Abstract. The rich and well-preserved bone material of six shrew species extracted from the filling of a karstic cavity near the town of Varshets (Prebalkan region, North Bulgaria) is described. The samples of *Beremendia fissidens*, *Asoriculus gibberodon*, *Sorex* cf. *minutus* and *S. runtonensis* represent relatively large forms of these species, while *Petenyia hungarica* does not grately differ from the other European populations. The Varshets record of *S. runtonensis* extends the stratigraphical range of the species into the Late Pliocene. The skull fragments determined as *Mafia* aff. *csarnotensis* show that this species has four upper antemolars; this number has not so far been known and the studied material contributes to the characteristic of this poorly known genus. The position of the Varshets assemblage within the context of the temporal and spatial variation of the species composition and structure of 23 Pliocene and Early Pleistocene shrew associations from Europe is assessed by correspondence analysis. The results point to a mosaic environment under a relatively warm and dry climate. On the basis of this analysis the ecological interpretation of *Asoriculus gibberodon* as a strict dweller in wet forests is questioned. The comparisons indicate that it tends to occur in shrew associations related to mosaic landscapes dominated by shrubby and open habitat patches.

Key words: fossil small mammals, Insectivora, Soricidae, Late Pliocene, morphology, morphometry, systematics, paleoecology.

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I. INTRODUCTION

The present paper is the second part of a series of studies on the extremely rich small mammal fauna from the karst fissure filling near the city of Varshets, western pre-Balkan region of North Bulgaria. The previous paper (POPOV 2001), dealing with members of the family Arvicolidae provides a description of the locality, a preliminary faunal list of small mammals, and a discussion on the age and of paleoenvironment. The arvicolid assemblage indicates a Late Pliocene age, in the middle of MN17. Here the author describes the remains of six soricid species. The presented material increases the knowledge on the morphological variability, taxonomy, and zoogeography of this group, poorly studied in this part of the continent. The scarce available Pliocene and Early Pleistocene data come predominantly from the Mediterranean part of the Balkan Peninsula (BRUIJN et al. 1970; WEERD et al., 1982; MALEZ & RABEDER 1984; REUMER & DOUKAS 1985; KOUFOS 2001).

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II. MATERIAL AND METHODS

The described specimens are housed in the collection of the Institute of Zoology, Bulgarian Academy of Sciences. The terminology and the majority of measurements employed here follow REUMER (1984) and RZEBIK-KOWALSKA (1976, 1988). The degree of posterior emargination of the large upper teeth was quantified by means of the PE-index (PEI), proposed by REUMER (1984).

The use of "cf." indicates that the form is " perhaps identical, but diagnostic elements missing", while "aff." signifies "close to, but different" (MATTHEWS 1973; LUCAS 1986).

In taxonomic drawings scale bars represent 1 mm. The measurements, presented in millimeters, were taken using a stereo-microscope fitted with micrometric lenses. In tables the following descriptive statistics are shown: sample size (N); minimal and maximum observed values (Min – Max); mean; standard deviation (SD).

The method of multidimensional scaling (MDS) is used to present in the most parsimonious fashion the correspondences and differences between the morphometric data in the literature and material from Varshets (Tables 1- 3, 5-6). The analysis follows the procedure described below. For each measurement (i) all possible differences (d_i) between means or rarely individual values (X_{ij} and X_{ik}) of two samples (j and k) have been calculated:

$$d_i = \frac{X_{ij} - X_{ik}}{X_{ij}} \cdot 100.$$

Subsequently, an overall pairwise distance (OD) was calculated as a mean of distances based on the individual dimensions (P):

$$OD = \frac{\sum_{i=1}^{P} d_i}{P}.$$

The signs of the obtained overall distances were ignored, i. e. they were considered positive. Given the low degree of integrity and the state of preservation of the fossils, the number of character distances used for calculations of the overall distances was changeable, ranging from 10 to 32. Four generic matrices containing the overall distances between pairs of samples in all possible combinations were constructed. The distance ranges within the matrices were as follows: *Sorex* – 0.1-30.2; *Petenyia* – 0.7-21.2; *Asoriculus* – 0.4-14.3; *Beremendia* – 0.2-12.6. The obtained dissimilarity matrices were analyzed by multidimensional scaling (STATISTICA for Windows, StatSoft, Inc. 1993) to achieve a two-dimensional final arrangement of samples, depicting their morphometric relationships. As usual in mammalian paleontology, the analyzed measurements were designed to describe each particular tooth, bone or bone fragment, in order to be compared and/or identified when find isolated. This lead to the situation that many of the measurements are correlated with the overall size. thus, the obtained results primarily reveal the size relationships among compared forms, and some of the two-dimensional MDS plots show a well pronounced arch effect. Regardless of these drawbacks, the analysis permits summarization in a repeatable way the "instinct" of an investigator when he compares samples of fragmentary fossil material on the basis of measurements available.

To arrange the Varshets shrew assemblage within the context of the spatial and temporal variation of species composition and structure of the Pliocene and Early Pleistocene shrew assemblages in Europe, a detrended correspondence analysis (DCA) is carried out by the CANOCO program, using the options "log transformation", "downweighting rare species", and "detrending by a second order of polynomial"(BRAAK 1987, 1990). The obtained ordination plots allow one to infer the effect of paleoenvironmental gradients (ordination axes) on the assemblage composition and structure, and to show the position of the species optima along these gradients. The diversity of shrew assemblages was evaluated by means of HILL's (1973) heterogeneity measure (N2). The same index was used to assess the species' spatio-temporal niche breadth. In this case it is known as Levin's measure of niche breadth and represents the eveness and range of distribution (BRAAK 1990).

III. SYSTEMATICS

Family Soricidae GRAY, 1821

Tribe Soricini FISHER VON WALDHEIM, 1817

Genus *Sorex* LINNAEUS, 1758

Sorex cf. *minutus* LINNAEUS, 1766

(Fig. 1)

Material. 39 mandibles and fragments of mandibles and 1 fragment of maxilla with A^5, P^4, M^1, and M^2 .

Measurements: see Table I.

Description. Upper dentition. The pigmentation is poor, pink.

A^5 is relatively large.

P^4: the parastylar crest is very low; the posterior emargination is moderate; a well-pronounced cingulum bordering the buccal half of the posterior emargination; without a well-individualized hypocone; with a wide valley between the anterior edge of the posterolingual ridge and the protocone; the protocone is connected with the base of the parastyle by a low ridge; with a small cingulum in front of the parastyle.

M^1-M^2: without metalophs; the posterior emargination is moderate (see PE-index in Table I) with a cingulum on the buccal half; the hypocone is poorly developed on the anterior edge of the relatively short ridge, surrounding the hypoconal flange; with a wide valley between proto- and hypocone.

Mandible. With a relatively long coronoid spicule – but this structure is not well individualized; in some specimens it is connected with a vertical ridge in the upper half of the posterior part of the external temporal fossa; the internal temporal fossa is high, reaching the tip of the coronoid process; sometimes, in the upper half of this fossa, there are traces of a horizontal bar; the mental foramen is situated under the anterior half of M_1.

Lower dentition. The teeth are poorly pigmented in pink; the most intense pigmentation occurs on the tip of I_1.

I_1 is tricuspidate; buccally, the tooth ends below the middle part of P_4; the buccal cingulum absent or poorly presented on the dorsal half of the posterior edge.

A_1 is relatively long buccally; about one third of its length is hidden underneath P_4; two-cusped, but the posterior cusplet is very low.

P_4 is two cusped with well-developed postero-lingual basin.

M_1-M_2: with mesoconids, well-visible on non-worn specimens; the entoconid crests are very high; both the buccal and lingual cingula are well pronounced, but the buccal one is narrow and sometimes undulate.

M_3: the talonid is not reduced – the tooth has five cusps; the talonid basin is well-developed.

Discussion. The MDS results (Fig. 2) show that the compared samples of the genus separate into two basic clusters along the first dimension. The small forms are located on the left-hand portion of the plot, while the larger ones occupy the right side. The second dimension depicts some smaller-scale size differences within each group. The position of the sample of the smaller *Sorex* species from Varshets on the MDS plane (Fig. 2) indicates that it represents a relatively large

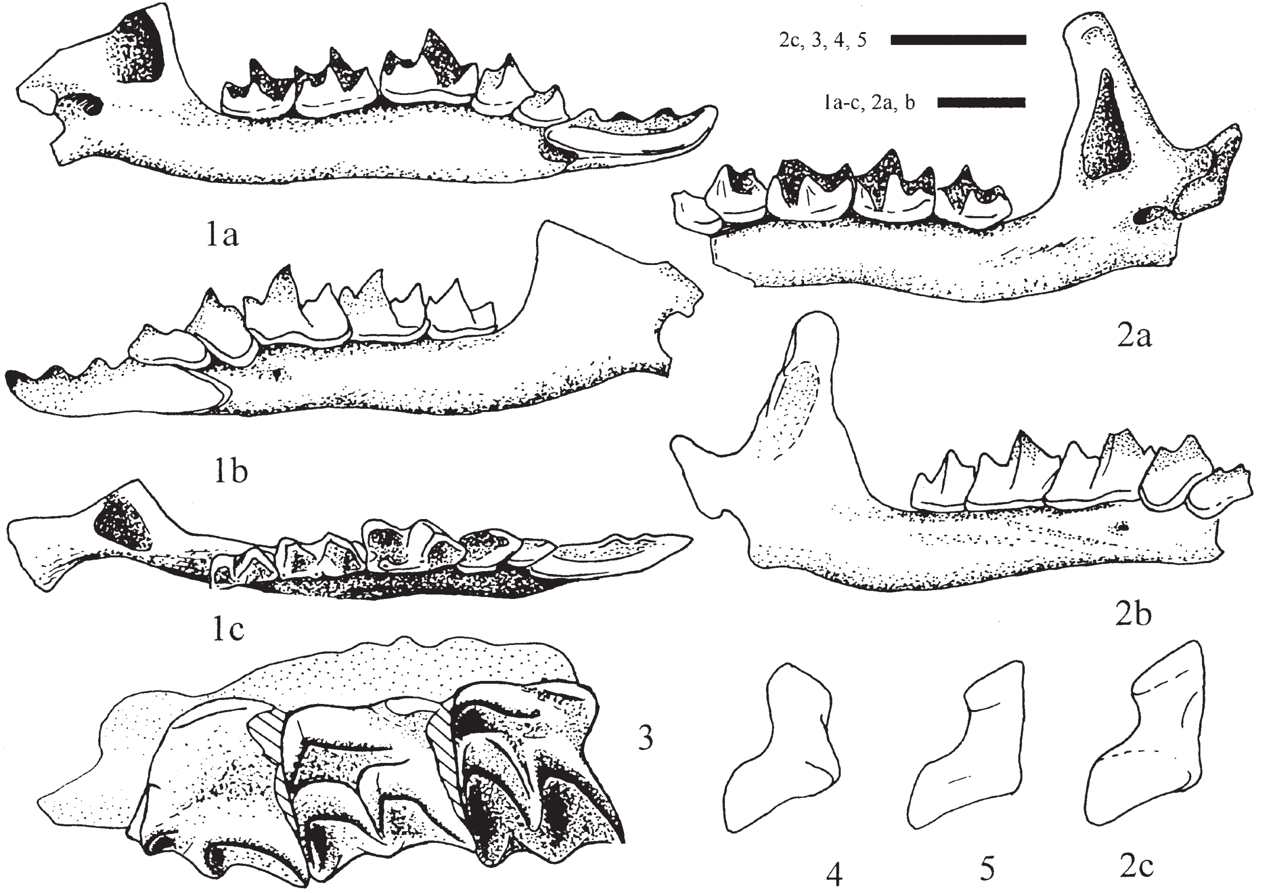

Fig. 1. *Sorex* cf. *minutus*. 1. left mandible, a. lingual view, b. labial view, c. occlusal view (Coll. No: V17-2). 2. fragment of right mandible with A_1-M_3 (Coll. No: V17-1), a – lingual view, b – labial view; 3. occlusal view of a fragment of right maxilla with P^4-M^2 (Coll. No: V98); 2c, 4, 5. condyloid processes in posterior view (Coll. No: V17-3, 4).

Table I

Measurements of *Sorex* cf. *minutus* from Varshets

Measurements	Abbreviations	N	Min	Mean	Max	SD
Length of mandible (cf. REUMER 1984)	LMd	15	3.70	4.11	4.40	0.168
Length of mandible with I_1	LMd+I_1	–	–	–	–	–
Height of processus coronoideus	HPC	23	3.07	3.19	3.32	0.067
H. of horizontal ramus under M_2	HMd/ M_2	46	0.75	0.91	1.10	0.071
Height of condyloid process	HC	23	1.07	1.28	1.32	0.118
Length of lower facet of condyle	LLF	28	0.82	0.95	1.25	0.085
Length of upper facet of condyle	LUF	24	0.50	0.59	0.75	0.057
Length of I_1-M_3	LI_1-M_3	2	5.50	–	5.92	–
Length of A_1-M_3	LA_1-M_3	10	4.10	4.25	4.50	0.128
Length of M_1-M_3	LM_1-M_3	24	3.02	3.16	3.32	0.084
Length of I_1	LI_1	3	2.62	2.69	2.75	–
Height I_1	HI_1	4	0.67	0.68	0.70	–
Buccal length of A_1	BLA_1	9	0.65	0.80	0.87	0.086
Width of A_1	W A_1	9	0.37	0.48	0.57	0.058
Buccal length of P_4	BLP_4	16	0.80	0.88	1.00	0.060
Width of P_4	WP_4	16	0.45	0.55	0.62	0.042
Lengtn of M_1	LM_1	28	1.20	1.34	1.45	0.052
Talonid width of M_1	TAWM_1	30	0.62	0.71	0.85	0.045
Trigonid width of M_1	TRW M_1	29	0.52	0..64	0.75	0.050
Lengtn of M_2	L M_2	39	1.10	1.18	1.35	0.058
Talonid width of M_2	TAW M_2	41	0.57	0.68	0.80	0.049
Trigonid width of M_2	TRW M_2	40	0.52	0.63	0.75	0.038
Length of M_3	L M_3	26	0.87	0.93	1.07	0.048
Width of M_3	WM_3	25	0.50	0.56	0.66	0.029
Palatine length	PALL	2	5.90	6.00	6.10	–
Width of interorbital constriction	Io	2	5.90	–	6.10	–
Length of A^1-A^5	LA^1-A^5	1	–	2.07	–	–
Length of P^4-M^3	LP^4-M^3	4	3.70	3.72	3.77	0.033
Length of M^1-M^3	LM^1-M^3	3	2.65	2.69	2.77	0.069
Buccal length of P^4	BLP^4	10	1.22	1.32	1.40	0.067
Length to posterior emargination of P^4	PE P^4	8	0.70	0.83	0.97	0.103
Lingual length of P^4	LL P^4	10	0.82	0.98	1.10	0.124
Width of P^4	W P^4	10	1.17	1.27	1.37	0.071
Buccal length of M^1	BLM^1	9	1.20	1.25	1.27	0.029
Length to posterior emargination of M^1	PE M^1	7	0.95	1.03	1.10	0.055
Lingual length of M^1	LL M^1	9	1.10	1.19	1.32	0.086
Anterior width of M^1	AW M^1	9	1.20	1.26	1.37	0.071
Posterior width of M^1	PW M^1	9	1.20	1.37	1.52	0.105
PE-index of M^1	M^1 (PEI)	7	0.08	0.17	0.22	0.064
Buccal length of M^2	BLM^2	6	1.07	1.15	1.20	0.052
Length to posterior emargination of M^2	PE M^2	9	0.85	0.93	0.95	0.035
Lingual length of M^2	LL M^2	9	0.95	1.08	1.15	0.066
Anterior width of M^2	AW M^2	9	1.15	1.31	1.52	0.157
Posterior width of M^2	PW M^2	6	1.20	1.27	1.37	0.077
PE-index of M^2	M^2 (PEI)	6	0.17	0.20	0.024	0.031
Length of M^3	LM^3	4	0.65	0.67	0.70	0.026
Width of M^3	W M^3	2	1.01	–	1.02	–

form, similar to *S. minutus* from Tegelen and *S. bor* from Osztramos 9 and 1, being definitively larger than the small form of *S. minutus* from Osztramos 7 (REUMER 1984). The form from Varshets, according to the height of the coronoid process, also approaches *S. fejfari* HORÁČEK & LOŽEK 1988. However, neither the diagnosis of *S. fejfari* and comparisons reveal unambiguous characters allowing discrimination between *S. minutus* and *S. fejfari*. According to RZEBIK-KOWALSKA (1991) most probably the typical material of *S. fejfari* belongs to *Sorex bor* REUMER, 1984. The last mentioned species approaches in size *S. minutus*, when they were allopatric or allochronic, but *S. minutus* is clearly smaller when the two species occurred together (REUMER, 1984; HORÁČEK & LOŽEK 1988; RZEBIK-KOWALSKA 1991), (see also Fig. 2). Besides size, these two species differ in some qualitative characters – *S. bor* shows a simple upper incisive (fissident in *S. minutus*) and lacks a vertical bar at the distal margin of external temporal fossa (present in *S. minutus*). Despite the absence of I^1 the present material has tentatively been referred to *S. minutus* on the basis of the occurrence of a vertical bar in the external temporal fossa, clearly visible in some specimens (Fig. 1: 2b).

Sorex runtonensis HINTON, 1911

(Fig. 3)

Material: 22 mandibles and fragments of mandibles.

Measurements: see Table II.

Table II

Measurements of *Sorex runtonensis* from Varshets. For explanation of abbreviations see Table I

Measurement	N	Min	Mean	Max	SD
LMd	10	4.50	4.87	5.15	0.189
LscMd (symphisis-condyle)	1	–	8.75	–	–
LMd+I_1	1	–	10.50	–	–
HPC	16	3.75	3.98	4.22	0.150
HMd/ M_2	24	1.05	1.16	1.32	0.071
HC	16	1.19	1.56	1.75	0.145
LLF	18	1.07	1.15	1.27	0.050
LUF	16	0.60	0.74	0.90	0.077
LI_1-M_3	2	6.85	–	7.25	–
LA_1-M_3	3	4.80	4.93	5.10	-
LM_1-M_3	18	3.40	3.54	3.77	0.086
LI_1	1	–	3.32	–	–
HI_1	3	0.90	0.96	1.02	–
BLA_1	5	0.91	1.01	1.07	0.066
W A_1	5	0.60	0.63	0.67	0.034
BLP_4	13	1.00	1.08	1.15	0.051
WP_4	13	0.51	0.69	0.85	0.080
LM_1	22	1.40	1.52	1.60	0.056
TAWM_1	21	0.80	0.86	0.97	0.055
TRW M_1	21	0.67	0.77	0.90	0.057
L M_2	20	1.21	1.32	1.45	0.060
TAW M_2	21	0.72	0.81	0.92	0.066
TRW M_2	21	0.70	0.75	0.85	0.051
L M_3	14	0.92	1.02	1.15	0.059
WM_3	13	0.60	0.65	0.72	0.035

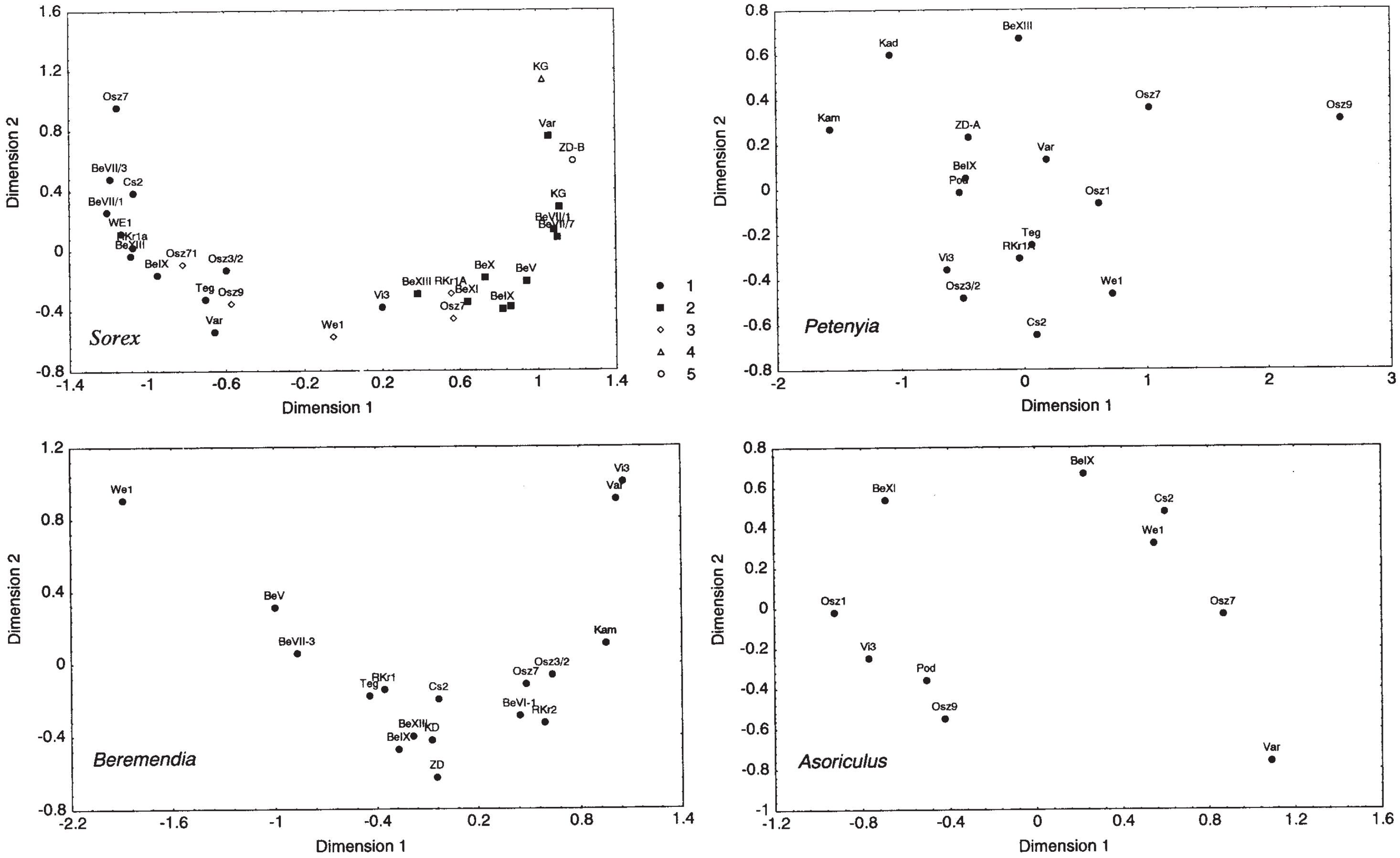

Fig. 2. Results of multidimensional scaling of generic dissimilarity matrices. Be – Betfia, Cs – Csarnota, Kad – Kadzielnia, Kam – Kamyk, KG – Kozi Grzbiet, Osz – Osztramos, Pod – Podlesice, RKr – Rębielice Królewskie, Teg – Tegelen, Var – Varshets, Vi – Villany, We – Węże, ZD – Zamkowa Dolana. 1. – *S. minutus*, 2. *S. runtonensis*, 3. *S. bor*, 4. *S. subaraneus*, 5. *S. casimiri*.

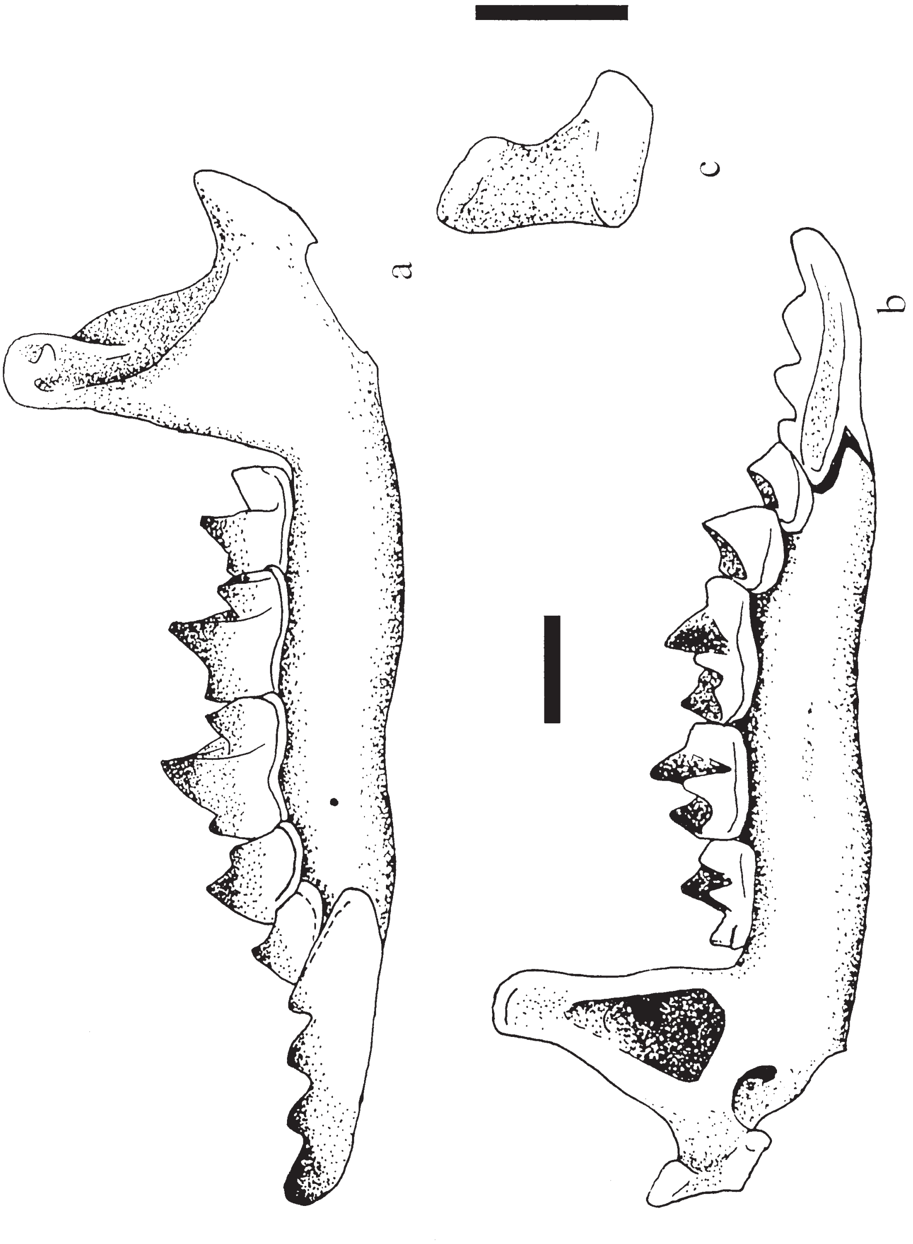

Fig. 3. *Sorex runtonensis*. Left mandible (Coll. No: V96), a – labial view, b – lingual view; c. – condyloid process in posterior view.

Description. Mandible. The horizontal ramus is relatively robust, its lower margin concave under M_1; the mental foramen is most often situated below the posterior part of P_4, sometimes between P_4 and M_1, rarely below the anterior part of M_1, but never more posteriorly than the anterior root of M_1; the ascending ramus is high and massive; the tip varies in shape but is more often relatively wide (spatulate) and rounded; the anterior edge of the coronoid process is slightly concave, while the posterior one is convex; the external temporal fossa is shallow, its lower margin reaching slightly below the level of the upper sigmoid notch; the coronoid spicule is small, sometimes indistinct, situated very close to the apex of the process; often this spicule is connected with a vertical ridge running downward to the posterior part of the external temporal fossa; the internal temporal fossa is triangular and relatively high, sometimes there being a slight horizontal bar inside; there are two mandibular foramina, situated in a common depression; the condyle is low with a wide interarticular area, which broadens downward but does not cover the whole width of the lower facet; the upper facet is oblique in relation to the lower one.

Lower dentition. The cusps of the teeth are stained light red.

I_1 shows three well-protruding undulations on the cutting edge; the tip is widely rounded; there is a poorly visible postero-dorsal cingulum.

A_1 is relatively long with a trace of a second peak; the tooth is hidden below the P_4 for a large part; there is a shallow postero-lingual basin.

P_4 has two peaks and a posterolingual basin which does not reach the cingulum.

M_1-M_2 are relatively long, with high entoconid crests; the buccal reentrant valleys open somewhat above the cingulum; the mesoconids are low, detectable only as a “rise” on the oblique crests.

M_3 has five cusps and an unreduced basined talonid.

The lower molars show cingula on both sides, lingually less strong than buccally.

Discussion. The MDS plot (Fig. 2) shows that the Varshets form is somewhat larger than *S. runtonensis* from Kozi Grzbiet, Betfia VII/1 and VII/4 and smaller than *S. subaraneus* from Kozi Grzbiet, being quite close to *S. casimiri* RZEBIK-KOWALSKA, 1991 from Zamkowa Dolna Cave B (RZEBIK-KOWALSKA 1991, 2000). Beside dimensions it differs from *Sorex runtonensis* HINTON, 1911 (= *S. araneoides* HELLER, 1930, = *S. helleri* KRETZOI, 1959,= *S. kennardi* HINTON, 1911), (JÁNOSSY 1965; MEULEN 1973; HARRISON 1996; RZEBIK-KOWALSKA 2000) in having a relatively long A_1 with a trace of a second peak, massive coronoid process, and somewhat more anterior position of the mental foramen. In these respects the form from Varshets is similar to a group of Pliocene species of comparable size, such as *S. casimiri*, *S. pseudoalpinus* RZEBIK-KOWALSKA, 1991, and *S. praealpinus* RZEBIK-KOWALSKA, 1991. The differences are as follows: in relation to *S. praealpinus* – *S. runtonensis* from Varshets has a shorter A_1 with a low and indistinct second cusp, wider interarticular area of the condyle; the posterolingual basin of its P_4 does not reach the cingulum; in relation to *S. pseudoalpinus* and *S. casimiri* – in having a small and sometimes indistinct coronoid spicule, situated much higher in the external temporal fossa. It may be supposed that the above mentioned peculiarities of the form from Varshets represent primitive characters for the European representatives of the genus. This assumption is confirmed by the circumstance that in these features the material from Varshets is similar to the early Pleistocene populations of *S. runtonensis* from Poland (RZEBIK-KOWALSKA 1991). Thus, although somewhat different, the Varshets form is considered to be a primitive form of *S. runtonensis*.

The species is characteristic for the Pleistocene. According to RZEBIK-KOWALSKA (1991, p. 374), the Pliocene records of the species from Poland and Hungary seem doubtful. Thus, the oldest record known so far is that from Deutsch-Altenburg 30A, Austria, a locality containing *Microtus* (*Allophaiomys*) *pliocaenicus* (FRANK and RABEDER 1984). In this context, the discovery of *S. runtonensis* in Varshets extends the range of the species downwards in geological time to the zone MN17. According to HORACEK (HORÁČEK & LOŽEK, 1988), *S. fejfari* from Vcelare 6/I (MN17) may be ancestral to *S. minutus* and *S. runtonensis*. In the light of the data presented here this assumption seems unlikely because these two species already existed during this time interval.

Tribe Blarinellini REUMER, 1998

Genus *Petenyia* KORMOS, 1934

Petenyia hungarica KORMOS, 1934

(Fig. 4)

Material: 36 fragmentary or intact mandibles; 9 maxillary fragments and some isolated teeth.

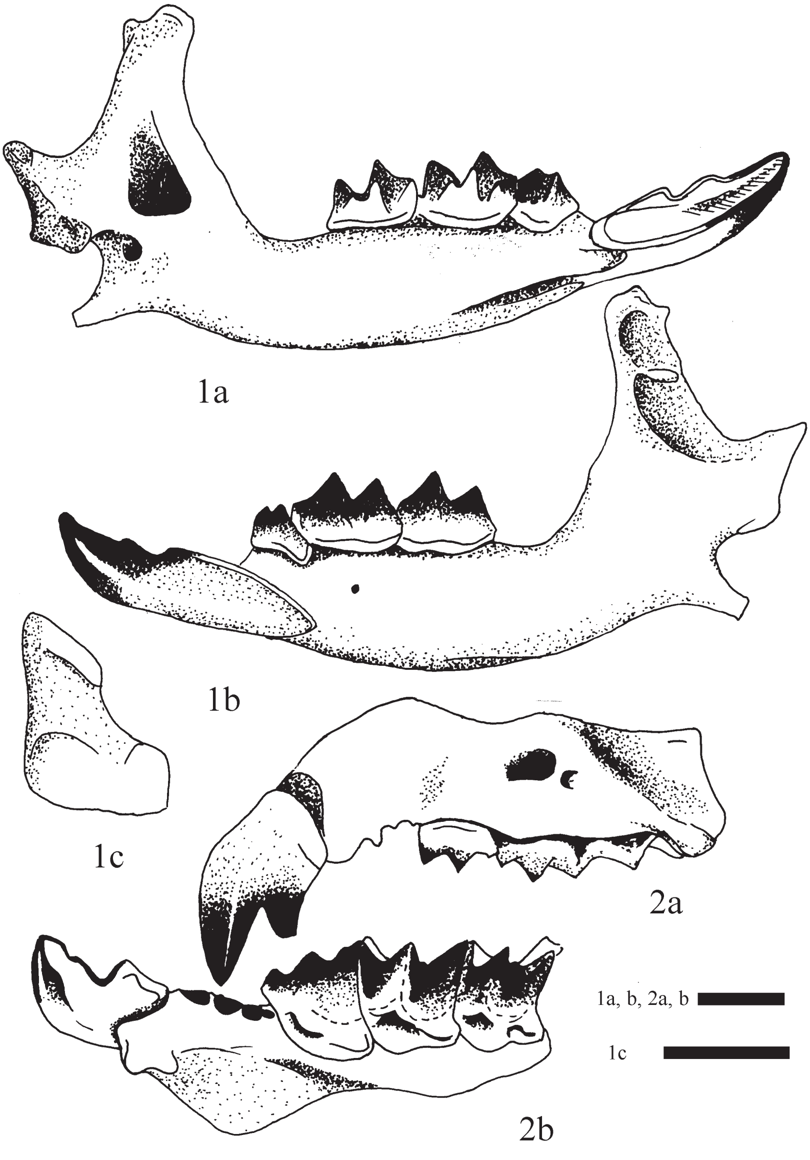

Fig. 4. *Petenyia hungarica*. 1. left mandible (Coll. No: V10), a – lingual view, b – labial view, c – posterior view of condyloid process; 2. left maxillary fragment with I^1, P^4-M^2 (Coll. No: V8), a – labial view, b – occlusal view.

Measurements: see Table III.

Table III

Measurements of *Petenyia hungarica* from Varshets. For explanation of abbreviations see Table I

Measurement	N	Min	Mean	Max	SD
LMd	33	4.07	4.26	4.60	0.109
LscMD	12	10.00	10.12	10.40	0.140
LMd+I1	14	8.10	8.33	8.67	0.198
HPC	39	4.00	4.18	4.37	0.092
HMd/ M$_2$	56	1.32	1.50	1.67	0.067
HC	42	1.52	1.86	2.07	0.113
LLF	41	1.00	1.30	1.40	0.077
LUF	41	0.65	0.93	1.10	0.101
LI$_1$-M$_3$	14	6.30	6.68	6.90	0.155
LA$_1$-M$_3$	12	4.50	4.66	4.80	0.114
LM$_1$-M$_3$	33	3.50	3.64	3.85	0.096
LI$_1$	22	3.00	3.73	4.02	0.222
HI$_1$	24	0.87	0.96	1.05	0.037
BLA$_1$	15	0.57	0.77	0.90	0.081
W A$_1$	15	0.55	0.63	0.75	0.050
BLP$_4$	28	0.95	1.07	1.17	0.067
WP$_4$	28	0.67	0.79	0.95	0.060
LM$_1$	53	1.35	1.49	1.65	0.066
TAWM$_1$	53	0.82	0.92	1.07	0.062
TRW M$_1$	52	0.72	0.83	1.00	0.052
L M$_2$	49	1.27	1.35	1.55	0.057
TAW M$_2$	49	0.75	0.86	1.00	0.055
TRW M$_2$	50	0.70	0.83	0.95	0.058
L M$_3$	36	1.00	1.08	1.17	0.039
WM$_3$	36	0.55	0.70	0.90	0.084
LI^1-A^4	1	3.07	3.07	3.07	–
LI^1	2	2.50	2.55	2.60	0.070
HI^1	3	1.35	1.41	1.55	0.115
BLP^4	8	1.45	1.48	1.52	0.026
PE P^4	8	1.12	1.23	1.40	0.093
LL P^4	8	1.10	1.21	1.40	0.109
W P^4	8	1.35	1.44	1.55	0.074
BLM^1	10	1.30	1.35	1.42	0.045
PE M^1	10	1.15	1.23	1.32	0.049
LL M^1	10	1.25	1.35	1.42	0.056
AW M^1	10	1.35	1.43	1.55	0.055
PW M^1	9	1.40	1.50	1.60	0.054
M^1 (PEI)	10	0.06	0.09	0.13	0.022
BLM^2	7	1.15	1.20	1.27	0.042
PE M^2	8	1.12	1.13	1.17	0.019
LL M^2	8	1.22	1.25	1.32	0.038
AW M^2	8	1.40	1.44	1.52	0.036
PW M^2	7	1.35	1.39	1.47	0.048
M^2 (PEI)	7	0.06	0.09	0.12	0.022

Description. Skull. The posterior margin of the anteorbital foramen is above the valley between para- and metastyle of M^1, while the lacrimal foramen is above the metastyle of M^1.

Upper dentition. I^1: the apex is not fissident and pointed; its dorsal outline is slightly convex; the buccal cigulum presents only along the lower (ventral) part of the posterior edge; its lower part is narrow, while the upper one is relatively wide; the dorsal and posterior edges make an almost straight or somewhat acute angle; the same is visible between the anterior edge of the talon and the ventral edge of the apex.

Only A^2-A^4 are available; A^2 and A^3 show well-developed lingual and buccal cingula, which form a shelf from which a tetrahedric cuspule with sharp angles arises; A^4 is extremely small, hidden behind the parastyle of P^4 when seen buccally.

P^4: there is no posterior emargination; the shape of the tooth is nearly triangular when seen occlusally; the protocone is not well pronounced – it is no more than a small protuberance on the almost continuous lingual ridge; the hypocone is even smaller or absent; the parastyle is prominent, connected with the paracone by a high parastylar crest.

M^1-M^2: the posterior emargination is very slight (see PE-index in Table III); there is a metaloph, the hypocone is not individualized; the hypoconal edge of the posterolingual ridge and protocone are usually separated by a shallow depression; in one specimen only (M^1) they are connected, forming a continuous endoloph.

Mandible. The ventral margin of the horizontal ramus below M_2 is straight or somewhat convex; the mental foramen is situated below the middle of M_1; the long and well-pronounced coronoid spicule is situated nearly at the middle of the external temporal fossa or slightly higher; this spicule points above the upper condylar facet; the external temporal fossa ends slightly bellow the upper sigmoid notch; the anterior margin of *processus coronoideus* is concave in its upper half , while it is convex at the base; the tip of the process is usually undulate, while in some specimens only it is rounded; the shape of the internal temporal fossa is subtriangular and relatively low; the mandibular foramen is at the middle of the internal temporal fossa; there is no horizontal bar in this fossa.

Lower dentition. The teeth are dark cherry pigmented; the most intense pigmentation (nearly black) occurs on I_1.

I_1 is bicuspulate with pointed apex; the buccal cingulum in some specimens is narrow, expressed only on the dorsal posterior edge; in some specimens the cingulum is absent; the posterior edge extends further back from the posterior margin of P_4.

A_1 is bicuspulate, without a posterolingual basin; the buccal cingulum is weak or, more often, absent; the lingual one is not well pronounced; the tooth is relatively long when seen from the buccal side.

P_4 is clearly bicuspulate; the postero-lingual basin is well pronounced, but situated relatively high – its posterolingual corner does not reach the cingulum; the buccal cingulum presents but most often it is relatively weak; the lingual one is relatively well-developed, only in one specimen is it missing.

M_{1}-$_{M2}$: the shape of the teeth is subrectangular in occlusal view, with a well-pronounced anterolingual corner; the entoconid crests are well-developed, rarely they are relatively low; the buccal cingula are well pronounced; the lingual ones are clearly visible along the whole length of the tooth base, but they are weak.

M_3 is subtriangular in shape – its anterobuccal corner is relatively sharp; the talonid is reduced to a single cusp (hypoconid); the talonid basin is not developed but in some specimens a shallow depression occurs on the lingual slope of the hypoconid; both the lingual and buccal cingula are clearly visible, but sometimes the lingual one may be weak.

Discussion. The structural details of the specimens examined correspond entirely to the descriptions and illustrations of *Petenyia hungarica* presented by REUMER (1984) and RZEBIK-KOWALSKA (1989). On the basis of measurements of a number of samples from Poland, which stratigraphical range comprises a very long time interval (from Ruscinian to late Biharian), the last author reveals a slight increase in size with geological age. A similar trend can be observed on Fig. 2, presenting the results of multidimensional scaling. The first dimension depicts the size differences between the small form from Oszrtramos 9 (lower part of MN14), determined as *P.* aff. *hungarica* (REUMER 1984), and the large form from Kamyk (Early Biharian, Q1). The sample from Varshets occupies an intermediate position along this axis. The second dimension also reveals some size differences – the smaller form from Betfia XIII is located in the uppermost part of the plot, while the larger forms from Osztramos 3/2 and Csarnota 2, are situated in the lowermost part of the diagram. The dimensions of the remains from Varshets are distinctly smaller (Lmd, HPC, TRW, and TAWM$_1$) than the materials from Osztramos 3/2 and Csarnota 2 (REUMER 1984), (Fig. 2). The comparisons with the Polish and Romanian data (RZEBIK-KOWALSKA 1989, 2000) reveal greater differences (Fig. 2). In general, the mandibles described by the present author are larger, especially in the height of the coronoid process, and height of the horizontal ramus of mandible below M$_2$. On the other hand, the teeth of the Varshets sample are greater, in particular, than in the earliest Polish populations (Węże I, Rębielice Królewskie 1A, 2). These differences however are not very impressive (Fig. 2) and most probably reflect some temporal and spatial differences in the environment. The maxillary measurements of our remains are nearly the same as in other European populations (REUMER 1984; RZEBIK-KOWALSKA 1989).

Tribe Blarinini KRETZOI, 1965

Genus *Mafia* REUMER, 1984

Mafia aff. *csarnotensis* REUMER, 1984

(Figs 5 and 6)

Material. 40 fragments of mandible, 5 rostral fragments of cranium with: left I^1-M^3; left P^4-M^2 and right P^4; left A^1-M^2, right A^4-M^3; left I^1 and right P^4-M^3; left A^2, P^4-M^3 and right P^4-M^2; 3 maxillary fragments with: I^1, P^4-M^3; P^4-M^2; M^1-M^2.

Measurements: see Table IV.

Description. Skull. The lacrimal foramen is above the mesostyle of M^1; the posterior edge of the antero-labial foramen is above the anterior part of M^1.

Upper dentition. The upper teeth are stained dark-red. The most intense pigmentation (almost black) occurs on the anterior part of upper incisive.

I^1 is relatively short with pointed, non-fissident apex; the ventral margin shows a slightly S-shaped outline; the ventral edge of the apex and the anterior margin of the talon almost form a right angle; the dorsal outline is straight or slightly convex and makes right angle with the posterior edge; the buccal cingulum is shown up to 3/4 of the buccal height of the talon; the posterior edge is straight.

A^1-A^4 : there are four antemolars; A^1 and A^2 are the largest ones, while the A^4 is the smallest; when seen from the buccal side; A^4 is completely hidden behind the parastyle of P^4; A^3 is half the size of A^2; A^1-A^3 show a poor antero-buccal and relatively large postero-lingual basins; buccal and especially lingual cingula, are broad; the first three antemolars bear well-pronounced cingular cusps with pigmented tips on their postero-lingual parts.

P^4: the parastyle has a rather anterior position; the parastylar crest is high; the paracone is situated at the middle of the buccal side; the protocone is conical and well-pronounced, situated at the antero-lingual corner of the tooth; it is separated by a valley from the anterior part of the postero-lingual ridge (there is no well-individualized hypocone); the bases of the protocone and parastyle are connected by a low ridge; the hypoconal flange is not bordered posteriorly by a cingular ridge.

M^1- M^2: there are no metalophs; the hypocone is not well individualized on the anterior edge of the postero-lingual cingulum; there is a small but distinct antero-lingual cingulum below the base of the protocone; the hypoconal flanges are deeply concave.

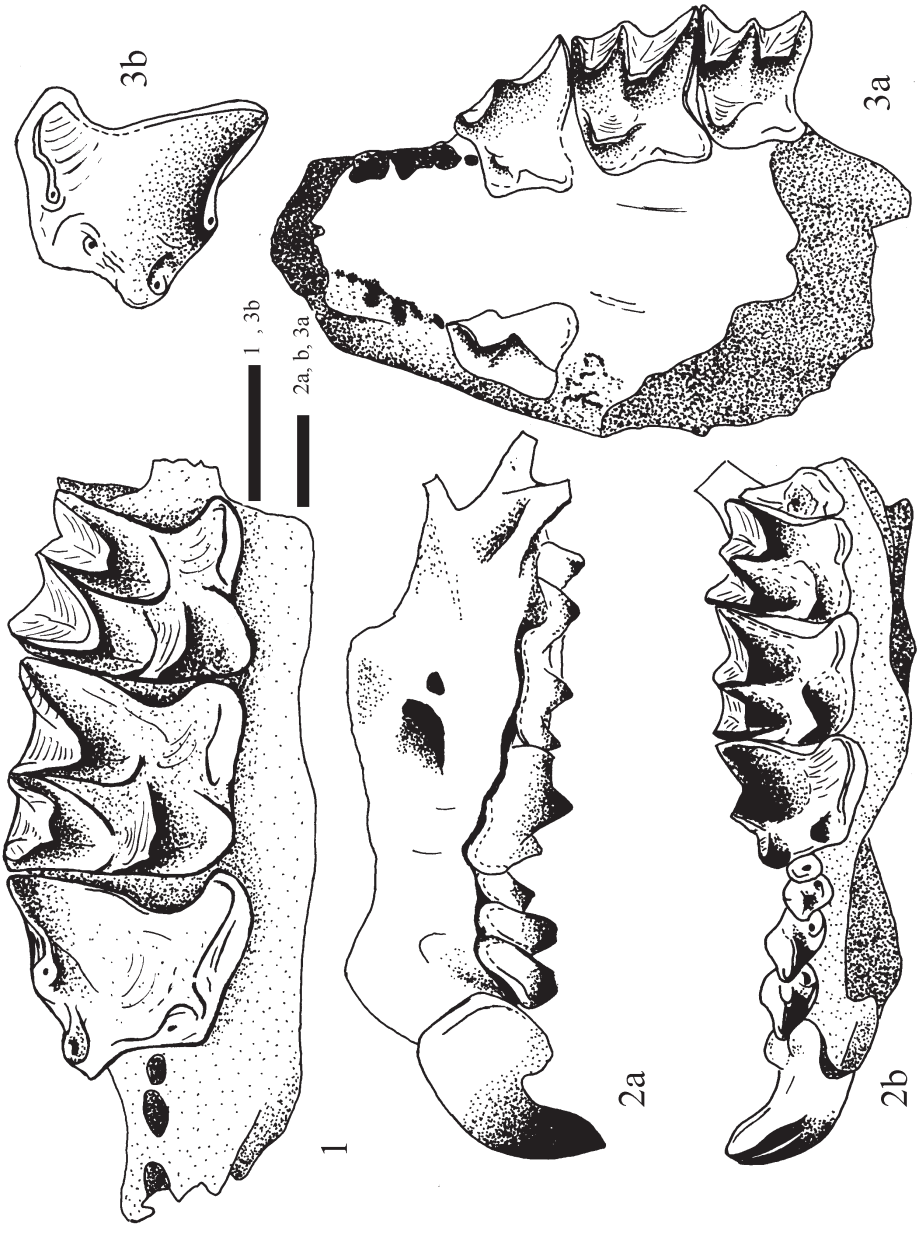

Fig. 5. *Mafia* aff. *csarnotensis*. 1. left maxillary fragment with P^4-M^2 (Coll. No: V72) in occlusal view; 2. left maxillary fragment with full dentition (Coll. No: V13), a. labial view, b. occlusal view; 3. fragment of skull (Coll. No: V21), a. ventral view, b. left P^4, occlusal view.

The posterior emargination of P^4-M^2 is considerable (see PE-index in Table IV).

M^3: the protocone is high; the lingual basin is large but not surrounded lingually by a well expressed ridge; there is low but distinct protocone on the anterolingual corner of the tooth.

Mandible. The lower margin of horizontal ramus is slightly concave below M_2; the mental foramen is under the reentrant valley of M_1 or rarely under its hypoconid; the upper half of the anterior margin of the coronoid process is concave, while its lower half is most often convex, sometimes

Table IV

Measurements of *Mafia* aff. *csarnotensis* fom Varshets. For explanation of abbreviations see Table I

Measurement	N	Min	Mean	Max	SD
LMd	31	4.10	4.52	4.90	0.201
LscMd	12	8.40	8.64	9.00	0.238
LMd+I_1	6	10.80	11.03	11.40	0.206
HPC	35	4.50	4.63	4.85	0.098
HMd/M_2	54	1.42	1.66	1.85	0.086
HC	40	2.12	2.37	2.75	0.164
LLF	46	1.40	1.61	1.85	0.089
LUF	40	0.90	1.08	1.27	0.099
LI_1-M_3	7	7.35	7.67	7.90	0.223
LA_1-M_3	9	5.15	5.32	5.60	0.176
LM_1-M_3	28	3.87	4.02	4.25	0.104
LI_1	10	4.05	4.39	4.75	0.202
H I_1	15	0.92	1.00	1.10	0.052
BL A_1	11	0.90	1.04	1.20	0.103
W A_1	11	0.65	0.77	0.92	0.097
BLP_4	25	1.17	1.37	1.60	0.119
W P_4	26	0.80	0.98	1.12	0.090
LM_1	48	1.52	1.73	1.95	0.096
TAW M_1	49	0.95	1.07	1.22	0.071
TRW M_1	48	0.87	0.99	1.17	0.079
LM_2	43	1.40	1.52	1.75	0.076
TAW M_2	45	0.77	0.91	1.05	0.051
TRW M_2	42	0.82	0.93	1.10	0.068
LM_3	33	1.02	1.14	1.25	0.058
W M_3	33	0.60	0.70	0.85	0.064
PALL	4	7.00	7.17	7.30	0.150
LI^1-A^4	1	3.80	3.80	3.80	–
LA^1-A^4	2	2.20	2.30	2.40	0.141
LP^4-M^3	5	4.50	4.78	5.10	0.213
LI^1-M^3	2	8.20	8.30	8.40	0.141
LM^1-M^3	6	3.07	3.24	3.40	0.130
LI^1	3	2.45	2.48	2.50	0.028
LT I^1	5	1.10	1.14	1.22	0.049
H I^1	6	1.47	1.57	1.67	0.080
BL P^4	11	1.55	1.63	1.80	0.077
PE P^4	9	1.00	1.11	1.25	0.097
LL P^4	9	1.22	1.36	1.57	0.113
W P^4	11	1.55	1.67	1.90	0.106
BL M^1	14	1.05	1.56	1.65	0.043
PE M^1	14	1.27	1.32	1.37	0.032
LL M^1	14	1.45	1.53	1.62	0.049
AW M^1	14	1.60	1.72	1.85	0.076
PW M^1	12	1.62	1.74	1.87	0.077
M^1 (PEI)	14	0.14	0.17	0.25	0.030
BL M^2	12	1.17	1.31	1.37	0.060
PE M^2	12	0.97	1.11	1.20	0.074
LL M^2	12	1.12	1.28	1.47	0.105
AW M^2	12	1.57	1.73	1.90	0.093
PW M^2	12	1.37	1.47	1.60	0.062
M^2 (PEI)	12	0.13	0.16	0.27	0.038
L M^3	6	0.50	0.55	0.62	0.050
W M^3	6	1.05	1.10	1.12	0.028

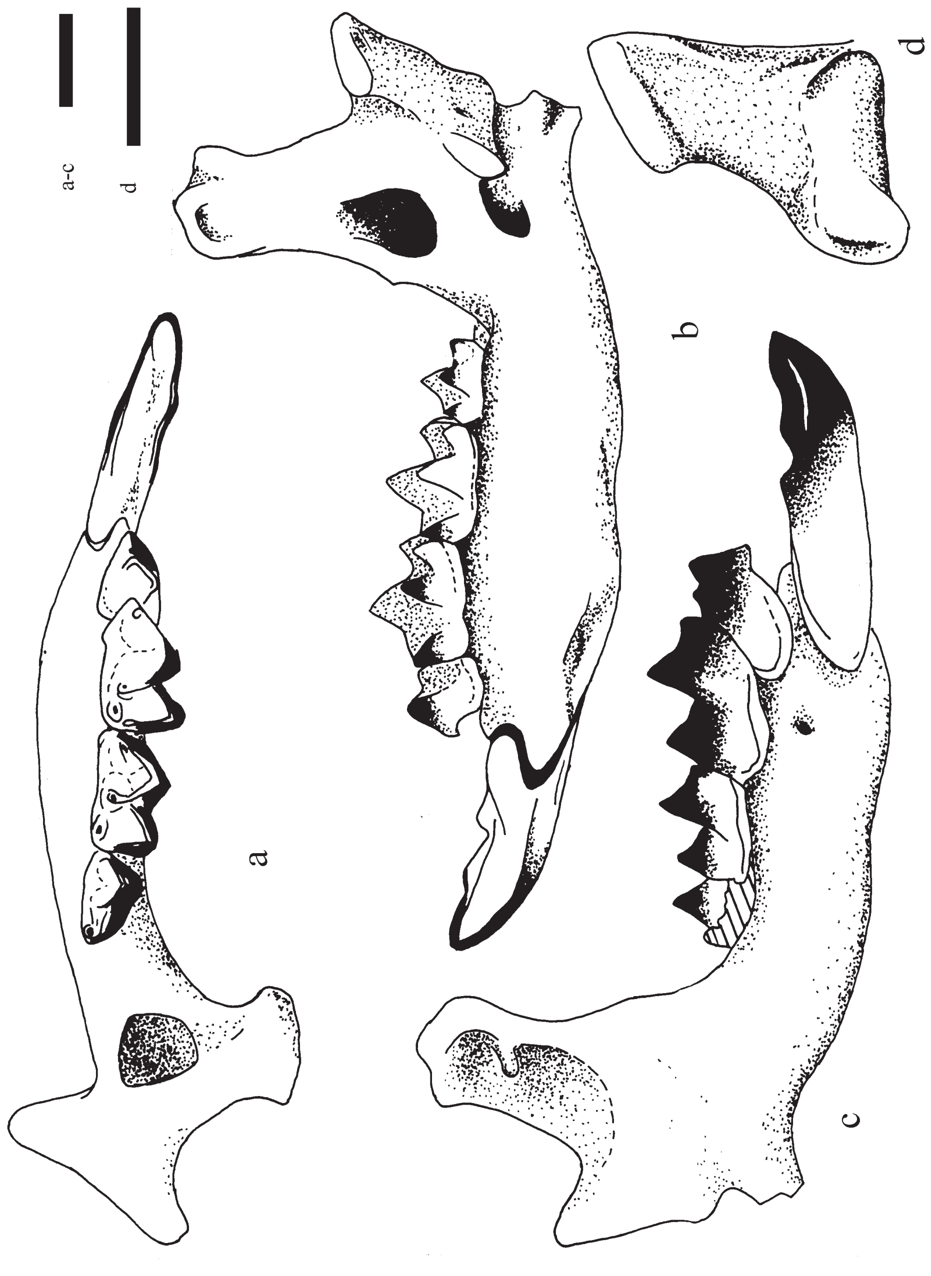

Fig. 6. *Mafia* aff. *csarnotensis*. Right mandible without A_1 (Coll. No: V11), a – occlusal view, b – lingual view, c – labial view, d – posterior view of the condyloid process.

with a small protrusion; only in a few specimens is this part of the edge entirely concave; the tip of the coronoid process is broad, sometimes more or less spatulate, undulate in upper outline, its posterior part becomes more prominent backwards; only in four out of 24 specimens the tip is rounded; the well individualized but short coronoid spicule is situated at two-thirds of the height of the external temporal fossa; as a rule this spicule points to the upper condylar facet; the external temporal fossa reaches downwards underneath the upper sigmoid notch (at one third of the condyle height); the internal temporal fossa is relatively low, rounded-triangular in shape; there is no horizontal bar inside; the mandibular foramen is relatively large, situated under the middle or anterior part of internal temporal fossa; the interarticular area of the condyle is broad; the lower articular facet is large, prominent lingually; its upper margin is undulate; the upper facet is oblique in relation to the lower one.

Lower dentition. The lower teeth are pigmented dark red; the degree of pigmentation changes along the tooth-row; the pigment is darker (nearly black) on the lower incisor than further back on the lower dentition; generally, the protoconids are more intensely stained than hypoconids; buccally the pigmented area reaches the bases of these conids, while lingually only the upper parts are coloured; often, the upper halves of para-, meta-, and entoconids are lightly pigmented.

I_1 is bicuspulate, a tendency towards a tricuspulate situation could be seen in some specimens due to a minute anterior protuberance; the undulations are well prominent; the buccal cingulum is either slight or thin, but well-visible on the dorsal edge of the posterior part of the tooth, not surrounding the corner; the tooth reaches back as far as the posterior margin of P_4; the apex is pointed.

A_1 is relatively long as seen from the buccal side; monocuspulate, but in some specimens a minute posterior cuspule appears; there are buccal and lingual cingula, which are relatively poor, although the lingual one is better developed.

P_4: the tooth appears two cusped from side view; there are well expressed buccal and lingual cingula, although the latter, is sometimes relatively weak; the postero-lingual basin is wide, reaching the cingulum in the postero-lingual corner of the tooth.

M_1- M_2: entoconid and metaconid are close to each other and their bases are connected; the entoconid crest is missing, so the entoconid is conical or slightly elongated antero-posteriorly; the buccal cingula are very well developed, while the lingual ones are weak, most often slightly visible under entoconid and paraconid only.

M_3 is with reduced talonid – the entoconid is absent; there is no trace of a talonid basin; the buccal cingulum is well-developed while the lingual one is weak or, very often, missing.

Discussion. The isolated cranial and mandibular fragments described above are considered as belonging to one species on the basis of size and tooth pigmentation pattern. The greater length of the upper tooth row in comparison with the lower one (Table IV) does not contradict this consideration. In shrews such differences are common within a species. For instance, the measurements taken from a large sample (N=34) of recent *S. araneus* (a shrew of comparable size) from one locality reveal differences of nearly the same magnitude: LI^1-M^3 = 7.8-8.3-8.7; LI_1-M_3 = 7.1-7.7-8.2 (Min-Mean-Max).

Among the shrew material presented in the locality only *Petenyia hungarica* shows some superficial similarity to the specimens described above. This is especially true for the colour and intensity of the tooth pigmentation. However, the separation of the remains of these two forms is quite easy – the specimens under consideration are larger (Table IV), lack an entoconid crest on M_1-M_2, and have stronger posterior emargination on P^4-M^2.

The Blarinini species *Sulimskia kretzoii* (SULIMSKI, 1962) is also somewhat similar to the material from Varshets, but it differs in having five upper antemolars, not so well pronounced posterior emargination on P^4- M^2 , not well individualized metalophs on M^1-M^2, wider cingulum on I^1, higher internal temporal fossa, higher coronoid process with a more spatulate apex, and a lower condyloid process.

The lower jaws from Varshets represent a form which is in most respects very similar to the type species of the genus *Mafia*, *M. csarnotensis,* described on the basis of a mandibular fragment from Csarnota 2, Hungary (REUMER 1984). Significant features of both forms include a conical entoconid devoid of entoconid crest, a condyle with wide interarticular area, a normal soricine P_4, well-developed lingual and poor buccal cingula, a moderately developed coronoid spicule, situated on the upper half of the external temporal fossa, etc. The Varshets mandibles differ, however, to some extent from the Hungarian material: they are somewhat smaller (LMD, HPC), have an oblique position of the upper condylar facet in relation to the lower one, a more spatulate apex of the coronoid process, a less posteriorly placed condyle, and a more anterior position of the mental foramen.

The upper teeth from Varshets compare well in size and morphology (strong posterior emargination of P^4-M^2, the non fissident I^1), with the isolated upper teeth from the type locality (REUMER 1984). However, in contrast to the material from Csarnota 2, the last upper antemolar in the form from Varshets is not shifted lingually, so the A^3 does not touch P^4.

Bearing in mind that the material from the type locality is rather scarce and fragmentary, it is hard to tell whether the above mentioned differences warrant taxonomic distinction. For the time being, the material from Varshets is tentatively determined as *M.* aff. *csarnotensis*. The distinction or identity between the two forms remains to be further substantiated.

The morphology of *Mafia csarnotensis*, the type species of the genus, has so far been poorly known. This is particularly true as far as the number of upper antemolars is concerned (REUMER 1984; RZEBIK-KOWALSKA 1990). The skull fragments from Varshets with their well-preserved upper dentitions clearly show that the number of the upper antemolars is four. Thus, the studied material improves the characteristic of the genus and questions the generic identity of the enigmatic species *Mafia dehneli* (KOWALSKI, 1956), which possesses five upper antemolars (REUMER 1984; RZEBIK-KOWALSKA 1990), taking into account that, as a rule, the number of upper antemolars is constant within a shrew genus. Moreover, the detailed description of *M. dehneli* presented by RZEBIK-KOWALSKA (1990) revealed that the species has very strong hypocones on P^4 and M^1-M^2.

Tribe Beremendiini REUMER, 1984

Genus *Beremendia* KORMOS, 1934

Beremendia fissidens (PETENYI, 1864)

(Fig. 7, 8)

Material: 172 mandibles and fragments of mandibles; 46 fragments of skull and upper dentitions and numerous isolated teeth.

Measurements: see Table V.

Description. Skull. The infraorbital foramen is pocketed, its posterior margin is sharp, situated above the posterior part of P^4 or above the anterior part of M^1; the lacrimal foramen is small, situated at the level of the middle part of the infraorbital foramen.

Upper dentition. The tooth pigmentation is darkred, not very intensive; the main cusps are stained downwards to their bases.

I^1 is fissident; the posterior edge is straight, making a right angle with the dorsal outline; a wide posterior external cingulum is present behind the talon. The tips are intensely pigmented in darkred.

A^1-A^4: the first two antemolars are about equal in size and the largest; A^4 is the smallest antemolar, situated lingually from the parastyle of P/4; on A^1-A^2 there are shallow basins, situated posterolingually from the central crest, surrounded by a well pronounced cingulum; sometimes there is a very small cuspule on the posterolingual end of this cingulum; the buccal cingulum is also conspicuous, and widens posteriorly; these teeth are unicuspid; only the very tips of A^1-A^2 are pigmented in pale red.

P^4: the protocone varies – usually it is a small protuberance at the middle part of the arc-shaped ridge, running from the base of the parastyle towards to the centre of the tooth; the variability concerns the development of the cusp or of the ridge – sometimes there being only a ridge, while the cusp is not individualized, and sometimes the ridge is reduced and instead only the cusp is present; as a rule the hypocone is not well-pronounced on the anterior part of the ridge, surrounding the hyponal flange; in most specimens there is a wide valley between this ridge and the ridge runing from the protocone to the centre of the tooth, but, in a few cases there is a low ridge connecting the hypocone and the posterior part of the "protoconal" ridge; the paracone and the parastyle are the

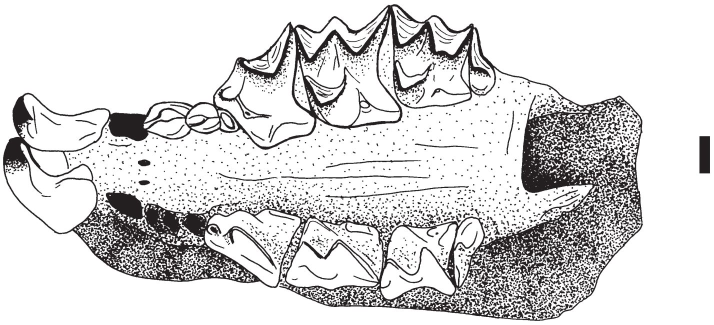

Fig. 7. *Beremendia fissidens*. Fragment of skull (Coll. No: V92), ventral view.

highest cusps, connected by a high parastyle crest; the posterior emargination is fairly conspicuous; a thin cingulum could be observed along the posterior tooth margin.

M^1-M^2: the hypocone is moderately developed; there is a low metaloph; the hypocone is separated from the protocone and metaloph by a wide valley, but in some specimens this valley is closed by a low ridge, connecting the hypocone with the metaloph; in some cases, a trace of thin cingulum could be observed underneath the protocone; the posterior emargination varies from moderate to conspicuous (see PE-index in Table V); a thin, not well individualized, posterior cingulum could be observed in some specimens.

M^3: the lingual basin is bordered posteriorly by a well-developed V-shaped ridge; the buccal one is opened posteriorly.

Mandible. The mental foramen is situated under the posterior part of M_1 or slightly anteriorly; the horizontal ramus is wider in its anterior part – under M_1 and narrower in its posterior part – behind M_3.

Lower dentition. I_1: the cutting edge is smooth; the apex is upturned; there is postero-buccal cingulum; the posterior edge of the tooth reaches backward as far as the posterior margin of P_4, or slightly posteriorly; the tip is strongly pigmented in dark-red.

A_1 is unicuspid (in some specimens a small posterior cusplet may exist), elongated, with barely pronounced buccal cingulum; the lingual cingulum is somewhat better developed; the posterolingual basin is poor.

P_4 is bicuspulate, elongated buccally with well pronounced both buccal and lingual cingula; the posterolingual cingulum is shallow and not well defined.

M_1-M_2: the buccal cingula are conspicuous; the ventro-buccal edge of M_1 is slightly undulated, while in M_2 as a rule it is straight; the lingual cingula are not so well developed; there is an entoconid crest and on some specimens it is very high; in M_1 the talonid is wider than the trigonid while in M_2 the situation is reversed.

M_3: the talonid is moderately reduced, basined, surrounded postero-buccally by a horseshoe-like ridge; there is no lingual cingulum.

Discussion. The qualitative characters of the above described remains suggest that they pertain to genus *Beremendia*, and the measurements imply that the material represents the larger of the two species belonging to the genus, *B. fissidens*. The MDS results (Fig. 2) indicate that the material from Varshets represents a relatively large form of the species, similar to some late Pliocene and Early Pleistocene populations from Hungary and Poland (Villany 3, Osztramos 3/2, Kamyk), (Reumer 1984; Rzebik-Kowalska 1976). At the same time, it is somewhat larger than the Early Pliocene form from Węże 1 and the Early Pleistocene populations from Romania (Rzebik-Kowalska 2000). Thus, the material under study corresponds well to the size fluctuations during Pliocene and Early Pleistocene recorded in other parts of Europe (Rzebik-Kowalska 2000, Fig. 8).

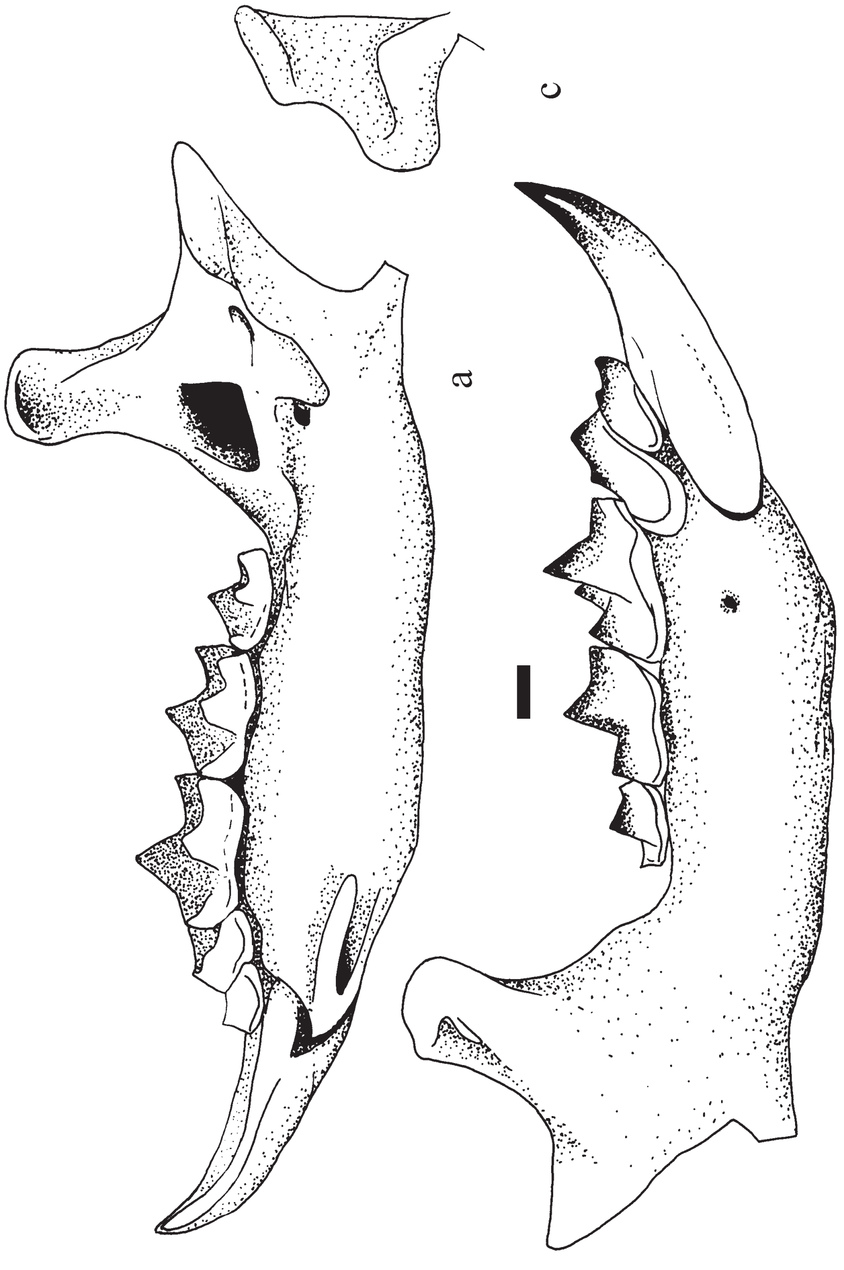

Fig. 8. *Beremendia fissidens*. Right mandible (Coll. No: V18-20-90), a – lingual view, b – labial view, c – posterior view of the condyloid process.

Table V

Measurements of *Beremendis fissidens* from Varshets. For explanation of abbreviations see Table I

	N	Min	Mean	Max	SD
LMd	61	6.65	7.31	8.30	0.372
LscMd	1	1.90	1.9	1.9	–
LMd+I$_1$	18	16.10	17.58	18.7	0.644
HPC	84	6.00	6.71	7.50	0.299
HMd/M$_2$	119	2.00	2.61	3.10	0.180
HC	84	3.15	3.79	4.4	0.255
LLF	82	2.17	2.72	3.25	0.215
LUF	84	1.50	1.93	2.7	0.163
LI$_1$-M$_3$	21	11.00	11.48	12.50	0.389
LA$_1$-M$_3$	44	7.55	8.13	8.80	0.309
LM$_1$-M$_3$	80	5.85	6.41	7.20	0.253
LI$_1$	45	5.75	6.51	7.25	0.320
H I$_1$	74	1.35	1.53	1.70	0.078
BLA$_1$	58	1.10	1.39	1.80	0.149
W A$_1$	56	0.77	1.10	1.29	0.092
BLP^4	91	1.55	1.89	2.25	0.149
W P^4	87	1.10	1.38	1.62	0.100
LM$_1$	124	2.57	2.87	3.25	0.122
TAW M$_1$	126	1.35	1.69	2.05	0.137
TRW M$_1$	123	1.00	1.56	1.92	0.132
LM$_2$	114	2.12	2.42	2.70	0.120
TAW M$_2$	114	1.00	1.45	1.75	0.129
TRW M$_2$	116	1.17	1.47	1.80	0.110
LM$_3$	88	1.20	1.75	1.97	0.105
W M$_3$	87	0.85	1.02	1.32	0.090
PALL	10	11.00	11.88	13.00	0.687
IO	4	6.20	6.77	7.20	0.434
LI^1-A^4	6	5.60	6.00	6.30	0.266
LA^1-A^4	10	3.20	3.81	4.10	0.282
LP^4-M^3	25	7.30	7.66	8.00	0.177
LM^1-M^3	24	5.00	5.26	5.57	0.189
LI^1	32	2.80	3.62	4.25	0.344
LT I^1	36	1.10	1.63	2.05	0.227
H I^1	38	2.20	2.39	2.70	0.120
BL P^4	50	2.60	2.92	3.15	0.127
PE P^4	50	1.45	1.82	2.17	0.152
LL P^4	51	1.85	2.14	2.57	0.205
W P^4	51	2.00	2.57	2.92	0.192
BL M^1	45	2.25	2.51	2.65	0.111
PE M^1	48	1.80	2.02	2.25	0.111
LL M^1	48	2.15	2.38	2.65	0.103
AW M^1	47	2.30	2.59	2.95	0.144
PW M^1	46	2.40	2.73	2.95	0.130
M^1 (PEI)	45	0.10	0.21	0.34	0.052
BL M^2	43	1.90	2.17	2.40	0.106
PE M^2	43	1.60	1.78	2.25	0.113
LL M^2	43	1.70	2.04	2.35	0.141
AW M^2	45	2.20	2.64	2.90	0.142
PW M^2	42	2.00	2.21	2.55	0.104
M^2 (PEI)	39	0.10	0.19	0.26	0.038
L M^3	27	0.80	0.93	1.05	0.079
W M^3	26	1.50	1.80	2.10	0.128

Tribe Neomyini MATSCHIE, 1909

Genus *Asoriculus* KRETZOI, 1959.

Asoriculus gibberodon (PETENYI, 1864)

(Fig. 9, 10)

Material: 250 complete or fragmentary mandibles; 4 skull fragments and 2 upper dentitions.

Measurements: see Table VI.

Description. Skull. The infraorbital foramen is rounded, situated above P^4 but sometimes its posterior edge is situated backwards as far as the anterior part of M^1; the lacrimal foramen is small, opening somewhat above the upper half of the interorbital foramen.

Upper dentition. Only the tips of the incisives, A^1-A^2 and the very tip of the paracone of P^4 are weakly pigmented in light yellow or orange.

I^1 is bifid, the posterior external cingulum is well pronounced, considerably wider in its upper half; the posterior external margin of the crown is concave; the lingual cingulum presents along the posterior margin of the talon only.

A^1-A^4: the first two antemolars are the largest ones, nearly equal in size; the third is somewhat smaller; A^4 is the smallest antemolar but not very much reduced – it could be observed from the buccal side; in occlusal view, the lingual part of the A^1-A^3 is shelf-like, and the cusp is high with a sharp anterior and posterior edges; on the lingual edge of the cingular "shelf" there is a small enamel undulation ("cuspule"), which is connected with the tip of the main cusp by a low lingual ridge; all antemolars show a well-pronounced buccal cingulum.

P^4: the parastyle is considerable protruding anteriorly; as a rule, a small cingulum exists in front of this cuspule; the proto- and hypocone are widely separated; the posterior part of the hypoconal base is sometimes surrounded lingually by the ridge of the hypoconal flange; the parastylar crest is moderately high; the posterior emargination is variable but always well-pronounced; some of the teeth are elongated in occlusal view, while the other ones are relatively short and wide; in buccal view a well pronounced cingulum could be observed.

M^1- M^2: the two morphotypes (A and B) described by REUMER (1984) could be found in the Varshets sample; the morphotype A is the commonest one and occurs more frequently in M^1's; in the authors' opinion these morphotypes have no systematic value because very often on the same dentition M^1 is of the morphotype A, while M^2 belongs to the morphotype B; the hypocone is well-developed, somewhat shifted lingually in relation to the protocone; the metalophs are present, but always low; on the M^1 the metastyle protrudes lingually, thus, the posterior part is wider than the anterior one, while on M^2 it is shortened (the tooth is wider anteriorly); the posterior emargination is moderate (see PE-index in Table VI); the lingual sides of these molars are concave in occlusal view.

M^3: is relatively small; the metacone is reduced to a posterior ridge.

Mandible. The mental foramen is below the M_1-hypoconid or, rarely, under the middle of M_1; the anterior margin of the coronoid process makes a slightly obtuse angle with the horizontal ramus; the tip of the coronoid process is relatively narrow, rounded, sometimes slightly bent anteriorly; the ventral margin of the external temporal fossa reaches downward at the middle of the condyle; the coronoid spicule is relatively short but distinct; sometimes its upper edge is sharp, while the ventral part passes gradually to the plane of the external temporal fossa; this spicule is situated nearly at the middle of the height of the fossa; the lower part of the internal temporal fossa is pocketed; its upper part is shallow, reaching the tip of the coronoid process; between these two parts of the fossa a poorly expressed horizontal bar could be observed in some specimens; this internal temporal fossa is somewhat shifted anteriorly; the pterygoid spicule is, as a rule, well pronounced, but small.

Lower dentition. A slight pale yellow or orange pigmentation could be observed on the tips of lower incisive P_4, and on the protoconids of unworn M_1- M_3.

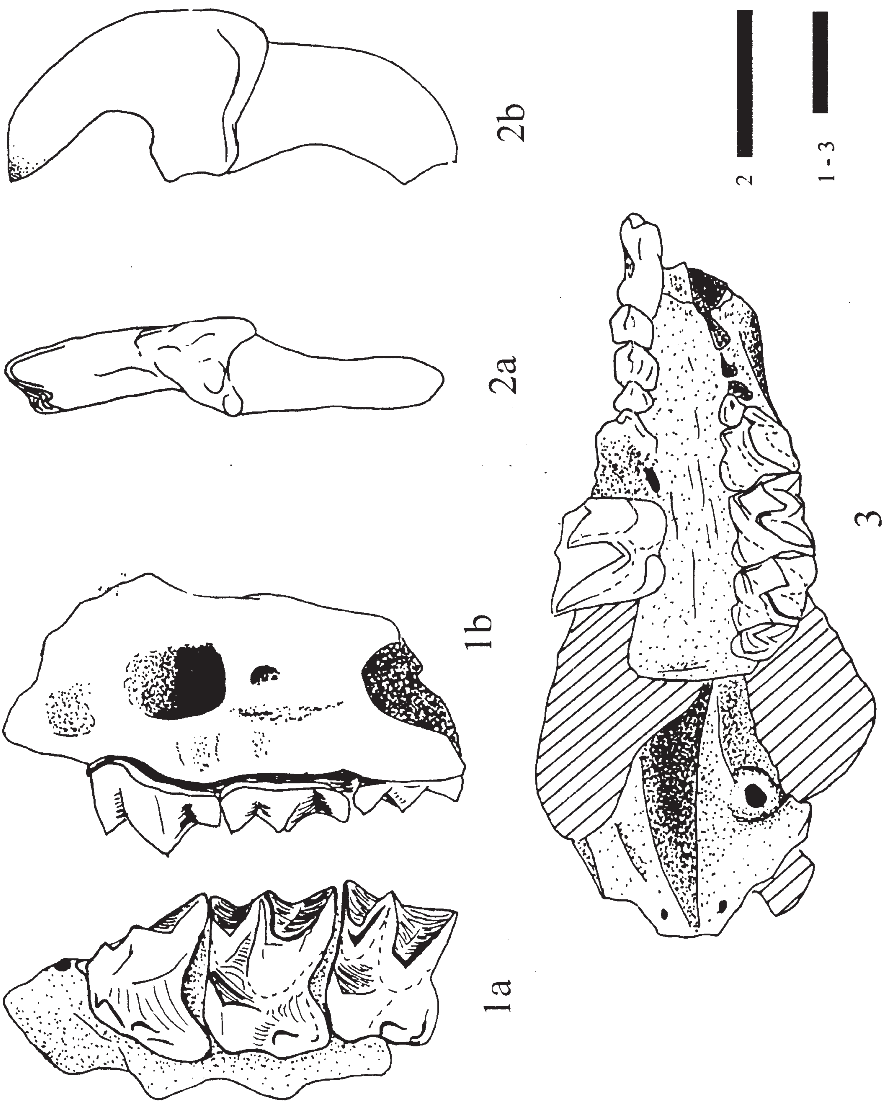

Fig. 9. *Asoriculus gibberodon*. 1. left maxillary fragment with P^4-M^2 (Coll. No: V3-1), a – occlusal view, b – lateral view; 2. left upper incisive (Coll. No: V3-3), a – ventral view, b – labial view; 3. fragment of skull, ventral view (Coll. No: V3-2).

I$_1$: the posterior cingulum present along the edge, but sometimes indistinct; bicuspulate, but the anterior cuspule is presented as a minor undulation, which disappears off the worn incisives; the tip is bent upwards; as a rule the incisive reaches backwards as far as the posterior end of P$_4$ or slightly before it.

A$_1$ is relatively long, unicuspid, with buccal and lingual cingula; a shallow triangular basin could be observed in occlusal view.

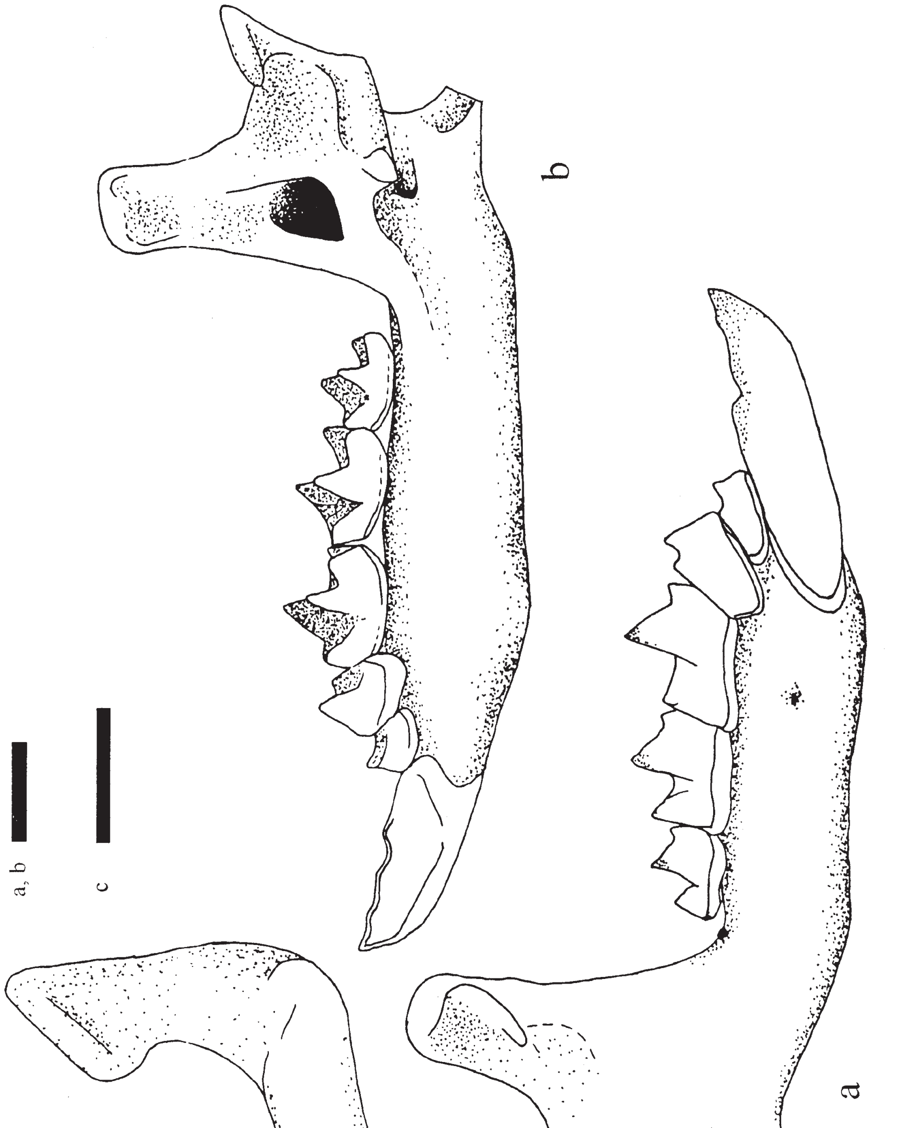

Fig. 10. *Asoriculus gibberodon.* Right mandible (Coll. No: V1), a – labial view, b – lingual view, c – posterior view of the condyloid process.

P_4 is relatively long, bicuspulate, basined, with buccal and lingual cingula – the later is weaker; the basin is subtriangular in occlusal view and relatively highly situated (it does not reach the cingulum posterolingually).

M_1-M_2: very similar to each other; buccally the ventral margin is slight but often undulated; the ventral lingual margin is either straight or convex (naviculare); the buccal cingulum is distinct while the lingual one is present but indistinct in some specimens; a small mesoconid could be seen on the

Table VI

Measurements of *Asoriculus gibberodon* from Varshets . For explanation of abbreviations see Table I

	N	Min	Mean	Max	SD
LMd	133	4.12	4.61	5.15	0.201
LMd+I$_1$	31	10.40	11.22	120	0.343
HPC	177	4.05	4.41	4.70	0.134
HMd/M$_2$	262	1.10	1.43	1.75	0.088
HC	188	1.95	2.36	2.87	0.166
LLF	198	1.27	1.64	1.95	0.108
LUF	186	0.80	1.02	1.20	0.087
LI$_1$-M$_3$	40	6.65	7.1	7.60	0.247
LA$_1$-M$_3$	65	4.80	5.19	5.55	0.190
LM$_1$-M$_3$	146	3.55	3.91	4.30	0.142
LI$_1$	58	3.07	3.69	4.15	0.203
H I$_1$	65	0.82	0.97	1.10	0.052
BLA$_1$	80	0.72	1.05	1.27	0.101
W A$_1$	79	0.62	0.74	0.87	0.059
BLP$_4$	128	0.92	1.27	1.47	0.114
W P$_4$	126	0.67	0.87	1.05	0.083
LM$_1$	195	1.45	1.68	1.90	0.082
TAW M$_1$	200	0.85	1.03	1.20	0.074
TRW M$_1$	196	0.75	0.92	1.20	0.072
LM$_2$	220	1.00	1.49	1.77	0.088
TAW M$_2$	222	0.77	0.93	1.12	0.076
TRW M$_2$	219	0.67	0.88	1.12	0.079
LM$_3$	160	0.92	1.11	1.27	0.060
W M$_3$	156	0.57	0.71	0.97	0.083
PALL	7	6.70	7.16	7.45	0.247
LI^1-A^4	3	3.17	3.44	3.65	0.248
LA^1-A^4	5	1.90	2.12	2.30	0.158
LP^4-M^3	15	4.40	4.58	4.95	0.170
LI^1-M^3	1	–	7.90	–	–
LM^1-M^3	14	3.05	3.19	3.45	0.131
L I^1	18	1.62	1.87	2.15	0.154
LT I^1	17	0.62	0.81	1.00	0.110
H I^1	18	1.27	1.36	1.45	0.055
BL P^4	35	1.55	1.65	1.80	0.073
PE P^4	33	0.87	1.07	1.30	0.099
LL P^4	33	1.00	1.22	1.50	0.118
W P^4	32	1.45	1.61	1.87	0.114
BL M^1	36	1.27	1.49	1.60	0.074
PE M^1	32	1.17	1.29	1.40	0.063
LL M^1	34	1.25	1.42	1.57	0.086
AW M^1	33	1.47	1.59	1.70	0.055
PW M^1	35	1.62	1.79	2.02	0.084
M^1 (PEI)	31	0.06	0.13	0.20	0.040
BL M^2	30	1.12	1.27	1.37	0.050
PE M^2	30	1.02	1.12	1.22	0.048
LL M^2	29	1.10	1.24	1.42	0.074
AW M^2	31	1.55	1.70	1.87	0.074
PW M^2	29	1.32	1.53	1.72	0.097
M^2 (PEI)	27	0.04	0.12	0.20	0.038
L M^3	17	0.57	0.65	0.77	0.056
W M^3	16	1.05	1.24	1.45	0.090

unworn teeth; the entoconid is present but its height is variable – as a rule being relatively low, while in some specimens it is high; the reentrant valley between the entoconid and the endostylid is rather narrow and situated high.

M_3: the talonid is narrow but not reduced, always basined with pointed ento- and hypoconids; the buccal cingulum is well-pronounced.

Discussion. According to HUTTERER (1994), the European fossil species traditionally referred to *Episoriculus* ELLERMAN & MORRISON- SCOTT, 1951 are different from the present-day forms of the genus from south-eastern Asia and should be attributed to a separate genus *Asoriculus*. Up to the present the following species names have been introduced for the forms referable to the genus: *A. gibberodon*, *A. kubinyii* (KORMOS, 1934), *A. castellarini* (PASA, 1947), *A. borsodensis* (JÁNOSSY, 1973), *A. tornensis* (JÁNOSSY, 1973), *A. thenii* (MALEZ & RABEDER, 1984), *A. maghrebensis* (RZEBIK-KOWALSKA, 1988) and *A. burgioi* MASINI & SARA, 1998. The description of *A. castellarini* is not very detailed and it is difficult to evaluate its status. The identity of *C. gibberodon* and *S. kubinyii* was suggested by KRETZOI (1956, p. 160, 162), and this assumption was accepted by later authors (JÁNOSSY 1973; REUMER 1984). GERAADS (1995) is of the opinion that *A. kubinyii* should be considered as a separate species. The recent analysis of the *Asoriculus* remains from some Hungarian localities made by REUMER (1984) pointed out that the small forms *A. borsodensis* (type locality Osztramos 1C) and *A. tornensis* (type locality Osztramos 13) fall within the range of variability of a single species and could be considered as synonyms of *A. gibberodon* (REUMER 1984). *A. thenii* and *A. burgoi* are larger than *A. gibberodon* (MALEZ & RABEDER 1984; MASINI & SARA 1998) and are well defined species. Thus, the genus seems to include three species.

As with *A. gibberodon*, there is a slight size increase from the oldest (MN14) to the youngest (Q1) populations (MEIN: in BRUJIN et al. 1970; REUMER 1984; RZEBIK-KOWALSKA 2000; MARCHETTI et al. 2000). The results of multidimensional scaling, presented on Fig. 2, do not agree with this statement. The samples clearly form two size groups. The smaller forms are located on the left side of the diagram while the larger ones are situated on the right side. Both groups comprise Pliocene as well as Early Pleistocene forms. These comparisons show that probably the effect of other factors may obscure the evolutionary drift (REUMER 1984; RZEBIK-KOWALSKA 2000). The relatively low maximum value among the overall distances within the dissimilarity matrix (see Material and Methods) indicates that most probably the two size groups belong to a single species, *A. gibberodon*. Thus the Varshets sample represents a large form of this species. In the size of the lower molars the form from Varshets overlaps the range of the variability of *A. thenii*, but this species has a much longer lower incisive (MALEZ & RABEDER 1984; RZEBIK-KOWALSKA 1988).

IV. DISCUSSION

Remarks on age and paleoecology

The comprehensive evaluation of the environmental significance of the Varshets local assemblage is possible only within the larger context of the compositional and structural variability of the fossil shrew assemblages from other parts of the continent. To depict in a parsimonious manner the position of Varshets assemblage within this wider perspective and to reveal the effect of particular paleoenvironmental gradients, twenty-three Pliocene and Early Pleistocene shrew assemblages were analysed by means of a detrended correspondence analysis (DCA). The shrew assemblages included in the analysis were chosen because of their detailed consideration with a comparable degree of taxonomic confidence and completeness, and because the data are presented in a way permitting quantitative comparisons (REUMER 1984; RZEBIK-KOWALSKA 1994, 2000).

The results of DCA are shown on Figs 11 a, b. Only the first two axes have eigenvalues greater than one, so further analysis was restricted to them. They account for 31.0 % and 19.3 %, respec-

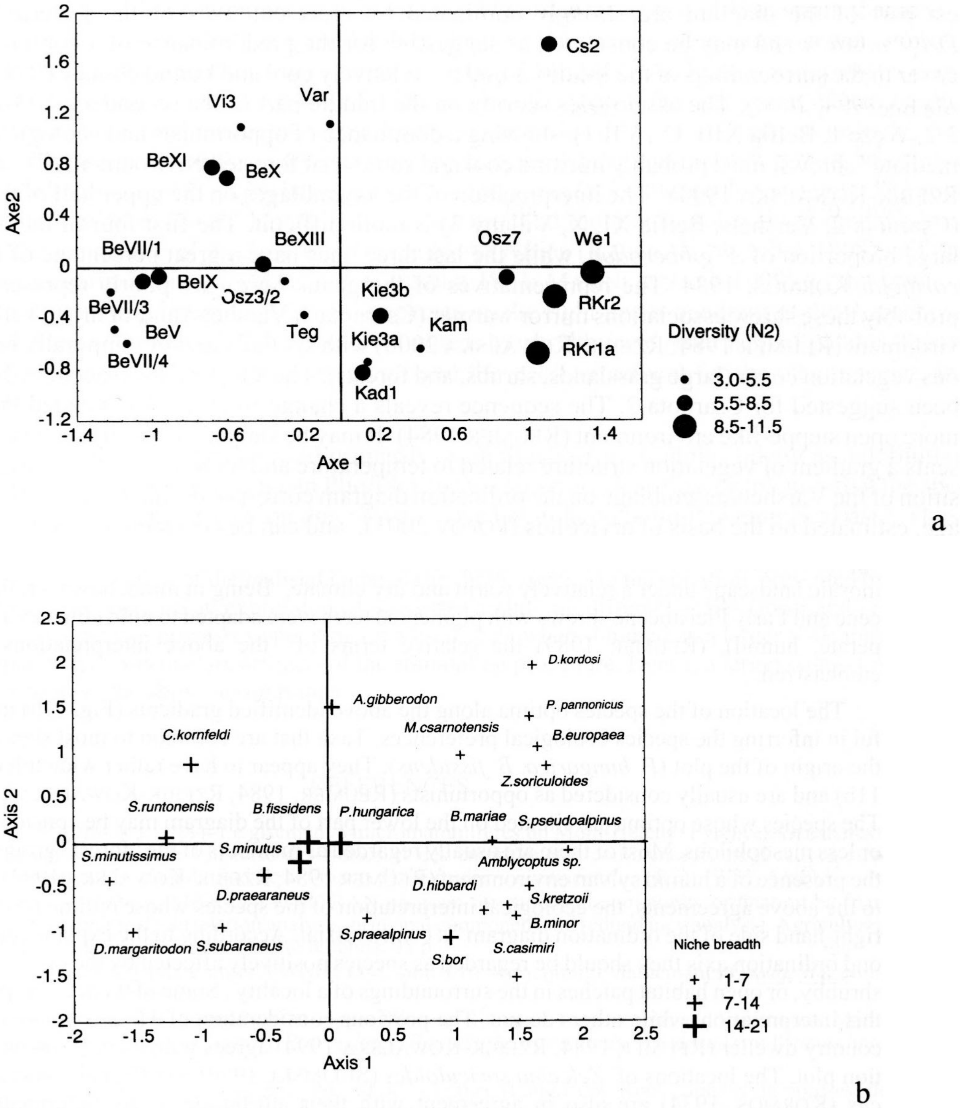

Fig. 11. Results of detrended correspondence analysis. a. ordination of shrew assemblages, for abbreviations see Fig. 2. Kie – Kielniki. The initial data are from REUMER 1984; RZEBIK-KOWALSKA 1994, 2000). b. ordination of species.

tively, of the variation within the data set. The first ordination axis reveals a rough chronostratigraphical gradient: MN15 and MN16A associations lay on the extreme right part of the diagram while those on the extreme left are Q2 associations; the MN17 and Q1 shrew associations occupy an intermediate position. It is worth noting that, in general, the assemblages on the right side of the plot are more diversified (Fig. 11a). Evidently, this axis represents a distinct faunal turnover during the time interval between Late Ruscinian and Late Biharian. These changes are probably related to a temperature decline during that time (REUMER 1984, 1989; RZEBIK-KOWALSKA 1995, 1998). So, the first axis may be identified as a temporal temperature gradient The second axis separates five assemblages, located on the upper part of the diagram (BeXI, BeX, Vi3, Var, and Cs2), from the remaining, situated on the lower part (Fig. 11a). The majority of the shrew associations from the lowest part of the diagram are strongly dominated by representatives of the genera *Sorex* and *Drepanosorex* and may be considered as suggestive for the predominance of a continuous forest cover in the surroundings of the localities under a relatively cool and humid climate (RZEBIK-KOWALSKA 1994, 2000). The assembales scoring on the middle part of the second axis (Osztramos 7, 3/2, Węże 1, Betfia XIII, IX, VII/1), showing a dominance of opportunists and ecologically "intermediate" shrews, most probably mirror a cool and somewhat forested environment (REUMER 1984; RZEBIK-KOWALSKA 1994). The interpretation of the assemblages on the upper half of the diagram (Csarnota 2, Varshets, Betfia XI, X, Villany 3) is more difficult. The first four of them contain a large proportion of *A. gibberodon*, while the last three ones have a great percentage of *Crocidura cornfeldi* KORMOS, 1934. The representatives of the genus *Sorex* are poorly represented. Most probably these shrew associations mirror warmer (Csarnota 2, Varshets) and/or drier (Villany 3) environment (REUMER 1984; RZEBIK-KOWALSKA 2000) with spatially and/or temporally heterogeneous vegetation cover (large grasslands, shrubs, and forests). The temporal heterogeneity has already been suggested for Csarnota 2. The sequence reveals a change from a more wooded biotope to a more open steppe-like environment (REUMER 1984). It may be supposed that the second axis represents a gradient of vegetation structure related to temperature and humidity. In this context, the position of the Varshets assemblage on the ordination diagram corresponds fairly well to its geological age, estimated on the basis of arvicolids (POPOV 2001), and can be considered as suggestive for a mosaic landscape under a relatively warm and dry climate. Being in mind, however, that the Pliocene and Early Pleistocene shrews with pigmented teeth were adapted to mild climates (warm, temperate, humid), (REUMER 1989) the relative terms of the above interpretations should be emphasized.

The location of the species optima along the above identified gradients (Fig. 11b) may be helpful in inferring the species ecological preferences. Taxa that are common to most sites occurs near the origin of the plot (*P. hungarica, B. fissidens*). They appear to have rather wide tolerances (Fig. 11b) and are usually considered as opportunists (REUMER, 1984; RZEBIK-KOWALSKA 1994, 2000). The species whose optima are situated on the lower part of the diagram may be considered as more or less mesophilous. Most of them are usually regarded as members of the "forest" group, indicating the presence of a humid sylvan environment (REUMER 1984; RZEBIK-KOWALSKA 1994). In contrast to the above agreements, the ecological interpretation of the species whose optima lie on the upper right-hand side of the ordination diagram is controversial. According to the explanation of the second ordination axis they should be regarded as species positively affected by the occurrence of dry, shrubby, or open habitat patches in the surroundings of a locality. Some of them correspond well to this interpretation, while others do not. The previous consideration of *M. csarnotensis* as an open country dweller (REUMER 1984, RZEBIK-KOWALSKA 1994) agrees with its position on the ordination plot. The locations of *Zelceina soriculoides* (SULIMSKI, 1959) and *Paenelimnoecus pannonicus* (KORMOS, 1934) are also in agreement with their attribution to an "intermediate" group (REUMER 1984, RZEBIK-KOWALSKA 1994). On the other hand, the positions of *Blarinella europaea* REUMER, 1984, *A. gibberodon*, and *Deinsdorfia kordosi* REUMER, 1984 on the ordination diagram is contradictory to earlier interpretations. These species were previously viewed as associated with forests (REUMER 1984; RZEBIK-KOWALSKA 1994, 2000). It should be mentioned however that for the time being the ecological requirements of these species have not been explicitly evaluated. The categorization of *D. kordosi* as a species associated with moist conditions and forests is based on its exoedaenodonty. This type of dentition has been considered as suggestive of a diet consisting of terrestrial mollusks which are especially abundant and active in a moist environment (REUMER 1984). However, according to RZEBIK-KOWALSKA (1994), this dentition was probably efficient not only in feeding on active snails but also to those hidden in shells. Thus, the shrews with such dentition were able to enter a more arid environment where snails were numerous but inactive in dry seasons. *B. europaea* has been attributed to the "forest" group on the basis of the ecological requirements of its living relative *B. quadraticauda* (MILNE-EDWARDS, 1872). According to STORCH & QIU (1996), however, the fossil European taxa show different dental morphology and it is better to place them outside this genus. Correspondingly, it is not necessary to expect similar ecology. A variety of ecological requirements have been postulated for *A. gibberodon*. REUMER (1984) states that it is a warmth-loving shrew which is "...assumed to be indicative for a rather moist and even wet environment, with a good covering of woody vegetation." According to RZEBIK-KOWALSKA 1994) it is indicative only for damp forests. CROCHET (1986) on the other hand found that in SW Europe this species becomes very abundant in the Upper Pliocene karstic localities (as in Varshets) which coincides with a forest regression associated with an appearance of a dry season (AGUILAR & MICHAUX 1984). Accordingly, *A. gibberodon* has been assumed as a species inhabiting forest edges. The consideration of *A. gibberodon* as characteristic for a warm and more or less dry environment corresponds to the occurrence of its close relatives in North Africa (RZEBIK-KOWALSKA 1998) and the Mediterranean parts of Europe (MALEZ & RABEDER 1984; MASINI & SARA 1998). In this context the ordination resulting interpretation of the species on the right upper quadrant of the diagram as forms associated with mosaic landscapes dominated by shrubby and open habitat patches seems more likely. This is especially true having in mind the good agreement for the other species, included in the ordination.

The present analysis is best viewed primarily as an illustrative example and not as a definitive study on the paleoecology of European Plio/Pleistocene soricids. A critical problem is that the species optima shown on the ordination diagram are based on relatively limited empirical data. Thus, these optima are a reflection of the realised niche of the shrew species in the situation, presented by the studied data set, and are an expression of processes acting on different scales (local and regional). It is possible that processes operating on a local scale when summed on a larger scale may produce apparent patterns that are artifacts of the summation procedure. Hence, a larger data set is necessary to confirm the above assumptions.

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