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Late Pliocene voles (Mammalia: Arvicolidae) from Varshets (North Bulgaria)

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Abstract. The filling of a karstic cavity near the town of Varshets (Prebalkan region, North Bulgaria) yielded at least 37 species of small mammals (insectivores, bats, lagomorphs, and rodents). The palaeoecological analysis shows that the assemblage is suggestive of a relatively humid and mild climate and a mosaic landscape with forests and meadows prevailing over the typical steppe vegetation. The extremely abundant and fairly well-preserved fossil remains of six vole species are described in detail. Special attention is paid to their evolutionary level within the context of the main evolutionary trend during this time – an increase in the hypsodonty of the molars. One new species, *Clethrionomys primitivus* n. sp., which represents the most primitive evolutionary stage within the genus, is described. On the basis of the arvicolid assemblage it is suggested that the age of the fauna is late Pliocene (MN 17 zone).

Key words: species composition, systematics, new species, measurements, evolution, palaeoecology, chronostratigraphy, MN17 zone.

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I. INTRODUCTION

In spite of the progress made during the last decades, the Pliocene small mammal fauna of the central territories of the Balkan peninsula is still poorly known. The main part of evidence comes from the Mediterranean areas of the peninsula (DE BRUIJN & VAN DER MEULEN 1979, VAN DER MEULEN & VAN KOLFSCHOTEN 1986, SEN & LEDUC 1996). In this respect the recently discovered paleontological locality Varshets is of particular importance, especially when taking into account its richness (number of remains, number of taxa) and the good state of preservation of the bone material. So far, numerous taxa of birds (BOEV 1995, 1997) and large mammals (SPASSOV 1997a, b) have been recognized and described. The present study reports the first data on the extremely rich small mammal fauna. The vole remains are described in greater detail since they provide the most important evidence of the age of the locality.

II. MATERIAL AND METHODS

The described fossils were found in the reddish clay sediments filling an old karst pot-hole exposed by ancient quarying on the southern slope of Gradichte hill. This hill (about 400 m above sea level) rises in the basin of the rivers of Botunia, Schugavitsa, and their affluents. It is situated about 6 km north-east of the town of Varshets, near the village of Dolno Ozirovo (43° 13' N, 23° 17' E) (Fig. 1). The bone bearing deposit consists of a yellow-reddish weathering residue of the limestone in places cemented by calcite. The sediment contains a small amount of fine, eroded, limestone rubble. The upper part of the sediments in the area near the fissures of the northern wall of the karst pothole (Fig. 2) was covered by fine laminated hidrothermal deposits.

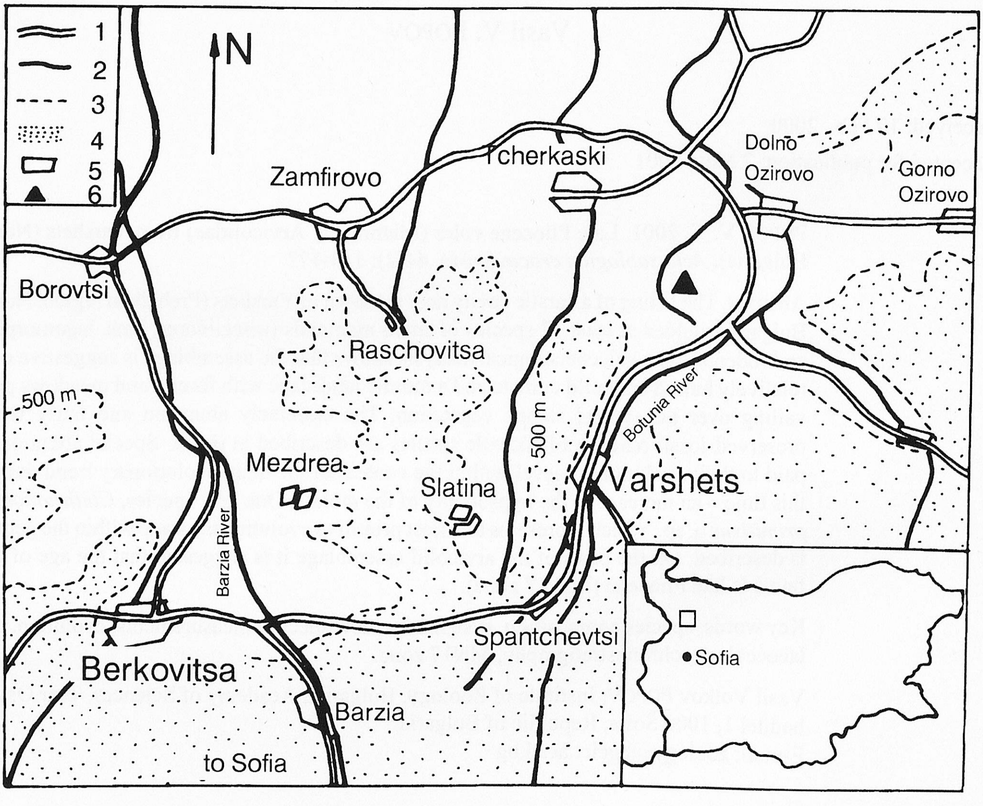

Fig. 1. Geographical situation of the locality. 1 – road; 2 – river; 3 – contour of 500 m a. s. l.; 4 – 500 m a. s. l.; 5 – village; 6 – locality.

During the field seasons of 1989 and 1990 a great amount of sediment was washed through screens (mesh size 0.8 mm) and numerous bones of small vertebrates were collected. Later (1991-1992) Dr. Z. BOEV collected further material, but unfortunately it was obtained by dry sieving (mesh size 2 mm), (BOEV 1995) so the smaller bones and teeth may have been lost. This material was kept separately and is used in the taxonomic part of the study only, while the quantitative palaeoecological analyses were based on the sample obtained by the wet sieving.

The list of species and their quantitative representation (number of molars, obtained by washing, in brackets) is as follows: *Erinaceus samsonowiczi* SULIMSKI, 1959 (5), *Desmana* cf. *polonica* PASHKOV et TOPACHEVSKY, 1990 (3), *Talpa* cf. *csarnotana* KRETZOI, 1959 (34), *Scalopoides* cf. *copernici* (SKOCZEŃ, 1980) (3), *Quyania polonica* (SKOCZEŃ, 1980) (2), *Sorex minutus* LINNAEUS,

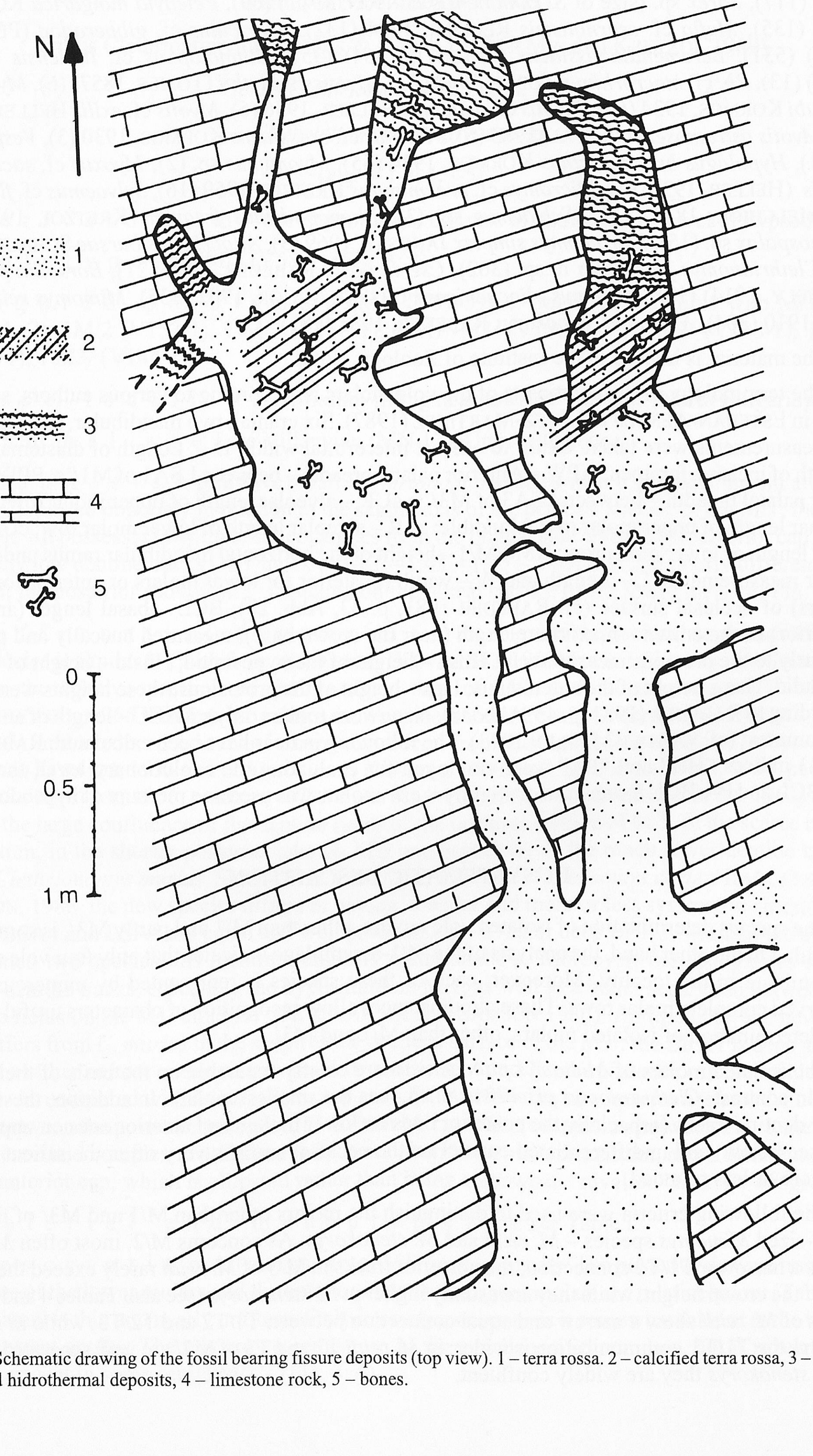

Fig. 2. Schematic drawing of the fossil bearing fissure deposits (top view). 1 – terra rossa. 2 – calcified terra rossa, 3 – laminated hidrothermal deposits, 4 – limestone rock, 5 – bones.

1766 (117), *Sorex* sp. (size of *S. runtonensis* HINTON, 1911) (69), *Petenyia hungarica* KORMOS, 1934 (135), *Mafia* cf. *csarnotensis* REUMER, 1984 (132), *Asoriculus* cf. *gibberodon* (PÉTENYI, 1864) (531), *Beremendia fissidens* (PÉTENYI, 1864) (357), *Rhinolophus* cf. *lissiensis* (MEIN, 1964) (13), *Rh.* cf. *macrorhinus* TOPAL, 1963 (43), *Myotis* cf. *blythii* (TOMES, 1857) (6), *Myotis* cf. *schaubi* KORMOS, 1934 (60), *Myotis* cf. *delicatus* HELLER, 1936 (6), *Myotis* cf. *exilis* HELLER, 1936 (9), *Myotis ostramosensis* TOPAL, 1983 (5), *Plecotus* cf. *crassidens* KORMOS, 1930 (3), *Vespertilio* sp. (1), *Hypolagus brachignathus* KORMOS, 1934 (45), *Myomimus* sp. (2), *Myoxus* cf. *sackdillingensis* (HELLER, 1930) (4), *Micromys* cf. *praeminutus* KRETZOI, 1959 (16), *Sylvaemus* cf. *flavicollis* (MELCHIOR, 1834) (33), *Sylvaemus* sp. (3), *Rhagapodemus frequens* KRETZOI, 1959 (2), *Nannospalax* sp. (15), *Estramomys simplex* JÁNOSSY, 1969 (3), *Allocricetus bursae* SCHAUB, 1930 (9), *Clethrionomys primitivus* n. sp. (362), *Cseria opsia* RABEDER, 1981 (21), *Borsodia petenyii* (MÉHELY, 1914) (10), *Mimomys pliocaenicus* FORSYTH MAJOR, 1902 (335), *Mimomys reidi* HINTON, 1910 (304), *Mimomys stenokorys* RABEDER, 1981 (181).

The material is housed in the Institute of Zoology, Sofia.

The terminology of different parts of the vole molars is, according to various authors, summarized in ESTEBAN-AENLLE & LÓPEZ-MARTINEZ (1987). Six cranial, two mandibular, and eight molar measurements were taken. Skull: Io – Least interorbital width; D – Length of diastema; IFL – Length of incisive foramen; APW – Anterior palatal breadth – between LSA1 of M1/'s; PPW – posterior palatal breadth – between LSA3 of M3/'s; aUR – alveolar length of upper molar row; cUR – coronar length of upper molar row. Mandible: aLR – alveolar length of lower molar row; cUR – coronar length of lower molar row; HMd/M/1 – height of the horizontal mandibular ramus under M/1. Molar measurements: L – Length and W – width (posterior for lower molars or anterior for upper molars) of occlusal surface (cf. RABEDER 1981, p. 43, Abb. 28), BCL – basal length (anterior-posterior) of the crown – maximum length (near the crown base), measured buccally and perpendicularly to the previous measurement; Hhsd – height of the hyposinuid; Hhsld – height of the hyposinulid; Has – height of the anterosinus; Hps – height of the protosinus,(these heights were taken according to RABEDER (1981, p. 46, Abb. 30), on unworn molars only); LACC – length of anteroconid complex, (cf. VAN DER MEULEN 1973). The following indices have been calculated: RABEDER's (1981) indices "HH" and "PA" were employed for evaluating the evolutionary level; the ratios HH/BCL and PA/BCL for unworn or slightly worn molars was used as a measure of hypsodonty.

III. SYSTEMATIC DESCRIPTION

The species determination of isolated vole molars, other than M/1 and partly M3/, is sometimes difficult. On the other hand, the analysis of the M/1-assemblage indicates that only four vole species predominate in the locality. Moreover, each of these species is represented by numerous well-preserved complete molar rows. These circumstances allow recognition of characters useful in species determination of isolated molars, other than M/1 and M3/.

The isolated molars of *Mimomys pliocaenicus* are clearly separable on the basis of their large size. In contrast, *Clethrionomys primitivus* n. sp. has the smallest molars. In addition, these show lower dentine tracks (especially the posterior ones on lower molars and anterior ones on upper molars, see below) and undifferentiated enamel on the occlusal surface; very often the salient angles are more or less rounded.

The following criteria were used to distinguish the molars other than M/1 and M3/ of the two small-sized *Mimomys* species – *M. reidi* and *M. stenokorys*. As concerns M/2, most often *M. reidi* shows a narrower T1/T2 connection; the posterior tracks in M/3 of *M. reidi* rarely exceed the lower half of the crown height, while they are usually higher in *M. stenokorys* (see also Tables 4 and 5); the M1/'s of *M. reidi* show a narrow and equal connection between T1/T2 and T2/T3, while in *M. stenokorys* the T1/T2 communication is wider; in *M. reidi* T2 and T3 of M2/ are well separated, while in *M. stenokorys* they are widely confluent.

Family Arvicolidae GRAY, 1821

Tribus Clethrionomyini HOOPER & HART, 1962 (= Myodini KRETZOI, 1969)

Genus *Clethrionomys* TILESIUS, 1850

Clethrionomys primitivus n. sp.

(Fig. 3: 1-8; 4: 1-5)

Derivato nominis: *primitivus* because of its rather low level of hypsodonty.

Holotype: right M/1 (V58-1) (Fig. 3: 3).

Figured paratypes: 6M/1 (V57-59), 2 fragm. of mandible with M/1-M/3 (V60 -1, 2), 1M/2 (V152-1), 1 M/3 (V158-1), 3 M1/-M3/ (V106: 1-3), 1 M1/ (V118-1), 1 M2/ (V127-1), 1 M3/ (V144-1).

Type locality: karst fissure filling near town of Varshets (North Bulgaria).

Mammal age: Late Villanyian (MN 17), Upper Pliocene.

Diagnosis. A primitive small *Clethrionomys* species with a simple ellipsoid anterior cap (AC), placed obliquely in relation to the sagital axis of the occlusal surface of the M/1; the M3/ is simple – it possesses only three salient angles from the lingual side and a short posterior cap (PC); relatively low dentine tracks (HH-index of M/1 – 1.43 – 1.75 – 2.09; thin and poorly differentiated enamel; the posterior root of M/2 is situated on the dorsal surface of the lower incisive (Fig. 3: 5).

Differential diagnosis. In the shape of the occlusal surface of M/1 the new species is similar to *Clethrionomys kretzoii* (KOWALSKI, 1958) but it differs from the latter species in the relative position of the posterior root of M/2 and incisive; from *C. sokolovi* TOPACHEVSKY, 1965 it differs in having a smaller size, shorter PC of M3/ (see TOPACHEVSKY 1973, fig. 50-3), and a reduced amount of crown cementum; from the Pleistocene species *Clethrionomys acrorhiza* KORMOS, 1933 and *C. hintonianus* KRETZOI, 1958 (=*C. hintoni* KORMOS, 1934, paeocc., = *C. solus* KRETZOI, 1956, praeocc, = *C. intrans* KRETZOI, 1958, = *C. sebaldi* HELLER, 1963) it differs in the large confluence of the dentine fields of the occlusal surface of M/1, in the scarce crown cementum, in the shorter posterior lobe on M3/ and especially in the much lower dentine tracks. From *Clethrionomys murius* SAVINOV & TUTKOVA, 1987 and *Visternomys cortezi* RADULESCO & SAMSON, 1986 the new species differs in having: a wider and more or less symmetric anterior cap — the BSA4 and LSA5 are equal and well pronounced – a rather deep BRA3, while in the abovementioned two species this reentrant angle is rather shallow. Moreover, the last species shows higher dentine tracks, especially the hyposinuid on M/1, as well as a better separation between the dentine fields on the M1/ and M2/ (cf. RADULESCO & SAMSON 1986). Additionally, the new species differs from *C. murius* in the shape of the occlusal surface of the M3/: the BRA1 is deep and as a result a rather narrow connection exists between the AL1 and T2; the posterior cap is considerably shorter. As compared with *Dinaromys allegranzii* SALA, 1996, the new species has broader confluences between the posterior triangles (T1-T3) on M/1, a wider connection between the elements of the anteroconid complex (T4-T5 and AC), more abundant crown cementum, and a different shape of the anterior cap, which is ellipsoid rather than being somewhat "nivaloid" as in *D. allegranzii*.

Material and measurements: see Table I.

Description. All molars except M1/ have two roots. The posterior dentine tracks on the sides of the lower molars and the anterior ones on the upper molars are relatively low (Table 1). The enamel is thin and nearly uniform. Only in some specimens is it somewhat thinner at the tips of the reentrant angles. There is crown cementum in the synclines of the molars, but it is relatively scarce, except in some senile M/1's (Fig. 3: 6).

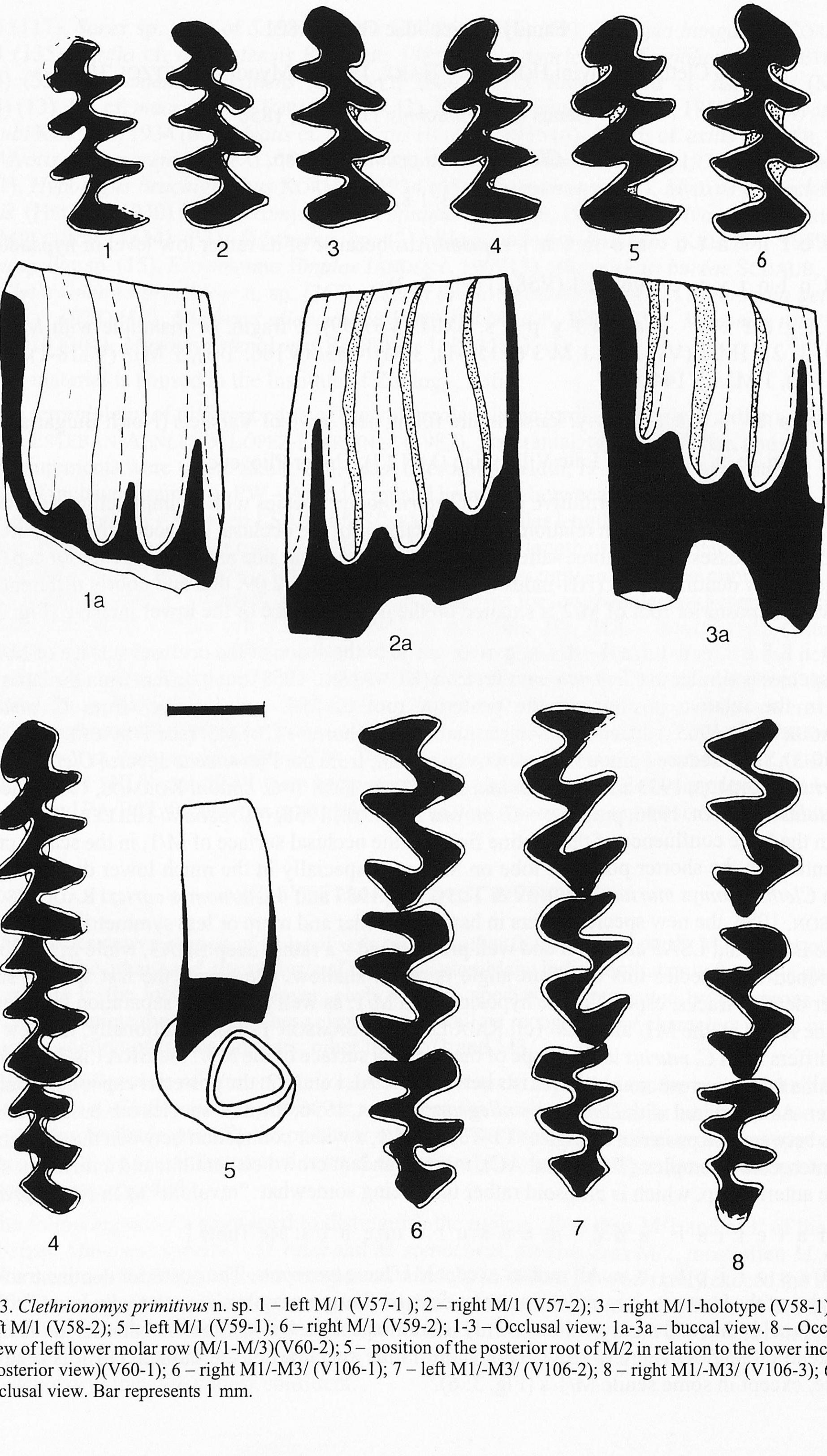

Fig. 3. *Clethrionomys primitivus* n. sp. 1 – left M/1 (V57-1); 2 – right M/1 (V57-2); 3 – right M/1-holotype (V58-1); 4 – left M/1 (V58-2); 5 – left M/1 (V59-1); 6 – right M/1 (V59-2); 1-3 – Occlusal view; 1a-3a – buccal view. 8 – Occlusal view of left lower molar row (M/1-M/3)(V60-2); 5 – position of the posterior root of M/2 in relation to the lower incisive (posterior view)(V60-1); 6 – right M1/-M3/ (V106-1); 7 – left M1/-M3/ (V106-2); 8 – right M1/-M3/ (V106-3); 6-7 – occlusal view. Bar represents 1 mm.

Table I

Measurements and ratios of the molars, mandibles and skull fragments of *Clethrionomys primitivus* n. sp. from Varshets. For abbreviations and manner of measurement see text

	Measurement	N	MIN	MAX	Mean	SD	CV(%)
M/1	L	107	2.00	2.50	2.25	0.109	4.87
	LACC	105	0.75	1.40	0.93	0.091	9.78
	W	105	0.82	1.15	0.97	0.061	6.30
	BCL	28	2.30	2.85	2.42	0.119	4.91
	LACC/L	104	32.00	46.50	41.17	2.44	5.93
	Hhsd	26	0.85	1.62	1.34	0.203	15.16
	Hhsld	26	0.70	1.60	1.09	0.232	21.20
	HH	26	1.43	2.09	1.75	0.182	10.41
	HH/BCL	26	0.60	0.88	0.72	0.071	9.88
M/2	L	97	1.32	1.65.	1.48	0.076	5.15
	W	92	0.72	1.00	0.85	0.068	8.03
	BCL	29	1.52	1.72	1.62	0.051	3.15
	Hhsd	29	0.45	1.42	1.06	0.247	23.23
	Hhsld	26	0.34	1.50	0.93	0.305	32.88
	HH	25	0.71	1.89	1.42	0.350	24.70
	HH/BCL	25	0.44	1.22	0.90	0.278	31.06
M/3	L	85	1.12	1.52	1.34	0.087	6.45
	W	80	0.52	0.87	0.69	0.069	10.00
	BCL	44	1.22	1.67	1.49	0.100	6.74
	Hhsd	36	0.20	1.90	0.84	0.459	54.66
	Hhsld	33	0.30	1.52	0.77	0.379	48.98
	HH	30	0.37	2.43	1.13	0.558	49.53
	HH/BL	30	0.29	1.67	0.752	0.371	49.39
Mandible	cLR	34	4.75	5.55	5.05	0.203	4.02
	aLR	16	5.20	6.05	5.68	0.281	4.95
M1/	L	92	1.82	2.20	2.01	0.085	4.23
	W	85	0.67	1.12	0.88	0.079	8.58
	BCL	65	1.92	2.30	2.12	0.079	3.71
	Has	61	0.35	2.00	1.02	0.360	35.24
	Hps	62	0.25	1.80	0.95	0.343	35.91
	PA	58	0.56	2.43	1.43	0.430	30.07
	PA/BCL	58	0.21	1.68	0.69	0.239	34.73
M2/	L	85	1.40	1.60	1.87	0.085	4.54
	W	86	0.75	1.12	0.87	0.066	7.64
	BCL	59	1.55	1.92	1.71	0.084	4.88
	Has	53	0.25	1.75	1.00	0.406	40.51
	Hps	49	0.20	1.50	0.61	0.293	48.10
	PA	48	0.49	2.19	1.21	0.438	36.11
	PA/BCL	47	0.35	1.29	0.71	0.266	37.38
M3/	L	38	1.20	1.80	1.51	0.125	8.28
	W	37	0.69	1.07	0.84	0.083	9.91
	BCL	20	1.25	2.15	1.82	0.246	13.52
	Has	15	0.32	1.17	0.726	0.292	40.17
	Hps	12	0.25	0.90	0.460	0.201	43.79
	PA	10	0.41	1.23	0.81	0.257	31.85
	PA/BCL	10	0.22	0.68	0.465	0.133	28.30
Skull	cUR	9	4.80	5.60	5.18	0.248	4.78
	aUR	9	5.30	6.00	5.64	0.271	4.80
	APW	3	2.55	2.70	2.65	–	–
	PPW	2	3.60	3.65	–	–	–
	D	2	5.60	6.50	–	–	–
	Io	2	3.70	4.90	–	–	–
	IFL	2	4.30	4.50	–	–	–

M/1. The triangles are largely confluent, especially the T1 and T2; all parts of the anteroconid complex (ACC) are in great confluence.

M/2-M/3. The occlusal surface shows three dentine fields; the semi-opposed triangles are in great confluence and form the first two rhomboid dentine fields, the third (posterior) field is the PC.

M1/ has three roots – there is an additional small but distinct root. The triangles, following the anterior loop on each M1/ or M2/, are alternating and the dental fields are more or less well separated.

M3/ is simple with three well-developed salient angles on each side; its posterior loop is rather short and sometimes bears an incipient fourth outer salient angle separated from the BSA3 by a shallow re-entrant fold; the dentine spaces are confluent in different combinations.

Comparison and discussion. In some respects (the shape of ACC, the simple M3/, the development of the dentine tracks) the remains described above come near to some primitive *Pliomys* and *Dinaromys* species (cf. DE BRUIJN & VAN DER MEULEN 1975, RABEDER 1981, NESIN & SKORIK 1989, TOPACHEVSKY & NESIN 1989, SALA 1996). However, some characters, such as the considerable confluence of the dentine fields of M/1, the normal development of the BSA2 on M3/, the poor enamel differentiation, and the shape of the anterior cap of the M/1 do not make it very probable that they belong to these evolutionary lineages.

The shape of the occlusal surface of the M/1 of the new species strongly resembles that of *Clethrionomys kretzoii,* described from Kadzielnia 1, Poland (KOWALSKI 1958). However, according to the position of the posterior root of M/2, the Varshets remains seem more primitive. This is in agreement with the chronostratigraphical position of the two localities – Varshets (see below) is older than Kadzielnia 1 (NADACHOWSKI 1989).

According to the position of the posterior root of M/2, the mandibles from Varshets are comparable with the Early Pleistocene species, *Clethrionomys sokolovi* (assemblage with *Microtus (Allophaiomys) pliocaenicus*) (TOPACHEVSKY 1965). On the other hand this species seems somewhat more evolved in having more abundant crown cementum, and more complicated M3/, as could be seen in a later publication by TOPACHEVSKY (1973). Moreover, it should be mentioned that the main part of the bank vole remains in these east European localities show a normal (pleurorhizal) position of the posterior root of M/2. They were reported as a separate form under the name *Clethrionomys* sp. The co-occurrence of two so similar forms in one locality seems unlikely. Most probably all these remains belong to a single species with an unstable position of the posterior root of M/2. Most probably *Clethrionomys sokolovi* is a synonym for *C. hintonianus* or *C. kretzoii* (TESAKOV 1996).

According to the data presented in the analysis of the evolution of east European – west Siberian bank voles, presented by TESAKOV (1996), the evolutionary stage of the population from Varshets corresponds to the most primitive forms (*Clethrionomys* sp.), known from the first half of the Late Villanyian (MN17) – Sablya (north Caucasus), Lebyazhie (Western Siberia). They are clearly more primitive (HH-index of M/1 ranges from 1.5 to 2.5) than the populations from the latest Villanyian and earliest Biharian, referred by this author to *Clethrionomys kretzoii*, whose HH-index of M/1 varies from 3.5 to 4.0. Moreover the last mentioned forms show a semipleurorhize position of the posterior root of M/2 (TESAKOV 1996).

On the basis of these comparisons and taking into account the relative chrostratigraphical position of the respective localities, the following phylogenetic lineage may be constructed: *Clethrionomys primitivus* n.sp. – *C. kretzoii* – *C. acrorhisa* (+*C. sokolovi*, + *C. hintonianus*) – *C. glareolus*.

In contrast to RABEDER's (1981) opinion, the co-occurence of *Clethrionomys primitivus* n. sp. and *Cseria opsia* (see below) in the assemblage from Varshets indicates that the first species is not a descendant of the *Cseria* – phyletic lineage, or at least that their division took place much earlier than the latest Pliocene.

Genus *Cseria* KRETZOI, 1959

Cseria opsia RABEDER, 1981

(Fig. 14: 3-9)

1981. *Cseria opsia* n. sp.; RABEDER, p. 59-63, Taf. 3, Fig. 1-3, Abb. 33-43.

Material and measurements: see Table II.

Table II

Measurements and ratios of the lower molars of *Cseria opsia* from Varshets. For abbreviations and manner of measurement see text

	Measurement	N	MIN	MAX	Mean	SD	CV(%)
M/1	L	18	2.17	2.57	2.32	0.115	4.97
	LACC	18	0.70	1.12	0.95	0.103	10.85
	W	18	0.85	1.01	0.96	0.070	7.29
	BCL	9	2.30	2.45	2.38	0.060	2.54
	LACC/L	18	32.26	46.28	40.84	3.719	9.11
	Hhsd	6	0.67	1.62	1.10	0.325	29.6
	Hhsld	6	0.45	0.60	0.515	0.061	11.95
	HH	6	0.81	1.70	1.22	0.310	25.41
	HH/BCL	6	0.35	0.73	0.518	0.137	26.41
M/2	L	3	1.42	1.52	1.46	–	–
	W	3	0.75	0.80	0.77	–	–
Mandible	aLR	2	5.50	5.75	–	–	–

Description. M/1. The anteroconid complex (ACC) is a simple dentine field, consisting of two triangles and an asymmetrical elongated, ovoid, anterior cap; only in one very young specimen is there a trace of an enamel islet; another aberrant specimen bears a vestigial trace of a "*Mimomys*" ridge; in the majority of specimens the dentinal spaces are largely confluent, but in some others, in advanced stages of wear, the triangles are rather tight. The enamel is not differentiated or, in some adult specimens, it is slightly thinner on the tips at the infolds and salient angles. There is no crown cementum. The dentine tracks, especially the posterior ones, are rather low (Fig. 14: 3a-5a).

M/2: the two pairs of the triangles are semi-opposed, forming two rhomboid dentine fields.

Remarks. The material described above is very similar to the samples from Stranzedorf D and F, denoted as *Cseria opsia* (RABEDER 1981). The differences are not impressive and concern only the somewhat higher values of the HH-index of the form from Varshets (Table II). This difference indicates that the Varshets chronopopulation is somewhat more progressive. This is confirmed by the circumstance that the size and height of the posterior dentine track of the single M/1 from layer G of Stranzedorf, designated as *Cseria* cf. *opsia* (RABEDER 1981), falls in the middle part of the range of variability of the Varshets sample.

Although the shape of the occlusal surface of M/1 of *Cseria opsia* is reminiscent of that of the Early Pleistocene species *Villanyia exilis* KRETZOI, 1956 (type locality Villany 5, Hungary), it is readily distinguishable by its higher dentine tracks and lower values of the LACC/L index (cf. TERZEA 1991). On the basis of the first character, the form from Varshets seems more evolved. In contrast, the relatively short anterior cap and the shorter anteroconid complex should be interpreted as primitive characters. These observations lead to the hypothesis that *Cseria opsia* represents an early specialized side branch in the phylogenetic derivation of the enigmatic group "*Cseria (? Ungaromys) – Villanyia* KRETZOI, 1956" and, in particular, is not a direct ancestor of *Villanyia exilis* (TERZEA 1991).

Tribus Lagurini KRETZOI, 1955

Genus *Borsodia* JÁNOSSY & VAN DER MEULEN, 1975

Borsodia petenyii (MÉHELY, 1914)

(Fig. 4: 6-7)

1914. *Mimomys Petenyii* n. sp. (partim), MÉHELY, p. 191-194, Taf. IV: 5-7, Taf. VIII: 2-3.

Material and measurements: see Table III:

Table III

Measurements of the lower molars of *Borsodia petenyii* from Varshets. For abbreviations and manner of measurement see text

L	W	BLC	HC	Hhsd	Hhsld
2.45	1.00	–	–	–	–
2.57	1.10	2.55	2.02	2.05*	2.12*
2.80	1.25	2.92	1.55	–	–
2.60	1.10	2.65	1.62	1.60*	1.82*
2.82	1.25	2.95	2.37	2.37*	2.70*

* the real values are higher since the teeth are relatively worn.

Description. The anteroconid complex (ACC) bears a *Mimomys* – ridge bordered by well expressed both prism- and isle-fold. As a rule the isle-fold is not far reaching downwards to the crown side. The prism fold is more extended, but it is wide and rather shallow. On the *Mimomys* -ridge there is always an enamel interruption (mimosinuid) which is a branch of the anterior dentine track (anterosinuid). The posterior dentine track (hyposinuid) is very high, reaching the occlusal surface at the earliest stages of tooth-wear. The enamel is thin and poorly differentiated – on some prisms it is somewhat thicker on the anterior walls. There is no crown cementum. The dentine fields of the basic triangles (T1-T3) are more or less well separated.

Remarks. In some respects the molars described above are reminiscent of certain *Mimomys* species, without an enamel islet on M/1, such as *Mimomys stenokorys*. The main differences between these genera concern the opposite type of enamel differentiation and the presence (in *Mimomys*) or the absence (in *Borsodia*) of crown cementum. On the other hand in some young *Mimomys* specimens the enamel is thin and not differentiated and the cementum is scarce and poorly visible. Such molars were separated from the true *Borsodia* specimens on the basis of their long isle fold reaching the basis of the crown and the lack or poor development of the mimosinuid.

Initially *Borsodia* was considered as a subgenus of *Mimomys*. Here RABEDER's (1981) opinion is followed that it should be considered as a separate genus, which represents a primitive evolutionary stage within the tribe *Lagurini*.

According to the shape of linea sinuosa (RABEDER 1981), the molars from Varshets are very similar to the two late Pliocene species – *Borsodia altisinuosa* RABEDER, 1981 from Starnzendorf

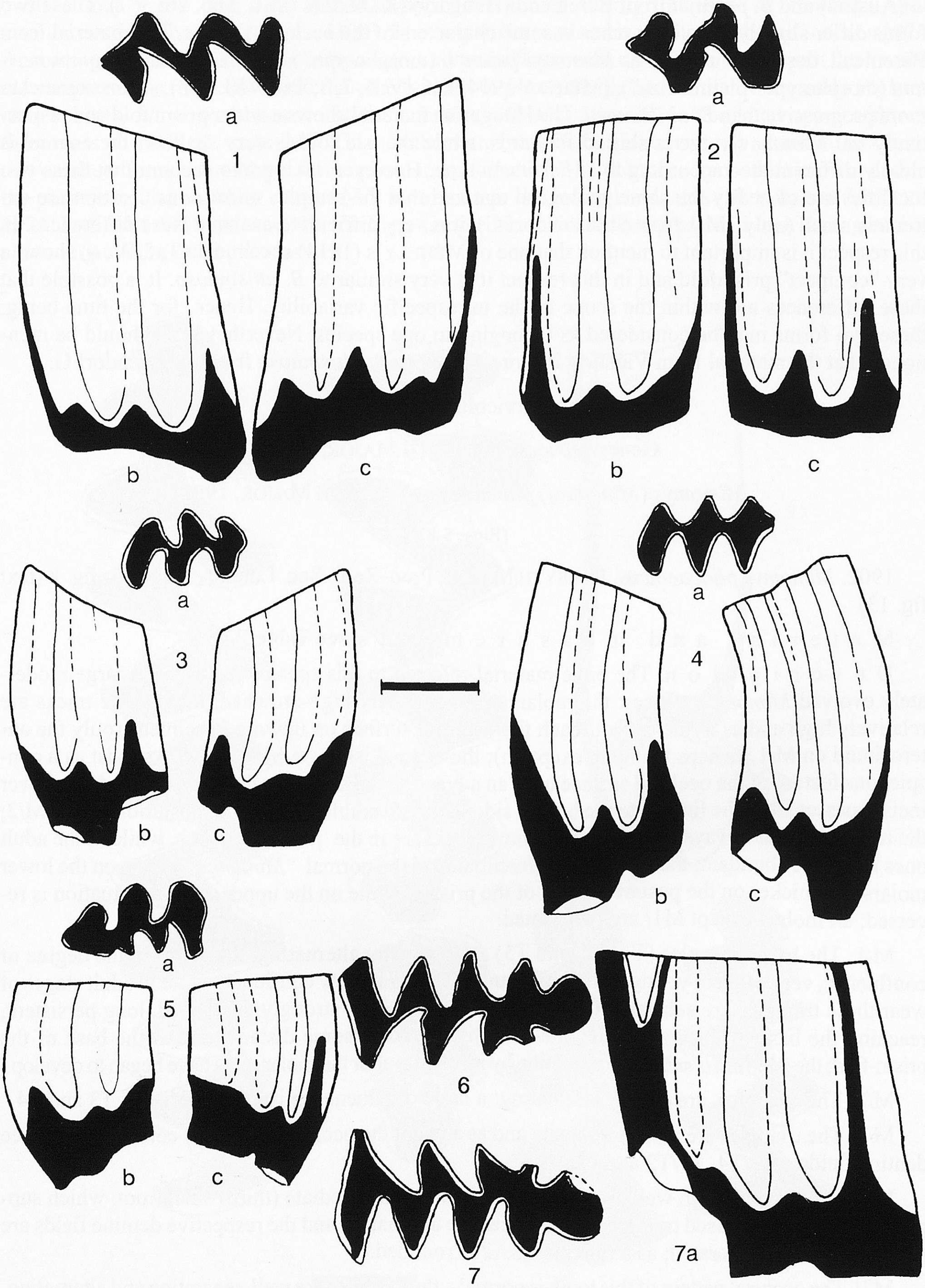

Fig. 4. *Clethrionomys primitivus* n. sp. 1 – left M1/ (V118-1) a. occlusal view, b. buccal, c. lingual; 2 – left M2/ (V127-1) a. Occlusal view, b. lingual, c. lingual; 3 – left M/3 (V158-1) a. occlusal view, b. buccal, c. lingual; 4 – left M/2 (V152-1) a. occlusal view, b. buccal, c. lingual; 5 – left M3/ (V144-1) a. occlusal view, b. buccal, c. lingual. *Borsodia petenyii* . 6 – right M/1 (V65-1), occlusal view; 7 – left M/1 (V65-2), occlusal view, 7a. buccal view. Bar represents 1 mm.

G (Austria) and *B. petenyii* from Beremend (Hungary) (RABEDER 1981, Abb. 46: 3, 7). These two forms differ slightly from each other in some characters of the occlusal surface. The material from Beremend, described initially as *Mimomys petenyii* (morphotype "acrorhiza") and *Mimomys newtoni* (morphotype "pleurorhiza"), (MÉHELY 1914, Taf. IV: 6, 7, 8; Taf. VIII: 2, 3), seems somewhat more progressive than *B. altisinuosa*. The Hungarian material shows a wider prism fold and respectively the *Mimomys* ridge is shifted forwards, while the isle fold is very shallow; the enamel is clearly differentiated according to "*Microtus*" -type. However, taking into account that these two localities are of nearly the same geological age and that the samples under consideration are extremely small (only 1M/1 from Stranzendorf G), it is very difficult to evaluate these differences. In this respect it is important to mention that one of MÉHELY's (1914) specimens (Taf. IV: 6) shows a very "compact" prismfold and in this respect it is very similar to *B. altisinuosa*. It is possible that these differences are within the scope of the intraspecific variability. Hence, for the time being, these two forms may be considered as belonging to one species. Nevertheless, it should be mentioned that the material from Varshets is more similar to *B. altisinuosa* from Stranzendorf G.

Tribus Arvicolini GRAY, 1821

Genus *Mimomys* FORSYTH MAJOR, 1902

Mimomys (*Mimomys*) *pliocaenicus* FORSYTH MAJOR, 1902

(Figs. 5-8)

1902. *Mimomys pliocaenicus,* FORSYTH MAJOR. Proc. Zool. Soc. London, 1, p. 103, fig. 8 (text fig. 13)

Material and measurements: see Table IV.

Description. The bone material referred to this species represents a large moderately evolved *Mimomys* species: the molars are moderately high-crowned; the dentine tracks are relatively high and as a rule do not reach the occlusal surface on unworn specimens (only the anterosinuid on M/1 perhaps being an exeption); the enamel islets on M/1 and M3/ persist as a conspicuous feature of the occlusal surface until an advanced stage of wear has been reached; the lower incisor passes from the lingual to the buccal side of the mandible beneath the posterior root of M/2; the reentrant folds always contain cementum; it is scarce in the juvenile molars, while in the adult ones it is more abundant; the enamel is differentiated to the normal "*Mimomys*" type – on the lower molars it is thicker on the posterior walls of the prisms, while on the upper ones the situation is reversed; all molars except M1/ are two rooted.

M/1. The basic triangles (T1, T2, and T3) are distinctly alternating; they vary in the degree of confluence, very often in young teeth the T1 and T2 being largely confluent, while in adult stages of wear these triangles are substantially closed; the prismfold is strongly developed, long persistent, reaching the base of the crown; the isle-fold disappears at some distance above the base of the prism-fold; the isle-fold is subject to reduction by insulation after the molar roots have began to develop.

M/2. The triangles are clearly alternating; a large confluence exists only between T3 and T4.

M/3. The triangles are almost opposite and as a result the occlusal surface is composed by three dentine fields – T3/T4, T1/T2 and PL.

M1/. On the teeth with well grown roots there is an intermediate (third) small root, which supports the inner first closed triangle; the triangles are alternating and the respective dentine fields are more or less well separated; as a rule the LSA2 is rounded.

M2/. The occlusal pattern of this tooth is normal – the triangles are well-separating and alternating.

M3/. The LRA3 is subject to reduction by insulation and the resulting enamel islet is a long persistent feature; the grinding surface consists of three well separated dentine fields – AL1, T2, and a posterior field, comprising T3, a weak vestige of T4 and PC.

Remarks. The teeth described above are almost exactly like those of *Mimomys pliocaenicus* as described by HINTON (1926). The only difference concerns the number of roots on M2/. According to HINTON (1926) *M. pliocaenicus* posesses three roots on M2/. In this respect the Varshets sample seems more advanced than the typical *M. pliocaenicus* and similar to the early Pleistocene species, *M. osztramonensis* JÁNOSSY & VAN DER MEULEN, 1975. The latter species shows three roots on M1/ and two on M2/. On the other hand, this species is more evolved and differs from the Varshets form in the much more ephemeral enamel islet, in the more hypsodont crown, and in the position of the posterior root of M/2 in relation to the incisive (JÁNOSSY & VAN DER MEULEN 1975, RABEDER 1981). Hence, the Varshets sample is considered a representative of a progressive chronopopulation of *M. pliocaenicus*.

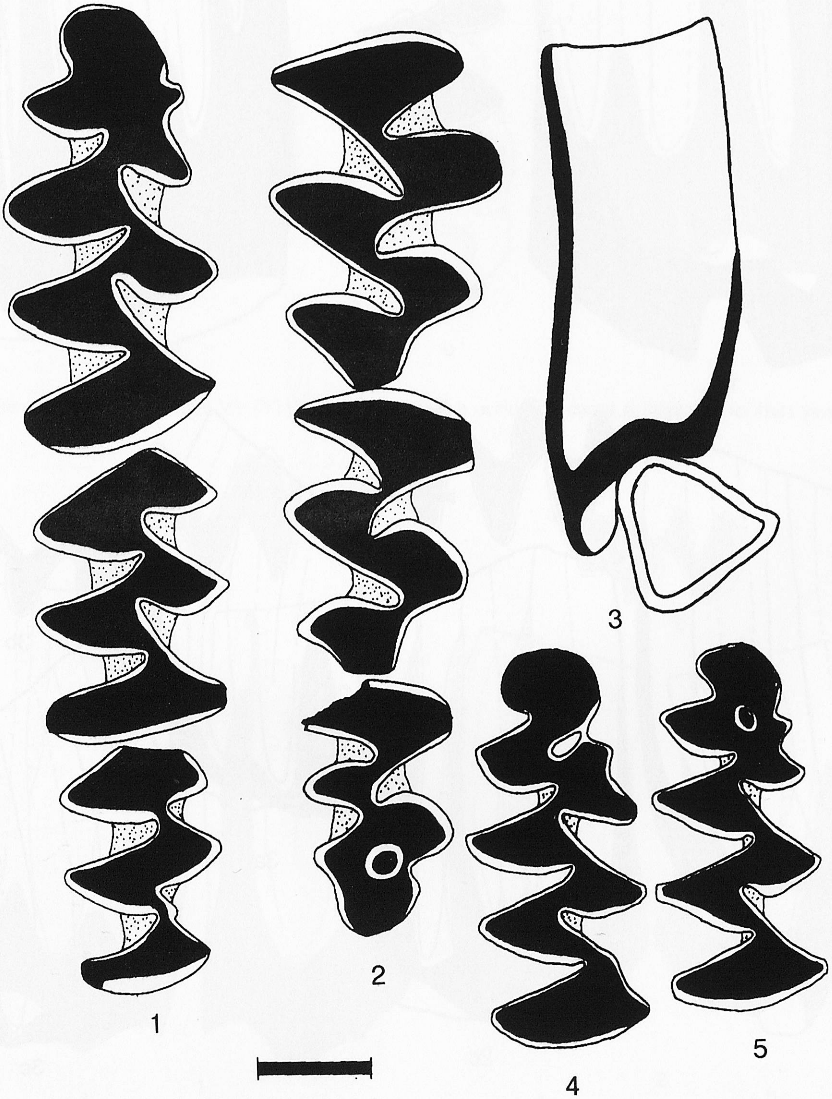

Fig. 5. *Mimomys pliocaenicus*. 1 – right M/1-M/3 (V41); 2 – right M1/-M3/ (V159); 3 – position of the posterior root of M/2 in relation to the lower incisive (posterior view); 4 – right M/1 (V35); 5 – right M/1 (V36). 1-2, 4-5 – occlusal view. Bar represents 1 mm.

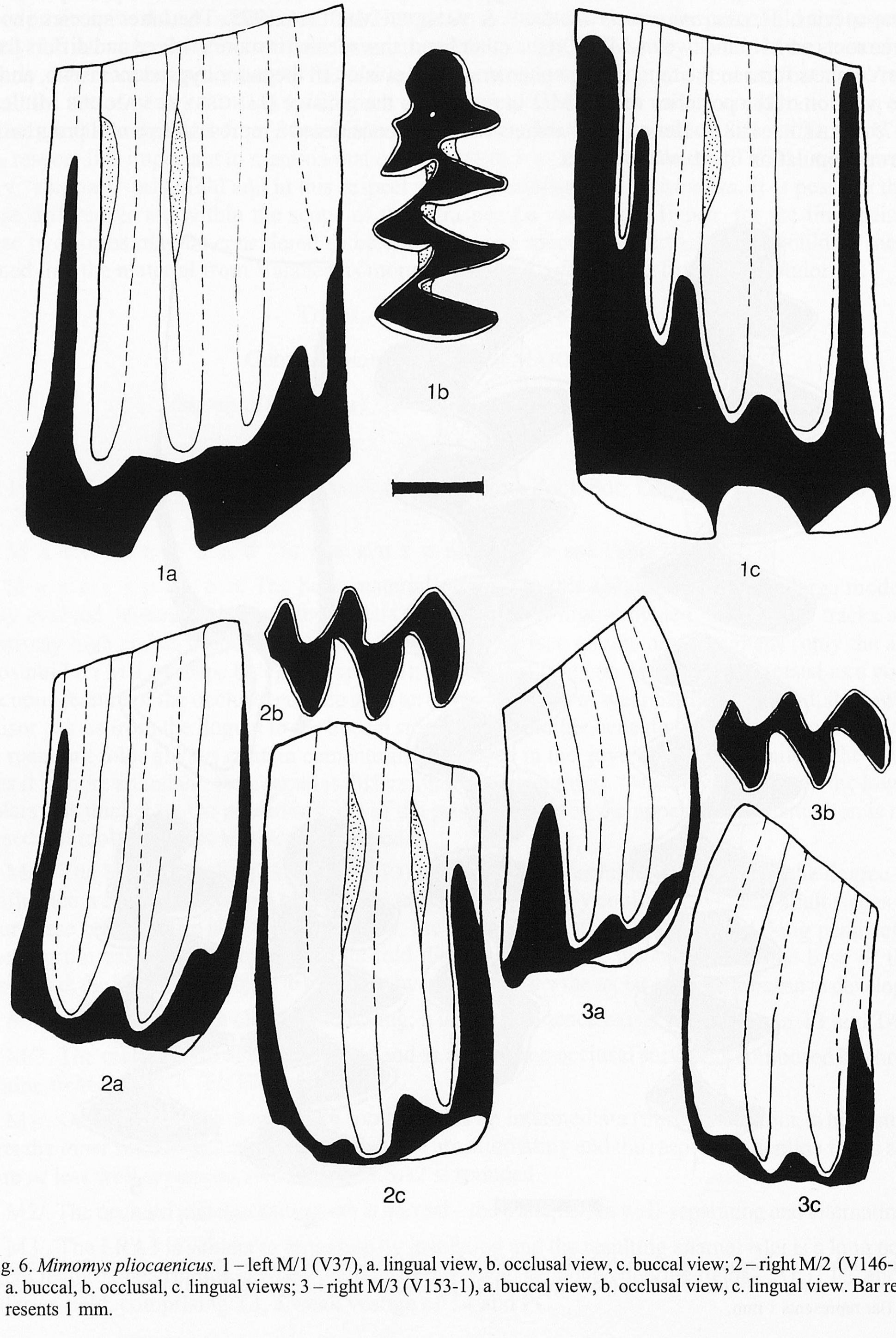

Fig. 6. *Mimomys pliocaenicus.* 1 – left M/1 (V37), a. lingual view, b. occlusal view, c. buccal view; 2 – right M/2 (V146-1), a. buccal, b. occlusal, c. lingual views; 3 – right M/3 (V153-1), a. buccal view, b. occlusal view, c. lingual view. Bar represents 1 mm.

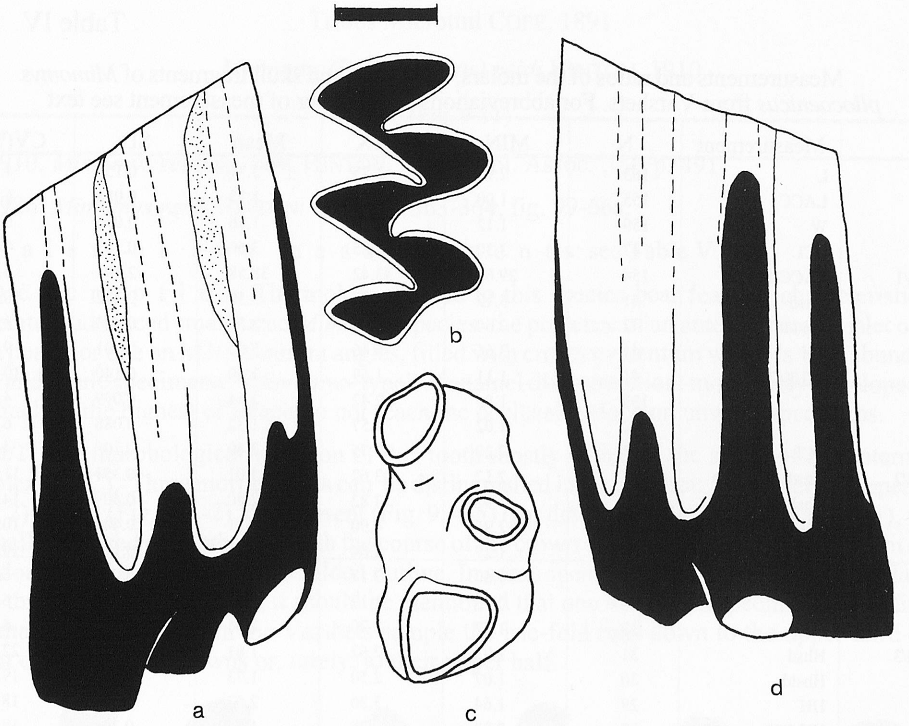

Fig. 7. *Mimomys pliocaenicus* : right M1/ (V113-1). a. buccal view; b. occlusal; c. dorsal, d. lingual views. Bar represents 1 mm.

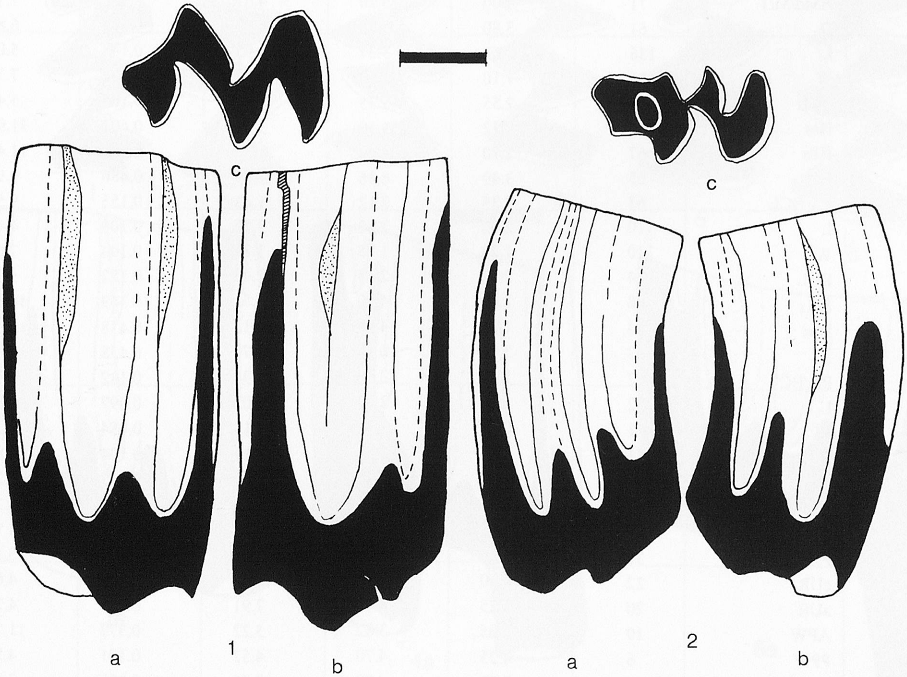

Fig. 8. *Mimomys pliocaenicus* 1 – right M2/ (V124-1), a. buccal view, b. lingual view, c. occlusal view; 2 – right M3/, a. buccal, b. lingual, c. occlusal views. Bar represents 1 mm.

Table IV

Measurements and ratios of the molars, mandibles and skull fragments of *Mimomys pliocaenicus* from Varshets. For abbreviations and manner of measurement see text

	Measurement	N	MIN	MAX	Mean	SD	CV(%)
M/1	L	163	2.95	3.75	3.31	0.159	4.80
	LACC	155	1.00	1.52	1.28	0.088	6.87
	W	159	1.12	1.80	1.46	0.095	6.50
	BCL	47	3.30	3.85	3.60	0.145	4.03
	LACC/L	154	29.60	43.42	38.58	2.19	5.68
	Hhsd	41	3.12	4.25	3.59	0.372	10.36
	Hhsld	42	2.60	4.62	3.50	0.460	13.14
	HH	41	3.66	6.46	5.02	0.501	9.98
	HH/BCL	41	1.11	1.69	1.40	0.140	10.04
M/2	L	139	1.85	2.42	2.14	0.099	4.67
	W	132	1.02	1.57	1.32	0.088	6.68
	BCL	41	2.20	2.75	2.40	0.108	4.48
	Hhsd	35	2.17	3.62	3.01	0.351	11.66
	Hhsld	29	1.92	3.82	2.80	0.409	14.59
	HH	29	2.96	4.90	4.11	0.440	10.71
	HH/BCL	29	1.27	2.04	1.71	0.175	10.23
M/3	L	94	1.60	2.17	1.87	0.096	5.17
	W	90	0.75	1.12	0.96	0.064	6.66
	BCL	32	1.87	2.20	2.04	0.091	4.45
	Hhsd	31	1.07	2.62	1.81	0.398	22.03
	Hhsld	30	1.07	2.50	1.73	0.329	19.01
	HH	29	1.64	3.30	2.52	0.464	18.40
	HH/BCL	29	0.82	1.72	1.24	0.231	18.61
Mandible	cLR	54	6.90	8.20	7.52	0.311	4.13
	aLR	53	7.70	8.80	8.20	0.359	4.38
	HMd/M/1	71	4.00	5.20	4.67	0.332	7.17
	D	61	3.80	5.80	4.59	0.313	6.83
M1/	L	136	2.62	3.37	2.95	0.148	5.02
	W	131	1.10	1.62	1.35	0.104	7.70
	BCL	74	2.55	3.35	3.01	0.165	5.49
	Has	66	2.22	4.50	3.36	0.401	11.93
	HPs	67	2.70	4.50	3.56	0.409	11.48
	PA	65	3.49	6.36	4.89	0.486	9.93
	PA/BCL	63	1.35	2.12	1.63	0.155	9.53
M2/	L	110	2.02	2.50	2.26	0.100	4.42
	W	110	1.20	1.75	1.37	0.104	7.64
	BCL	74	2.12	2.45	2.43	0.122	5.05
	HAs	68	2.50	4.30	3.52	0.369	10.51
	Hps	64	1.32	4.40	3.12	0.438	14.06
	PA	63	3.41	6.15	4.70	0.458	9.74
	PA/BCL	62	1.41	2.36	1.94	0.182	9.38
M3/	L	72	1.80	2.20	2.02	0.097	4.83
	W	71	0.85	1.37	1.16	0.084	7.24
	BCL	45	1.85	2.32	2.12	0.104	4.89
	Has	41	1.60	3.30	2.50	0.407	16.26
	Hps	39	1.55	2.85	2.00	0.326	16.28
	PA	37	2.33	4.24	3.18	0.469	14.73
	PA/BCL	37	1.06	1.97	1.49	0.226	15.13
Skull	cUR	22	6.70	7.85	7.25	0.292	4.04
	aUR	20	7.25	8.40	7.91	0.335	4.23
	APW	10	2.65	3.82	3.22	0.377	11.71
	PPW	6	4.25	4.70	4.52	0.191	4.24
	D	7	8.20	9.00	8.55	0.309	3.62
	Io	2	4.50	4.60	–	–	–
	IFL	3	5.25	5.80	5.85	–	–

Tribus Microtini COPE, 1891

Mimomys (Pusillomimus) reidi HINTON, 1910

(Fig. 9-11)

1910. *Mimomys reidi* sp. nov. HINTON, Proc. Geol. Assoc. , 21, p. 491.

1926. *Mimomys reidi* HINTON: HINTON: 363-364, fig. 99-66a.

Material and measurements: see Table V.

Description. The molars referred to this species bear features characteristic of a moderately advanced small sized *Mimomys* species: the presence of an anterior enamel islet on M/1 and a posterior one on M3/; reentrant angles, filled with crown cementum which is very abundant in adult and senile specimens; "*Mimomys*- type" of enamel differentiation; moderately developed dentine tracks – the highest of which do not reach the occlusal surface on unworn specimens.

M/1. The morphological variation of this tooth mostly concerns the shape of the anteroconid complex (ACC). Three morphotypes can be distinguished in this respect: 1) enamel islet open (Fig. 9: 3), 2) closed (Fig. 9: 1-2), or 3) absent (Fig. 9: 4-5) (for details see BACHELET et al. 1991), which gradually replaced each other through the course of the crown wear. In only one slightly worn specimen does the enamel islet show a folded outline. In some specimens this islet disappears relatively early through wear. However, it should be mentioned that one very worn specimen still maintains this character. As a rule, in the Varshets sample the isle-fold runs down to the upper third of the height of the unworn crowns or, rarely, to their upper half.

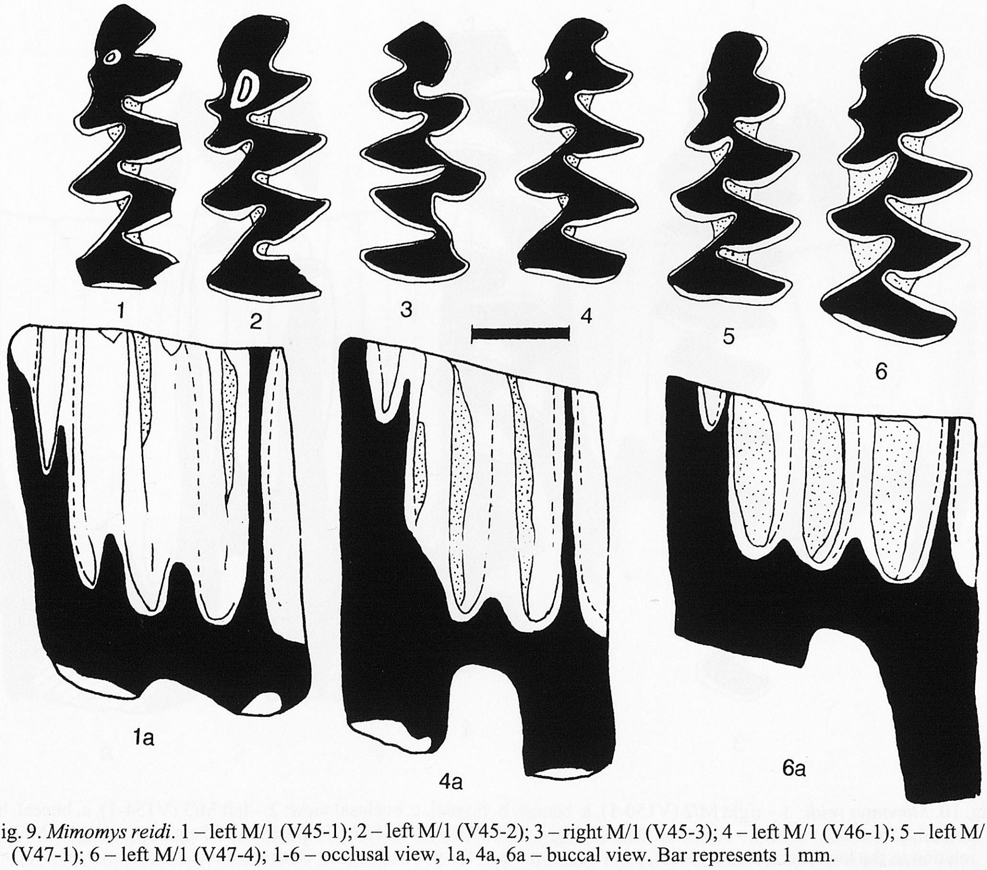

Fig. 9. *Mimomys reidi*. 1 – left M/1 (V45-1); 2 – left M/1 (V45-2); 3 – right M/1 (V45-3); 4 – left M/1 (V46-1); 5 – left M/1 (V47-1); 6 – left M/1 (V47-4); 1-6 – occlusal view, 1a, 4a, 6a – buccal view. Bar represents 1 mm.

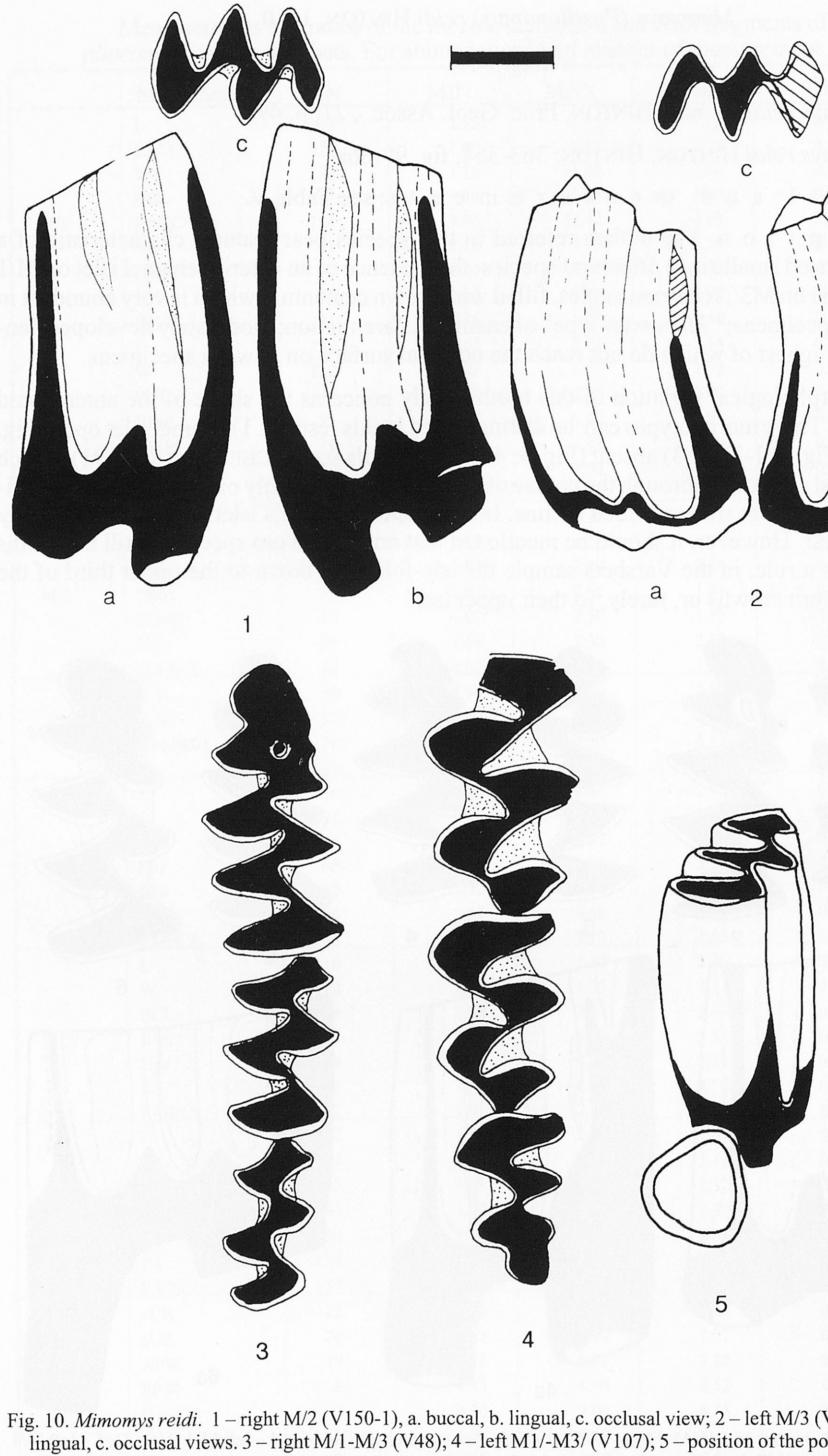

Fig. 10. *Mimomys reidi*. 1 – right M/2 (V150-1), a. buccal, b. lingual, c. occlusal view; 2 – left M/3 (V154-1), a. buccal, b. lingual, c. occlusal views. 3 – right M/1-M/3 (V48); 4 – left M1/-M3/ (V107); 5 – position of the posterior root of M/2 in relation to the lower incisive (V49-12), 3-4 - occlusal view; 5 – posterior view. Bar represents 1 mm.

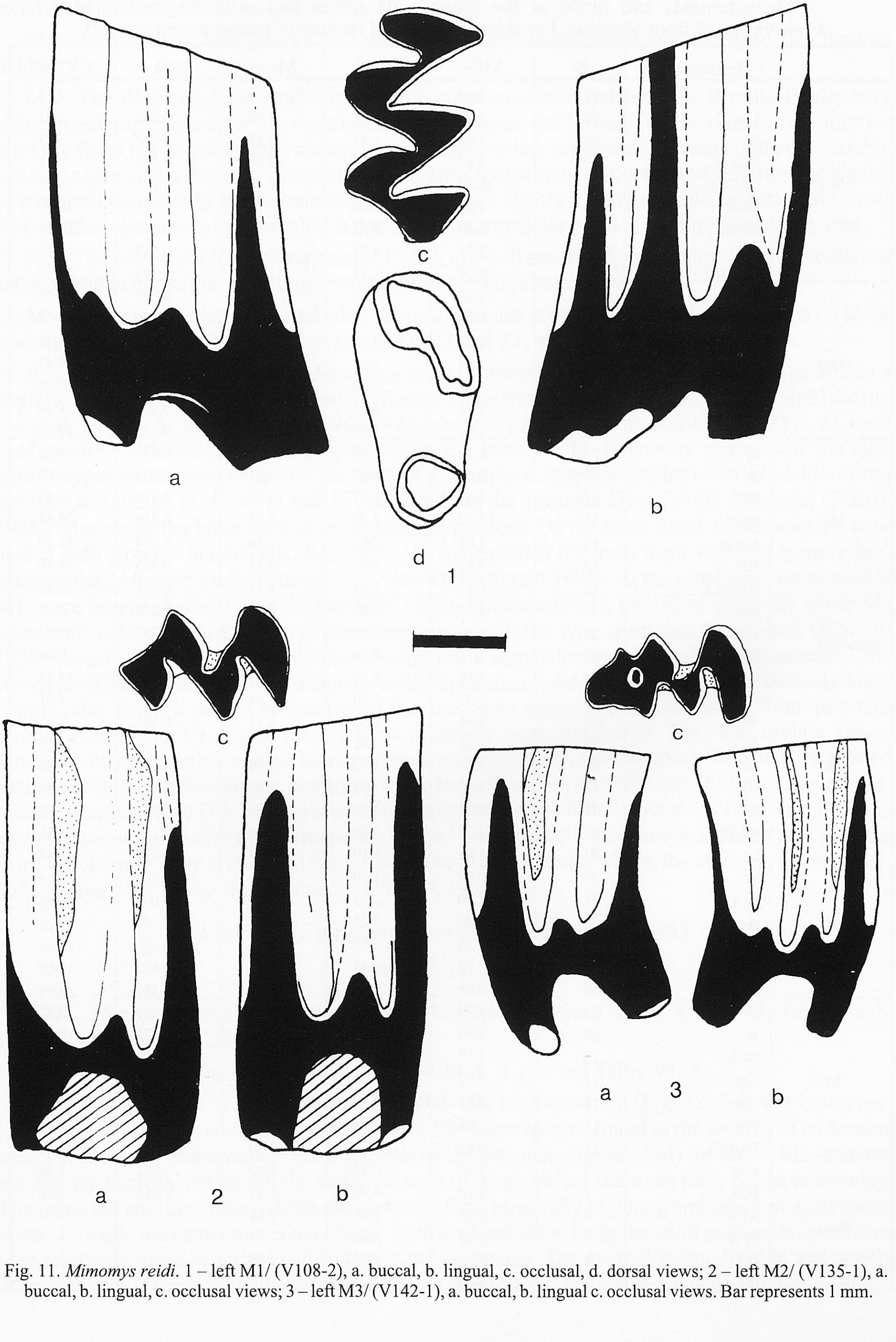

Fig. 11. *Mimomys reidi*. 1 – left M1/ (V108-2), a. buccal, b. lingual, c. occlusal, d. dorsal views; 2 – left M2/ (V135-1), a. buccal, b. lingual, c. occlusal views; 3 – left M3/ (V142-1), a. buccal, b. lingual c. occlusal views. Bar represents 1 mm.

Table V

Measurements and ratios of the molars, mandibles and skull fragments of *Mimomys reidi* from Varshets. For abbreviations and manner of measurement see text

	Measurement	N	MIN	MAX	Mean	SD	CV(%)
M/1	L	92	2.40	3.10	2.78	0.118	4.24
	LACC	92	0.57	1.27	1.02	0.096	9.41
	W	95	1.00	1.37	1.20	0.082	6.83
	BCL	29	2.67	3.32	2.87	0.153	5.32
	LACC/L	92	28.57	45.69	36.58	3.26	8.91
	Hhsd	16	1.35	3.00	2.30	0.477	20.80
	Hhsld	16	1.45	3.32	2.21	0.517	23.43
	HH	16	2.25	4.33	3.20	0.619	19.31
	HH/BCL	16	0.79	1.55	1.11	0.193	17.34
M/2	L	93	1.60	2.00	1.80	0.090	5.03
	W	86	0.90	1.27	1.08	0.076	7.08
	BCL	27	1.72	2.15	1.92	0.104	5.39
	Hhsd	10	1.92	2.67	2.34	0.245	10.47
	Hhsld	7	1.82	2.40	2.09	0.226	10.80
	HH	7	2.82	3.46	3.19	0.268	8.39
	HH/BCL	7	1.44	1.94	1.66	0.194	11.70
M/3	L	75	1.40	1.90	1.60	0.099	6.22
	W	70	0.60	1.05	0.81	0.078	9.62
	BCL	27	1.47	1.97	1.71	0.110	6.43
	Hhsd	16	1.12	2.50	1.47	0.359	24.48
	Hhsld	14	1.02	2.02	1.36	0.314	23.10
	HH	12	1.63	2.87	2.11	0.395	18.76
	HH/BCL	12	0.92	1.55	1.23	0.191	15.58
Mandible	cLR	37	5.90	6.80	6.37	0.265	4.16
	aLR	29	5.90	7.10	6.53	0.297	9.94
	HMd/M/1	53	2.70	4.20	3.49	0.347	9.94
	D	24	3.10	4.50	3.67	0.353	13.22
M1/	L	89	2.22	2.70	2.42	0.097	4.01
	W	86	0.90	1.32	1.11	0.100	9.05
	BCL	55	2.32	2.82	2.53	0.116	4.59
	Has	25	1.92	3.55	2.56	0.460	17.94
	HPs	22	2.45	3.50	2.85	0.281	9.86
	PA	22	3.21	4.70	3.87	0.457	11.79
	PA/BCL	21	1.14	1.90	1.53	0.177	11.58
M2/	L	61	1.82	2.10	1.94	0.072	3.68
	W	59	0.97	1.30	1.15	0.064	5.56
	BCL	41	1.90	2.35	2.06	0.095	4.62
	Has	28	1.95	3.25	2.48	0.352	14.22
	Hps	25	1.75	3.05	2.36	0.370	15.62
	PA	25	2.70	4.46	3.46	0.452	13.06
	PA/BCL	40	0.49	2.07	1.34	0.389	28.99
M3/	L	29	1.50	1.90	1.73	0.101	5.82
	W	29	0.80	1.15	1.00	0.077	7.70
	BCL	16	1.65	1.92	1.79	0.077	1.79
	Has	11	0.85	2.40	1.61	0.519	32.17
	Hps	11	0.55	2.10	1.44	0.499	34.69
	PA	11	1.08	3.12	2.17	0.683	31.44
	PA/BCL	11	0.65	1.78	1.20	0.358	29.78
Skull	cUR	7	5.90	6.50	6.20	0.202	3.26
	aUR	7	6.10	6.70	6.47	0.218	3.38
	APW	3	2.30	2.65	2.48	–	–
	PPW	2	3.50	3.60	–	–	–
	D	3	6.75	7.35	7.03	–	–
	IFL	2	4.40	4.50	–	–	–

M/2. The T3 and T4 are widely confluent, while the other dentine triangles are more or less separated; the PL is the best isolated dentine field; the posterior root treads on the dorsal surface of the incisive, somewhat shifted buccally (Fig. 10: 5).

M/3. Two pairs of triangles (T3/T4 and T1/T2) are widely confluent and form two dentine fields.

M1/. The deep reentrant angles leave little communication between the dentine fields; only some juvenile specimens show a wide connection between the T3 and T4; as a rule the two anterior roots are fused but in some senile molars they are more or less separated; the root number is variable – in some specimens there are two roots – an anterior root which is a compound structure consisting of an anterior large fang and a coalescent, although still clearly distinguishable, intermediate small root; in other specimens their number is three – the intermediate small root being completely free.

M2/. The dentine fields, and especially T2-T3, are well separated; the molar bears two roots, the anterior one being larger, resulting from a fusion of two primary roots.

M3/. There is no anterior enamel islet; the posterior one is present relatively often, even on some worn teeth; the dentine fields, and in particular T2 and T3, are well isolated.

Remarks. In this paper *Mimomys reidi* is considered as an evolutionary stage within a phyletic lineage, comprising the following forms: *Mimomys stehlini* KORMOS, 1931 (sensu BACHELET et al. 1991) – *M. minor* FEJFAR, 1961 (= *M. hintoni* FEJFAR, 1961, in RABEDER 1981) – *M. reidi* – *M. pusillus* (MÉHELY, 1914). In general, on the basis of the frequency changes of the isle-morphotypes with crown wear, the Varshets M/1 -sample is intermediate between *M. stehlini* from Seynez (BACHELET et al. 1991) and *M. pusillus* from the Temnata Cave (North Bulgaria) (POPOV 1986). Moreover, the latter form is much more hypsodont. On the other hand, the characters, connected with crown – height (HH, PA, Table V), indicate that the form from Varshets is more progressive than *Mimomys minor* from Strazendorf D (RABEDER 1981). At the same time, the available M1/'s are nearly identical with the two M1/'s from Stranzendorf G, described under the name *Mimomys* cf. *reidi* (RABEDER 1981). The comparison with the type specimen of *M. reidi* (HINTON 1926) reveals that the M/1-sample under study has a somewhat more primitive appearance – the crown is slightly lower and the frequency of the specimens with an enamel islet is relatively high. On the other hand, it should be mentioned that the lower crown may result simply from the small sample, comprising by chance mainly some relatively worn specimens. The other molars, represented by larger samples, exhibit more pronounced hypsodonty, comparable with that in the related species, *Mimomys plioceneicus,* occurring in the locality, which is presumably at a comparable evolutionary stage (Table IV). These observations indicate that the form under study is nearer, although somewhat more primitive (high frequency of the "enamel-islet" morphotypes), to *Mimomys reidi* from Weybourne Crag (HINTON 1926) than to the previous stage within the above presented phyletic lineage - *M. minor* from Hajnáčka (FEJFAR 1961).

Mimomys (*Pusillomimus*) *stenokorys* RABEDER, 1981

(Fig. 12-14: 1-2)

1981. *Mimomys stenokorys* n. sp., RABEDER, Beitr. Paläont. Österr., 8, p. 147, Taf. 6, Abb. 77-80, 94-96, Sinugr. 4, 5

Material and measurements: see Table VI.

Description. The morals are relatively high-crowned (Fig. 12: 5a), this being particularly evident when compared with the other *Mimomys* species found in the locality. The dentine tracks at the sides of the molars are high, especially the anterosinuid (Asd) on M/1. This structure reaches the occlusal surface in the earliest stages of wear, before the roots have began to develop. The reentrant angles contain a little crown cementum, especially in young and medium aged specimens. As a rule the cementum is not visible from occlusal view. Only the adult and senile specimens bear relatively more abundant cementum in the reentrants. The enamel is usually thin and poorly differentiated. If there is any differentiation, as a rule in adult specimens, it is of *Mimomys*-type.

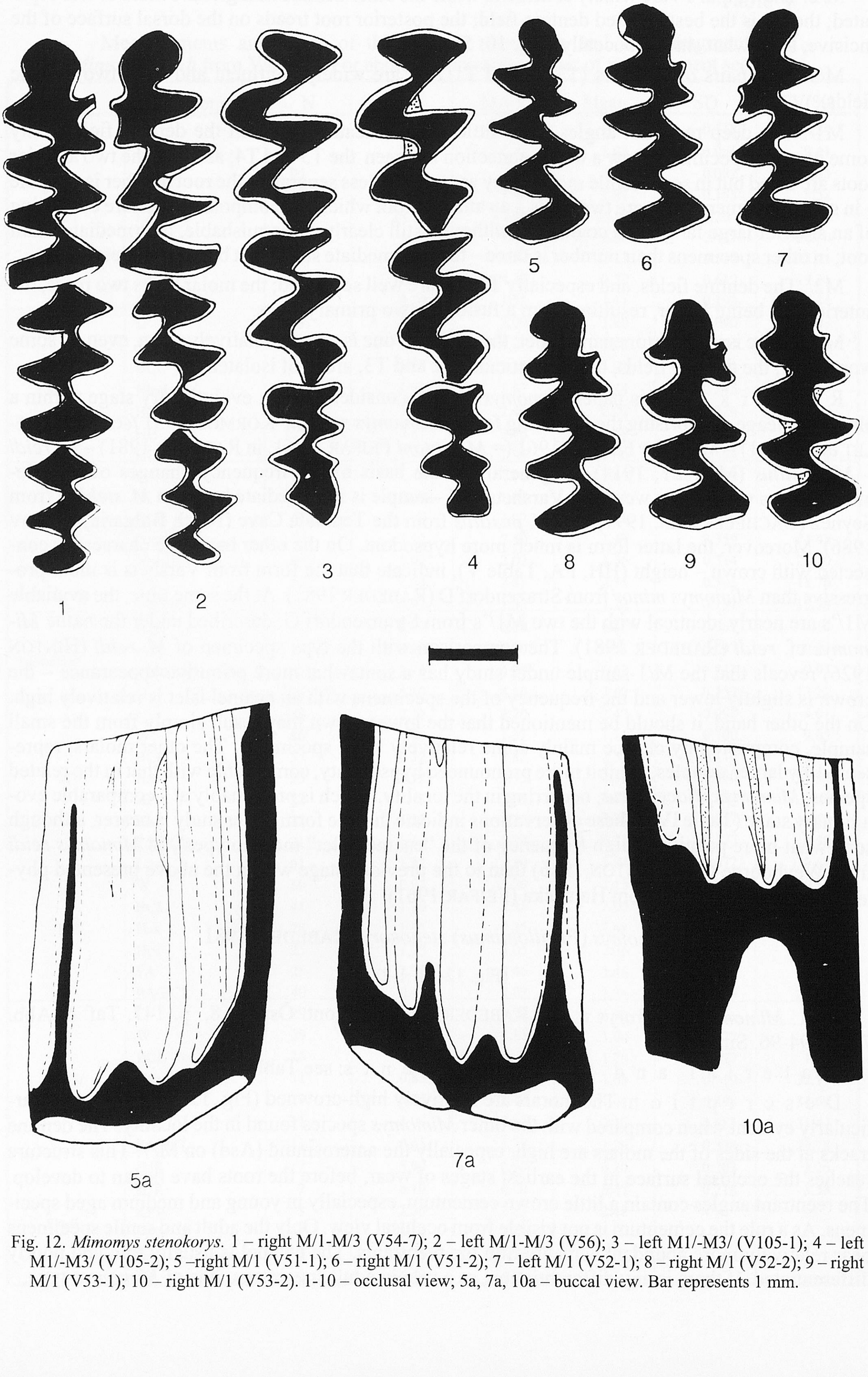

Fig. 12. *Mimomys stenokorys.* 1 – right M/1-M/3 (V54-7); 2 – left M/1-M/3 (V56); 3 – left M1/-M3/ (V105-1); 4 – left M1/-M3/ (V105-2); 5 –right M/1 (V51-1); 6 – right M/1 (V51-2); 7 – left M/1 (V52-1); 8 – right M/1 (V52-2); 9 – right M/1 (V53-1); 10 – right M/1 (V53-2). 1-10 – occlusal view; 5a, 7a, 10a – buccal view. Bar represents 1 mm.

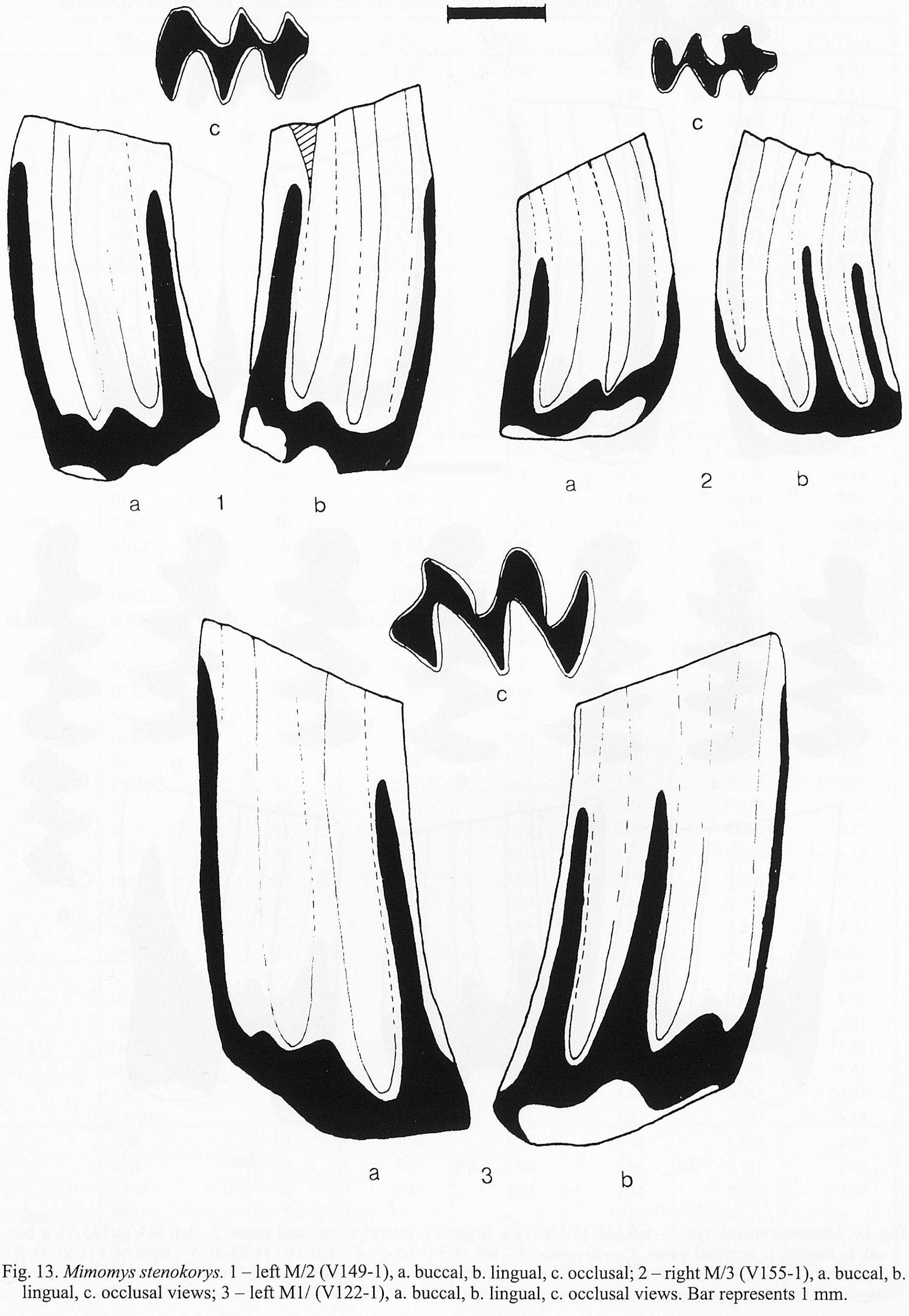

Fig. 13. *Mimomys stenokorys*. 1 – left M/2 (V149-1), a. buccal, b. lingual, c. occlusal; 2 – right M/3 (V155-1), a. buccal, b. lingual, c. occlusal views; 3 – left M1/ (V122-1), a. buccal, b. lingual, c. occlusal views. Bar represents 1 mm.

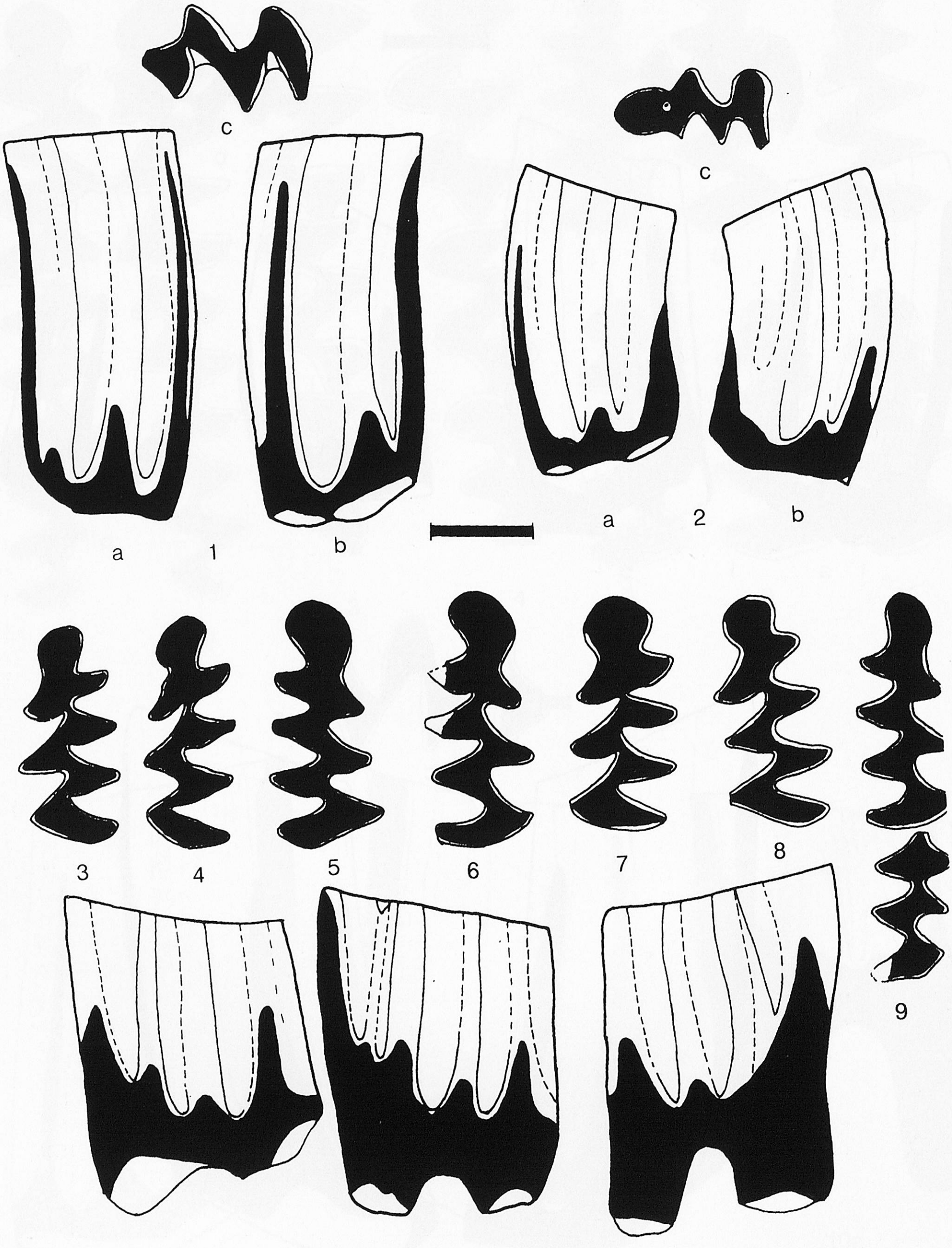

Fig. 14. *Mimomys stenokorys.* 1 – left M2/ (V136-1), a. lingual, b. buccal, c. occlusal views; 2 – left M3/ (V143-1), a. buccal, b. lingual, c. occlusal views. *Cseria opsia.* 3 – left M/1 (V63-1); 4 – left M/1 (V63-2); 5 – right M/1 (V63-3); 6 – right M/1 (V63-4); 7 – M/1 left M/1 (V63-5); 8 – left M/1 (V63-6); 9 – right M/1-M/2 (V64-1); 3-9 – occlusal view; 3a, 4a, 5a. – buccal view. Bar represents 1 mm.

Table VI

Measurements and ratios of the molars, mandibles and skull fragments of *Mimomys stenokorys* from Varshets. For abbreviations and manner of measurement see text

	Measurement	N	MIN	MAX	Mean	SD	CV(%)
M/1	L	65	2.30	2.92	2.60	0.128	4.92
	LACC	65	0.82	1.35	1.06	0.094	8.83
	W	62	0.95	1.27	1.08	0.079	7.31
	BCL	13	2.57	3.37	2.82	0.200	7.10
	LACC/L	65	28.90	48.00	40.73	3.82	9.39
	Hhsd	13	2.65	3.50	3.12	0.239	7.64
	Hhsld	12	2.17	3.32	2.77	0.339	12.21
	HH	12	3.50	4.78	4.17	0.372	8.92
	HH/BCL	12	1.24	1.77	1.48	0.133	8.99
M/2	L	68	1.52	1.85	1.66	0.082	4.93
	W	65	0.82	1.15	0.97	0.079	8.19
	BCL	32	1.65	2.07	1.84	0.101	5.50
	Hhsd	19	2.00	3.15	2.47	0.334	13.52
	Hhsld	17	1.55	2.95	2.32	0.493	21.21
	HH	16	2.73	4.31	3.47	0.450	12.97
	HH/BCL	16	1.65	2.11	1.89	0.172	9.14
M/3	L	47	1.27	1.85	1.47	0.108	7.38
	W	44	0.55	1.07	0.74	0.105	14.18
	BCL	24	1.42	1.87	1.65	0.118	7.17
	Hhsd	10	1.07	1.90	1.46	0.244	16.68
	Hhsld	9	0.82	2.05	1.47	0.443	30.10
	HH	9	1.55	2.80	2.12	0.388	18.27
	HH/BCL	9	0.87	1.60	1.28	0.251	19.57
Mandible	cLR	20	5.40	6.15	5.76	0.229	3.98
M1/	L	58	2.10	2.55	2.24	0.092	4.11
	W	57	0.80	1.17	0.98	0.074	7.55
	BCL	34	2.20	2.65	2.40	0.113	4.73
	Has	29	2.32	3.82	2.92	0.343	11.73
	HPs	28	2.10	3.80	3.07	0.406	13.23
	PA	27	3.38	5.23	4.26	0.464	10.88
	PA/BCL	27	1.40	2.03	1.77	0.177	10.00
M2/	L	87	1.55	2.00	1.74	0.079	4.57
	W	84	0.82	1.17	1.01	0.082	8.17
	BCL	36	1.77	2.17	1.92	0.099	5.19
	Has	25	2.27	3.45	2.99	0.324	10.83
	Hps	27	1.95	3.10	2.67	0.330	12.36
	PA	25	3.07	4.60	4.04	0.395	9.79
	PA/BCL	24	1.57	2.49	2.10	0.216	10.32
M3/	L	35	1.32	1.80	1.57	0.093	5.95
	W	34	0.82	1.07	0.89	0.076	8.53
	BCL	28	1.57	1.90	1.69	0.090	5.31
	Has	19	1.75	2.90	2.34	0.360	15.36
	Hps	22	1.12	2.50	1.88	0.332	17.63
	PA	18	2.46	3.73	3.07	0.441	14.37
	PA/BCL	18	1.38	2.32	1.83	0.277	15.14
Skull	cUR	5	5.30	5.55	5.44	0.108	1.99
	aUR	4	5.70	6.00	5.90	0.141	2.40
	APW	4	2.25	2.82	2.54	0.236	9.30
	PPW	1	–	–	3.65	–	–
	D	1	–	–	6.40	–	–
	Io	1	–	–	4.00	–	–
	IFL	1	–	–	4.45	–	–

M/1. The outer re-entrant folds (the BRA1, BRA2, and isle-fold) are shallow, so the dentine spaces of the basic triangles (T1, T2, and T3) are largely confluent in different combination. These folds, as well as the inner ones, become shallower in lower parts of the crown, so that in advanced stages of wear these triangles and all dentine fields are more confluent. However, as a rule, the basic triangles are substantially separated from the posterior loop and from the anteroconid complex. In the young specimens the LRA4 is relatively deep and the rounded LSA5 is well pronounced. In later stages of wear the latter structure is often obsolete. The prism-fold and *Mimomys*-ridge are well developed and long persistent. There is no trace of enamel islet – the respective re-entrant fold persists as a normal fold throughout the crown instead of being subject to reduction by insulation of its inner part. The relative antero-posterior width of the prism-fold is variable – in old stages of wear the *Mimomys*-ridge shifts anteriorly and this fold becomes wide and shallow (Fig. 12: 10). The mimosinuid is poorly developed or, most often, not pronounced. This feature is very important in distinguishing the young M/1's of this species (which lack crown cementum and the enamel is not well differentiated) from one of the rarest cementless vole species in the locality, *Borsodia petenyii*, a representative of the tribe Lagurini.

M/2 and M/3. The triangles are not perfectly alternating, semi-opposed, and form two widely confluent pairs which are more or less well-isolated from each other and form the posterior loop behind.

M1/. In occlusal view, the tooth consists of a well-separated anterior loop (AL2) and four more or less confluent dental triangles. Most frequently, especially in worn specimens, a large connection exists between T1 and T2, from the one hand and between T3 and T4 from the other. As a rule, in contrast to the other salient angles, the LSA2 is rounded. The M1/ of adult specimens (with more or less well grown roots) bears three roots – two large ones and a comparatively slender intermediate root, supporting the first lingual prism. In one very old specimen this fang is fused with the anterior main root.

M2/. The most characteristic feature of this tooth is the large confluence between the alternating dentine fields of the anterior pair of triangles, T2 and T3, forming a characteristic rhomboid structure, distinctly isolated from the anteriorly and posteriorly situated fields. The number of roots is two. The posterior root is on the dorsal surface of the lower incisor.

M3/. The occlusal surface of this tooth consists of two dentine fields. The anterior one is formed by the large confluence between the AL1 and T2, while the posterior one comprises the T3, the poorly developed T4, and PC. In some specimens these two fields are widely confluent, forming a continuous dentine space. In some unworn teeth there is a trace of a posterior enamel islet, resulting from the reduction of LRA3. However, this structure is almost completely absent in the majority of the available M3/'s.

Remarks. The molars described above fit the definition of subgenus *Pusillomimus* (RABEDER 1981), which is considered to combine some chronologically successive forms. The upper Pliocene part of this phyletic lineage comprises the following three species – *Mimomys stranzendorfensis* RABEDER, 1981 *M. stenokorys* RABEDER, 1981 and *M. jota* RABEDER, 1981. These species have the profile of Stranzendorf, Austria, as their type locality. The Varshets teeth show a distinct similarity with these three forms in general size and dental pattern. The main difference between these forms concerns the development of the dentine tracks (RABEDER 1981), but they are not well-differentiated in this respect, there being a considerable overlap in the respective indices. Nevertheless, it should be mentioned that the M/1 sample of *Mimomys stranzedorfensis* (Stranzendorf D) has a more primitive appearance in having somewhat lower values of the HH-index. As a rule, the variability of the dentine track height and the respective indices (HH, PA) in the *Mimomys* species, presented in the locality by large samples, is considerable (Tables IV-VI). Thus, taking into account the small samples from Stranzendorf, it may be supposed that at least *Mimomys stenokorys* and *M. jota* should be considered as representatives of one species, which according to the rules of zoological nomenclature should be named *Mimomys stenokorys*. The material from Varshets is almost identical with these forms and covers their compiled variability (Table VI).

IV. DISCUSSION

Palaeoecology

The small mammal assemblage from Varshets is dominated by two groups – shrews and voles. According to the palaeoecological analysis, presented by REUMER (1984), the most abundant shrew species, *Asoriculus* cf. *gibberodon*, is "indicative for a rather moist or even wet environment, with a good covering of woody vegetation". The remaining species can be considered as opportunists, living in forests, grasslands, marshes, and shrubby areas (REUMER 1984). Nevertheless, bearing in mind the ecology of the still living species, *Sorex minutus*, it may be supposed that these ubiquitous shrews had a preference for a more or less mesophilous environment with a good covering of vegetation.

Three species of almost equal abundance dominate amongst the voles – *Clethrionomys primitivus* n. sp., *Mimomys pliocaenicus,* and *Mimomys reidi.* As pointed out above, *Clethrionomys primitivus* n. sp. is assumed to be at the beginning of the phyletic lineage leading to the recent bank vole, *Cethrionomys glareolus.* Thus it can be supposed that the fossil form, like its modern-day descendant, preferred wooded landscapes under a relatively humid climate, inhabiting the forest wedges. Analogously, it can be assumed that *Mimomys pliocaenicus* had a habitat preference similar to its living descendant *Arvicola terrestris* (CHALINE & LAURIN 1986) i.e. vegetated banks of rivers and streams, or mesophilous bushes and meadows (TOPACHEVSKY et al. 1987). These actualistic extrapolations are based on the presumption that the fossil and extant taxa are end points of two anagenetic phyletic lineages, i. e. each of them evolved within a constant ecological niche. The other two abundant species, *Mimomys reidi* and *Mimomys stenokorys*, having a more or less evolved structure of their molars, probably lived in an environment similar to that of the recent Microtini. Perhaps they inhabited more or less mesophilous open territories. This assumption is confirmed by the circumstance that these species are relatively rare in the simultaneous faunas (Khaprovian faunal complex) from the supposedly dry steppe landscapes of the southern part of the Russian plain (TOPACHEVSKY & NESIN 1989, TOPACHEVSKY et al. 1987) and the southern part of western Siberia (ZAZHIGIN 1980). In contrast, *Borsodia petenyii,* which represents an early evolutionary stage within the phyletic lineage, leading to the typical Quaternary steppe dwellers of the tribe Lagurini (RABEDER 1981), is in low number in the assemblage from Varshets, while it is among the dominant species in the respective eastern faunas (from the southernmost part of the Russian plain to south-east Kazakhstan) (TOPACHEVSKY et al. 1987). Its descendants or close relatives, belonging to the genera *Lagurodon, Prolagurus, Lagurus*, and *Eolagurus* are usually in great quantity in the Pleistocene assemblages in this part of the country, even in the semi-mountain areas. This indicates that the climate which existed when the bones were being accumulated was not so dry and continental, and that the open patches, which no doubt occurred in the surroundings, were covered by meadows, not steppes. In the same direction can be interpreted the poverty of some other steppe elements, such as the small hamsters and the underground inhabitants such as *Cseria opsia* and *Nannospalax* sp. The scarcity of some species preferring dry and shrubby habitats, such as *Erinaceus samsonowiczi, Miomymus* sp., and *Rhagapodemus* cf. *frequens* leads to the same conclusion.

The occurrence of a mesophilous environment under relatively mild and even climate is confirmed by the (presumed) ecological preferences of some other species. The proximity of a water basin or river is indicated by the presence of *Desmana* cf. *polonica*. It is likely that *Micromys* cf. *praeminutus* also preferred relatively wet biotopes, such as the vegetated banks of these water basins. The occurrence of some "exotic", for this part of Eurasia, species such as *Scalopoides* cf. *copernici* and *Quyania polonica,* deserves special attention. Some of their relatives are still living in restricted areas of East Asia (Japan) and North America (the Pacific coast) this being a relic situation. Today, the extant species occur under relatively humid and mild conditions and require a cover of trees or shrubs. The presence of *Talpa* cf. *csarnotana*, *Myoxus* cf. *sackdillingensis, Sylvaemus* cf. *flavicollis*, *Sylvaemus* sp. is further evidence of fairly humid conditions with a good covering of woody vegetation. The postcranial morphology of *Hypolagus brachignathus* indicates that this hare was relatively heavy and sturdy, not so adapted to running on dry terrain as the recent species, *Lepus capensis* Linnaeus, 1758 (SYCH 1965). Most probably the fossil species favoured more mesophilous open and bushy habitats.

On the basis of these analyses it can be seen that the assemblage is dominated entirely by mesophilous species. Most of them are suggestive of wooded landscape. On the other hand, the meadow dwellers and species preferring wet biotopes also show a considerable quantitative representation. The more or less xerophilous species indicative of dry habitats such as rocky areas and patches of steppes are very few and scarce. This ecological composition doubtless indicates a relatively humid climate and forested environment with large meadows and open water.

On the basis of the species composition of the association of large mammals, and especially taking into account the considerable predominance of deer remains, SPASSOV (1997a,b) presents a similar environmental reconstruction – a mosaic landscape of forests, park-forests, shrubbery, and open terrain.

The division between arvicolids and murids in Plio-Pleistocene assemblages is often used as an indication of the prevailing climatic conditions. This approach may also serve as a check on the indications arrived at along the above lines of reasoning. The representatives of the first group are usually considered to be characteristic of a temperate climate, while the second group is assumed to be indicative of a relatively dry and warm climate (VAN DER MEULEN & VAN KOLFSCHOTEN 1986). Thus, the poverty of murids in the Varshets assemblage most probably indicates a cool and fresh climate, especially bearing in mind that this group tends to be better represented in karst fissure assemblages. On the other hand, the composition of the bat assemblage, and particularly the presence of horseshoe bats (*Rhinolophus* spp.), suggests a moderately worm climate, similar to the recent one in this part of the country. This is confirmed by the circumstance that many of the most abundant species, such as *Asoriculus gibberodon*, *Beremendia fissidens*, *Petenyia hungarica*, and *Mafia csarnotensis* disappeared completely during the early Pleistocene, which might be explained by the effect of a general trend towards a cooling and drying of the climate.

In conclusion, the mammal assemblage from Varshets suggests a relatively humid and mild climate and a mosaic landscape with forests and meadows prevailing over the typical steppe vegetation.

Age of the fauna

A characteristic feature of the Varshets assemblage is that it contains only voles with rooted molars. MEIN (1979) draws the Neogene/Quaternary boundary (MN17/Q1) on the basis of the appearance of the first rootless voles of genus *Microtus*. Hence, the assemblage under consideration should be referred to the Pliocene.

The evolution of *Mimomys* species in Europe, and especially of the large forms, has been the subject of recent studies (KOWALSKI 1960, JÁNOSSY & VAN DER MEULEN 1975, RABEDER 1981, CHALINE & LAURIN 1986) and provides possibilities for more detailed chronostratigraphical correlations. In this respect *Mimomys pliocaenicus* seems to be the best stratigraphical marker among the voles presented in the assemblage, indicating the lower half of the Villanyian stage – the so-called Beremendian (sensu RABEDER 1981). This is confirmed by the fact that the beginning of the next phase of Villanyian is marked by the first appearance of voles with rootless molars – the representatives of the genera *Lagurodon* and *Microtus (Allophaiomys)*.

As follows from RABEDER's (1981) study on the molar evolution within some vole phyletic lineages, based on evidence from some Austrian localities, the well-stratified profile in Stranzendorf covers the entire timespan of this chronostratigraphical unit (Beremendian). The evolutionary level of the Varshets voles, such as *Mimomys pliocaenicus, M. stenokorys, Borsodia petenyii, Cseria opsia*, is nearly the same as in the respective species from the middle part of this section – Stranzendorf G (for details see the taxonomic part). According to the absolute dates this layer is slightly older than 2.14 Ma (RABEDER 1981). Taking into account that, in some cases, the biometrical variability within the large species samples from Varshets covers the ranges of more than one of the "chrono-species" from Stranzendorf (for example *Mimomys jota – M. stenokorys*, *Borsodia altisinuosa – B. petenyii*), it may be assumed that the time span of Varshets lies between 2.04 Ma – Stranzendorf I (layer with *M. jota*) and 2.4 Ma – Stranzendorf D (the voles in this layer are distinctly more primitive).

On the basis of an analysis of the large mammals, SPASSOV (1997a, b) comes to a similar conclusion, that is to say that the fauna should be referred to the middle part of biochronological zone MNQ 17 (about 2.23 Ma B. P.), somewhat earlier than the reference locality St.-Vallier (France).

These correlations suggest that the relatively humid and warm time span represented by the "forest-meadow" small mammal assemblage from Varshets corresponds with the Tegelen interglacial, recorded from Northern Europe (ZAGWIJN 1975). It could be assumed that these palaeoenvironmental conditions affected the entire Europe. This is confirmed by the investigations in the European part of the former USSR. VELICHKO (1987) noted that this interglacial comprised several climatic oscillations. For the areas bordering the northern coasts of both the Black and Caspian Seas, CHEPALIGA (1987) recorded some climatic cycles – three warm periods alternating with cool ones. The warm phases comprise the following time intervals – 3.3 – 2.9, 2.4 – 2.0 and 1.8 – 1.6 Ma. Therefore, both the tentative chronostratigraphical correlation presented above and the ecological appearance of the assemblage agree with this scheme and allow the conclusion that it represents a warm phase during the middle part of the Tegelen interglacial.

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