Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria)

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ABSTRACT

The micromammals from the sediment filling of an ancient cave located near the village of Muselievo (Pleven district) are studied. At least 35 species representing 28 genera from 15 families are identified. The lipotyphlans are represented by scarce remains of five species: *Blarinoides mariae*, *Deinsdorfia kordosi*, *Mafia* cf. *csarnotensis*, *Asoriculus gibberodon*, and *Talpa minor*. The main part of bones belongs to bats: *Rhinolophus wenzensis*, *Rh. mehelyi birzebbugensis*, *Rh.* ex gr. *euryale*, *Myotis blythii longicaninus* n. ssp., *Myotis* cf. *bechsteinii*, *Myotis* sp., and *Miniopterus* cf. *approximatus*. The four lagomorphs (*Ochotonoma csarnotanus*, *Hypolagus beremendensis*, *Trischizolagus dumitrescuae*, and *Pliopentalagus dietrichi*) are among the most numerous components of the assemblage. Most of the species belong to the rodents, dominated quantitatively by the voles: *Dolomys occitanus*, *Dolomys* cf. *nehringi*, *Propliomys* cf. *hungaricus*, *Bjornkurtenia canterranensis*. The other rodents are represented by sciurids (*Pliopetaurista dehneli*, *Sciurus* sp., *Tamias orlovi*, ?*Spermophilus* sp.), glirids (*Myomimus complicidentatus* n. sp., *Dryomimus eliomyoides*, *Glis minor*), mice (*Rhagapodemus* cf. *hautimagnensis*, *Rhagapodemus* sp., *Sylvaemus dominans*), cricetids (*Allocricetus bursae*, *A. ehiki*, *Trilophomys depereti*), a mole rat (*Pliospalax* cf. *macoveii*), and a porcupine (*Hystrix* sp.). The presence of *Dolomys occitanus*, slightly more advanced than the population from the type locality (Sète, France) speaks for the late Ruscinian age (MN15b-zone). According to the biogeographical comparative analyses and the appearance of the bat assemblage, it can be supposed that the climate was similar to the recent one. The assemblage points to a complex landscape, composed probably of savanna-steppes on the plain, shrubs on the slopes, and tall forests along the rivers.

KEY WORDS
Mammalia,
Soricidae,
Talpidae,
Rhinolophidae,
Vespertilionidae,
Lagomyidae,
Leporidae,
Sciuridae,
Gliridae,
Muridae,
Cricetidae,
Arvicolidae,
Trilophomyidae,
Spalacidae,
Hystricidae,
Pliocene,
Ruscinian,
Bulgaria,
biochronology,
paleoecology.

RÉSUMÉ

Les petits mammifères pliocènes (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) de Muselievo (Bulgarie du Nord).

Les micromammifères découverts dans le sédiment remplissant une ancienne grotte près du village de Muselievo (district de Pleven) sont étudiés. Nous avons identifié au moins 35 espèces appartenant à 28 genres et 15 familles. Les Lipotyphla sont représentés par les restes de cinq espèces : *Blarinoides mariae*, *Deinsdorfia kordosi*, *Mafia* cf. *csarnotensis*, *Asoriculus gibberodon* et *Talpa minor*. La majeure partie des os sont attribuables à des chauve-souris : *Rhinolophus wenzensis*, *Rh. mehelyi birzebbugensis*, *Rh.* ex gr. *euryale*, *Myotis blythii longicaninus* n. ssp., *Myotis* cf. *bechsteinii*, *Myotis* sp. et *Miniopterus* cf. *approximatus*. Les quatre lagomorphes (*Ochotonoma csarnotanus*, *Hypolagus beremendensis*, *Trischizolagus dumitrescuae* et *Pliopentalagus dietrichi*) fournissent l'un des plus abondants composants de l'association faunique. La majorité des espèces appartient aux rongeurs, dominés quantitativement par les campagnols : *Dolomys occitanus*, *Dolomys* cf. *nehrengi*, *Propliomys* cf. *hungaricus*, *Bjornkurtenia canterranensis.* Les autres rongeurs sont représentés par les sciuridés (*Pliopetaurista dehneli*, *Sciurus* sp., *Tamias orlovi*, ? *Spermophilus* sp.), les gliridés (*Myomimus complicidentatus* n. sp., *Dryomimus eliomyoides*, *Glis minor*), les muridés (*Rhagapodemus* cf. *hautimagnensis*, *Rhagapodemus* sp., *Sylvaemus dominans*), les cricétidés (*Allocricetus bursae*, *A. ehiki*, *Trilophomys depereti*), un rat-taupe (*Pliospalax* cf. *macoveii*) et un porc-épic (*Hystrix* sp.). La présence d'un *Dolomys occitanus* légèrement plus évolué que la population de la localité type (Sète, France) indique un âge ruscinien terminal (zone MN15b). Selon les analyses biogéographiques et l'association des chauve-souris on peut supposer que le climat était similaire à celui d'aujourd'hui. L'association faunique indique un paysage complexe fait de steppes-savanes dans les plaines, broussailles sur les versants et forêt-galeries le long des rivières.

MOTS CLÉS
Mammalia,
Soricidae,
Talpidae,
Rhinolophidae,
Vespertilionidae,
Lagomyidae,
Leporidae,
Sciuridae,
Gliridae,
Muridae,
Cricetidae,
Arvicolidae,
Trilophomyidae,
Spalacidae,
Hystricidae,
Pliocène,
Ruscinien,
Bulgarie,
biochronologie,
paléoécologie.

INTRODUCTION

The Pliocene small mammal fauna in Bulgaria is still poorly known. Up to now only late Pliocene arvicolids and soricid from Varshets (N Bulgaria) have been studied in detail (Popov 2001, 2003). For the earlier parts of the Pliocene, the only available data concern the preliminary species lists from Dorkovo (MN14), the Rhodopy Mts, S Bulgaria (Thomas *et al.* 1986) and the present locality (Popov 1994). The scarcity of data is regrettable having in mind the geographical position of the country on the Balkan Peninsula, acting as a large bridge between North and South and being a natural door, in the past as in present, for migrations of mammals from Asia to Europe and *vice versa*. The present paper aims at filling up partially this gap by providing a detailed description of the Pliocene small mammals remains from Muselievo. This assemblage can be considered as complementary to the mammalian fauna of Ciuperceni-2, which is similar in age and known from the bedded deposits on the opposite side of the Danube in South Romania (Fig. 1) (Terzea 1981, 1997). The importance of Muselievo is corroborated by its intermediate geographic position between the well known Central European localities of comparable age, such as Csarnóta-2 (Hungary), and the intensively studied during the last

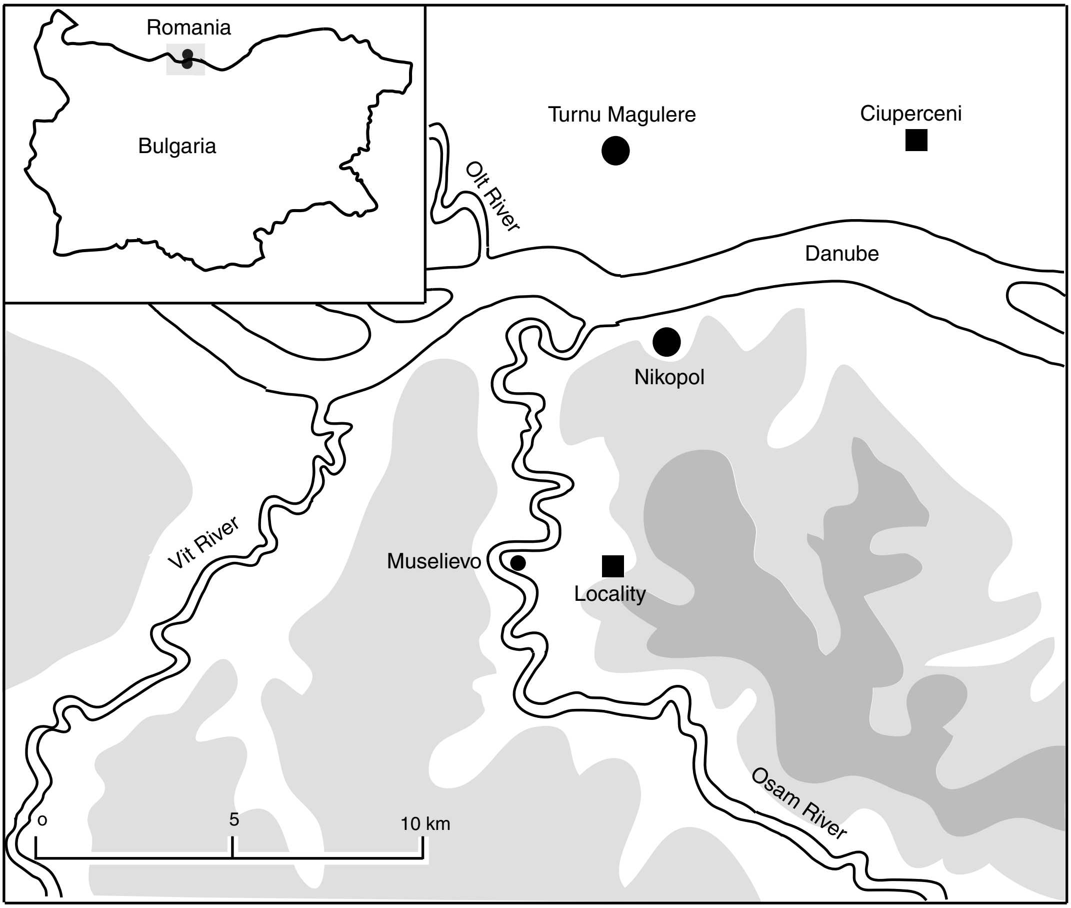

FIG. 1. — Sketch map showing of the geographical position of the fossil locality “Muselievo” in North Bulgaria. The relief is marked by a gray gradation from white (up to 100 m above sea level), moderate (up to 200 m a.s.l.), and high (up to 300 m a.s.l.). Symbols: ●, towns; •, village; ■, palaeontological localities.

decades Pliocene faunas in the Aegean area (Van der Meulen & Van Kolfschoten 1986; Sen & Leduc 1996).

The geographic position of the locality is shown in Figure 1. It is situated 1 km northeast from the village of Muselievo (Pleven district) (43°36’N, 24°50’E; UTM: LJ23; 150 m above sea level) and represents a yellowish clay deposit, filling an ancient cave, revealed on the wall of an abandoned limestone carry. The former karstic hollow is entirely filled with the sediment, in which different strata cannot be identified.

The locality was discovered by I. Petrov, an amateur paleontologist from Pleven, in the summer of 1988. Systematic excavations were made under the guidance of the present author during the autumn of 1988 and the summer of 1989.

MATERIAL AND METHODS

The fossils were collected from one place of the sediment exposure, situated near to the eastern wall of the ancient hollow. The sample comprises about 500 kg of sediment. The individual subsamples (about 10 kg each) were sieved in water using mesh bags of 0.8 mm apertures. The washed residue was dried and re-sieved through

2 mm and 0.8 mm conventional metal sieves. The content of each sieve was poured onto a table and sorted by hand.

All determinable specimens (predominantly isolated teeth) were measured with a binocular microscope and ocular micrometer (ocular 8 × and objective 4 × or 2 ×). The distance between successive marks on the micrometer was 0.025 mm and 0.05 mm, respectively. All measurements are given in millimeters. In most cases, the measurements of individual teeth were taken on the occlusal surface of the teeth and their maximum length (L) and width (W) were represented. For shrews, the measuring system of Reumer (1984) was adopted: H, height of upper incisive; HC, height of the condyle; LUF, length of the condylar upper facet; LLF, length of the condylar lower facet. The bat remains were measured according to Popov & Ivanova (2002): trW, trigonid width; taW, talonid width; BL, buccal length; PW, posterior width; HPC, height of coronoid process; HMd/m1, height of mandibular ramus under m1 measured lingually; HMd/m2, the same under m2; LSy, length of symphysis. In most cases the tooth row lengths represent coronar lengths; in some cases when the alveolar lengths were measured the values are given in brackets; a value in a semi-bracket indicates an alveolar-coronar length. Arvicolid dimensions follow Van der Meulen (1973): a, anteroconid length of m1. Statistical abbreviations on tables of measurements are as follows: M, mean; Min, Max, minimal and maximal values within a sample; SD, standard deviation of the mean; CV, coefficient of variation (%); N, number of specimens measured.

The dental terminology is according to the following sources: Soricidae (Reumer 1984), Chiroptera (Van Valen 1966), Lagomorpha (Lopez Martinez 1980, 1986), Sciuridae (Cuenca Bescos 1988), Gliridae (Daams 1981), Muridae (Van de Weerd 1976); Cricetidae (Mein & Freudental 1971); Arvicolidae (Van der Meulen 1973; Rabeder 1981; Maul 1996); Spalacidae (Topachevsky 1969).

The material is deposited in the collections of Institute of Zoology, Bulgarian Academy of Science, Sofia.

SYSTEMATICS

Order LIPOTYPHLA Haeckel, 1866
Family SORICIDAE Gray, 1821
Genus *Deinsdorfia* Heller, 1963

Deinsdorfia kordosi Reumer, 1984
(Fig. 2E, F)

Deinsdorfia kordosi Reumer, 1984: 52-55, pl. 13, figs 7-10, pl. 14, fig. 2.

MATERIAL EXAMINED. — 1 I1 (Ms145); LI1 = 2.20; HI1 = 1.40.

DESCRIPTION

This upper incisive shows light pigmentation on the apex and on the anteriormost part of the talon. The buccal posterior edge is rounded, gradually passing into the convex dorsal margin. The apex and the talon are placed at a sharp angle. The talon is two-cusped. The cingulum is broad and well pronounced only in the lower two thirds of the crown height. The ventral margin of the talon is slightly concave.

REMARKS

The measurements fall within the range of variability of *Deinsdorfia kordosi* from Csarnóta-2 (Hungary), i.e. it is larger than the remaining Pliocene species of the genus, known from the Hungarian localities (Reumer 1984). The other overall features also agree well with the original description. Up to now, the species has been known from Csarnóta-2 (Reumer 1984), Rebielice Krolewskie 1A (cf.) (Rzebik-Kowalska 1990a), and Wölfersheim (Dahlmann 2001).

Genus *Mafia* Reumer, 1984

Mafia cf. ***csarnotensis*** Reumer, 1984
(Fig. 3)

MATERIAL EXAMINED. — 1 I1 (Ms146), fragment of mandible with m1 (Ms376).

MEASUREMENTS. — I1: LI1 = 2.45; HI1 = 1.67; m1 (L × W) = 1.82 × 1.10; HMd/m2 = 1.85; Lm1-m3 = 4.25; HC = 2.25; LLF = 1.65; LUF = 1.05.

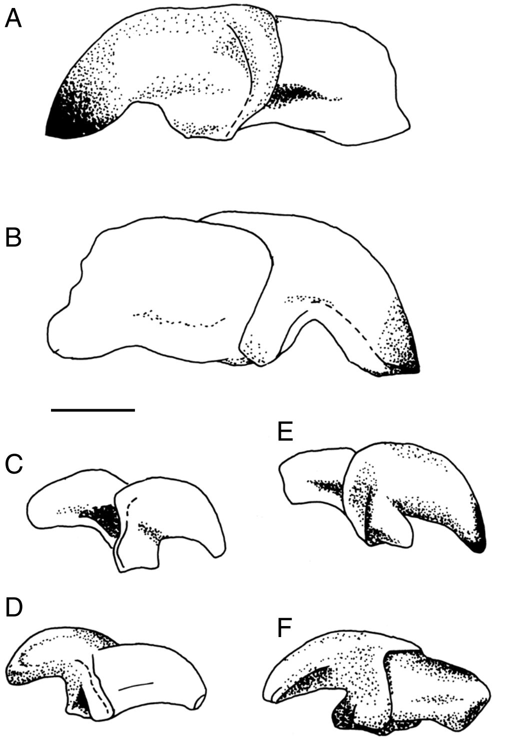

FIG. 2. — **A**, **B**, *Blarinoides mariae* Sulimski, 1959; **A**, left upper incisor, Ms145, buccal view; **B**, the same, lingual view; **C**, **D**, *Asoriculus gibberodon* (Pétenyi, 1864); **C**, right upper incisor, Ms148, buccal view; **D**, the same, lingual view; **E**, **F**, *Deinsdorfia kordosi* Reumer, 1984; **E**, right upper incisor, Ms145, buccal view; **F**, the same, lingual view. Scale bar: 1 mm.

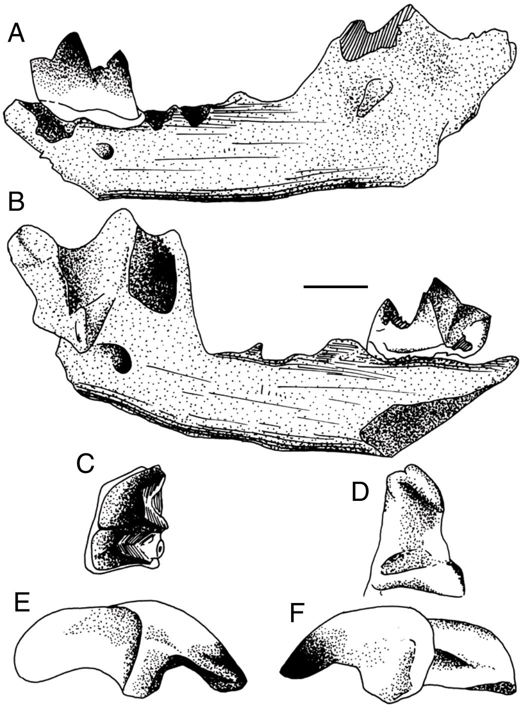

FIG. 3. — *Mafia* cf. *csarnotensis* Reumer, 1984; **A**, left fragment of mandible, Ms376, labial view; **B**, the same, lingual view; **C**, the same, occlusal view of m1; **D**, the same, posterior view of condyloid process; **E**, left upper incisor, Ms146, lingual view; **F**, the same, buccal view. Scale bar: 1 mm.

DESCRIPTION

I1: the non-fissident apex is intensely pigmented in dark red. The posterior buccal edge of the crown is slightly convex. The cingulum is not well pronounced, especially in the uppermost part of the crown height. The apex and talon are separated by a shallow groove.

Mandible: m1: the upper part of the crown is intensely stained in dark red; the entoconid crest is lacking and the entoconid is nearly conical, slightly elongated antero-posteriorly; the buccal and lingual cingula are relatively broad and well pronounced; the buccal ventral margin of the crown is concave in its middle part. The mental foramen is situated under the second half of the crown of m1. The condyle possesses a broad interarticular area. The upper facet is obliquely oriented in relation to the lower one.

REMARKS

The measurements of the bones and teeth available, as well as their structural details, generally correspond to the original material from Csarnóta-2 (Reumer 1984). However, some differences should be mentioned. According to Reumer (1984), the facets of the condyle in the Hungarian specimens are nearly parallel. The cingulum of the upper incisive from Muselievo is rather weak in comparison with the material from Csarnóta-2. For the time being the scarce and poorly preserved material available does not permit to ascertain whether these differences have systematic value or not, and the determination remains tentative. The species is known from Hungary (Reumer 1984), Poland (Rzebik-Kowalska 1990b), Turkey (Reumer 1998), and Bulgaria (Popov 2003).

Genus *Blarinoides* Sulimski, 1959

Blarinoides mariae Sulimski, 1959
(Fig. 2A, B)

Blarinoides mariae Sulimski, 1959: 144. — Reumer 1984: 83-86, pl. 26.

MATERIAL EXAMINED. — 1 I1 (Ms147); LI1 = 2.87.

DESCRIPTION
The tooth is non-fissident. The apex is pigmented in dark red. The buccal cingulum is visible in the lower two third of the crown. It is rather broad in its upper part. Buccally, the posterior and dorsal margins form a slightly obtuse angle.

REMARKS
The general shape and size of the incisive from Muselievo correspond to the material from Csarnóta-2 (Reumer 1984) and Wölfersheim (cf.) (Dahlmann 2001).

Genus *Asoriculus* Kretzoi, 1959

Asoriculus gibberodon (Petényi, 1864)
(Fig. 2C, D)

Crocidura gibberodon Petényi, 1864: 73, pl. I, fig. 7. — Kormos 1911: 167-196.

Asoriculus gibberodon – Kretzoi 1959: 238; 1962: 353, pl. II, fig. 1.

Soriculus gibberodon – Sulimski 1962: 477, fig. 2.

Episoriculus gibberodon – Repenning 1967a: 48. — Rzebik-Kowalska 1981: 245-247, fig. 6.

MATERIAL EXAMINED. — 1 I1 (Ms148); LI1 = 1.55; HI1 = 1.30.

DESCRIPTION
Although the available incisive is rather worn, it is clearly visible that it is fissident. The apex is slightly pigmented in pale red.

REMARKS
Both the size and shape of the tooth leave no doubt that it belongs to *Asoriculus gibberodon*, a species common in many European Pliocene and early Pleistocene faunas (Popov 2003).

Family TALPIDAE Fischer von Waldheim, 1817
Genus *Talpa* Linnaeus, 1758

Talpa minor Freudenberg, 1914

MATERIAL EXAMINED. — 1 fragmentary humerus (Ms377-1), 1 cubitus and 3 fragments of cubitus (Ms377-2). Minimal width of humerus = 4.00; length of cubitus = 10.30.

REMARKS
The two postcranial bones found in Muselievo reveal features of the genus *Talpa*. Their measurements are intermediate between the medium-sized Pleistocene forms, usually denoted as *Talpa fossilis* Petényi, 1864, and the smaller species *Talpa minor*. In this respect, they correspond to the Pliocene species *Talpa csarnotana* Kretzoi, 1959, described from Csarnóta (Hungary). This species is of the size of *T. minor*, but differs in a stronger development of the proximal area of the humerus and a shorter shaft. Storch (1978) provided an illustration of the humerus of this form. However, the available fragment of humerus does not permit detailed comparisons. Nevertheless, it seems "unlikely that Csarnóta contains a different smaller *Talpa* species that other Hungarian localities of similar age" and it seems likely "that *T. csarnotana* is a junior synonym of *T. minor*" (Van Cleef-Roders & Van den Hoek Ostende 2001). The differences in size can be related to local environmental peculiarities as it is the case in the present-day populations of *T. europaea* Linnaeus, 1758 and *T. levantis* Thomas, 1906 in Bulgaria (Popov & Miltchev 2001).

Order CHIROPTERA Blumenbach, 1779
Family RHINOLOPHIDAE Lesson, 1827

Genus *Rhinolophus* Lacépède, 1799

According to the size, three groups of European rhinolophids can be considered: 1) large-sized

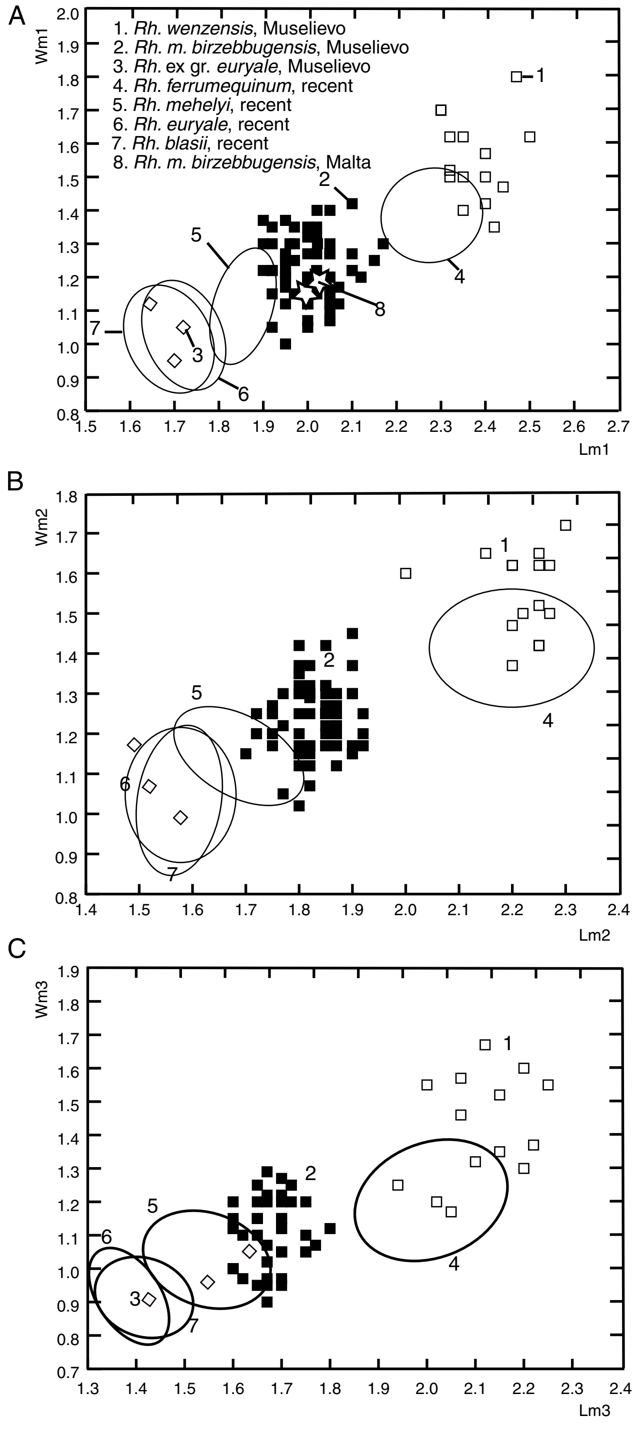

FIG. 4. — Scatter diagrams showing length (L) and width (W) of lower molars (mm) of fossil and recent rhinolophid bats; **A**, m1; **B**, m2; **C**, m3. The recent species are presented by 5% confidence ellipses.

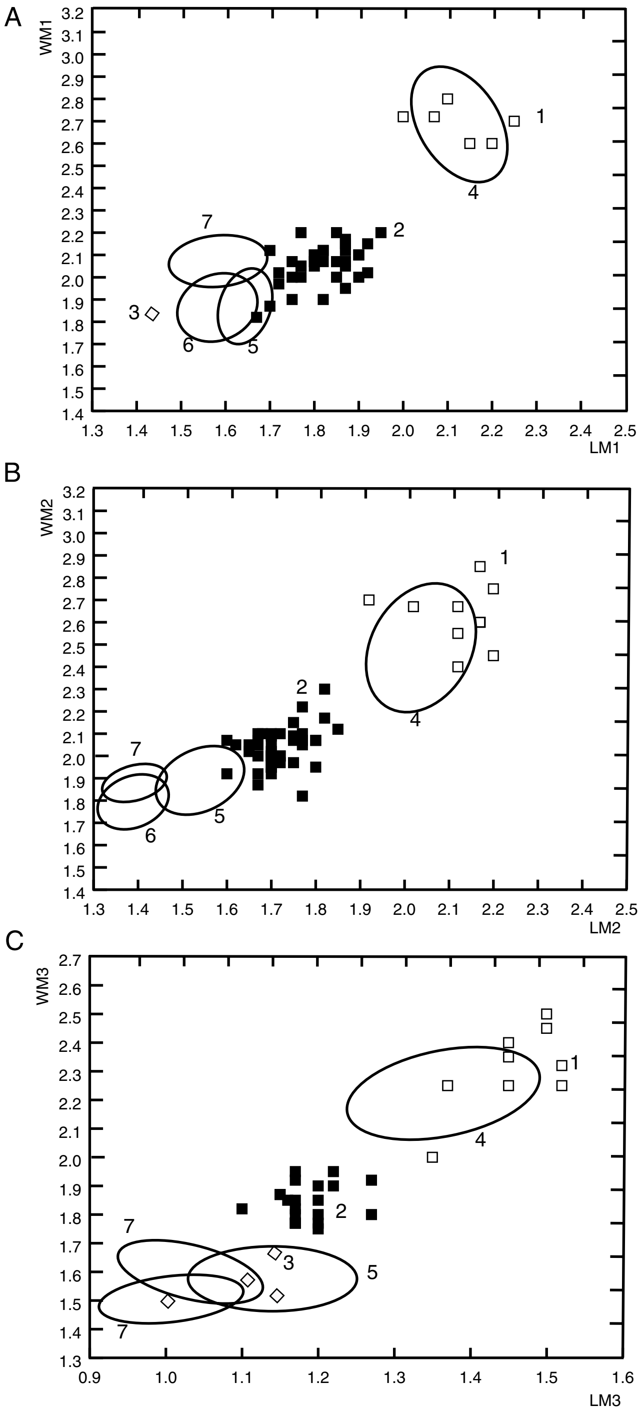

FIG. 5. — Scatter diagrams showing length (L) and width (W) of upper molars (mm) of fossil and recent rhinolophid bats; **A**, M1; **B**, M2; **C**, M3. For explanations see Fig. 4.

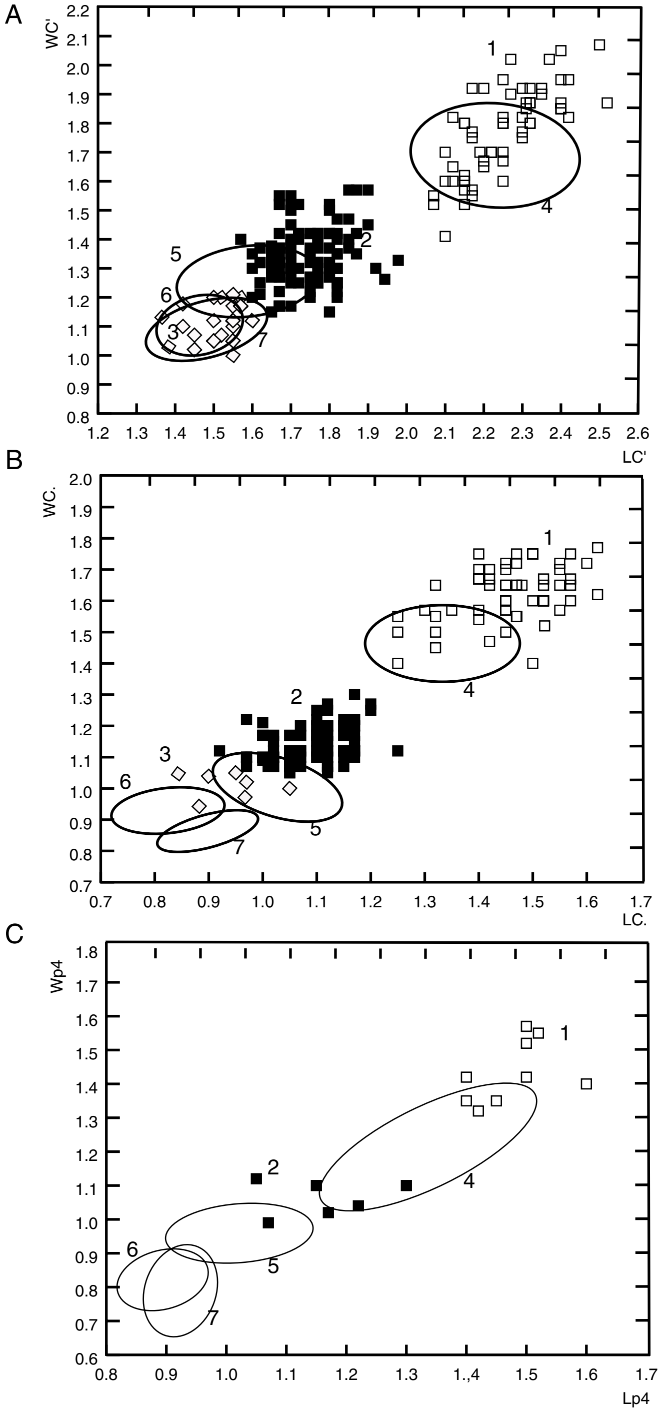

FIG. 6. — Scatter diagrams showing length (L) and width (W) of upper canine (**A**), lower canine (**B**), and p4 (**C**) (mm) of fossil and recent rhinolophid bats. For explanations see Fig. 4.

species, like the recent *Rhinolophus ferrumequinum* (Schreber, 1774); 2) medium-sized species, comparable with the present-day species *Rh. mehelyi* Matschie, 1901, *Rh. euryale* Blasius, 1853, and *Rh. blasii* Peters, 1867; and 3) small-sized species similar to the modern *Rh. hipposideros* (Bechstein, 1800). The remains from Muselievo represent three forms, which can be related to the first two groups (Figs 4-6).

The large-sized horseshoe bats from the Miocene, Pliocene, and Pleistocene of Europe are relatively well known thanks to Gaillard (1899), Revillod (1919), Kretzoi (1951, 1977), Topál (1963b, 1979) and Woloszyn (1988). Based on an analysis of the morphological and biometrical variation in coherent and successive fossils and in living populations of large horseshoe bats, Topál (1979) outlined their phylogenetic relationships and recognized some evolutionary lineages that diverged since late Miocene. The main evolutionary trend during Pliocene and Pleistocene was toward a reduction of the anterior part of both upper and lower tooth rows. For instance, the c1-p4 and C1-P4 lengths were considerably greater in the Pliocene and early Pleistocene forms due to the somewhat longer c1, C1, p4, and especially to the less reduced P2 and p2.

Bogdanowicz (1992) in his comparative phenetic study on Rhinolophidae suggested that the small premolars in modern Ethiopian and Palaearctic rhinolophids present a great degree of reduction, especially in medium and large-sized forms. It can be assumed that this evolutionary trend represents a specialization towards a hard-shelled insect eating (Freeman 1979). Additional adaptations in this direction include abbreviated third upper molars and reduction of the talonid in m3 (Freeman 1979, 1981). In this respect the retention of P2 and p3 in line with tooth row should be considered as a primitive feature for the recent horseshoe bats (Anderson 1905).

Rhinolophus wenzensis Woloszyn, 1988
(Fig. 7)

Rhinolophus wenzensis Woloszyn, 1988: 243-248, pl. 11: 2, tables 12-15.

MATERIAL EXAMINED. — 10 fragments of mandible (Ms174-183), 33 left c1 (Ms184), 28 right c1 (Ms185), 9 p4 (Ms186), 13 m1 (Ms187), 12 m2 (Ms188), 11 m3 (Ms189), 35 left C1 (Ms190), 22 right C1 (Ms191, 197), 2 P4 (Ms192), 6 M1 (Ms193, 198), 10 M2 (Ms194, 199), 12 M3 (Ms195, 200), 25 fragments of humerus (Ms196).

MEASUREMENTS. — See Table 1.

DESCRIPTION AND COMPARISONS

C1: the tooth is more massive than in the comparative material of modern *Rhinolophus ferrumequinum* (Schreber, 1774) from North Bulgaria. The crown outline in occlusal view is irregularly oval, elongated antero-posteriorly; the postero-labial margin is convex, while the postero-lingual one is slightly concave. The tooth is less compressed antero-posteriorly in comparison with the tooth of the modern species, so, from the labial view, the posterior undulation of the cingulum forms a right angle (sharp in the recent species).

P4: the tooth is elongated transversely; the talonid is well developed postero-lingually; the anterior margin is slightly concave.

M1-M2: these molars are relatively large. The posterior emargination is well pronounced, especially on M1; this tooth also shows a well developed talon. In these respects, the teeth resemble those of the recent *Rh. ferrumequinum*. As compared with *Rh. wenzensis* (Woloszyn 1988) the width of molars from Muselievo is considerably greater. At the same time, they are slightly narrower than the molars of *Rh. kowalskii* Topál, 1979, *Rh. estramontis* Topál, 1979, and *Rh. macrorhinus anomalidens* Topál, 1979 (Topál 1979). Most probably, these disagreements reflect some differences in the measurement systems used by the various authors.

M3: this tooth is relatively large and more massive than in the recent species and in *Rh. macrorhinus anomalidens*. In this respect, it is similar to *Rh. kowalskii* and *Rh. estramontis*.

c1: it is somewhat compressed oro-caudally (more than in the recent species) in occlusal outline. In size it is comparable with *Rh. macrorhinus anomalidens* and *Rh. wenzensis* (Table 1) and is more massive than in the recent species.

TABLE 1. — Measurements (mm) of *Rhinolophus wenzensis* Woloszyn, 1988 from Muselievo in comparison with other Pliocene large sized rhinolophids from Europe. For abbreviations see Material and methods.

	Rhinolopus wenzensis **Muselievo**						***R. kowalskii*** **Podlesice**			***R. estramontis*** **Osztramos 1f**		
	N	Min	M	Max	SD	CV	holotype	Min	Max	holotype	Min	Max
LC1	59	2.02	2.25	2.52	0.111	4.96	-	2.08	2.41	-	2.27	2.31
WC1	59	1.41	1.77	2.07	0.155	8.76	-	1.72	2.00	-	1.81	1.95
LP4	2	1.45	-	1.47	-	-	-	1.31	1.59	-	1.36	1.45
WP4	2	2.17	-	2.59	-	-	-	2.27	2.68	-	2.31	2.41
BLM1	6	2.00	2.13	2.25	0.090	4.26	-	1.95	2.31	-	2.03	2.36
PWM1	6	2.60	2.69	2.80	0.078	2.89	-	2.95	3.32	-	2.95	3.40
BLM2	10	1.92	2.12	2.20	0.088	4.17	-	1.90	2.18	-	2.00	2.27
PWM3	10	2.40	2.62	2.85	0.135	5.14	-	2.64	2.95	-	2.68	2.95
LM3	11	1.35	1.47	1.62	0.074	5.05	-	1.27	1.63	-	1.36	1.45
WM3	10	2.00	2.33	2.50	0.161	6.49	-	2.08	2.45	-	2.23	2.41
HMd/m1	4	2.00	2.12	2.20	-	-	2.13	1.95	2.23	2.18	-	-
HPC	1	-	4.27	-	-	-	-	3.60	4.40	4.14	-	-
Lc1	57	1.25	1.45	1.62	0.090	6.18	-	-	-	1.22	-	-
Wc1	57	1.40	1.62	1.77	0.090	5.49	-	-	-	1.47	-	-
Lp4	13	1.30	1.45	1.60	0.074	5.07	1.27	1.27	1.50	1.36	-	-
Wp4	12	1.27	1.42	1.57	0.106	7.46	1.22	1.09	1.36	1.22	-	-
Lm1	18	2.32	2.39	2.50	0.057	2.40	2.27	2.08	2.45	2.27	-	-
Wm1	18	1.35	1.55	1.80	0.124	8.03	1.45	1.22	1.63	1.45	-	-
Lm2	12	2.15	2.23	2.30	0.041	1.84	2.03	2.00	2.31	2.18	-	-
Wm2	12	1.37	1.57	1.72	0.104	6.66	1.45	1.36	1.59	1.54	-	-
Lm3	12	2.00	2.12	2.25	0.083	3.90	2.00	1.88	2.18	1.95	-	-
trWm3	12	1.17	1.44	1.67	0.164	11.4	-	-	-	-	-	-
taWm3	12	1.05	1.27	1.45	0.147	11.6	1.18	1.00	1.31	1.27	-	-

	R. macrorhinus anomalidens **Osztramos 8**			***R. wenzensis*** **Weze 1**			
	holotype	Min	Max	Min	M	Max	SD
LC1	-	2.08	2.45	2.16	2.23	2.31	0.079
WC1	-	1.72	2.08	1.86	1.91	1.98	0.049
LP4	-	1.22	1.50	1.47	1.56	1.70	0.088
WP4	-	2.13	2.54	1.91	2.06	2.24	0.134
BLM1	-	1.90	2.23	1.98	2.09	2.21	0.107
PWM1	-	2.72	3.32	1.97	2.17	2.33	0.133
BLM2	-	1.72	2.08	1.95	2.01	2.15	0.095
PWM3	-	2.41	3.00	1.96	2.10	2.31	0.159
LM3	-	1.18	1.40	-	-	-	-
WM3	-	2.03	2.31	-	-	-	-
HMd/m1	2.08	1.95	2.23	-	-	-	-
HPC	-	-	-	4.00	-	4.31	-
Lc1	1.50	-	-	1.23	1.32	1.37	-
Wc1	1.72	-	-	1.50	1.62	1.75	-
Lp4	1.36	1.18	1.45	1.36	1.51	1.62	0.071
Wp4	1.40	1.13	1.40	1.27	1.44	1.56	0.083
Lm1	2.13	2.00	2.27	2.34	2.40	2.45	0.046
Wm1	1.54	1.31	1.54	1.46	1.55	1.60	0.076
Lm2	2.00	1.90	2.13	2.18	2.27	2.32	0.076
Wm2	1.50	1.27	1.54	1.48	1.61	1.71	0.118
Lm3	1.95	1.81	2.03	2.10	2.14	2.20	0.053
trWm3	-	-	-	1.36	1.46	1.52	0.087
taWm3	1.18	1.04	1.27	1.21	1.36	1.49	0.141

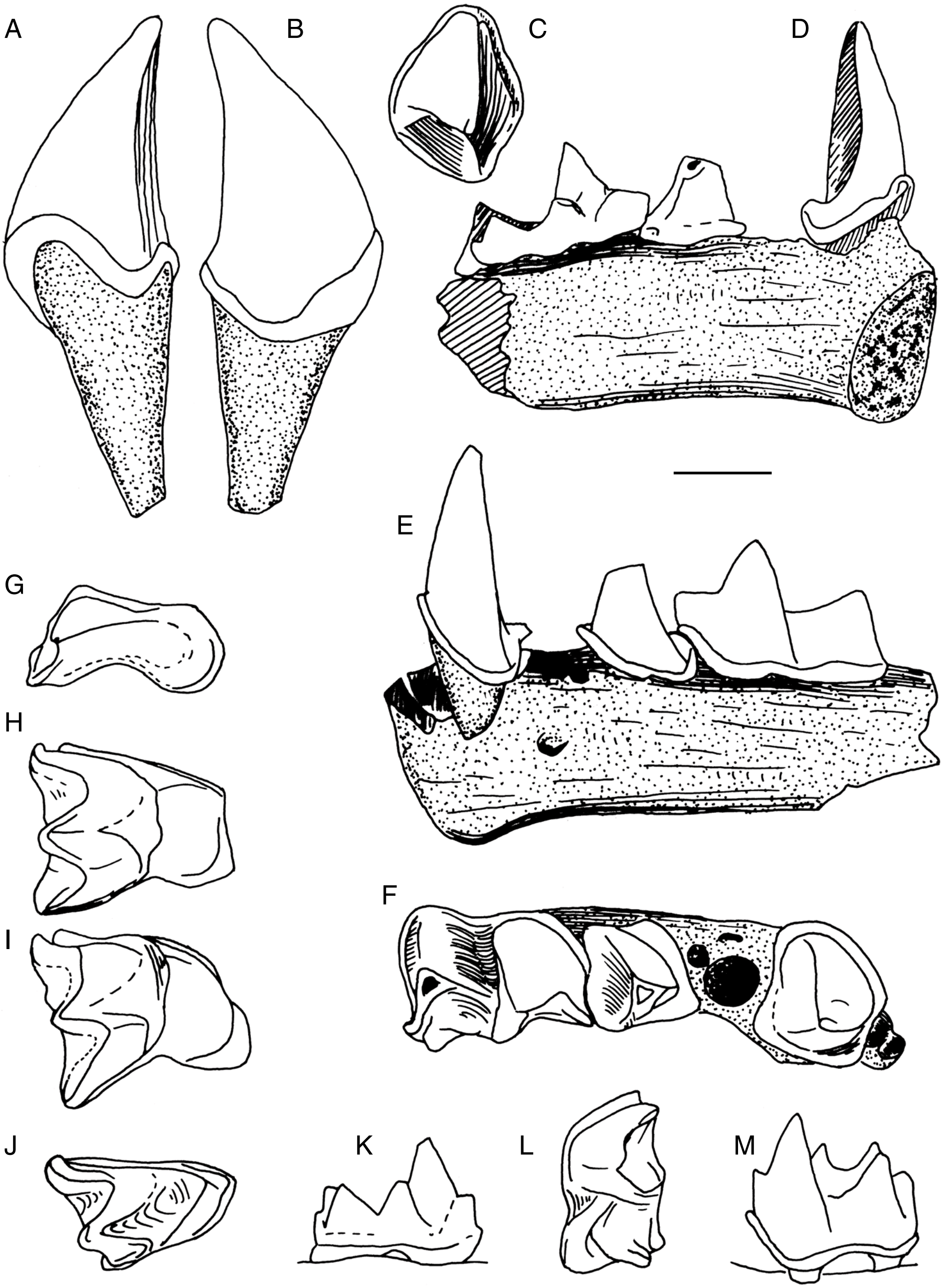

FIG. 7. — *Rhinolophus wenzensis* Woloszyn, 1988; **A**, right upper canine, Ms197, buccal view; **B**, the same, lingual view; **C**, the same, occlusal view; **D**, left fragment of mandible with c1, p4, and m1, Ms174, lingual view; **E**, the same, labial view; **F**, the same, occlusal view; **G**, right P4, Ms192, occlusal view; **H**, right M2, Ms199, occlusal view; **I**, right M1, Ms198, occlusal view; **J**, right M3, Ms200, occlusal view; **K**, left m1, Ms176, lingual view; **L**, the same, occlusal view; **M**, the same, buccal view. Scale bar: 1 mm.

p3: this tooth is lacking, but judging by the size and position of the alveolus it can be said that it is larger and not so displaced labially as in *Rh. estramontis* from Osztramos-1f and especially in comparison with the recent species. Most probably, the crowns of p2 and p4 were not contiguous as in the case of modern *Rh. ferrumequinum*. At the same time, p3 seems more reduced than in some specimens of *Rh. kowalskii* from Podlesice and *Rh.* cf. *kowalskii* ssp. from Csarnóta-2 (Topál 1979). In this respect, it is similar to *Rh. wenzensis* (Woloszyn 1988).

p4: p4 is robust. In occlusal view, the outline of the crown is a shortened irregular trapezium with the shorter and slightly convex base oriented labially. This tooth exceeds in dimensions those of *Rh. kowalskii*, *Rh. macrorhinus anomalidens* and the recent species *Rh. ferrumequinum*. In this respect it is similar with *Rh. wenzensis* although this species shows a slightly, on average, more elongated p4 (Table 1).

m1 and m2: m1 and m2 are nyctalodontic and massive. They are larger than the respective molars in *Rh. kowalskii*, *Rh. estramontis*, *Rh. macrorhinus anomalidens* and the modern comparative material of *Rh. ferrumequinum*.

m3: nyctalodontic. The talonid is relatively large, wider than in the modern *Rh. ferrumequinum* (taWm3 recent = 0.92-1.02-1.35, N = 20), *Rh. kowalskii* and *Rh. macrorhinus anomalidens*, being nearly identical with *Rh. wenzensis* (Table 1).

REMARKS

The teeth available have a structure and arrangement characteristic for the large sized species of horseshoe bats, belonging to "*ferrumequinum*" group. They are however larger than in the modern species from Bulgaria (Figs 4A-C; 5B, C; 6A-C) and similar in this respect to the fossil species *Rh. kowalskii*, *Rh. estramontis*, *Rh. macrorhinus anomalidens* (Topál 1979), although in some measurements the material from Muselievo shows even larger values. According to the teeth dimensions, and especially those of p4 and m3, the examined material is practically identical with *Rh. wenzensis* (Woloszyn 1988). In general, the size, teeth structure and arrangement of the form from Muselievo correspond to the original diagnosis of *Rh. wenzensis* (Woloszyn 1988): "A large representative of *Rhinolophus*, close in dimensions to *Rh. kowalskii* Topál, 1979 differing from this species in its massive teeth, a robust p4, whose crown is almost square in outline, a massive talonid on m3 and more strongly reduced p2".

The remains from Muselievo show that with regard to the structure of the anterior part of dentition we deal with an early-specialized form. In this respect, the examined material substantiates the Woloszyn's (1988) suggestion that "*Rh. wenzensis* is more progressive than other Miocene and Pliocene species of that group". On the other hand, this species retains some less specialized features such as the relatively large talonid on m3, not so reduced p3, moderately displaced outward from the tooth row so that the crowns of p2 and p4 are probably not contiguous. For the time being, the described remains are the second record of the species. Its presence in Muselievo constitutes an important fact, indicating that it is not an endemic form as supposed by Woloszyn (1988).

Rhinolophus mehelyi birzebbugensis
Storch, 1974
(Fig. 8)

Rhinolophus mehelyi birzebbugensis Storch, 1974: 414-417, abb. 4, 14-17.

Rhinolophus mehelyi – Sevilla 1988: 147-153, figs 25, 26: 1-3, 28, 29: 1-4.

MATERIAL EXAMINED. — 67 fragments of mandible (Ms149:1-67), 1 fragment of maxillae with P4-M3 (Ms150), 118 right C1 (Ms150), 113 left C1 (Ms152), 4 P4 (Ms153), 33 M1 (Ms154), 46 M2 (Ms155), 19 M3 (Ms156), 44 left c1 (Ms157), 72 right c1 (Ms158), 6 p4 (Ms159), 59 m1 (Ms160), 46 m2 (Ms161), 28 m3 (Ms162), 2 fragments of maxillae with P4-M1 and M1-M3 (Ms163), 3 fragments of maxillae with P4-M1, M3 and M2-M3 (Ms164), 18 fragments of humerus (Ms165).

MEASUREMENTS. — See Table 2.

TABLE 2. — Dental measurements (mm) of *Rhinolophus mehelyi birzebbugensis* Storch, 1974 from Muselievo in comparison with the recent *Rhinolophus mehelyi* Matschie, 1901 from Bulgaria. For abbreviations see Material and methods.

	Rhinolophus mehelyi birzebbugensis **Muselievo**					***Rhinolophus mehelyi*** **N Bulgaria, recent, N = 14**			
	N	Min	M	Max	SD	Min	M	Max	SD
LC1	213	1.60	1.72	2.00	0.080	1.45	1.57	1.75	0.031
WC1	213	1.10	1.31	1.57	0.101	1.10	1.24	1.32	0.024
LP4	3	0.97	1.14	1.27	-	1.02	1.09	1.20	0.019
WP4	3	1.70	1.85	1.97	-	1.62	1.80	1.97	0.043
LM1	33	1.67	1.81	1.95	0.070	1.62	1.66	1.70	0.007
WM1	33	1.82	2.06	2.20	0.093	1.72	1.90	2.00	0.021
LM2	45	1.60	1.72	1.85	0.056	1.50	1.56	1.62	0.015
WM2	45	1.87	2.03	2.30	0.087	1.70	1.85	2.07	0.027
LM3	20	1.15	1.19	1.27	0.036	1.05	1.13	1.25	0.020
WM3	19	1.75	1.84	1.95	0.061	1.57	1.63	1.70	0.017
Lc1	112	0.92	1.09	1.25	0.060	0.95	1.04	1.15	0.020
Wc1	112	1.07	1.14	1.30	0.055	0.95	1.02	1.12	0.017
Lp4	6	1.05	1.16	1.30	0.093	0.92	1.04	1.12	0.023
Wp4	6	0.99	1.06	1.12	0.052	0.85	0.95	1.05	0.022
Lm1	58	1.90	2.01	2.17	0.060	1.80	1.85	1.94	0.015
Wm1	58	1.00	1.21	1.42	0.090	1.00	1.09	1.25	0.030
Lm2	47	1.72	1.84	1.92	0.050	1.62	1.70	1.80	0.022
Wm2	47	1.07	1.23	1.45	0.090	1.02	1.11	1.25	0.024
Lm3	28	1.60	1.68	1.80	0.050	1.50	1.57	1.67	0.018
trWm3	27	0.90	1.10	1.29	0.109	0.87	1.00	1.10	0.026
taWm3	28	0.85	0.99	1.17	0.093	0.77	0.89	1.02	0.026

DESCRIPTION AND COMPARISONS

The material from Muselievo is described in comparison with the three medium-sized extant species of horseshoe bats (*Rh. mehelyi* Matschie, 1901; *Rh. euryale* Blasius, 1853; and *Rh. blasii* Peters, 1866) from Bulgaria (Popov & Ivanova 2002). Since the form from Muselievo overlaps in many measurements with some modern populations of *Rhinolophus ferrumequinum* (cf. Sevilla 1988), comparisons with this species have also been included.

C1: the crown is more or less oval, when seen from above; the postero-lingual margin presents a slight concavity, similar in this respect to the three modern medium-sized species, and differing from the recent comparative material of *Rh. ferrumequinum*, which possesses a convexity in this part of the tooth margin, and showing a depression on the postero-buccal margin of the tooth, resulting of the pressure of P2. In the fossil material, from labial view, the cingulum runs slightly downwards up to the posterior part of the crown, where it starts to run upwards, forming in this way an obtuse angle. In this feature the available upper canines are similar to the recent medium sized species and differ from the recent *Rh. ferrumequinum* in which the anterior and posterior parts of this cingulum form a right or sharp angle, due to the antero-posterior compression of this tooth.

P2 is not present in the material examined, but the size and position of the alveolus (specimen Ms150), indicate that this tooth must have been of moderate size and slightly displaced labially. In this respect, the fossil material is similar with *Rh. blasii*, which possess a relatively large P2, laying in the tooth row. As a result, there is a well pronounced depression on the middle part of the anterior margin of P4, pointing to the presence of a pressure from P2. In the other modern species, the P2 is quite reduced, positioned labially to the tooth row, and there is no impression of this tooth on the anterior margin of P4.

P4: the tooth is moderately elongated transversely with respect to the tooth row. This tooth

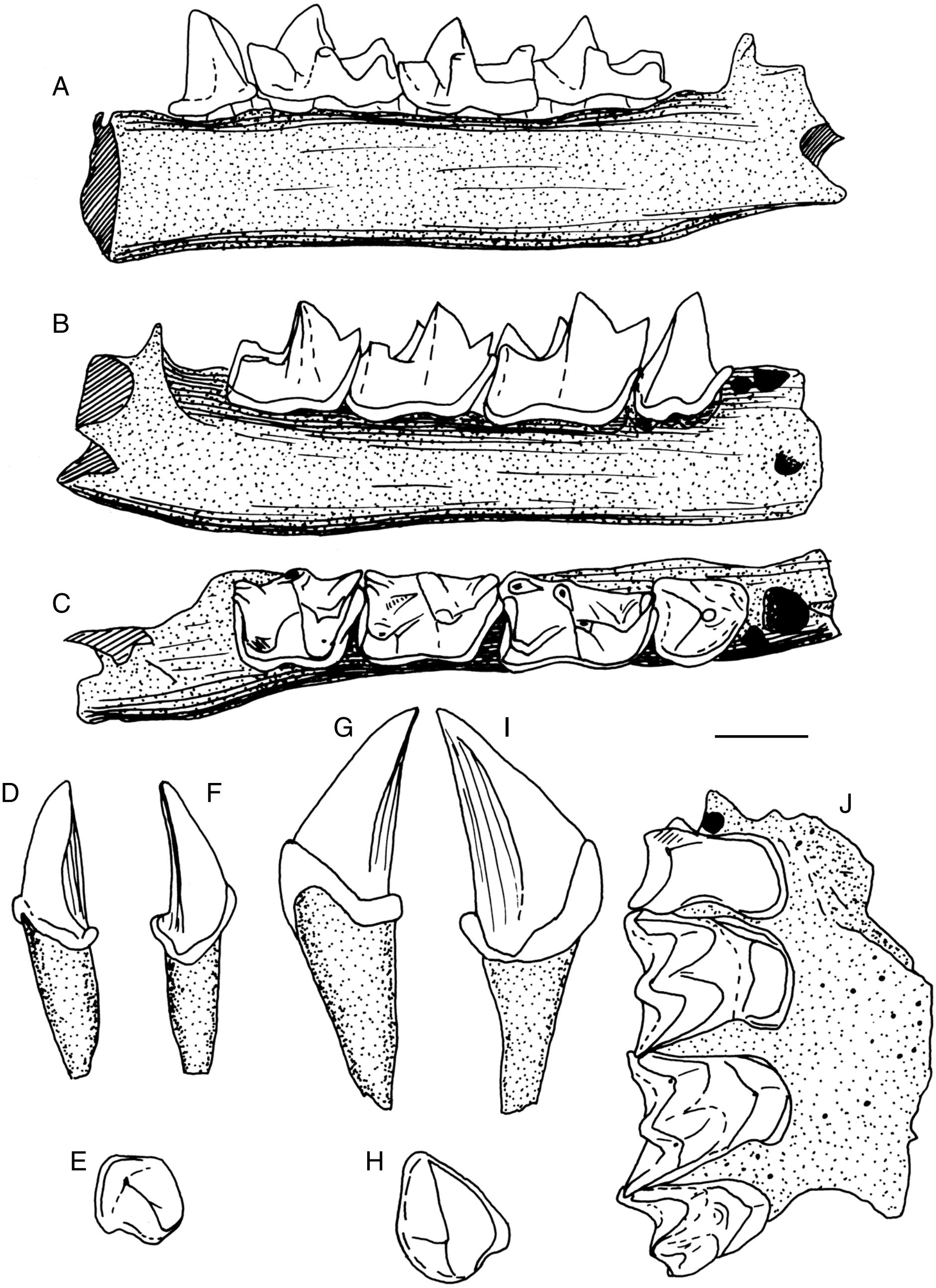

FIG. 8. — *Rhinolophus mehelyi birzebbugensis* Storch, 1974; **A**, right fragment of mandible with p4-m3, Ms149, lingual view; **B**, the same, labial view; **C**, the same, occlusal view; **D**, right lower canine, Ms158-1, lingual view; **E**, the same, occlusal view; **F**, the same, buccal view; **G**, right upper canine, Ms151, buccal view; **H**, the same, occlusal view; **I**, the same, lingual view; **J**, right palatal fragment with P4-M3, Ms150, occlusal view. Scale bar: 1 mm.

is slightly more elongated in the recent *Rh. mehelyi* and *Rh. euryale* and much more in *Rh. blasii*.

M1-M2: the posterior emargination of these teeth is shallow like in the three modern medium-sized species, whereas in *Rh. ferrumequinum* the rear margin of the crown has a well pronounced emargination. The recent *Rh. blasii* differs considerably from the remaining two medium-sized species in having a strongly developed talon on these molars and especially on M1. So, these molars are strongly elongated transversely. In this respect, the fossil material is similar to *Rh. mehelyi* and *Rh. euryale*.

M3: the tooth is massive and more elongated transversely than in the recent *Rh. mehelyi*. In this respect, it is similar with the other two modern medium-sized species. On the other hand, the fossil material differs from the three comparative species in having a proportionately larger M3.

c1: in the crown outline the tooth is an irregular trapezium with convex labial and concave posterior margins. The anterolingual corner is poorly pronounced and rounded as in the modern *Rh. mehelyi*, whereas in the comparative specimens of *Rh. euryale* it is sharp. In contrast, this corner is not developed in *Rh. blasii*, and the outline of its crown in occlusal view is triangular.

p3: this tooth is not preserved, but judging by the size and position of the alveolus, it may be assumed that p3 must have been similar with the recent species *Rh. euryale* and in a lesser degree with *Rh. blasii.* These species present moderately reduced p3 situated in the tooth row (some specimens of *Rh. blasii*) or slightly shifted laterally (some specimens of *Rh. blasii* and *Rh. euryale*). At the same time it differs from *Rh. mehelyi* which has more reduced p3 and displaced further labially.

p4 in the outline of crown is a triangle with rounded corners, with a well developed anterolingual cingular shelf, and straight or slightly concave lingual margin. In these respects, the available teeth are similar to those of the modern comparative specimens of *Rh. mehelyi*. In the other two medium-sized species, the outline of the crown is a shortened (*Rh. euryale*) or more or less elongated (*Rh. blasii*) trapezium. In *Rh. ferrumequinum* the p4 is almost square with a poorly developed cingular shelf and convex lingual margin.

m1-m2: the structure of these nyctalodontic molars is similar to those of the recent *Rh. mehelyi* from Bulgaria though differing in some proportions and dimensions. The m1 deserves special attention in this respect. The length of this tooth is considerably greater than in the recent comparative material, while there is a broad overlap in the talonid breadth (Table 2). Storch (1974) reported similar relations between the recent and fossil (early Pleistocene) populations of *Rh. mehelyi*, though the talonid width of m1 in the Mediterranean modern form is even greater, nearly equal to the average value of the population from Muselievo.

m3: nyctalodontic. As compared with the modern medium-sized species, the form from Muselievo differs in having broadest talonids and larger size of this molar.

Palate: the posterior emargination of the palate is shallow (specimen Ms150) and anteriorly reaches the middle part of the M3. In this respect, the fossil specimen is quite different from the three recent medium-sized species in which this emargination is quite deep, reaching anteriorly the posterior or middle part of the crown of M2.

REMARKS

The above descriptions and comparisons suggest that the material examined presents a horseshoe bat of medium size close to the contemporary species *Rh. mehelyi*. It differs considerably, however, from the modern comparative material in its generally greater size, more elongated m1, etc. In this respect the specimens from Muselievo fit well to the description of the limited early Pleistocene material from Malta, designated as a separate subspecies, *Rhinolophus mehelyi birzebbugensis*

TABLE 3. — Dental measurements (mm) of *Rhinolophus* ex gr. *euryale* Blasius, 1853 from Muselievo in comparison with the recent *Rhinolophus euryale* from Bulgaria. For abbreviations see Material and methods.

	***Rhinolophus* ex gr. *euryale* Muselievo**					***Rhinolophus euryale* Bulgaria, recent, N = 80**			
	N	Min	M	Max	SD	Min	M	Max	SD
LC1	26	1.42	1.52	1.67	0.057	1.00	1.52	1.67	0.085
WC1	26	1.00	1.10	1.20	0.064	0.90	1.11	1.35	0.056
LM1	1	-	1.42	-	-	1.42	1.58	1.67	0.049
WM1	1	-	1.87	-	-	1.57	1.86	2.07	0.088
LM2	2	1.50	-	1.52	-	1.35	1.43	1.52	0.034
WM2	2	1.82	-	2.00	-	1.60	1.74	1.86	0.064
LM3	4	1.00	1.10	1.15	-	0.92	1.02	1.17	0.050
WM3	4	1.52	1.60	1.67	-	1.40	1.54	1.62	0.048
Lc1	8	0.85	0.94	0.97	0.060	0.77	0.87	0.95	0.040
Wc1	8	0.95	1.01	1.05	0.038	0.85	0.95	1.05	0.037
Lm1	1	-	1.50	-	-	1.57	1.69	1.82	0.042
Wm1	1	-	1.00	-	-	0.85	1.02	1.20	0.077
Lm2	3	1.55	1.57	1.60	-	1.45	1.56	1.67	0.035
Wm2	3	1.02	1.08	1.15	-	0.92	1.04	1.22	0.069
Lm3	1	-	1.57	-	-	1.32	1.41	1.52	0.046
trWm3	1	-	1.00	-	-	0.80	0.95	1.15	0.091
taWm3	1	-	0.92	-	-	0.63	0.76	0.92	0.067

(Storch 1974). The rich material from Muselievo and the above comparisons reveal some additional peculiarities of this form: relatively large p4, P4, m3 and M3, less reduced talonid on m3, and probably relatively large P2 and p3 not very shifted from the tooth row, a shallow posterior emargination of the palate.

Having in mind the morphologic evolutionary trends in large horseshoe bats and the general direction of specialization in recent rhinolophids (see above), the characters that differentiate the Muselievo material from the modern *Rh. mehelyi* are of less specialized nature. In this respect, it is somewhat similar to the smaller recent species *Rh. euryale* and especially to *Rh. blasii*. However, considering that, according to the recent situation, the large forms should be more specialized in the above respects, the form from Muselievo would fit better in the evolutionary line of *Rh. mehelyi* and might even be regarded as an ancestor of the recent species. That is why, following Storch (1974), I considered the fossil form as a chrono-subspecies of *Rh. mehelyi*.

***Rhinolophus* ex gr. *euryale* Blasius, 1853**
(Figs 9; 10)

MATERIAL EXAMINED. — 2 fragments of mandible with p3-m1 and m1-m2 (Ms166, 167), 4 c1 (Ms168, 169), 1 M1 (Ms170), 2 M2 (Ms171), 4 M3 (Ms172), 20 C1 (Ms173).

MEASUREMENTS. — See Table 3.

DESCRIPTION AND COMPARISONS

C1: the crown outline in occlusal view is elongated and oval, tapering anteriorly. The modern *Rh. mehelyi* differs from the fossil form in having an extensively developed linguo-distal part of this tooth. In recent *Rh. euryale* the occlusal outline is more oval, not tapering anteriorly, possessing a postero-lingual depression, lacking in the fossil material.

M1-M2: the posterior emargination and talons are poorly developed, so the molars are, to some extent, similar to those in *Rh. euryale* (poor emargination, but more developed talon) and *Rh. mehelyi* (weak talon but more pronounced emargination). The molars of the modern *Rh. blasii* are quite different in having a well developed talon and respectively much wider crowns (see above).

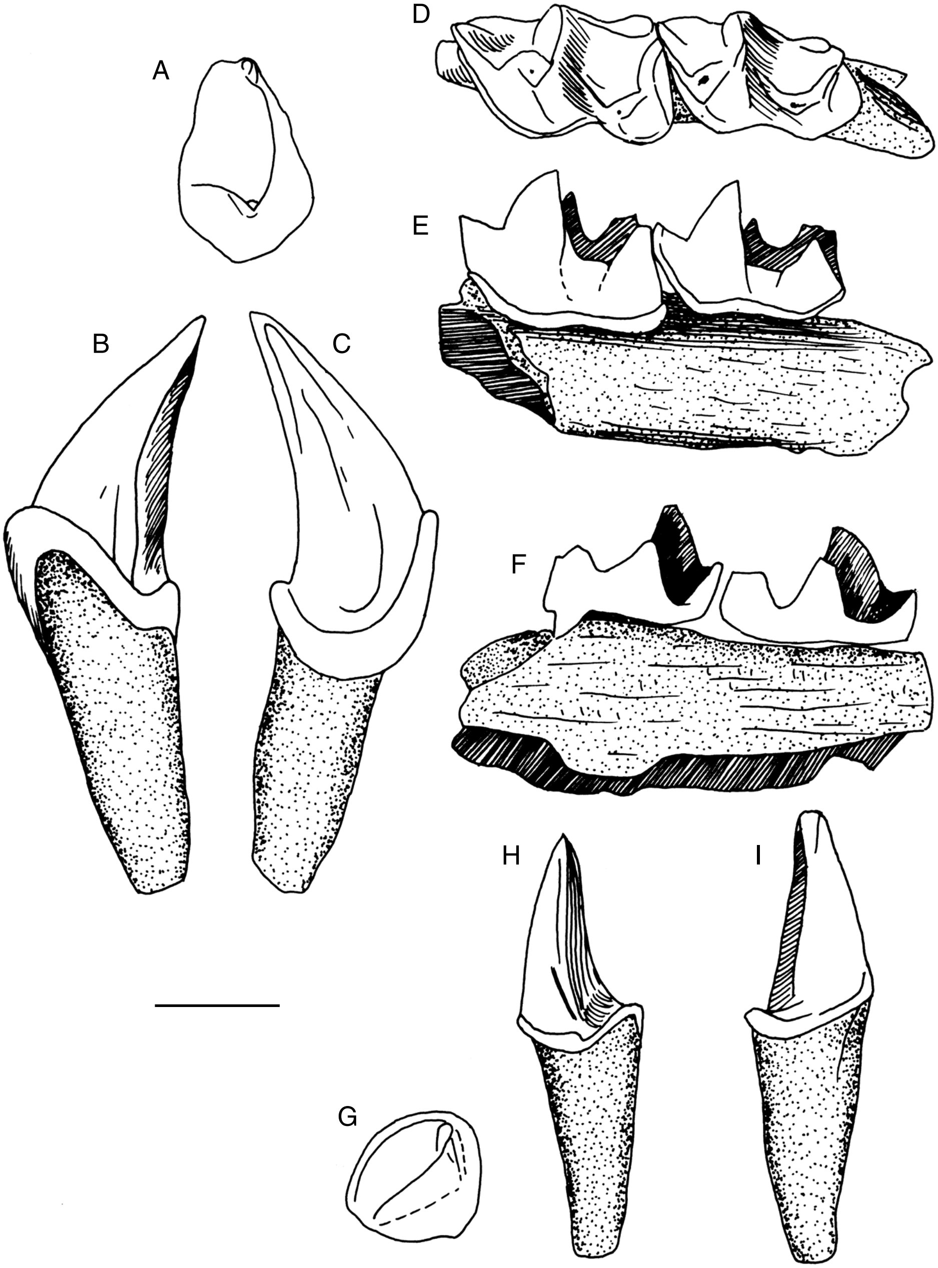

FIG. 9. — *Rhinolophus* ex gr. *euryale* Blasius, 1853; **A**, right upper canine, Ms173, occlusal view; **B**, the same, buccal view; **C**, the same, lingual view; **D**, fragment of right mandible with m2-m3, Ms167, occlusal view; **E**, the same, labial view; **F**, the same, lingual view; **G**, left lower canine, Ms168, occlusal view; **H**, the same, buccal view; **I**, the same, lingual view. Scale bar: 1 mm.

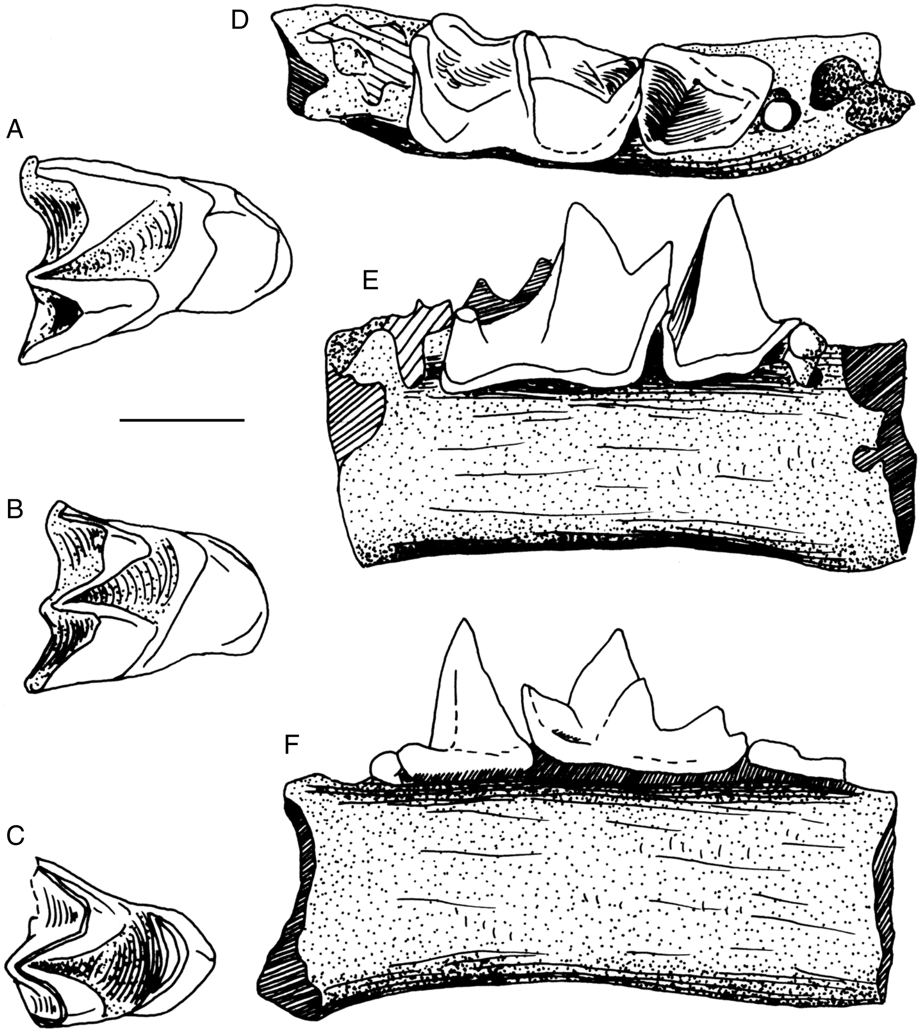

FIG. 10. — *Rhinolophus* ex gr. *euryale* Blasius, 1853; **A**, right M1, Ms170, occlusal view; **B**, right M2, Ms171, occlusal view; **C**, right M3, Ms172, occlusal view; **D**, right fragment of mandible with p4-m1, Ms166, occlusal view; **E**, the same, labial view; **F**, the same, lingual view. Scale bar: 1 mm.

M3: the crown outline is triangular, similar to *Rh. euryale* but with more developed posterior (metacone-metastyle) loop.

c1: in occlusal outline, it is an oval or shortened trapezium with rounded corners. The tooth possesses a well developed talon in its posterior part. It is similar to the recent *Rh. euryale* but differs in having larger size and a rounded anterolingual part.

p3 is relatively large, almost round and lies in the tooth row, situated in such a way that the alveolus of p2 is shifted anteriorly and the crowns of p2 and p4 were probably not contiguous. In this respect, it is similar to some specimens of recent *Rh. blasii* and *Rh. euryale* from Bulgaria. However, in general, the three modern species seem more specialized than the fossil form in having more tightly spaced p2 and p4.

p4 in crown outline resembles an elongated trapezium with its base facing lingually. Its cingulum is well developed, forming a large shelf anteriorly. The tooth is more elongated than in the recent *Rh. euryale* but close to *Rh. blasii*. The shape of p4 in the modern *Rh. mehelyi* is nearly triangular and thus it is quite different from the fossil material and the other two medium-sized modern species.

m1-m2 are nyctalodontic and elongated, close in their form to the present-day *Rh. euryale*. The molars are less massive and narrower in comparison with those in recent *Rh. mehelyi*.

m3: this nyctalodontic tooth possesses a massive talonid similar to the less specialized modern *Rh. blasii*. In contrast, the talonids of the other two medium-sized species are more delicate.

REMARKS

The above descriptions and comparisons show that the fossil material is nearer to *Rhinolophus euryale* than to the other two medium-sized species. At the same time it differs from the contemporary species in some important features: a relatively large p3, situated near to the longitudinal axis of the tooth row; more elongated p4; better developed talonid on m3; more massive lower canine with weaker (rounded) antero-lingual corner; the occlusal outline of the crown of the upper canine is tapered in its posterior part and does not show any postero-lingual emargination. In some of these characters, the level of specialization is about that of the less specialized (in some respects) recent species of this group, *Rh. blasii*. Most probably, these similarities correspond to the low evolutionary level of the fossil form and do not indicate that they belong to the same evolutionary lineage. The differences with the modern *Rh. mehelyi* are greater because it is more specialized, according to the criteria mentioned above.

As compared with the fossil forms, the measurements of the material from Muselievo are close to *Rh. neglectus* Heller, 1936 and *Rh. euryale praeglacialis* Kormos, 1934. Unfortunately, the original descriptions of these species are incomplete and do not permit detailed comparisons. In general, these two forms are slightly larger than the recent *Rh. euryale*. More detailed information is available for *Rh. neglectus* from Mala Cave and Rebielice Krolewskie 2, Poland (Woloszyn 1988). The determination of this material is based on a direct comparison with the holotype. The comparison with the data presented by Woloszyn (1988) reveals some differences such as shorter teeth (p4, m1, m2, M2) and less massive upper canines in the Muselievo material. At the same time, the only available mandible from Muselievo is similar with *Rh. neglectus* in the premolar arrangement. Most probably, this similarity is a shared plesiomorphic feature of the Pliocene forms and is not necessarily an indication for their close relationship. According to Woloszyn (1988), *M. neglectus* should be considered as a form closely related with *Rh. mehelyi*. On the other hand, the above considerations show that the fossil sample under study is more similar to *Rh. euryale*. The only assumption one can draw so far is that the material from Muselievo belongs to a primitive form within the phyletic lineage leading to the contemporary *Rhinolophus euryale*.

Family VESPERTILIONIDAE Gray, 1821

Genus *Myotis* Kaup, 1829

Some more or less complete mandibular fragments were referred to this genus on the basis of the following features: three premolars; myotodont lower molars with a rounded emargination of the paralophid in labial view (not angular as in *Plecotus*); a bluntly rounded tip of the coronoid process (not pointed as in *Plecotus*); and a relatively elongated p4 (not antero-posteriorly compressed as in large *Eptesicus*). The size and morphology of the teeth on these more or less complete specimens served as a reference sample and allowed to ascribe to this genus a large number of isolated lower teeth. The fact that the available mandibular fragments belong to only three genera

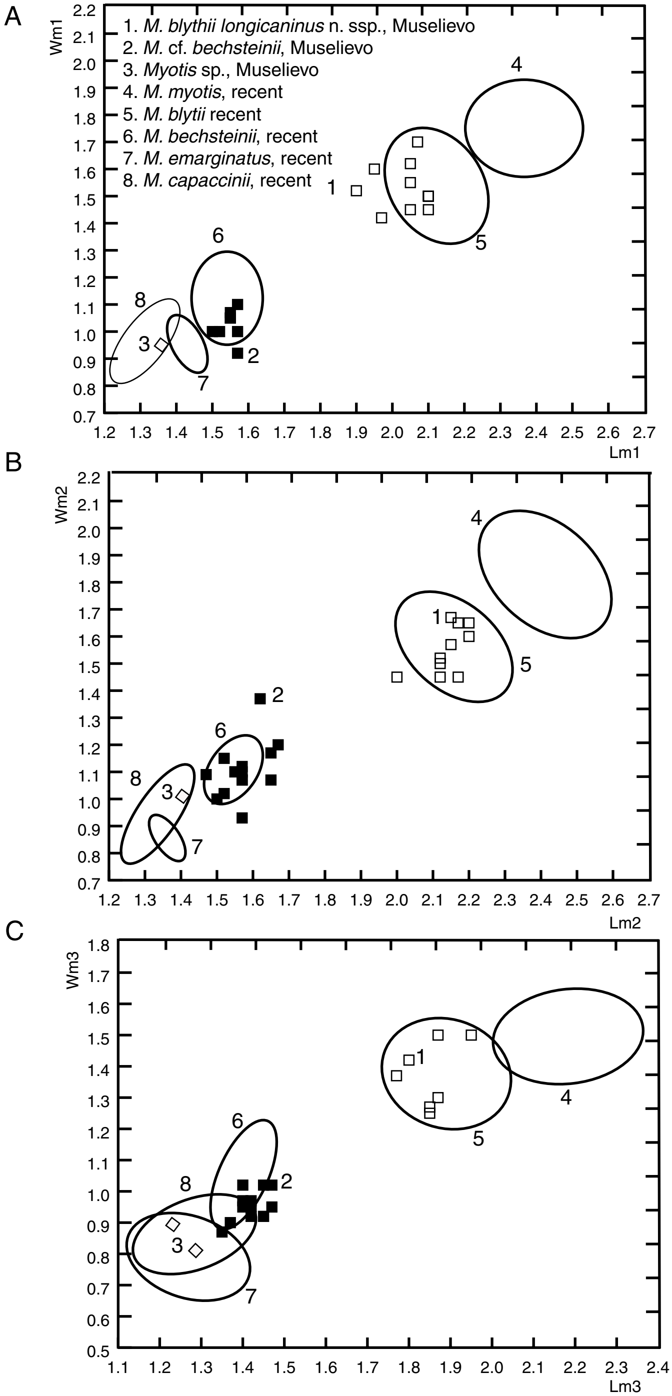

FIG. 11. — Scatter diagrams showing length (L) and width (W) of lower molars (mm) of fossil and recent *Myotis* spp.; **A**, m1; **B**, m2; **C**, m3. The recent species are presented by 5% confidence ellipses.

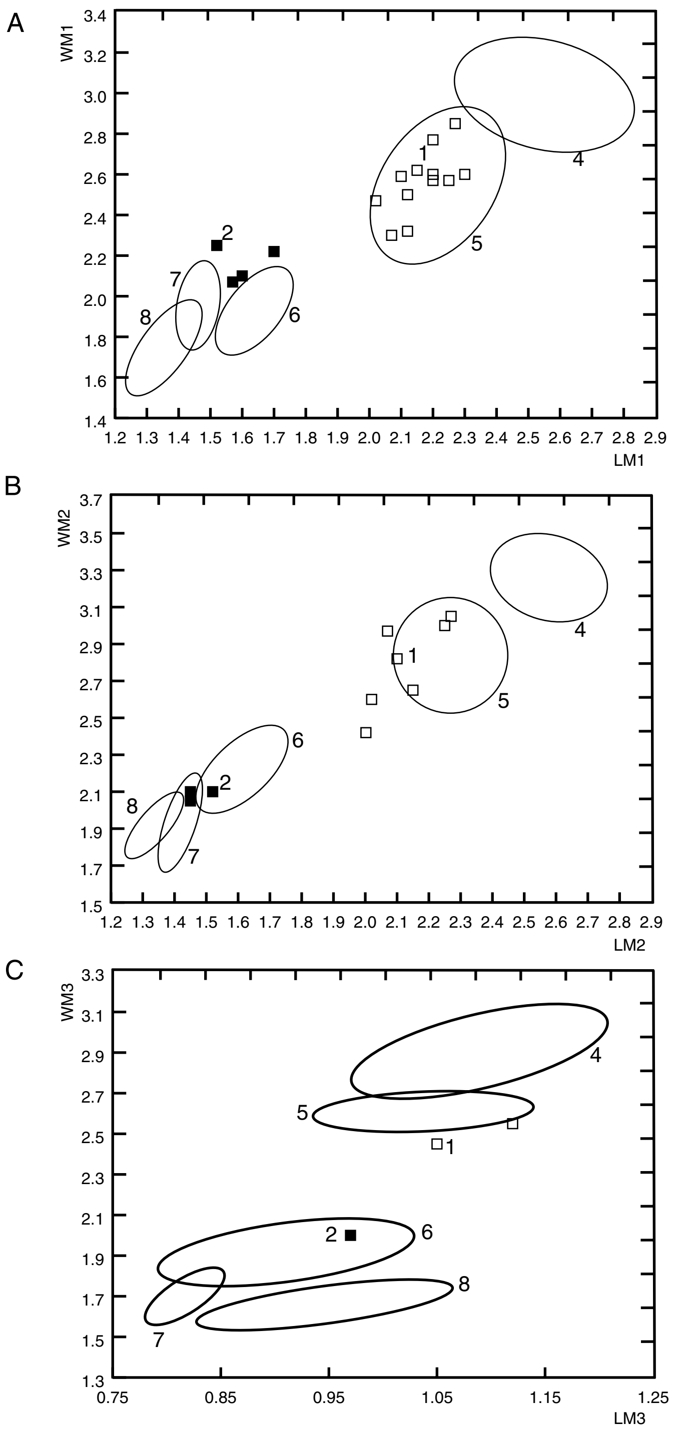

FIG. 12. — Scatter diagrams showing length (L) and width (W) of upper molars (mm) of fossil and recent *Myotis* spp.; **A**, M1; **B**, M2; **C**, M3. For explanations see Fig. 11.

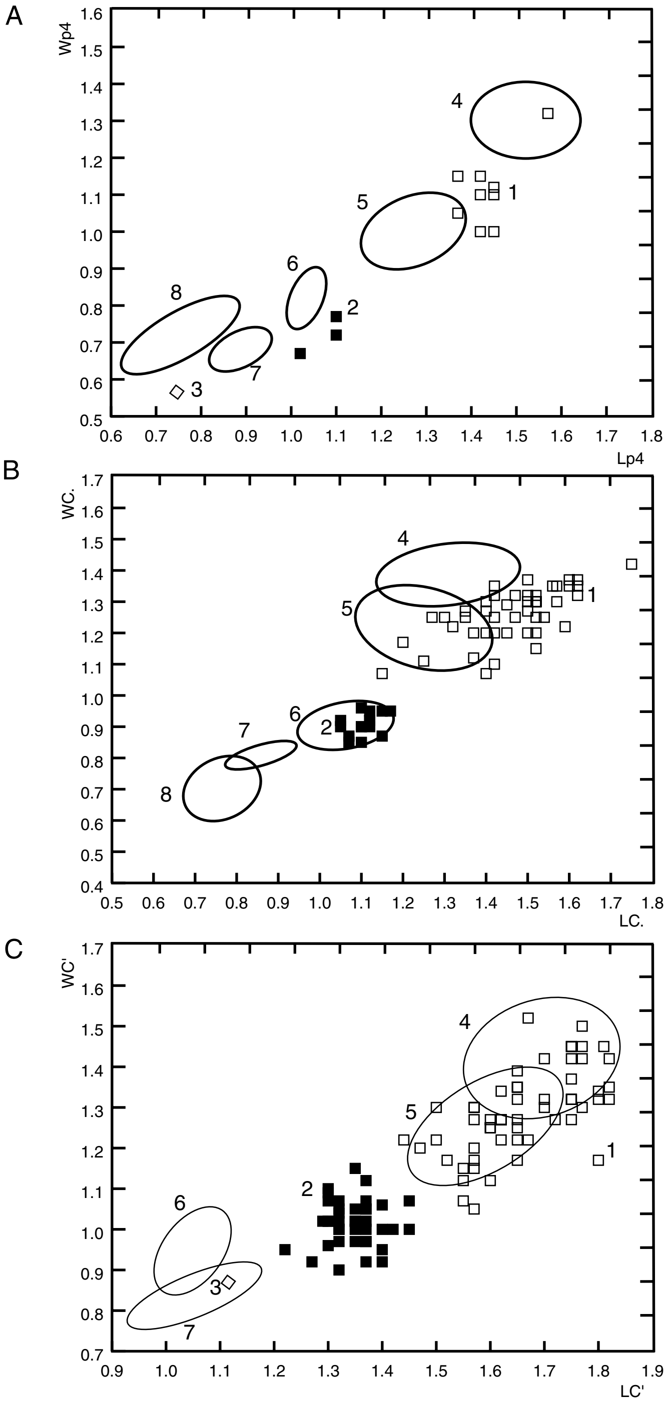

FIG. 13. — Scatter diagrams showing length (L) and width (W) of p4 (**A**), lower canine (**B**), and upper canine (**C**) (mm) of fossil and recent *Myotis* spp. For explanations see Fig. 11.

(*Rhinolophus*, *Miniopterus*, and *Myotis*) allows attribution of all upper teeth, other than these of *Rhinolophus* and *Miniopterus*, to the genus *Myotis*. The measurements of the mandibular fragments referable to *Myotis* (see below) indicate that they belong to at least three size groups. The values of length and width of the available isolated fossil teeth, plotted on scatter diagrams together with comparative samples of some recent species, confirm the occurrence of three size groups within the material from Muselievo (Figs 11-13). The largest remains belong to a form similar in size to the two recent closely related species *M. blythii* (Tomes, 1857) and *M. myotis* (Borkhausen, 1797). The second group is close to the present day *M. bechsteinii* (Kuhl, 1818), whereas the smallest remains are comparable to some medium-sized species such as *M. emarginatus* (Geoffroy, 1806), *M. nattereri* (Kuhl, 1818), and *M. capaccinii* (Bonaparte, 1837).

As in rhinolophids, a general evolutionary trend within the genus *Myotis* is the shortening of the tooth rows, which affects primarily the incisive-premolar part of the dentition (Kuz'akin 1950; Topál 1963c, 1983; Rybàø 1976). Another evolutionary trend involves the simplification of occlusal surface of teeth, especially of the incisives and upper molars alongside with the reduction of the talonid on m3 and the overall length of M3 (Menu 1987).

Myotis blythii longicaninus n. ssp.
(Figs 14; 15)

HOLOTYPE. — 1 fragment of mandible with p4 (Ms352, Fig. 14F-H).

FIGURED PARATYPES. — 1 fragment of mandible with m2-m3 (Ms350); 1 left C1 (Ms361-1); 1 left P4 (Ms361-2); 1 right M1 (Ms361-3); 1 left M2 (Ms361-4); 1 right M3 (Ms361-5); 1 left c1 (Ms361-7); 1 left m1 (Ms361-8).

ETYMOLOGY. — *Longicaninus* because of its elongated canines.

TYPE LOCALITY. — Muselievo, Bulgaria.

OTHER MATERIAL EXAMINED. — 10 small fragments of mandible with one tooth (p4, m1, m2, m3) each (Ms349-358, 362), 11 fragments of mandible without teeth (Ms359-360), 35 left C1 (Ms363), 38 right C1 (Ms368), 3 P4 (Ms365), 7 left and 4 right M1 (Ms366), 4 left and 2 right M2 (Ms367), 1 right M3 (Ms368), 30 right c1 (Ms369), 38 left c1 (Ms370), 3 left and 5 right p4 (Ms371), 5 right m1 (Ms372), 5 right and 4 left m2 (Ms373), 1 left and 1 right m3 (Ms374), 1 distal fragment of humerus (Ms375).

MEASUREMENTS. — For summary data on isolated teeth see Table 4.
Holotype: LSy = 3.50; HMd/m1 = 2.50; Lp4 = 1.42, Wp4 = 1.00.
Mandibular fragments: LSy = 2.87; 3.37; 3.40.
HMd/m1 = 2.62; 2.37; 2.42; 2.37; 2.50; 2.12; 2.57.
Lp2-p4 = (2.87); (2.62); (2.50); (2.30); (2.25); (2.55).
HPC = 5.55.
M1 (L × W) = 2.10 × 1.45; 2.05 × 1.45; 2.07 × 1.70; 1.97 × 1.42.
M2 (L × W) = 2.00 × 1.45; 2.20 × 1.60; 2.20 × 1.42.
M3 (L × trW × taW) = 1.80 × 1.42 × 1.02; 1.77 × 1.25 × 0.92; 1.87 × 1.30 × 1.02; 1.85 × 1.25 × 1.02; 1.95 × 1.50 × 1.05.

DIAGNOSIS. — A large *Myotis* species with elongated canines and p4s.

DIFFERENTIAL DIAGNOSIS. — *Myotis blythii longicaninus* n. ssp. has smaller molars than the recent *M. myotis*, being similar in this respect with *M. blythii*, but differs from the recent form in having considerably longer canines, a larger p4, more anterior position of the mental foramen, more oblique position of the symphysis, ellipsoidal basal cross-section of the upper canine (not pear-like as in the recent species), better developed mesial cingula on M1 and M2, less anteroposteriorly reduced M3, slender and elongated m1-m2, less reduced talon on m3, without interruption of the middle part of the labial cingulum on m3. The form from Muselievo differs from *Myotis ghardalamensis* Storch, 1974 in having more elongated p4 and m1-m2, and less reduced M3.

DESCRIPTION AND COMPARISONS

The holotype (Ms352) is a mandibular fragment with p4, which lingual margin is slightly eroded; the alveoli of the canine, p2, p3, and i3 and the symphysis are also preserved. The crown outline of p4 is rectangular (elongated antero-postereriorly) with rounded corners (occlusal view). In the recent species this tooth is shortened antero-posteriorly with a trapezoidal outline, somewhat widened out posteriorly. The anterior margin of the cingulum of the p4 overlaps the posterior rim of the alveolus of p3, in contrast to the recent species, in which

TABLE 4. — Measurements (mm) of isolated teeth of *Myotis* (s.s.) *blythii longicanninus* n. ssp. from Muselievo in comparison with the recent species from North Bulgaria and some fossil forms. For abbreviations see Material and methods.

	***Myotis blythii longicanninus* n. ssp. Muselievo**					***M. blythii* recent, North Bulgaria, N = 20**			***M. myotis* recent, North Bulgaria, N = 20**			***M. ghadalensis* early Pleist., Malta**	***M.* cf. *blythii* middle Pliocene, Osztramos 9, Hungary**
	N	Min	M	Max	SD	Min	M	Max	Min	M	Max	Min-Max	Min-Max
Lc1	47	1.15	1.46	1.75	0.118	1.15	1.27	1.40	1.17	1.34	1.50	-	-
Wc1	46	1.07	1.26	1.42	0.083	1.17	1.23	1.32	1.32	1.42	1.50	-	-
Lp4	8	1.37	1.44	1.57	0.063	1.20	1.28	1.37	1.42	1.53	1.62	-	1.36
Wp4	8	1.00	1.12	1.32	0.094	0.92	1.04	1.12	1.12	1.28	1.42	1.20	-
Lm1	6	1.90	2.02	2.10	0.082	1.97	2.09	2.20	2.20	2.31	2.47	-	1.90-2.15
Wm1	6	1.50	1.55	1.62	0.051	1.35	1.51	1.70	1.50	1.76	1.95	-	-
Lm2	8	2.12	2.15	2.20	0.029	2.07	2.16	2.27	2.30	2.44	2.60	-	2.15
Wm2	8	1.45	1.56	1.67	0.091	1.42	1.57	1.70	1.60	1.84	2.07	1.56-1.60	-
Lm3	2	1.85	-	1.87	-	1.80	1.87	2.00	1.97	2.16	2.32	1.84-1.88	3.03
trWm3	2	1.27	-	1.50	-	1.25	1.36	1.55	1.32	1.52	1.67	1.32-1.36	1.22
taWm3	2	0.95	-	1.10	-	0.82	0.93	1.02	0.82	0.96	1.20	-	0.92
LC1	57	1.47	1.66	1.82	0.098	1.50	1.59	1.70	1.59	1.69	1.85	-	-
WC1	57	1.05	1.29	1.52	0.104	1.10	1.26	1.40	1.42	1.49	1.62	-	-
LP4	3	1.40	1.61	1.80	-	1.35	1.56	1.72	1.72	1.93	2.10	-	1.68
WP4	2	1.27	-	1.45	-	1.27	1.40	1.65	1.60	1.80	2.05	-	1.59
LM1	12	2.02	2.17	2.30	0.084	2.10	2.22	2.32	2.20	2.52	2.77	-	2.08
WM1	12	2.30	2.56	2.85	0.157	2.15	2.54	2.85	2.80	3.06	3.30	-	2.82
LM2	7	2.02	2.12	2.27	0.102	2.15	2.24	2.42	2.35	2.59	2.70	-	2.08-2.27
WM2	7	2.42	2.79	3.05	0.237	2.60	2.86	3.17	3.12	3.45	3.70	-	3.00-3.22
LM3	2	1.05	-	1.12	-	0.95	1.05	1.20	1.00	1.08	1.17	1.08	-
WM3	2	2.45	-	2.55	-	2.15	2.55	2.67	2.62	2.93	3.17	2.64	-

the anterior end of p4 does not reach the alveolus of p3. The foramen mentale is situated under the portion between c1 and p2 (in front of the root of p2), while in the recent species it is shifted posteriorly, located on the level of the root of p2 or behind it, i.e. between p2 and p3.

c1: in general the tooth is similar to this one of the modern *M. blythii*, but in some specimens the posterior shelf is better developed and its distal part is curved upwardly. There is no cingular cusplet at the mesiolingual margin of the tooth.

p4: the available teeth are large, rectangular in crown outline. The labial cingulum shows two concavities, each towards a root. In labial view, the overall orientation of the ventral margin of the crown is horizontal or slightly oblique, while in the recent species it is clearly oblique, with a definitely more ventral position of the posterolabial corner of the crown than the antero-labial one.

m1 and m2 : they are slender and more elongated than in the recent species. Their talonids are longer than the trigonids. In the modern species the lengths of the trigonids are nearly equal with the lengths of the talonids, or the trigonids are longer. In the fossil m1s the upper margin of the cingulum strongly ascends at the base of the protoconid. The entocristids are well developed and somewhat higher than in the recent species.

m3: the talonid shows no distinct reduction, in contrast to the recent species. The labial cingulum is equally thick along the crown, while in the recent species it is weaken or interrupted between the protoconid and hypoconid.

C1: the basal cross-section of the crown is ellipsoidal. There are two shallow grooves: one on the labial face, one on the lingual face. In the recent species these grooves are better pronounced and very often there is a trace of an

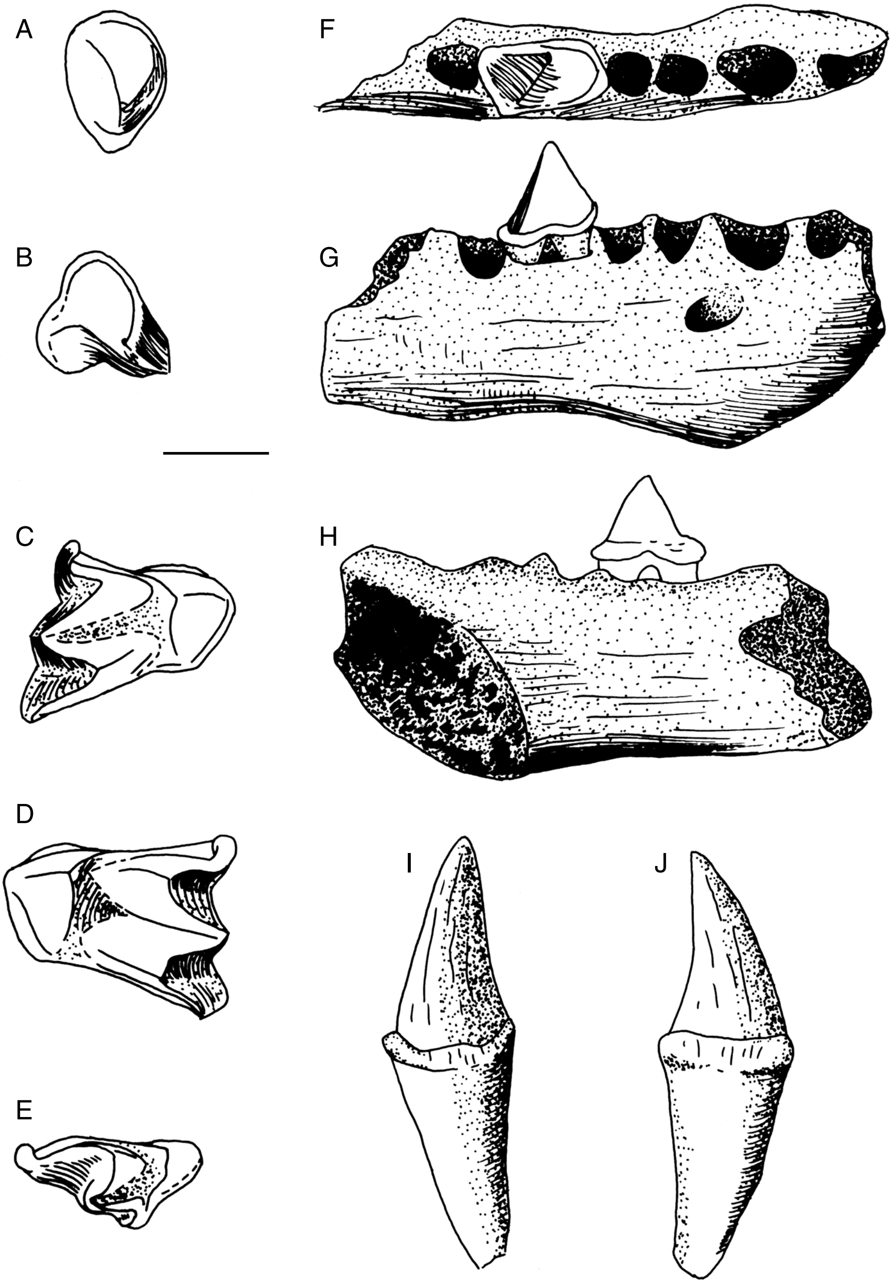

FIG. 14. — *Myotis blythii longicaninus* n. ssp.; **A**, right upper canine, Ms364-1, occlusal view; **I**, the same, buccal view; **J**, the same, lingual view; **B**, left P4, Ms365-1, occlusal view; **C**, right M1, Ms366-1, occlusal view; **D**, left M2, Ms367-1, occlusal view; **E**, right M3, Ms368, occlusal view; **F**, right fragment of mandible with p4, Ms352 (holotype), occlusal view; **G**, the same, labial view; **H**, the same, lingual view. Scale bar: 1 mm.

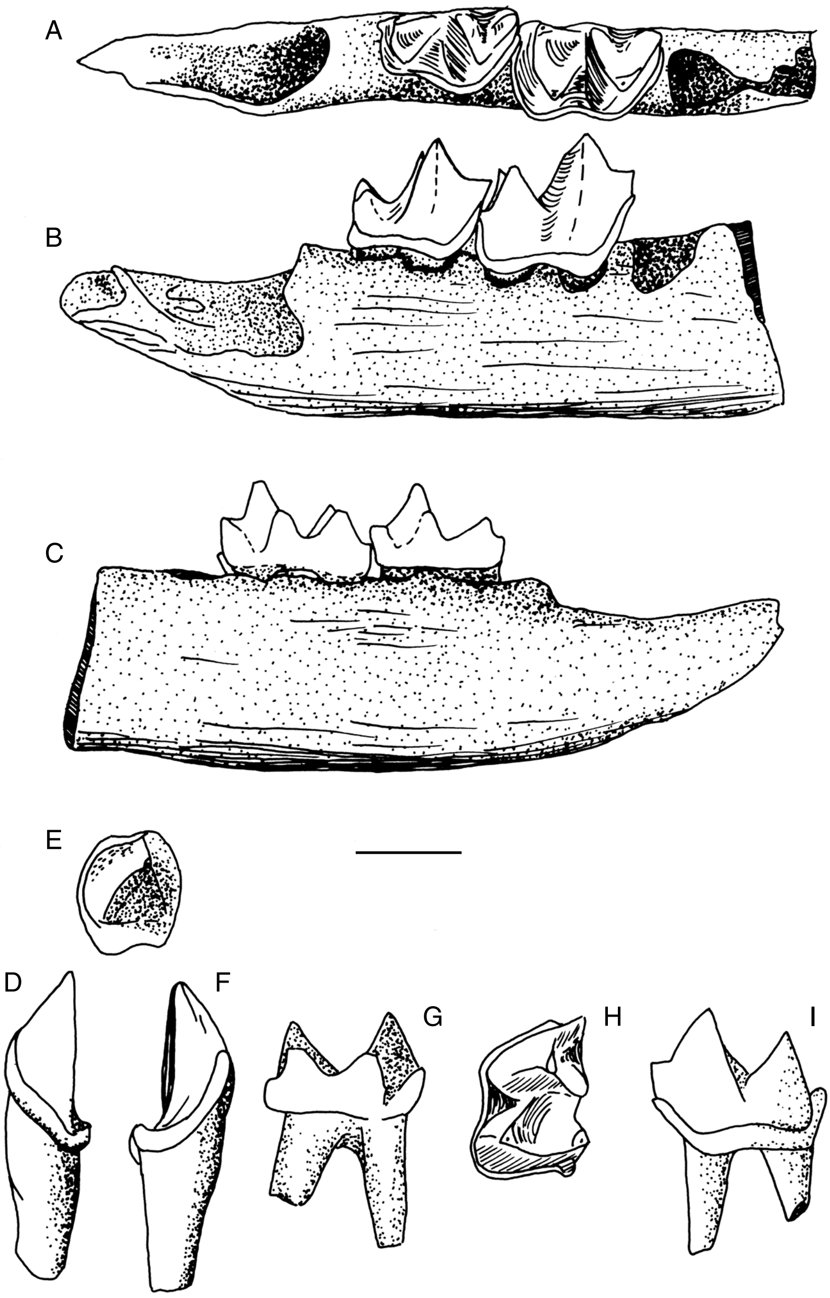

FIG. 15. — *Myotis blythii longicaninus* n. ssp.; **A**, right fragment of mandible with m2-m3, Ms350, occlusal view; **B**, the same, labial view; **C**, the same, lingual view; **D**, left lower canine, Ms370-1, buccal view; **E**, the same, occlusal view; **F**, the same, lingual view; **G**, left m1, Ms372-1, lingual view; **H**, the same, occlusal view; **I**, the same, buccal view. Scale bar: 1 mm.

antero-labial groove, which never occurs in the fossil form. The lower margin of the crown is sharp and well differentiated from the root, while in the recent species the transition between these parts of the tooth is gradual.

P4: in one unworn tooth there is an indistinct accessory tubercle on the mesio-lingual margin of the cingulum. This cingular cusplet is always missing in the recent comparative material of *M. blythii*. The lingual portion of the crown (talon) is better developed than in the modern species.

M1-M2: the occlusal surface of the two first upper molars is simplified: without heel, paraloph, metaloph, and metaconule, similar in these respects to the recent species. The differences concern the wider mesial cingula in the fossil teeth, which usually incorporate the parastyles. This feature reflects the loose arrangement of P4-M1-M2 in the fossil form.

M3: the outline of the crown is transversely triangular, with a rather massive metacone protruding posteriorly. In the recent species this cusp is indistinct, transversely elongated as an extension of the premetacrista.

REMARKS

The L × W plots of the fossil molars (Figs 11; 12) show that they are of approximately the same size as the teeth of the recent *M. blythii*. In the same time the ranges of variability of the fossil p4s and especially of the lengths of the canines are larger, covering the variability of both recent species, *M. myotis* and *M. blythii* (Fig. 13). These data indicate that we deal with one species, similar in size to *M. blythii* but with longer canines and larger p4s.

The size of molars from Muselievo is nearly identical with the middle Pliocene material from Osztramos 9 and 13, determined as *Myotis* cf. *blythii* (Topál 1983). The Hungarian form has a relatively wide talonid on m3 (trWm3 = 1.22, taWm3 = 0.92; taW/trW = 83.63%), which, according to Topál (1983), "seems to be a primary and more ancient feature". The form from Muselievo also shows a relatively wide talonid. The values of the taW/trW ratio in the two specimens from Muselievo are 73.3 and 74.8%, while in 20 recent specimens of *M. blythii* this ratio ranges between 63.08 and 73.08% with a mean value of 68.78%. This ratio is even lower in the recent closely related species *M. myotis* (62.12-71.85%). Based on this feature and on the reduced premolar rows, *M. myotis*, according to Topál (1963c), is more evolved than *M. blythii*. In this context, the differences between the fossil and the recent samples of *M. blythii*, presented above, indicate that the remains from Muselievo represent an unspecialized and primitive form.

***Myotis* cf. *bechsteinii* (Kuhl, 1818)**
(Fig. 16)

MATERIAL EXAMINED. — 15 mandibular fragments (1 with p4 and m1, 2 with p4, m1 and m2, 1 with m1-m2, 5 with m2-m3, 2 with m1, 1 with m2, 3 with m3) (Ms320-334), 15 c1 (Ms335-336), 1 p4 (Ms337), 4 m1 (Ms338), 7 m2 (Ms339), 2 m3 (Ms340), 39 C1 (Ms378), 1 P4 (Ms342), 7 M1-2 (Ms343-344), 1 M3 (Ms345).

MEASUREMENTS. — See Table 5.

DESCRIPTION AND COMPARISON

Mandible: the horizontal ramus is rather massive. The mental foramen lies between the roots of the canine and p2 as in the recent *M. emarginatus* (Geoffroy, 1806) and *M. nattereri* (Kuhl, 1818), while in the modern comparative material of *M. bechsteinii* (Kuhl, 1818) it is situated under the p2. The anterior margin of the horizontal branch of mandible is more oblique in lateral view than in the modern *M. emarginatus*. In this respect it is similar to *M. bechsteinii*.

c1: the posterior shelf of the cingulum is not well developed; its distal part is not curved upwards as in the modern *M. emarginatus*, *M. nattereri*, and especially in *M. bechsteinii*.

p3: judging by the size and position of the alveolus, this premolar should be relatively large, situated close to p4, in such a way that their crowns were probably contiguous, differing in this respect from the modern *M. emarginatus* in which the premolars are loosely spaced.

TABLE 5. — Measurements (mm) of *Myotis* sp. and *M.* cf. *bechsteinii* (Kuhl, 1818) from Muselievo in comparison with some recent species of the genus from Bulgaria. For abbreviations see Material and methods.

	Muselievo						**Bulgaria, recent**					
	***Myotis* sp.**	***M.* cf. *bechsteinii* N = 2 - 8**					***M. bechsteinii* N = 4**				***M. emarginatus* N = 4**	***M. nattereri* N = 4**
	Min-Max	N	Min	M	Max	SD	Min	M	Max	SD	Min-Max	Min-Max
Lsy	1.75-2	1	-	2.55	-	-	2.67	-	2.82	-	-	-
Hmd/m1	1.4-1.6	4	1.85	-	1.95	-	1.55	1.64	1.80	0.087	-	-
Hmd/m2	1.37	10	1.82	-	2.07	-	1.62	-	1.72	-	1.60-1.80	1.45-1.50
Lp4-m3	-	1	-	(5.20)	-	-	5.17	-	5.22	-	4.77-4.90	4.30-4.80
Lm1-m3	3.85	1	-	(4.30)	-	-	4.20	4.33	4.60	0.129	3.85-4.00	3.65-3.95
Lc1	-	15	1.05	1.11	1.17	0.036	1.00	1.08	1.15	0.055	0.85-1.00	0.77-0.85
Wc1	-	15	0.85	0.91	0.96	0.036	0.85	0.91	0.97	0.042	0.77-0.85	0.64-0.75
Lp4	0.77	5	0.97	1.04	1.10	0.053	1.01	1.05	1.07	0.017	0.90-0.95	0.70-0.91
Wp4	0.57	5	0.67	0.73	0.77	0.038	0.77	0.82	0.92	0.049	0.65-0.70	0.61-0.75
Lm1	1.35-1.37	10	1.50	1.56	1.62	0.032	1.45	1.50	1.57	0.046	1.42-1.45	1.27-1.35
Wm1	0.82-0.97	11	1.00	1.04	1.10	0.055	0.95	1.10	1.22	0.099	0.85-1.00	0.82-1.05
Lm2	1.40	16	1.47	1.56	1.67	0.058	1.50	1.56	1.65	0.047	1.32-1.42	1.23-1.40
Wm2	1.05	16	0.92	1.09	1.20	0.072	1.07	1.16	1.27	0.082	0.85-1.00	0.84-1.05
Lm3	1.25-1.35	10	1.35	1.41	1.47	0.036	1.36	1.41	1.46	0.034	1.20-1.32	1.24-1.30
trWm3	0.85-0.90	12	0.95	0.95	1.02	0.048	0.92	1.04	1.15	0.097	0.77-0.90	0.74-0.97
taWm3	0.75 (2 X)	12	0.72	0.79	0.87	0.053	-	-		-	-	-
LC1	1.12	39	1.22	1.34	1.45	0.047	1.01	1.09	1.15	0.033	1.01-1.18	0.90-1.01
WC1	0.87	39	0.90	1.01	1.15	0.056	0.90	0.96	1.05	0.064	0.81-0.88	0.74-0.82
LP4	-	1	-	1.20	-	-	1.15	1.26	1.50	0.124	1.06-1.09	0.98-1.12
WP4	-	1	-	1.15	-	-	0.95	1.11	1.20	0.061	0.90-0.97	0.94-1.05
LM1	-	4	1.52	1.60	1.70	-	1.55	1.62	1.75	0.063	1.36-1.42	1.31-1.41
WM1	-	4	2.07	2.16	2.25	-	1.75	1.91	2.12	0.131	1.64-1.75	1.58-1.85
LM2	-	3	1.45	1.47	1.52	-	1.50	1.61	1.80	0.085	1.34-1.39	1.28-1.34
WM2	-	3	2.05	2.07	2.10	-	2.02	2.12	2.32	0.125	1.92-1.97	1.74-2.03
LM3	-	1	-	0.97	-	-	0.85	0.91	0.92	0.059	0.78-0.85	0.81-0.92
WM3	-	1	-	2.00	-	-	1.72	1.88	2.02	0.089	1.65-1.77	1.50-1.82

p4: this tooth is rectangular in occlusal view with a medial constriction and, in crown outline, it resembles the respective teeth of the recent *M. emarginatus* and *M. bechsteinii*. However, the posterior edge has no impression for m1 as in the recent *M. bechsteinii*. In the modern species, this feature resulted from a strong mesio-distal compression of the tooth row anterior portion. Another consequence of this compression is the strong overlapping between the crowns of p3 and p4 in modern *M. bechsteinii*. The arrangement of p3, p4 and m1 in the fossil material corresponds more or less to that of the recent *M. emarginatus*. In particular, in both forms the p4 and m1 barely contact at the margins of the cingula. On the other hand, the available p4s differ from the respective teeth of *M. emarginatus* in having a less developed antero-labial cingular shelf, and a labial cingulum not considerably bent upwards, being only gently curved as in the recent *M. nattereri*.

m1 and m2: these myotodont molars are rather condensed antero-posteriorly as compared with the modern *M. bechsteinii* but not so much as in the available comparative material of *M. nattereri*. In this respect, they are similar to the molars of the recent *M. emarginatus*, but the fossil teeth are larger. The anterior half of the labial cingulum is thicker than in the recent *M. emarginatus*. In this respect, it is somewhat similar to the present-day *M. nattereri*.

m3: myotodont. The talonid is rather broad and massive. In this feature, the fossil species is quite

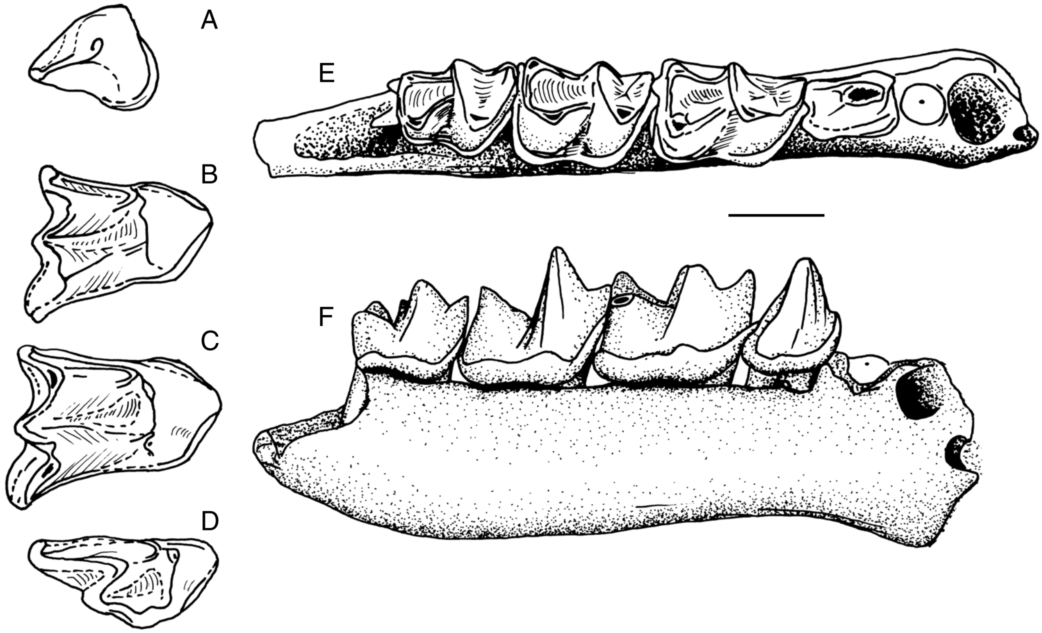

Fig. 16. — *Myotis* cf. *bechsteinii* (Kuhl, 1818); **A**, right P4, Ms342, occlusal view; **B**, right M1, Ms343-3, occlusal view; **C**, right M2, Ms343-2, occlusal view; **D**, right M3, Ms345, occlusal view; **E**, right fragment of mandible with p4-m3, Ms322, occlusal view; **F**, the same, labial view. Scale bar: 1 mm.

different from the modern species *M. bechsteinii* and *M. emarginatus* in which the talonid is conspicuously smaller. The fossil material is somewhat similar to the comparative sample of *M. nattereri*, but in this species the talonid is shorter and more gracile. In all recent species, the lateral margin of the crown (between the trigonid and talonid) is deeply concave in occlusal view, while in the fossil teeth this concavity is less pronounced.

C1: this tooth is rather elongated. The antero-lingual ridge of the crown is indistinct and rounded and the respective groove is shallow. In this respect, it is similar to the modern *M. emarginatus*. In contrast, M. *bechsteinii* possesses a rather sharp ridge along the antero-lingual side of the crown.

P4: the anterior cingulum is poorly developed in contrast to the modern *M. bechsteinii* and *M. emarginatus*.

M1-M2: with protoconule, paraloph, metaloph, and metaconule (well pronounced on M2) as in the recent *M. emarginatus*. These elements are also present in the comparative material of the modern *M. bechsteinii* but variably pronounced and generally poor. Although similar in size to the molars of the recent *Nyctalus leisleri* (Kuhl, 1817), the fossil specimens differ in having interruption of the lingual cingulum at the base of the protocone; this cingulum is complete in the recent comparative sample of *N. leisleri*. In this respect the fossil teeth are comparable with the recent *M. bechsteinii* and other *Myotis* species.

M3: although more massive, it is similar to the respective tooth of *M. emarginatus*.

Remarks

The comparisons of the sample from Muselievo with the Pliocene species *M. gundersheimensis* Heller, 1936 from Poland (Podlesice) and Hungary (Osztramos 9) (Godawa 1993) show that, although similar in size, this species has shorter molars. *M. gundersheimensis* seems more specialized than the recent *M. bechsteinii* in having shorter c1-p4 row, being similar in this respect to the middle Pleistocene *Myotis kretzoii* Topál, 1981. The last species, however, differs from both *M. gundersheimensis* and *M. bechsteinii* in having three cusps on the lower incisors (Topál 1981). Unfortunately, *M. gundersheimensis* Heller, 1936, originally described from Gundersheim (Germany, MN15b, Koenigswald & Tobien 1990), is, up to now, very superficially known on evidence of a mandibular material, and it is impossible to compare the upper molars which are of a particular phylogenetic and taxonomic importance. Nevertheless, according to the multivariate analysis on the mandibles of fossil and recent *Myotis* species, presented by Topál (1985), *M. bechsteinii* and *M. gundersheimensis* seem very similar.

The fossil molars from Muselievo are nearly identical in dimensions with the comparative sample of the recent *M. bechsteinii* from Bulgaria (Figs 11; 12). In this respect it is also similar with the Pleistocene remains of this species from La Fage (France) (Mein 1975). The fossil form from Muselievo, however, has a more massive mandible, more complicated occlusal surface of the upper molars, relatively wider talonid on m3, more loosely arranged lower premolars, and considerably longer upper canines (Fig. 13C). As mentioned above, these differences indicate that the fossil form is at a lower level of specialization in comparison with the modern species. In its massive mandible the form from Muselievo is similar to *Myotis bechsteinii robustus* Topál, 1963, described from the early Pleistocene of Hungary (Repashuta) (Topál 1963a). This form is also reported from the early Pleistocene of the isle of Malta (Storch 1974) and Hundsheim (Austria) (Rabeder 1972). The individual teeth from these localities correspond in size to the remains from Muselievo and to the recent comparative material from Bulgaria. Unfortunately, the data on the dimensions of upper canines of the forms from Malta and Austria are scarce.

The above comparisons indicate that the early fossil forms similar in size to the recent *M. bechsteinii* need detailed study, especially in order to reveal their relationships with the present-day species. For the time being, on the basis of the similarity in size and morphology of the molars, I tentatively refer the material from Muselievo to *M. bechsteinii*. The long upper canines probably indicate that we deal with a relatively primitive and unspecialized form.

Myotis sp.

MATERIAL EXAMINED. — 2 fragments of mandible with m1-m3 and m3 (Ms346-347), 2 m1 (Ms348), 1 p4, 1 m3 (Ms379-1, 2).

MEASUREMENTS. — See Table 5.

DESCRIPTION AND COMPARISONS

Mandible: the foramen mentale is located between c1 and p2.

m1-m2: these myotodontic molars are relatively short and wide as compared with the modern *M. emarginatus*, but not so much as in *M. nattereri*.

m3: as a whole this tooth is somewhat more elongated than in the modern *M. nattereri*, especially well pronounced in the talonid length, and the trigonid is less compressed antero-posteriorly.

REMARKS

The size of the remains under study is comparable with some recent medium-sized mouse-ear bats, such as *Myotis emarginatus*, *M. nattereri*, and to a lesser extends with *M. capaccinii*. The last species, however, is under the range of variability of the fossil form in some dimensions. The remains from Muselievo differ from the modern *M. emarginatus* in having not so elongate and generally smaller p4. They show a greater similarity with *M. nattereri* but the modern comparative material has more gracile upper canines.

A wide range of fossil forms of comparable size is known from the Pliocene and early Pleistocene of Europe (Heller 1936; Topál 1983; Godawa 1993). In some measurements, the scarce remains from Muselievo fall in the upper range of

TABLE 6. — Measurements (mm) of *Miniopterus* cf. *approximatus* Woloszyn, 1988 from Muselievo in comparison with the recent species *M. schreibersii* (Kuhl, 1819) from North Bulgaria. For abbreviations see Material and methods.

	***M.* cf. *approximatus*, Muselievo**					***M. schreibersii*, recent**				
	N	Min	M	Max	SD	N	Min	M	Max	SD
Lsy	6	(1.80)	1.92	2.07	0.09	5	2.16	2.25	2.35	0.078
HMd/m1	6	1.42	1.59	1.67	0.09	-	-	-	-	-
HMd/m2	10	1.45	1.57	1.75	0.115	5	1.46	1.53	1.57	0.047
Lm1-m3	1	-	(3.87)	-	-	5	3.92	4.04	4.10	0.069
Lp2-p4	5	(1.82)	1.85	1.90	0.037	5	1.85	1.90	1.95	0.035
Lc1	1	-	0.72	-	-	5	0.76	0.80	0.87	0.042
Wc1	1	-	0.80	-	-	5	0.77	0.81	0.90	0.053
Lp2	1	-	0.55	-	-	5	0.56	0.59	0.66	0.041
Wp2	1	-	0.57	-	-	5	0.60	0.65	0.67	0.034
Lp3	1	-	0.65	-	-	5	0.56	0.60	0.65	0.033
Wp3	1	-	0.57	-	-	5	0.63	0.68	0.77	0.055
Lp4	1	-	0.80	-	-	5	0.78	0.82	0.85	0.038
Wp4	1	-	0.77	-	-	5	0.74	0.81	0.95	0.087
Lm1	5	1.47	1.53	1.60	0.050	5	1.46	1.49	1.59	0.057
Wm1	6	0.92	1.01	1.15	0.083	5	0.88	1.02	1.15	0.113
Lm2	10	1.35	1.46	1.57	0.069	5	1.36	1.41	1.51	0.059
Wm2	10	0.90	1.00	1.17	0.098	5	0.85	0.95	1.02	0.068
Lm3	5	1.22	1.27	1.32	0.040	5	1.25	1.28	1.34	0.037
Wm3	5	0.75	0.83	0.87	0.047	5	0.74	0.85	0.91	0.071
LC1	35	0.97	1.10	1.20	0.050	12	1.05	1.09	1.12	0.031
WC1	35	0.81	0.93	1.05	0.056	12	0.82	0.87	1.06	0.033
LM1	2	1.40	-	1.45	-	4	1.37	1.44	1.50	0.054
WM1	2	1.80	-	1.81	-	4	1.82	1.88	2.00	0.085
LM2	4	1.32	1.41	1.47	0.067	4	1.40	1.44	1.52	0.054
WM2	4	1.80	1.91	2.00	0.085	4	1.82	1.89	1.92	0.089

variability or above it, of *Myotis exilis* Heller, 1936, *M. janossyi* Topál, 1983 and *M. danutae* Kowalski, 1956 from Podlesice (Poland) and Osztramos 9, 13 (Hungary) (Topál 1983; Godawa 1993). They are nearly identical with *Myotis delicatus* Heller, 1936, and especially with the population of this species from Podlesice (Poland) (Godawa 1993). However, according to Kowalski (1956), the p4 in the Polish population, described initially as *Myotis dasycneme subtilis* Kowalski, 1956, is almost squared (0.70 × 0.75 mm). At the same time the only available p4 from Muselievo is clearly elongated (Table 5). The fossil forms mentioned above show well pronounced differences in the height of coronoid process. Unfortunately the scarce and fragmentary material from Muselievo does not permit detailed comparisons. Therefore, I refrain from a conclusive determination until complete mandibles will be known.

Miniopterus cf. *approximatus* Woloszyn, 1988
(Figs 17; 18)

MATERIAL EXAMINED. — 8 fragments of mandible with: c1-m1 (Ms201), m2-m3 (Ms202, 212), m1-m2 (Ms207), m1 (Ms213), m2 (Ms208, 209), m3 (Ms210); 7 mandibular fragments without teeth (Ms211, 221); 36 C1 (Ms203, 217, 218); 2 M1 (Ms204, 220); 4 M2 (Ms205, 220); 1 M3 (Ms206); 4 c1 (Ms214); 6 m1-2 (Ms215); 1 m3 (Ms218); 4 distal fragments of humerus (Ms222).

MEASUREMENTS. — See Table 6.

DESCRIPTION AND COMPARISONS

C1: the basal cross-section is elliptical with longer axis parallel to tooth row; the cingulum is well developed; there are four grooves along the crown, the anterior furrow is particularly narrow and deep.

M1: in occlusal view, the outline of this tooth is subrectangular with a well pronounced posterolingual talon; the parastyle is well developed forming a right angle with the preparacrista; the tooth is provided with a metaconule, paraloph and metaloph; both lingual and posterior cingula are well developed while the anterior one is lacking.

M2: the tooth resembles the M1, except for the smaller talon and the obtuse angle between the parastyle and preparacrista.

M3: in occlusal view, the tooth has a subtriangular crown, elongated transversely with respect to the tooth row; the parastyle is similar to that of other upper molars, but smaller; the preparacrista is the longest crista.

c1: it possesses a rounded postero-lingual edge, while in the recent species it is better developed and sharper. The lingual cingulum is poorly pronounced slightly incurved upwards, forming anteriorly a poor protrusion; in the modern species, *Miniopterus schreibersii* (Kuhl, 1819), this cingulum is well developed, clearly bent up, rising higher upward, and forming a distinct antero-lingual swelling. The talonid is poorly pronounced, forming a small surface in the postero-lingual border of the crown, while in the modern species it is well developed along the whole rear margin of the crown.

The crowns of p2 and p3 are loosely spaced and barely touch at the margins of the cingula. The crowns of p3 and p4, although contiguous, do not overlap in their lingual margins and, as a consequence, in p4 there is not a protruding antero-lingual corner; in contrast, in the recent species the lingual parts of the crowns overlap and as a results there is a well pronounced antero-lingual angle on p4. In general, the crowns of p2-p4 are less compressed antero-posteriorly than in the recent species. In particular, in labial view, the ventral margins of the crowns of p2 and p3 are slightly convex in the fossil form, whereas in the recent species the margins projects considerably ventrally and as a result their cingula have a form of an asymmetrical V in labial view. The crowns of p3 and p4 are longer than wide, while in the modern species the situation reversed.

In labial view, the crown of p2 is slightly lower than that of p3, while in the recent species they are equally high.

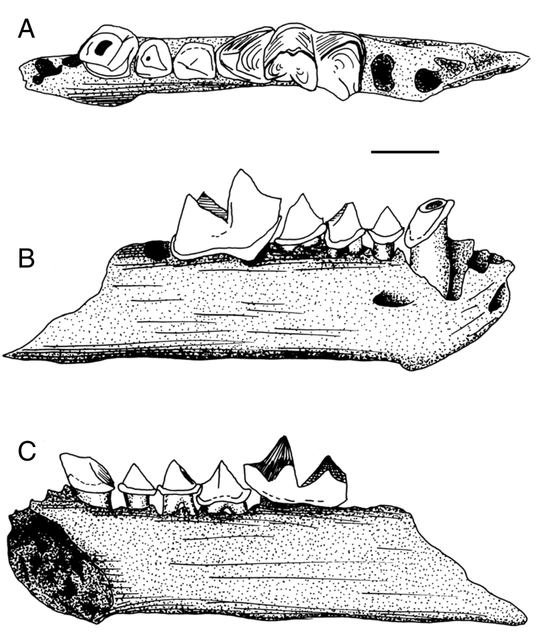

FIG. 17. — *Miniopterus* cf. *approximatus* Woloszyn, 1988; **A**, right fragment of mandible with p4-m1, Ms201, occlusal view; **B**, the same, labial view; **C**, the same, lingual view. Scale bar: 1 mm.

p2 has no tubercle on the antero-lingual cingular margin, while in the modern species this bulge is well developed; the crown cross-section is irregularly oval.

p3 is two-rooted; in occlusal view, the crown is trapezoidal or subrectangular.

p4 shows trapezoidal outline in occlusal view, orally tapering, with nearly straight labial margin; it is longer than wide. In the living species this tooth is wider than long, at most squarish, with a clearly convex labial margin (occlusal view). The labial ridge running from the tip reaches the postero-lingual edge of the crown, forming a well pronounced angle at this place. In the recent comparative material, this ridge does not reach the crown margin and there is no postero-lingual angle as seen in occlusal view. The labial cingulum on m1 is wider under hypo- and protoconid, while on m2 it is uniformly narrow.

m1-m2: nyctalodontic. In labial view the ventral margin of the crown has two convexities each

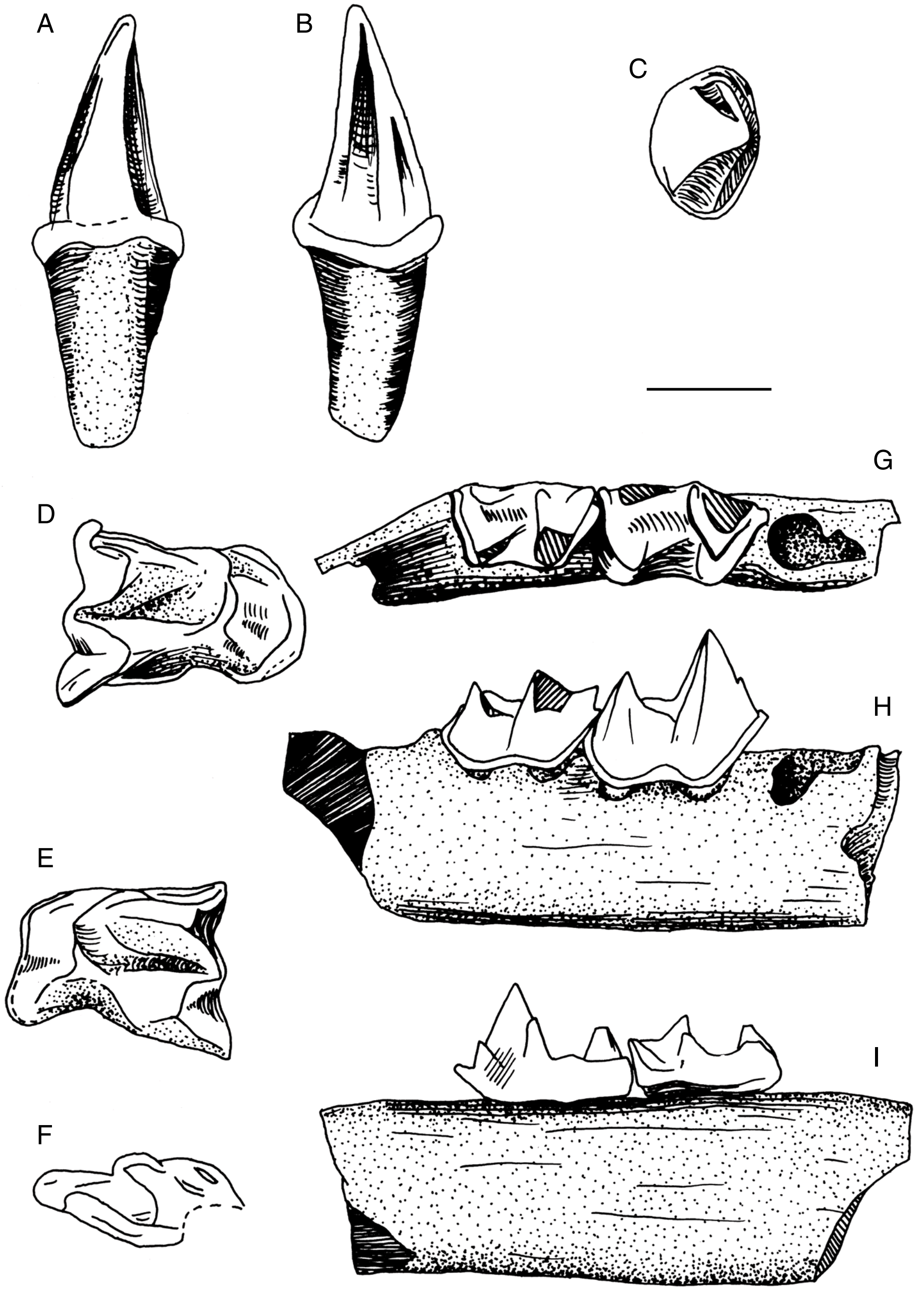

FIG. 18. — *Miniopterus* cf. *approximatus* Woloszyn, 1988; **A**, right upper canine, Ms203, labial view; **B**, the same, lingual view; **C**, the same, occlusal view; **D**, right M2, Ms205, occlusal view; **E**, left M1, Ms204, occlusal view; **F**, right M3, Ms206, occlusal view; **G**, fragment of right mandible with m2, m3, Ms202, occlusal view; **H**, the same, labial view; **I**, the same, lingual view. Scale bar: 1 mm.

towards a root, and a concavity between the roots; this medial concavity is however shallower than in the recent species, indicating that these molars are not so compressed antero-posteriorly as in the modern species. The labial cingulum of m1 is wider under the hypo- and protoconid, while this cingulum is uniformly narrow in m2 and m3.

m3: nyctalodontic; in labial view, the ventral margin of the crown is nearly straight. The talonid is slightly narrower than the trigonid.

REMARKS

Many features of the available remains such as a two rooted p3, nyctalodontic lower molars, a well developed postero-lingual talon on M1 and M2, etc., clearly indicate that they are referable to the genus *Miniopterus*. In general morphology the material is similar to the extant species *Miniopterus schreibersii*, though the lower right mandible from Muselievo, carrying c1-m1, shows some differences. These concern the anterior part of the lower tooth row: it is more elongated because the canine and premolars, especially p3 and p4, are less compressed oro-caudally and these teeth are more loosely spaced than in the modern species. Having in mind that the shortening of the anterior part of tooth row, as shown above and as pointed out by Topál (1979), is one of the best markers of the evolutionary degree in many bat phyletic lineages, it might be considered that the characters that differentiate the fossil material from Muselievo are in less evolved state than in the modern species from North Bulgaria. In this respect it is similar to the Pliocene (MN14) species, *Miniopterus approximatus*, described from Podlesice, Poland (Woloszyn 1988). On the other hand, the material from Muselievo differs considerably in having longer lower molars. In this respect, it is closer to the extant species. These comparisons, as well as the age of our material (see below), younger than the form from Podlesice, show that the remains from Muselievo represent an intermediate evolutionary stage between the Pliocene form from Poland and the modern species. The presence of such a transitive form in Muselievo constitutes an important fact, which substantiates the Woloszyn's (1988) assumption for "the probable phylogenetic links" between *M. approximatus* and the present-day *M. schreibersii*. Unfortunately, owing to a lack of sufficient material it is at present impossible to analyze these relationships in a reliable detail. For the time being, the remains from Muselievo are tentatively referred to *M. approximatus* based on their less specialized nature.

Order LAGOMORPHA Brandt, 1855
Family LAGOMYIDAE Lilljeborg, 1866
Genus *Ochotonoma* Sen, 1998

Ochotonoma csarnotana (Kretzoi, 1959)
(Fig. 19)

Ochotonoides csarnotanus Kretzoi, 1959: 244; 1962: 312, abb. 6. — Terzea & Boroneant 1979: 179-181, fig. 4. — Bazarov *et al.* 1976: 63, pl. II, fig. 9. — Erbaeva 1988: 81, pl. 19, fig. 2. — Terzea 1997: 654, fig. 3.

Ochotonoma csarnotana – Sen 1998: 367.

MATERIAL EXAMINED. — 8 p3 (Ms59-67), 2 p3 (Ms380), 1 dp4 (Ms381, 19 lower cheek teeth (Ms382), 1 fragment of mandible with m1 (Ms76), 14 upper incisors (Ms383), 1 dP2 (Ms79), 1 P2 (Ms75), 3 dP2 (Ms384), 1 P2 (Ms385), 2 dP4 (Ms77-78), 8 dP4 (Ms386), 2 P4 or M1 (Ms71-72), 2 M2 (Ms73-74), 7 M2 (Ms387), 20 upper cheek teeth (Ms388).

MEASUREMENTS. — See Table 7.

DESCRIPTION

P2 and dP2: an oblique and deep paraflexus separates the occlusal surface in two parts.

P3: the occlusal surface of the tooth is ellipsoidal, bearing a crescent shaped paraflexus, filled with crown cementum. The lingual margins of both hypocone and protocone are angular. The enamel is thin or lacking on the postero-buccal margin of the occlusal surface.

dP4: the occlusal surface is elongated. The inner part of the hypoflexus forms a kidney-shaped enamel islet.

The occlusal surface of P4 and M1 consists of two transverse lophs (anteroloph and posteroloph), separated by a deep hypoflexus, filled

TABLE 7. — Measurements (mm) of isolated teeth of *Ochotonoma csarnotana* (Kretzoi, 1959) from Muselievo. For abbreviations see Material and methods.

Upper teeth					**Lower teeth and mandible**					
	N	Min	M	Max		N	Min	M	Max	SD
LP2	1	-	0.72	-	Lp3	11	1.36	1.50	1.75	0.143
WP2	1	-	1.37	-	Wp3	8	1.32	1.74	2.05	0.253
LdP2	1	-	0.95	-	Lm1	1	-	1.65	-	-
WdP2	1	-	1.82	-	Wm1	1	-	2.00	-	-
LP3	3	1.02	1.13	1.25	Lp3-m3	1	-	(8.6)	-	-
WP3	3	1.95	2.33	2.85	HMd/p4	1	-	4.3	-	-
LP4 or M1	2	1.22	-	1.37	HMd/m2	1	-	6.5	-	-
WP4 or M1	2	2.25	-	2.77						
LM2	2	1.30	-	1.55						
WM2	2	2.12	-	2.60						

with crown cementum. Posteroloph and anteroloph are about equal in width.

M2: anteroloph is wider than posteroloph. There is a postero-lingual process.

p3: the outline of the occlusal surface is nearly triangular. It consists of two lophs, anterior (anteroconid) and posterior ones, which are separated by two deep reentrant folds, paraflexid and protoflexid. The two parts of the occlusal surface are linked by a narrow dentine isthmus. The paraflexid is directed obliquely backward, or, in one specimen, it is nearly parallel to the median axis of the occlusal surface. The protoflexid is transverse. In most specimens, the flexid's margins are smooth. In two teeth, a slight irregular waviness can be observed. The shape of anteroconid is rhomboidal and its variability concerns the presence or absence of additional anterior reentrant folds. Two specimens (Ms59 and 67) possess two well developed anterior reentrant folds, filled with crown cementum. These teeth are similar to the materials known from Csarnóta-2 and Ciuperceni (see below). Other specimens have only buccal reentrant valley (Ms63, 64, 66) with variable depth. Three other teeth (Ms63, 64 and 66) show no traces of anteroflexid, or bear very shallow grooves without cementum. The posterior loph has a deep hypoflexid obliquely directed posteriorly. On two specimens, a trace of a mesoflexid occurs on the posterolingual margin. The enamel thickness is variable. It is thick in some parts of crown perimeter, while it is very thin or lacks in some others.

REMARKS

The available p3s differ from the members of the genus *Pliolagomys* Erbaeva, 1983 – *P. kujalnikensis* (Topacevski & Scorik, 1977) and *P. danubicus* (Topacevski & Scorik, 1977) –, described from the area of Odessa (the northern Black Sea coast), in having a more symmetrically situated anteroconid and smaller size. Moreover, the paraflexid of those species is nearly perpendicular to the sagital axis of the p3 occlusal surface. The oblique position of both paraflexid and protoflexid on the specimens from Muselievo corresponds to the morphology of *Ochotonoides csarnotanus*, known from Csarnóta-2 (Erbaeva 1988) and Ciuperceni (Terzea & Boroneant 1979). The available p3s are considerably smaller than those of the east Asiatic species of the genus *Ochotonoides* – *O. primitivus* Zheng & Li, 1982 and *O. complicidens* Boule & Teilhard de Chardin, 1928. In addition, the material from Muselievo differs from the second species in having smooth margins of paraflexid and protoflexid. These differences clearly show that the west Palearctic members of this morphologic group should be distinguished as a separate genus. This was done by Sen (1998) who, based on the material from the Pliocene locality Çalta

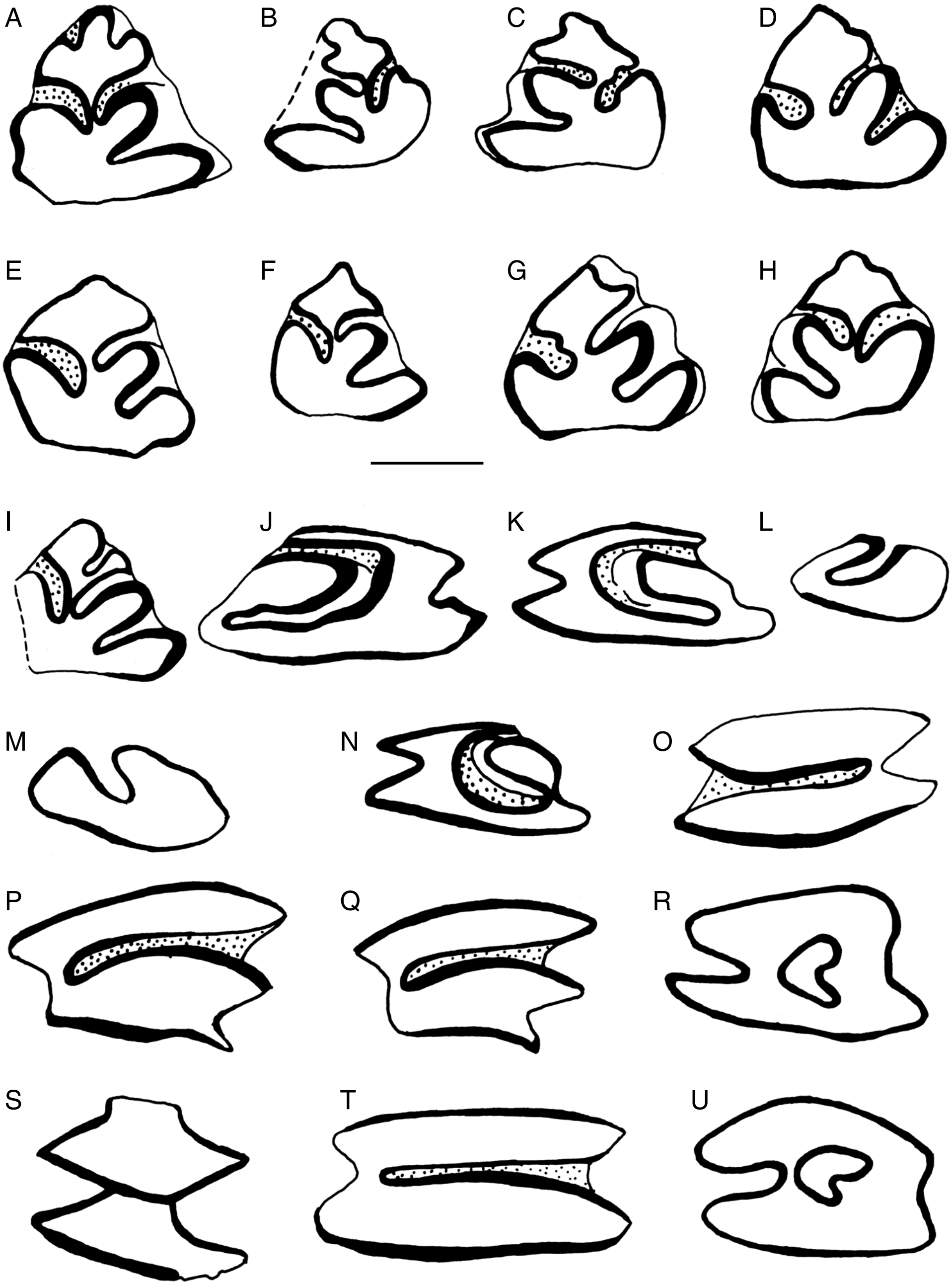

FIG. 19. — *Ochotonoma csarnotana* (Kretzoi, 1959), teeth in occlusal view; **A**, right p3, Ms59; **B**, left p3, Ms67; **C**, left p3, Ms61; **D**, right p3, Ms62; **E**, right p3, Ms63; **F**, right p3, Ms64; **G**, right p3, Ms65; **H**, left p3, Ms66; **I**, right p3, Ms60; **J**, right P3, Ms69; **K**, left P3, Ms70; **L**, left P2, Ms75; **M**, right dP2, Ms79; **N**, left P3, Ms68; **O**, left P4/M1, Ms72; **P**, right M2, Ms74; **Q**, right M2, Ms73; **R**, left dP4, Ms78; **S**, right m1, Ms76; **T**, right P4/M1, Ms71; **U**, left dP4, Ms77. Scale bar: 1 mm.

(MN15), Anatolia, Turkey, described the genus *Ochotonoma*. The type species of the new genus is *O. anatolica* Sen, 1998, to which the material from Muselievo is very similar. The differences concern some details of the shape of p3: the more oblique paraflexid and the lack of a mesoflexid (only two specimens bear a trace of mesoflexid) in the sample from Muselievo. Additionally, the form from Muselievo seems slightly larger. In these respects, the material under study compares better with the few specimens from Hungary and Romania, originally referred to *Ochotonoides csarotanus* (Kretzoi 1959, 1962; Terzea & Boroneant 1979). The variability of the form from Muselievo is great and includes specimens similar to both species. The co-occurrence of two species seems however unlikely, especially having in mind that the extreme morphotypes are connected by intermediate states. In this respect, the form from Muselievo can be considered as a link between the European and Anatolian forms, which corresponds to its intermediate geographical location. The distinction or identity between *O. csarnotana* and *O. anatolica* remains to be further substantiated based on further material from Csarnóta-2.

Family LEPORIDAE Gray, 1821

Since the species determination of the isolated teeth of Leporidae, others than p3, is problematic when isolated, they are considered separately. Teeth were divided with respect to their morphology into groups referred to as morphotypes. In some cases, it is possible to refer tentatively some morphotypes to one or another species already identified based on p3.

P2 (Fig. 20): the sample consists of 14 teeth (Ms93, 93-1, 2, 97-107, 107-1). Three morphotypes can be singled out based on the degree of development of hypoflexus, paraflexus and mesophlexus: 1) the paraflexus is only pronounced (Fig. 20J): two specimens (Ms107, 107-1). Similar teeth are known in *Trischizolagus maritsae* De Bruijn, Dawson & Mein, 1970; 2) the paraflexus and mesoflexus present but the latter is shallow and wide: six specimens (Ms100-105) (Fig. 20E-I). This pattern occurs in *Hypolagus beremendensis* (Petényi, 1864) (Sych 1965: pl. III, 4a, b); and 3) the three reentrant folds are well pronounced; the paraflexus is the deepest one and tends to have slightly crenulated margins: four teeth (Ms93, 93-1, 93-2, 97-99) (Fig. 20A-D). Similar teeth are known in *Pratilepus kutschurganicus* Topachevsky, 1980 (Topachevsky 1980: figs 16, 17).

The last two morphotypes are not well individualized because they are connected by many intermediates with variable deepness of the hypoflexus and mesophlexus (Ms106, 93-1, 93-2) (Fig. 20I). Some variants of these two morphotypes are known in *Pliopentalagus dietrichi* (Fejfar, 1961) (Daxner & Fejfar 1967).

Upper molariform teeth (P3-M2): four morphotypes can be distinguished based on the degree of waviness of the margins of the hypostria: 1) teeth with wavy walls of the hypostria; 1a) both walls of the hypostria are considerably and irregularly undulated: 21 teeth (Ms108-109, Ms389) (Fig. 21A, C); 1b) the walls are regularly folded, forming a sinusoid with a great amplitude but with a short period. The peaks and depressions of the walls are strictly opposite: nine teeth. Most probably, these two subgroups reflect the differences between molariform teeth within the same row, likewise in the recent species *Pentalagus furnessi* (Stone, 1900) (Gureev 1964: fig. 58). As concern the fossil forms, the morphotype 1a is known for *Pliopentalagus dietrichi* (Fejfar 1961a; Daxner & Fejfar 1967) and for the genus *Pratilepus* Hibbard, 1939 (Hibbard 1939); 2) both walls of the hypostria are no more than slightly wavy or one of them is smooth: 11 teeth (Ms110 and Ms390, Fig. 21F); and 3) nearly smooth walls of the hypostria: 2 teeth (Ms111, Fig. 21E).

The last two morphotypes may be recognized as characteristic of *Hypolagus beremendensis* (Sych 1965) and *Trischizolagus maritsae* (De Bruijn *et al.* 1970). However such teeth are also known for M1 and M2 in species whose premolars and M1s show heavily folded walls of the hypostria, for

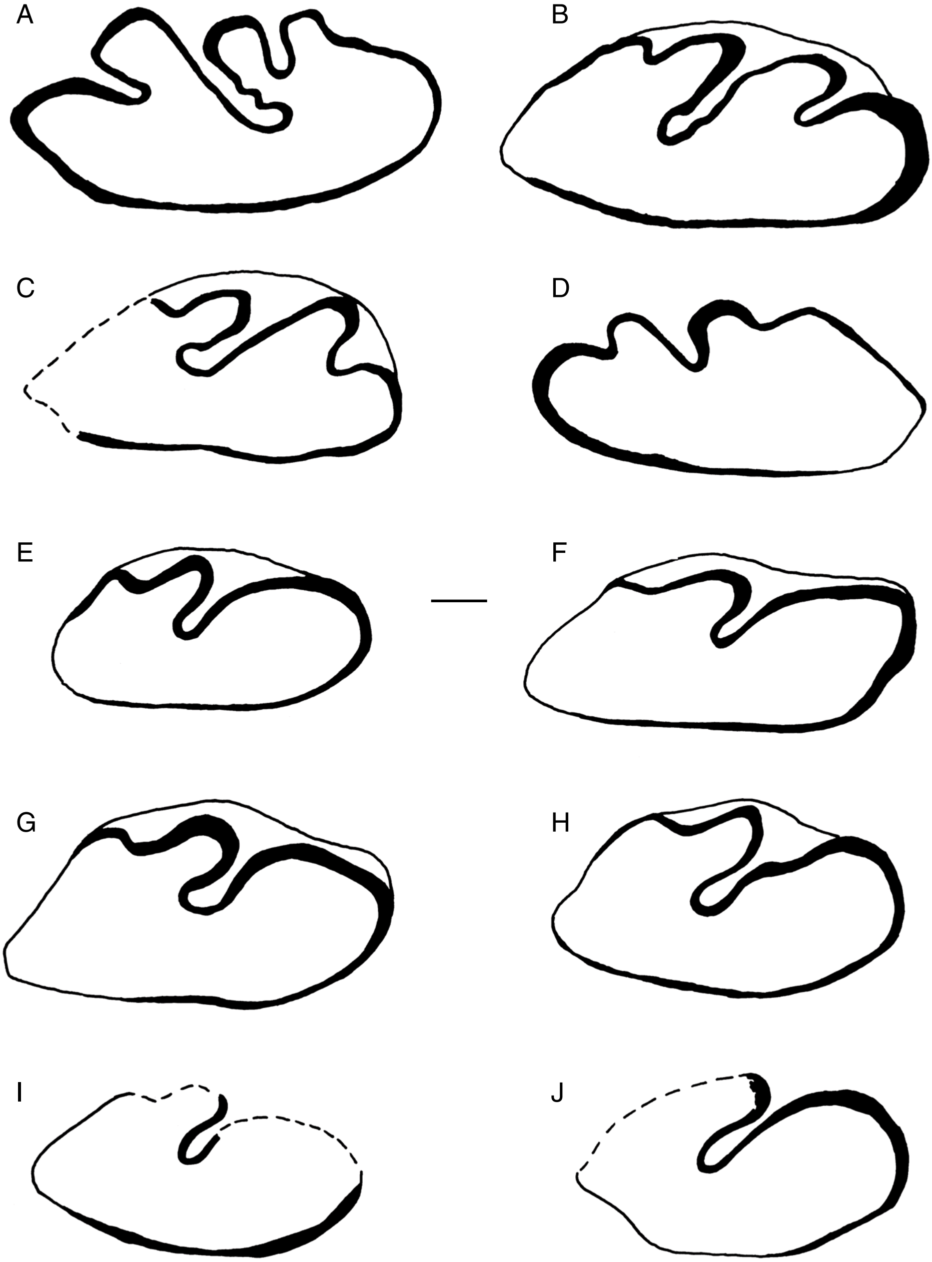

FIG. 20. — Leporidae indet., P2 in occlusal view; **A**, left, Ms93; **B**, right, Ms97; **C**, left, Ms98; **D**, right, Ms99; **E**, left, Ms100; **F**, left, Ms101; **G**, left, Ms102; **H**, left, Ms103; **I**, left, Ms106; **J**, left, Ms107. Scale bar: 1 mm.

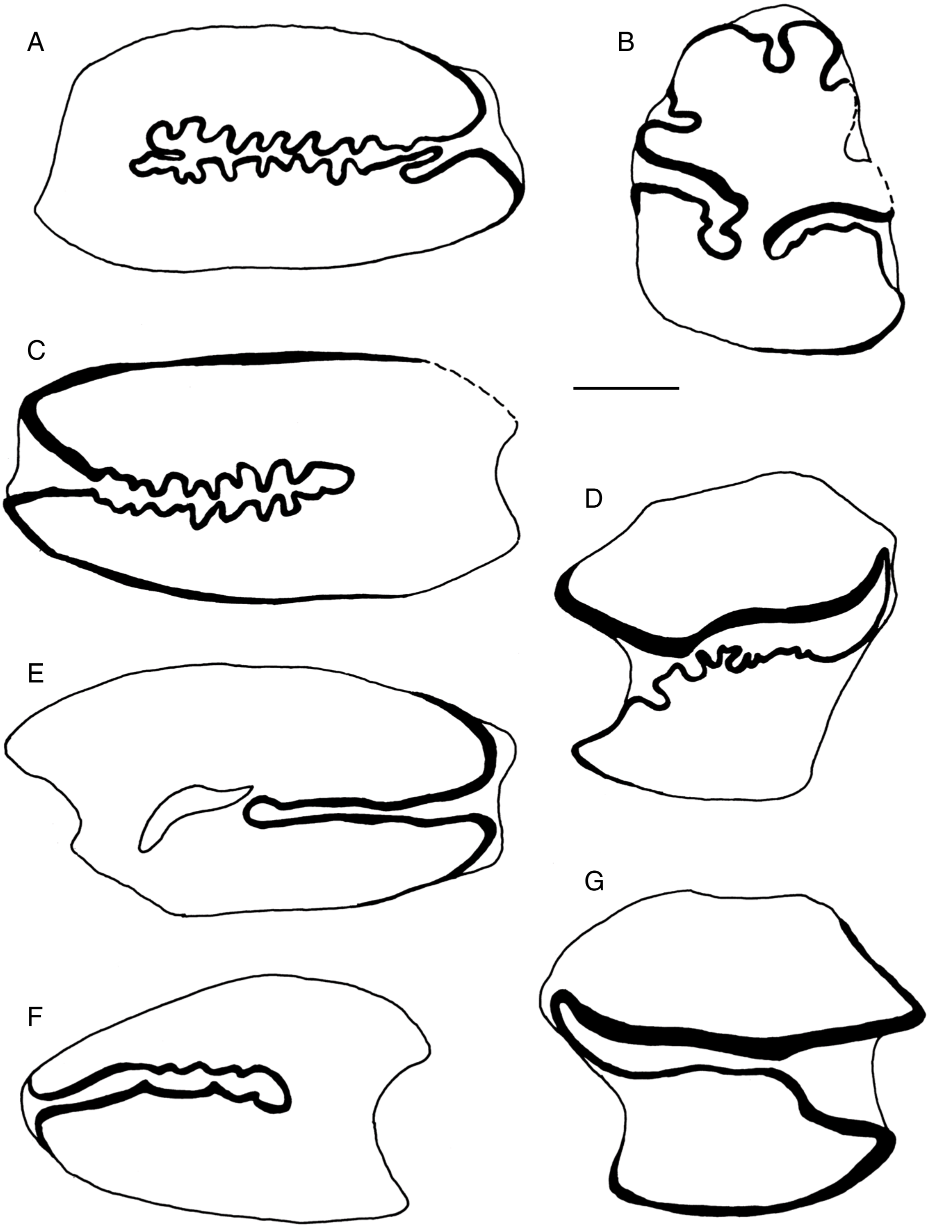

FIG. 21. — **A**, Leporidae, left upper molariform tooth, Ms108, occlusal view; **B**, *Pliopentalagus dietrichi* (Fejfar, 1961), right p3, Ms92, occlusal view; **C**, Leporidae, right upper molariform tooth, Ms109, occlusal view; **D**, Leporidae, left lower molariform tooth, Ms113, occlusal view; **E**, Leporidae, left upper molariform tooth, Ms11, occlusal view; **F**, Leporidae, right, Ms110, occlusal view; **G**, Leporidae, right lower molariform tooth, Ms112, occlusal view. Scale bar: 1 mm.

instance some species of the genera *Pratilepus*, *Pliopentalagus* Gureev & Konkova, 1964, and *Pentalagus* Lyon, 1943.

Lower molariform teeth (p4-m2): the distinction of the three morphotypes is based on the shape of the anterior wall of talonid: 1) the wall is heavily folded (Fig. 21D): five teeth (Ms113 and Ms391). Such teeth occur in *Pliopentalagus dietrichi* (Fejfar 1961a; Daxner & Fejfar 1967). Most probably all these teeth belong to this species. The degree of undulation is lower than in the recent *Pentalagus furnessi*; 2) the wall is slightly wavy or nearly smooth (Fig. 21G): 12 teeth (Ms112 and Ms392). This pattern occurs in *Hypolagus beremendensis* (Sych 1965: fig. 5), *Trischizolagus* (De Bruijn *et al.* 1970) (= *Alilepus* Dice, 1931 from Malusteni, Daxner & Fejfar 1967: fig. 5), *Pratilepus* (Hibbard 1939). It is difficult to find any additional features to permit the separation of these teeth between the species identified in the locality (see below).

The sample of Leporinae involves also: 9 upper incisives, 3 lower incisives, 11 upper milk premolars, 19 dp3, 13 dp4, 9 m3 (Ms393).

Genus *Hypolagus* Dice, 1917

Hypolagus beremendensis (Petényi, 1864)
(Fig. 22G-I)

Lepus beremendensis Petényi, 1864: 77.

Pliolagus beremendensis – Kormos 1934a: 65-78, figs 1-3.

Pliolagus tothi Kretzoi, 1941: 308-335, figs 1-7.

Hypolagus brachignathus – Sych 1965: 2-88, pls I-VII, figs 1-30.

Hypolagus beremendensis – Janossy 1963: 125.

MATERIAL EXAMINED. — 5 p3 (Ms94-96, Ms394).

MEASUREMENTS. — p3 (L × W): 3.3 × 3.0; 3.25 × 3.07; 2.75 × 3.12; 3.15 × - .

DESCRIPTION

p3: the occlusal surface is nearly triangular. There are two reentrant folds on the buccal side. The anterior one (protoflexid) is shallow; the posterior one (hypoflexid) is deep, reaching the medial axis of the occlusal surface. In two specimens, the posterior wall of this reentrant fold is slightly undulated. In one tooth, there is an enamel islet near the end of hypoflexid.

REMARKS

The available p3s are clearly smaller than the late Miocene rabbit, *Hypolagus igrmovi* Gureev, 1964 (Averianov 1996). In size and morphology they are similar to the Pliocene and early Pleistocene forms of the genus that are often considered to belong to two different species: *H. beremendensis* and *H. brachignathus*, respectively. According to Fladerer & Reiner (1996), they should be considered as two chronosubspecies. According to Sych (1965), the difference between *H. brachignathus* and *Pliolagus tothi* concerning the size and the occurrence of a lingual reentrant fold on p3 in the last form fall within the ontogenetic variability of the first species. Two out of the three p3s available belong to the primitive morphotypes as defined by Fladerer (1987) and Fladerer & Reiner (1996) (edged margin of the talonid; short, triangular trigonid; undulated distal wall of the hypoflexid) characteristic for the Pliocene form. One p3 is slightly more advanced in having an enlargement of the mesial margin of the trigonid and in the presence of an enamel islet. Thus, the form from Muselievo can be considered as a progressive stage of *H. beremendensis beremendensis.*

Genus *Trischizolagus* Radulesco & Samson, 1967

Trischizolagus dumitrescue
Radulesco & Samson, 1967
(Fig. 23)

Trischizolagus dumitrescue Radulesco & Samson, 1967: 544-563. — Terzea 1997: 656, fig. 4D-F.

Alilepus sp. – Daxner & Fejfar 1967: 43-46, taf. I, figs 1-4; abb. 5a-e.

Pratilepus kutschurganicus Topachevsky, 1980: 38, 39, figs 1-17.

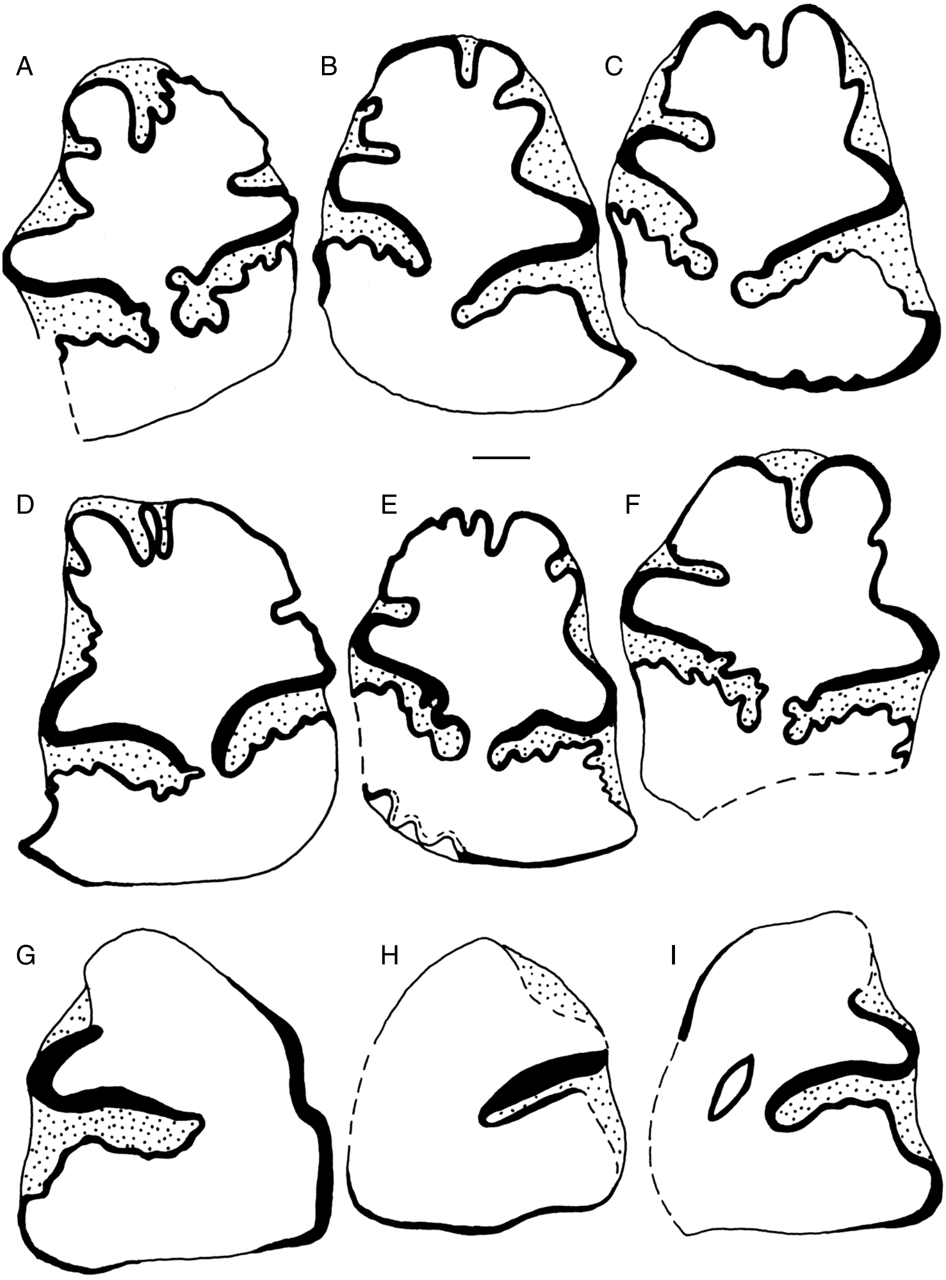

FIG. 22. — **A**-**F**, *Pliopentalagus dietrichi* (Fejfar, 1961), p3 in occlusal view; **A**, left, Ms86; **B**, right, Ms87; **C**, right, Ms88; **D**, left, Ms91; **E**, right, Ms89; **F**, right, Ms90; **G**-**I**, *Hypolagus beremendensis* (Petényi, 1864), p3 in occlusal view; **G**, left, Ms95; **H**, right, Ms94; **I**, right, Ms96. Scale bar: 1 mm.

MATERIAL EXAMINED. — 6 p3 (Ms80-85).

MEASUREMENTS. — p3 (L × W) = 3.3 × 3.5; 3.12 × 3.2; 3.57 × 3.00; 3.42 × 3.45; 2.6 × 2.95.

DESCRIPTION

Both hypoflexid and metaflexid are well developed, reaching near the sagital axis of the occlusal surface, and as a result the dentine bridge between the anterior and posterior segments of the occlusal surface is narrow, or absent (one specimen: Ms82). In one tooth only (Ms85) the metaflexid is relatively shallow. In some teeth, the posterior wall of these reentrant folds is slightly wavy. The paraflexid and protoflexid are well pronounced. The anteroflexid is clearly visible on most teeth as a broad and shallow reentrant valley with slightly folded margins in some specimens.

REMARKS

The p3s under consideration show greatest resemblance with *Trischizolagus dumitrescuae* and *Pratilepus kutschurganicus* Topachevsky, 1980 (waviness of the posterior wall of the hypoflexid and metaflexid). According to Topachevsky (1980), these species are very similar and the main difference concerns the presence of reentrant folds on the anterior wall of P2. However, it is debatable whether it is justified to lump certain types of upper premolars with groups of lower premolars having in mind the great diversity of leporids during this time. This author did not provide any clear argumentation in this respect. Some P2s with poorly developed lateral reentrant valleys, similar to those of *Trischizolagus*, have been referred to another species described from the locality, *Pratilepus ucrainicus* Topachevsky, 1980. Moreover, as in Muselievo, the presence of representatives of the genus *Pliopentalagus*, for instance *P. moldaviensis* Gureev & Konkova, 1964 is also possible. Based on these considerations, for the time being, I regard *Pratilepus kutschurganicus* as a junior synonym of *Trischizolagus dumitrescuae*. The same opinion has been recently presented by Averinov & Tesakov (1997) regarding the leporids from Novopetrovka and Kuchurgan (*Pratilepus kutchurganicus*, *P. ukrainicus*, and *Seregnetilagus orientieuropaeus* Topachevsky, 1987) as *Trischizolagus* cf. *dumitrescuae*. The teeth from Malusteni, reported under the name *Alilepus* sp. (Daxner & Fejfar 1967) without doubt also belong to *T. dumitrescue*, described from the same locality (Radulesco & Samson 1967). One tooth from Muselievo (Ms85) shows similarity with *Trischizolagus maritsae* De Bruijn, Dawson & Mein, 1970 in having a relatively broad connection between anterior and posterior parts of the occlusal surface. According to De Bruijn *et al.* (1970), this is a primitive feature. Since this peculiar pattern is presented only in one tooth in the studied material, it can be supposed that the form from Muselievo is more advanced than *T. maritsae*. The same suggestion derives

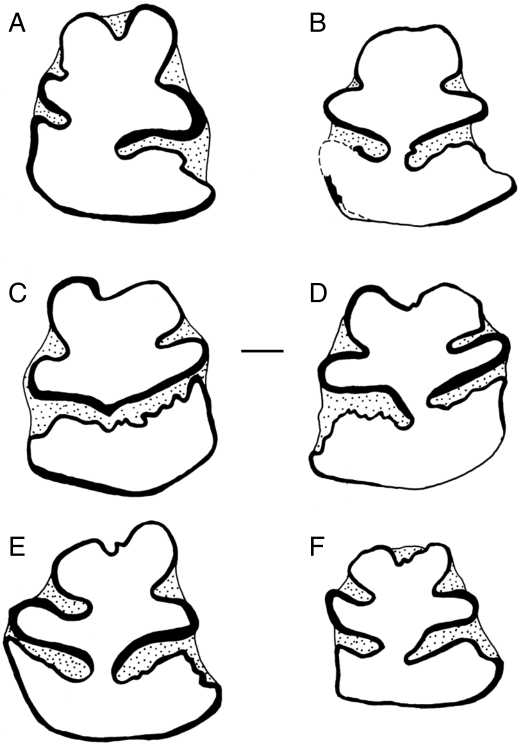

FIG. 23. — *Trischizolagus dumitrescue* Radulesco & Samson, 1967, p3 in occlusal view; **A**, right, Ms85; **B**, right, Ms81; **C**, left, Ms82; **D**, left, Ms80; **E**, right, Ms83; **F**, right, Ms84. Scale bar: 1 mm.

from the comparisons of the measurements of p3. According to Averianov & Tesakov (1997), this tooth shows a gradual increase in size from the early to the late Ruscinian. The p3s from Muselievo are larger than those from Maritsa (MN14) and cover the range of the sample of *T. dumitrescuae* from Malusteni and Beresti (MN15) (Radulesco & Samson 1967). Based on the broad overlap of the samples of different age, Averianov & Tesakov (1997) consider all the material they studied, including *T. maritsae*, belong to a single species, *T. dumitrescuae*. The above comparisons allow concluding that the p3 sample from Muselievo is very similar to *T. dumitrescuae* from the late Ruscinian (MN15) localities from Romania and Moldavia (Radulesco & Samson 1967; Daxner & Fejfar 1967; Averianov & Tesakov 1997). The difference concerns the constant occurrence of very deep para- and protoflexids on the trigonid of p3s from Muselievo. Based on the drawings presented by Averianov & Tesakov (1997) it seems that these reentrants are more frequent within the MN15 samples, although they are not so deep as in the studied material. In this respect, the available p3s show similarity with the recent *Pronolagus crassicaudatus* (Geoffroy, 1832) from East Africa and seem more derived than *T. dumitrescuae* from the type locality. For the time being, having in mind the limited available sample and the possible ontogenetic variation of the deepness of the para- and protoflexids (Averianov & Tesakov 1997), I consider these differences not enough for the species distinction of the form from Muselievo.

Genus *Pliopentalagus* Gureev & Konkova, 1964

Pliopentalagus dietrichi (Fejfar, 1961)
(Figs 21B; 22A-F)

Alilepus dietrichi Fejfar, 1961a: 261-276, figs 1-6.

Pliopentalagus dietrichi – Gureev 1964: 130, 131, fig. 57. — Daxner & Fejfar 1967: 8-43, taf. I, figs 5-7, abb. 1-4a.

MATERIAL EXAMINED. — 10 p3 (Ms86-92, Ms395).

MEASUREMENTS. — p3 (L × W) = 3.90 × 2.80; 4.00 × 3.00; 4.00 × 3.20; 4.00 × 3.10; 4.00 × 2.90; 4.20 × 3.00; 3.80 × 2.90; 3.90 × -; 4.10 × -.

DESCRIPTION

p3: the main reentrant valleys (hypoflexid and metaflexid) show heavily crenulated walls, especially the posterior ones. The three reentrant folds on the anterior lobe are well pronounced. In some specimens, they are plicated, forming smaller subordinate folds.

REMARKS

There is close resemblance between the pattern of p3 and some of the available P2, P4-M2 in the material from Muselievo, from one hand, and *Pliopentalagus dietrichi*, from the other (Fejfar 1961a; Gureev 1964; Daxner & Fejfar 1967). In the same time, the p3 differs from the closely related species *Pliopentalagus moladaviensis* (Gureev 1964: fig. 56), which shows an asymmetrical pattern of the occlusal surface.

Order RODENTIA Bowdich, 1821
Family SCIURIDAE Gray, 1821
Subfamily SCIURINAE Gray, 1821
Genus *Sciurus* Linnaeus, 1758

Sciurus sp.
(Fig. 24B)

MATERIAL EXAMINED. — 1 M1-2 (Ms142).

MEASUREMENTS. — M1-2 (L × W) = 2.35 × 2.77.

DESCRIPTION

The tooth is rectangular in occlusal outline with rounded lingual wall. The main cups and ridges are low; the mesostyle is well developed. The tooth has three roots.

REMARKS

This tooth is clearly larger than the upper molars of *Sciurus maltei* Dahlmann, 2001 from Wölfersheim (Germany) and nearly identical with the comparative material of the recent *Sciurus vulgaris*. It is also similar with the

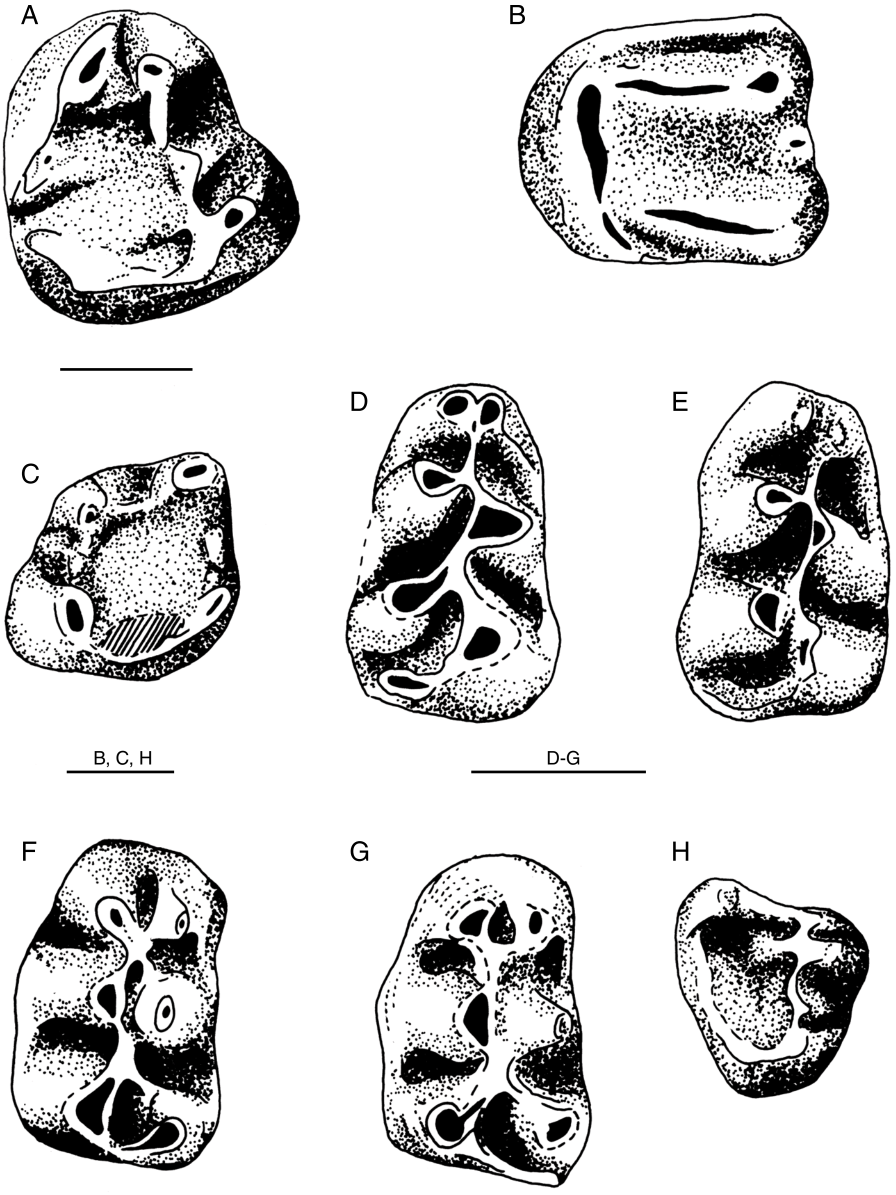

FIG. 24. — **A**, *Pliopetaurista dehneli* (Sulimski, 1964), left p4, Ms141, occlusal view; **B**, *Sciurus* sp., left M1-2, Ms142, occlusal view; **C**, ?*Spermophilus* sp., right p4, Ms143, occlusal view; **D**-**G**, *Allocricetus bursae* Schaub, 1930; **D**, right m1, Ms309, occlusal view; **E**, right m1, Ms310, occlusal view; **F**, left M1, Ms313, occlusal view; **G**, left M1, Ms311, occlusal view; **H**, *Tamias orlovi* (Sulimski, 1964), left M3, Ms144, occlusal view. Scale bars: 1 mm.

respective remains of *Sciurus warthae* Sulimski, 1964 from Weze 1. The scarce material available does not permit closer comparisons.

Subfamily MARMOTINAE Pocock, 1923
Genus *Tamias* Illiger, 1811

Tamias orlovi (Sulimski, 1964)
(Fig. 24H)

Eutamias orlovi Sulimski, 1964: 165-169.

Tamias orlovi – Black & Kowalski 1974: 466.

MATERIAL EXAMINED. — 1 m3 (Ms144); (L × W) = 2.02 × 1.8.

DESCRIPTION
The metalophid is short; the anteroconid is not distinct, incorporated in the anterolophid. The metastylid is very small, situated at the base of the metaconid. The mesolophid is relatively large. There is a well developed antero-buccal reentrant valley. The tooth has four roots but the central lingual root is fused with the posterior one.

REMARKS
The Muselievo specimen differs from the early Miocene species *Tamias eviensis* De Bruijn, Van der Meulen & Katsikatsos, 1980 in having larger size and somewhat simplified occlusal pattern; the entoconid is not well individualized on the end of the posterolophid, the mesostylid and anteroconid are poorly developed on the anterolophid. In the same time, this tooth is indentical to that of *Tamias orlovi* from Weze 1 (Sulimski 1964).

Genus *Spermophilus* Cuvier, 1825

? ***Spermophilus*** sp.
(Fig. 24C)

MATERIAL EXAMINED. — 1 p4 (Ms143); (L × W) = 2.12 × 2.07.

DESCRIPTION
The dental pattern is dominated by four large cups: metaconid, protoconid, hypoconid and entoconid. The metaconid is slightly larger than protoconid. These cusps are separated by a wide trigonid basin, open anteriorly and closed distally by a low but well pronounced metalophid. The ectolophid and mesoconid are present as two low tubercles. The metastylid is low and indistinct. A proper anteroconid is absent, however a slight enamel protuberance at the anterior wall of the metaconid may be considered as a remnant of this cusp. The tooth is two rooted.

REMARKS
This tooth is tentatively referred to the subfamily Marmotinae on the basis of the arrangement of the anterior tubercles: they are set apart and separated by a wide trigonid basin. According to both the structural details and dimensions, the tooth is similar with *Spermophilus* (*Urocitellus*) cf. *nogaici* (Topachevski, 1957) from Kotlovina (middle and upper layers) (Topachevsky & Nesin 1989). The limited material however does not permit detailed considerations.

Subfamily PETAURISTINAE Simpson, 1945
Genus *Pliopetaurista* Kretzoi, 1962

Pliopetaurista dehneli (Sulimski, 1964)
(Fig. 24A)

Pliosciuropterus dehneli Sulimski, 1964: 172-179, pl. IV; text-figs 5, 6, 7-2a-d; 8-2a-c.

Pliopetaurista dehneli – Mein 1970: 39, figs 60-66.

MATERIAL EXAMINED. — 1 p4 (Ms141); (L × W) = 2. 55 × 2. 70.

DESCRIPTION
The metastylid is well pronounced but it is relatively small, connected with the metaconid. The meta- and protoconids are separated by a narrow valley. The metaconid is prominent on the entolophid. There is an incipient hypolophid, which is connected with the entolophid and directed towards to the bottom of the talonid basin. There is shallow postflexid behind the hypoconid. The tooth is two rooted. The anterior root is round in cross-section, while the posterior one is flattened antero-posteriorly.

TABLE 8. — Molar measurements (mm) (L x W) of fossil and extant *Myomimus* spp. from Bulgaria.

	***Myomimus complicidentatus* n. sp., Muselievo**	***M. roachi* (Bate, 1937) recent, S Bulgaria**
m1	1.57 × 1.30; 1.64 × 1.45	1.37 × 1.15; 1.27 × 1.17; 1.32 × 1.10; 1.50 × 1.27
m2	1.50 × 1.48; 1.39 × 1.43; 1.43 × 1.43; 1.38 × 1.38	1.40 × 1.37; 1.37 × 1.27; 1.40 × 1.32
M1	1.27 × 1.60	1.27 × 1.30; 1.30 × 1.40
M2	1.32 × 1.74; 1.32 × 1.61 (holotype)	1.32 × 1.55; 1.30 × 1.52; 1.32 × 1.47
M3	1.05 × 1.37	1.07 × 1.35; 1.05 × 1.32

REMARKS

This premolar is shorter but wider than the respective tooth of *Pliopetaurista pliocaenica* (Depéret, 1897) (Mein 1970). The occlusal pattern of the tooth entirely conforms to *Pliopetaurista dehneli* from Weze 2, Poland (Sulimski 1964: fig. 5). It differs however by its slightly larger size and in having only two roots. In this respect, it is similar with *Pliopetaurista schaubi* (Sulimski, 1964) from Weze 1. However, the original material does not include p4, so it is difficult to make direct comparisons. On the other hand, some authors questioned the specific distinction between these forms (Mein 1970; Terzea 1980). Moreover, two rooted p4s were also found in *P. dehneli* (Sulimski, 1964). It is possible that *P. shaubi* is an extreme variant of *P. dehneli* (Terzea 1980). Such a large form, described as *P. dehneli*, is known from Ciuperceni, Romania (Terzea 1980). Another closely related species, *Pliopetaurista moldaviensis* Baranova & Konkova, 1974, is described from Moldavia and the Russian plain. According to Terzea (1980), this form is also identical with *P. dehneli*.

Family GLIRIDAE Thomas, 1897
Genus *Myomimus* Ognev, 1924

Myomimus complicidentatus n. sp.
(Fig. 25A-I)

HOLOTYPE. — Right M2, Ms129 (Fig. 25H).

FIGURED PARATYPES. — 2 m1 (ms122, 123), 3 m2 (ms124, 125, 126), 1 m1 (ms128), 2 m2 (ms127, 129), 1 m3 (ms130).

ETYMOLOGY. — *Complicidentatus* because of its complicated occlusal surface of the upper molars.

TYPE LOCALITY. — Muselievo, Bulgaria.

OTHER MATERIAL EXAMINED. — 1 m2 (Ms125-1).

MEASUREMENTS. — See Table 8.

DIAGNOSIS. — A large *Myomimus* species with broad upper molars bearing centrolophs.

DIFFERENTIAL DIAGNOSIS. — *Myomimus complicidentatus* n. sp. has larger molars than *Myomimus dehmi* (De Bruijn, 1966) and *Myomimus maritsensis* De Bruijn, Dawson & Mein, 1970. It differs from *Myomimus qafzensis* (Haas, 1973) and the Quaternary populations of *M. roachi* (Bate, 1937) in having broader upper molars, larger lower molars, and more complicated occlusal pattern of the upper molars, which always bear well developed centrolophs and some times an anterior extra ridge present.

DESCRIPTION

Lower molars (m1-2): the teeth show three roots. There are four main ridges on the concave occlusal surface – anterolophid, metalophid, mesolophid, and posterolophid. There is a posterior extra ridge in the valley between the mesolophid and posterolophid.

Upper molars (M1-2): three roots. The occlusal surface is clearly concave. In two specimens, the anteroloph is separated from the paracone as well as from the protocone. In one tooth (Ms127), it is connected with the protocone. The protoloph and metaloph meet and form a symmetrical arc. The posteroloph connects these ridges lingually. In most cases the anterior and posterior centrolophs are well developed, connected to the protoloph and metaloph, respectively. The anterior centroloph is usually larger.

M3: there are two centrolophs. The anterior one is longer, separated from the paracone.

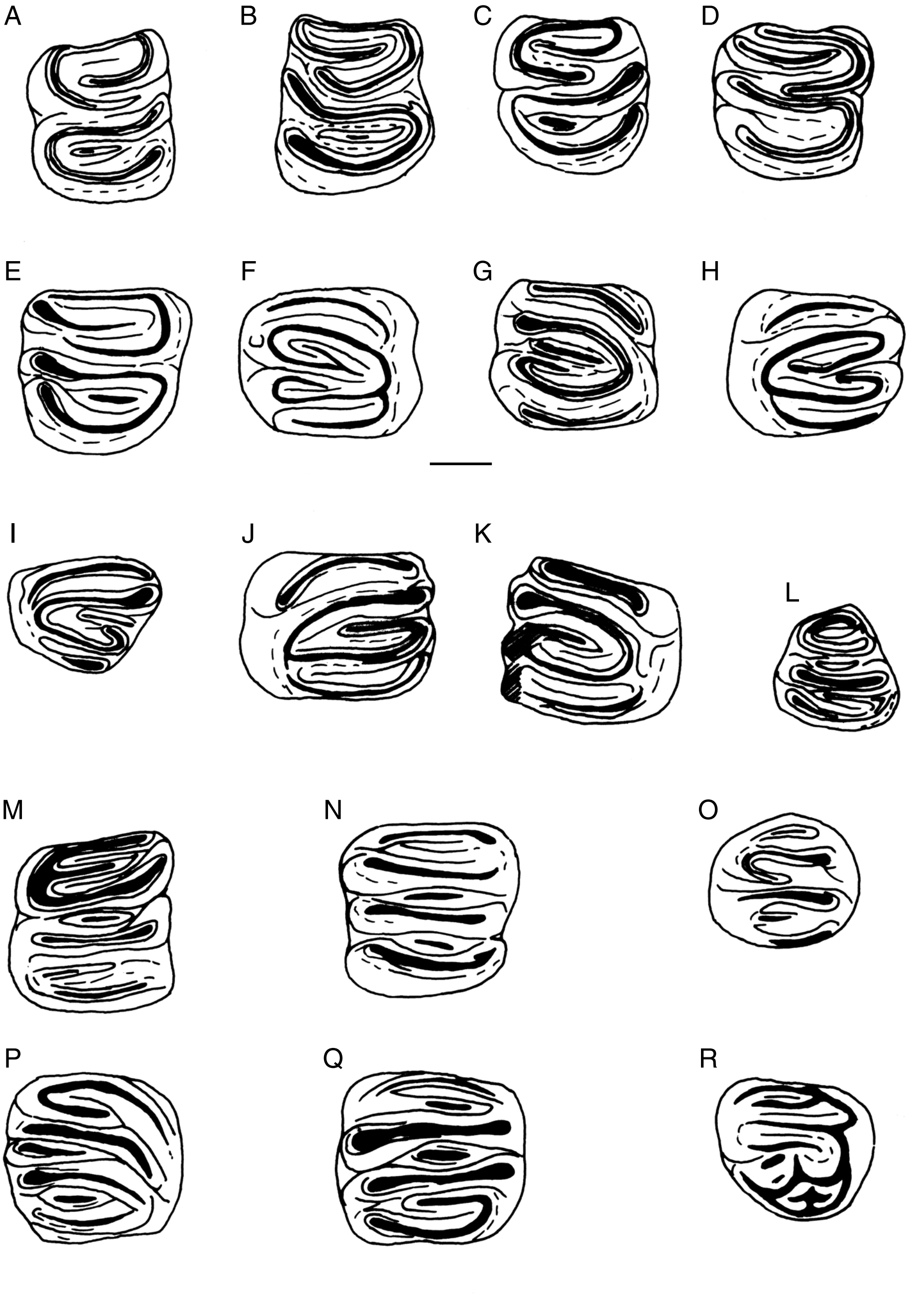

FIG. 25. — **A**-**I**, *Myomimus complicidentatus* n. sp.; **A**, left m1, Ms122, occlusal view; **B**, right m1, Ms123, occlusal view; **C**, left m2, Ms125, occlusal view; **D**, right m2, Ms126, occlusal view; **E**, right m3, Ms124, occlusal view; **F**, left M1-2, Ms127, occlusal view; **G**, left M1-2, Ms128, occlusal view; **H**, right M2, Ms129, occlusal view (holotype); **I**, right M3, Ms130, occlusal view; **J**, **K**, *Dryomimus eliomyoides* Kretzoi, 1959; **J**, right M1-2, Ms132, occlusal view; **K**, left M1-2, Ms131, occlusal view; **L**-**R**, *Glis minor* Kowalski, 1956; **L**, right p4, Ms133, occlusal view; **M**, left M2, Ms134, occlusal view; **N**, right M2, Ms135, occlusal view; **O**, right P3, Ms136, occlusal view; **P**, right M1-2, Ms138, occlusal view; **Q**, right M1-2, Ms137, occlusal view; **R**, right M3, Ms139, occlusal view. Scale bar: 1 mm.

REMARKS

The teeth from Muselievo are larger than those of the fossil species of the genera *Myomimus*, *Peridyromys* Stehlin & Schaub, 1951, *Microdyromys* De Bruijn, 1966 and *Ramys* Garcia Moreno & Lopez Martinez, 1986 with similar dental pattern (De Bruijn & Rumke 1974; Van de Weerd 1973; Storch 1975; Daams 1981; Hugueney 1968; Aguilar 1974): *Myomimus maritsensis* De Bruijn, Dawson & Mein, 1970, *M. dehmi* (De Bruijn, 1966), *Myomimus* sp., *M. roachi* (Bate, 1937), *M. qafzensis* (Haas, 1973), *Microdyromys koenigswaldi* De Bruijn, 1966, *Peridyromys murinus* (Pomel, 1953), *P. aquatilis* (De Bruijn & Moltzer, 1974) and *Ramys multicrestatus* (De Bruijn, 1966), (the taxonomy is after Daams & De Bruijn 1995). In size, the form from Muselievo is similar to the Miocene species *Miodyromys aegercii* (Baudelot, 1972) but it possesses a greater number of extra ridges (Aguilar 1980).

In general, the teeth from Muselievo show rather complicated occlusal pattern, comparable with the earlier forms of the genus: *Myomimus dehmi* and *M. maritsensis* (Daams 1981). The dental pattern of the molars under study differs from that of *Myomimus maritsensis* by having somewhat more complicated occlusal surface: the constant presence of a posterior centroloph on M1-2 and posterior extra ridge on m1-2.

The occlusal pattern of the M1-2s available is more complicated in comparison with the Quaternary populations of *Myomimus roachi* (Daams 1981; Van der Meulen & Doukas 2001). On the other hand, some specimens of the upper Pleistocene species *Myomimus qafzensis* (Israel) also show a rather complicated occlusal surface: presence of centrolophs (M1-2). Nevertheless, the populations from Israel look more progressive (see below) since these ridges are shorter (Daams 1981: pl. 3). An additional difference concerns the great frequency of the endoloph of M2s in the populations of *Myomimus qafzensis* (morphotypes C, Ce of M1-2, cf. Daams 1981). This ridge lacks in the small sample from Muselievo. As concern the lower molars, some middle and upper Pleistocene populations of *M. roachi* and *M. qafzensis* include specimens with posterior extra ridge. In these cases, again, the Pleistocene populations look more advanced in comparison with the material from Muselievo in having shorter extra ridges (Daams 1981: pl. 2). Some of the available lower molars fall in the upper part of the size variability of these populations (Daams 1981). The small size of the sample from Muselievo does not permit detailed comparisons, but the above-mentioned size differences do not allow to refer the material available to these species.

According to Daams (1981) the main trend within *M. dehmi-M. roachi* evolutionary lineage is towards a simplification of the dental pattern and size increase. The simplification includes the loss of the posterior extra ridge and the shortening of the centrolophid in the lower molars, while the M1-2s lose extra ridges and centrolophs. It is not clear whether the size differences between populations are due to spatio-temporal environmental variation or to evolution (Daams 1981). The population from Muselievo fits well within this pattern. Having in mind the age of the locality (MN15b, see below), it can be supposed that the new species is a direct descendant of *M. dehmi* (MN9-12; Daams 1981). The northern position of the locality probably additionally strengthens the considerable size increase in comparison with the populations of *M. dehmi* from Spain and Greece (Daams 1981). The earlier East Mediterranean species, *M. maritsensis* (MN14; Daams 1981), seems more progressive than the population from Muselievo in having a more simplified M1 occlusal pattern (Daams 1981: fig. 30). *Myomimus complicidentatus* n. sp. can be considered as a potential ancestor of the upper Pleistocene *M. qafzensis* from Israel. The smaller size of the southern Pleistocene species can be attributed to a geographical variation.

Genus *Dryomimus* Kretzoi, 1959

Dryomimus eliomyoides Kretzoi, 1959
(Fig. 25J, K)

Dryomimus eliomyoides Kretzoi, 1959: 240.

Dryomimus aff. *eliomyoides* – De Bruijn & Van der Meulen 1975: 332-334, pl. 5, figs 8-10, 12, 13.

MATERIAL EXAMINED. — 2 M1-2 (Ms131, 132); (L × W) = 1.43 × 1.62; 1.27 × 1.67.

DESCRIPTION

Medium sized glirid. The anteroloph is disconnected from the protocone as well as from the paracone. The posterior centroloph is strong. The posteroloph is not connected to the metacone but links lingually to the protocone.

REMARKS

The original description of Kretzoi (1959) is rather laconic without designation of a holotype. Thus, it is difficult to make direct comparisons with the Hungarian material. The Muselievo specimens are identical with the respective teeth from Toukobounia I (early Pleistocene, Greece) (De Bruijn & Van der Meulen 1975). These authors mentioned the great similarity between the Pliocene genus *Dryomimus* and the Miocene *Pseudodryomys* De Bruijn, 1965 from Spain. Most probably, this similarity results of a parallel evolution. Therefore, the use of a separate name for the Pliocene genus seems reasonable (De Bruijn & Van der Meulen 1975). The genera *Dryomimus* and *Myomimus* were synonymized by Kowalski (1963). However, the occurrence of a posterior centroloph only is a rather unusual feature for glirids, and consequently this opinion is rejected (De Bruijn *et al.* 1970). The material from Muselievo is similar to the molar from Kotlovina (lower and middle layers) (Topachevsky & Nesin 1989), described as *Myomimus* cf. *eliomyoides*. This damaged specimen is possibly a little smaller but the limited material from both localities does not allow further comparisons.

Genus *Glis* Brisson, 1762

Glis minor Kowalski, 1956
(Fig. 25L-R)

Glis sackdillingensis minor Kowalski, 1956: 384-386, pl. IV, fig. 8; text. fig. 2-f; 1963: 545-550, figs 8-10.

Glis minor – Kretzoi 1959: 240. — Kowalski 1963: 545-550.

Glis sackdillingensis – De Bruijn & Van der Meulen 1975: 334, 335, pl. 5, figs 14-17.

MATERIAL EXAMINED. — 1 p4 (Ms133), 2 m1 (Ms134), 1 m2 (Ms135), 2 P4 (Ms136), 7 M1-2 (Ms138, 139, 139-1-5), 1 M3 (Ms139).

MEASUREMENTS (L × W). — p4 = 1.08 × 1.02; m1 = 1.58 × 1.54; 1.57 × 1.45; m2 = 1.57 × 1.57; P4 = 1.15 × 1.34; 1.15 × 1.20; M1-2 = 1.53 × 1.60; 1.50 × 1.53; 1.45 × 1.60; 1.57 × 1.50; 1.62 × 1.55; 1.52 × 1.57; 1.40 × 1.60; M3 = 1.22 × 1.48.

DESCRIPTION

p4 has one root. The shape of the occlusal surface is triangular with rounded angles. There are four main and two extra ridges.

The lower molars are with two roots. The dental pattern of the lower molars consists of four main ridges, one centrolophid and two extra ridges in the anterior and posterior basins, respectively.

P4 shows rounded occlusal surface with six ridges.

The upper molars are three rooted. They possess four main ridges, one centroloph and two extra ridges (between anteroloph and protoloph, and between metaloph and posteroloph). The occlusal surface of M3 shows similar pattern.

REMARKS

The proposed synonymy between *Glis minor* and *G. sackdillingens* (Heller, 1930) (De Bruijn & Van der Meulen 1975) seems unlikely since these forms differ in size and show complementary stratigraphic ranges. Kowalski (1963), based on the teeth proportions, considered *Glis minor* as a specialized form, which probably is not in direct evolutionary relationship with the recent species. The overall appearance of the material from Muselievo agrees well with *Glis minor* from Weze (Kowalski 1963), and Gundersheim-4 (Gernamy (Fejfar & Storch 1990). Some of the available teeth are slightly smaller than the teeth of *G. minor* from Wölfersheim (Germany) (Dahlmann 2001).

TABLE 9. — Molar measurements (mm) of *Rhagapodemus* cf. *hautimagnensis* Mein & Michaux, 1970 from Muselievo. For abbreviations see Material and methods.

Lower molars						**Upper molars**					
	N	Min	M	Max	SD		N	Min	M	Max	SD
Lm1	16	2.02	2.17	2.35	0.09	LM1	18	2.07	2.30	2.50	0.115
Wm1	16	1.10	1.31	1.45	0.09	WM1	18	1.42	1.52	1.72	0.081
Lm2	10	1.40	1.58	1.90	0.135	LM2	7	1.30	1.49	1.62	0.106
Wm2	11	1.25	1.36	1.50	0.069	WM2	7	1.40	1.50	1.70	0.126
Lm3	3	1.42	-	1.57	-	LM3	3	1.12	-	1.25	-
Wm3	3	1.32	-	1.40	-	WM3	3	1.12	-	1.25	-

Family MURIDAE Gray, 1821
Genus *Rhagapodemus* Kretzoi, 1959

Rhagapodemus* cf. *hautimagnensis
Mein & Michaux, 1970
(Figs 26; 27A-H)

Rhagapodemus hautimagnensis Mein & Michaux, 1970: 2782. — Van de Weerd 1979: 140, 141, pl. 2, figs 10-14.

MATERIAL EXAMINED. — 23 m1 (Ms223-235), 1 mandibular fragment (Ms236), 10 m2 (Ms235-241), 5 m3 (Ms261-263), 18 M1 (Ms243-251, 264), 7 M2 (Ms252-258), 3 M3 (Ms242, 259, 260).

MEASUREMENTS. — See Table 9.

DESCRIPTION

m1: the anterocentral tubercle is fairly well developed and isolated on unworn teeth. In the latter stages of wear, it fuses with the anterior pair of cusps. In unworn teeth, the anterior and middle pairs of cusps are separated by a narrow valley. In some worn specimens, they are connected by a sagital pass. The posterior lamina is always isolated. The talonid is of medium size, oval and slightly elongated transversally. The labial accessory cusps are variable in size and number. The posterior one is always well developed, rounded and quickly becomes confluent with the hypoconid with wear. The other accessory cusps may lack, but more often, they are two, adjacent to the anterior and the middle pairs of cusps, respectively. In some specimens additional weak buds may occur.

m2: the accessory labial cusps, beside the anterior one, are poor (near the hypoconid) or lacking.

m3: there is a weak anterior add cusp.

M1: these molars possess three roots. The *t1* is considerably pushed to the back and is separated from the *t2*. In some specimens *t3* has a labially directed spur reaching the base of the *t6*. Most often, the *t4* and *t7* are not connected until the late stages of wear. Sometimes the *t8* and *t9* are also separated. The *t7* is elongated and looks like a broad ridge. The posterior cingulum (*t12*) is well developed.

M2: the majority of teeth have three roots, but some specimens show 4 or 5 roots. The *t1* is larger than the *t3* and they are set apart. The pairs of adjacent cusps, *t4*/*t7* and *t8*/*t9*, are separated during the early and middle wearing stages. The *t7* is elongated.

M3: the tooth is three rooted. The *t3* is lacking. The other cusps are connected in various combinations.

REMARKS

Some species of large murids, showing pronounced hypsodonty and presence of *t7* on M1 and M2, are known from Europe. The first described species is *Rhagapodemus frequens* Kretzoi, 1959, from the late Pliocene of Csarnóta (Carpathian basin, Hungary). This species is also recorded in Poland (Weze 1, Sulimski 1964). Subsequently, a more evolved form, *Rh. frequens athensis* De Bruijn & Van der Meulen, 1975, was reported from the south of Greece (the early

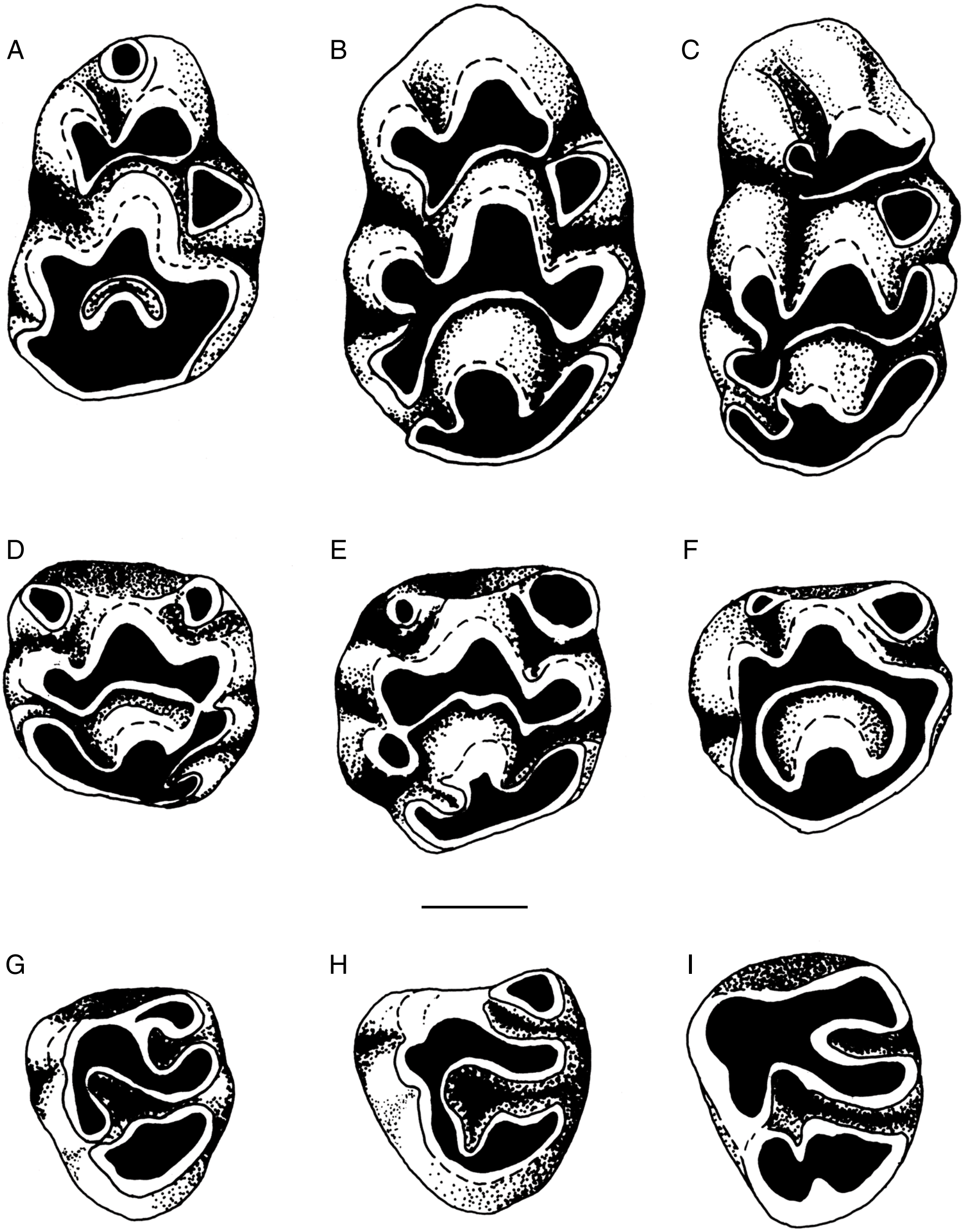

FIG. 26. — *Rhagapodemus* cf. *hautimagnensis* Mein & Michaux, 1970, upper molars in occlusal view; **A**, right M1, Ms243; **B**, right M1, Ms244; **C**, right M1, Ms246; **D**, left M2, Ms253; **E**, right M2, Ms254; **F**, right M2, Ms255; **G**, right M3, Ms259; **H**, right M3, Ms260; **I**, right M3, Ms242. Scale bar: 1 mm.

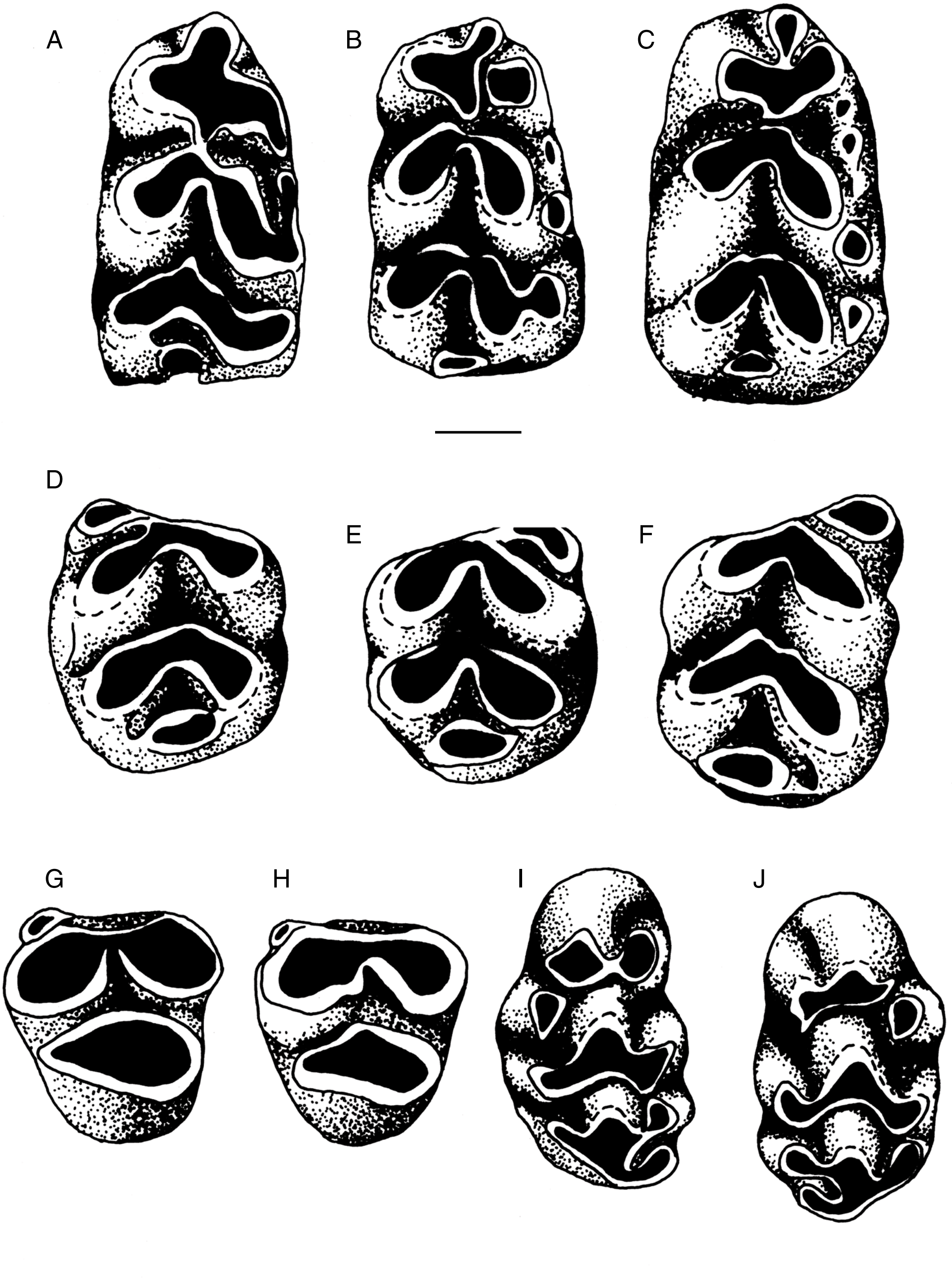

Fig. 27. — **A**-**H**, *Rhagapodemus* cf. *hautimagnensis* Mein & Michaux, 1970, lower molars in occlusal view; **A**, right m1, Ms233; **B**, right m1, Ms234; **C**, right m1, Ms229; **D**, left m2, Ms237; **E**, right m2, Ms238; **F**, right m2, Ms235; **G**, left m3, Ms261; **H**, left m3, Ms262; **I**, **J**, *Rhagapodemus* sp., M1 in occlusal view; **I**, left, Ms302; **J**, right, Ms303. Scale bar: 1 mm.

Pleistocene locality of Tourkobounia). This form is considered as a separate species by Martin Suarez & Mein (1998). Two closely related species differing in size were described from France: *Rhagapodemus hautimagnensis* Mein & Michaux, 1970 (large), and *Rh. ballesoi* Mein & Michaux, 1970 (small). The first species is also known from the early Ruscinian of Greece (Van de Weerd 1979). Another species, *Rh. wandeweerdi* De Bruijn & Van der Meulen, 1975, was reported from the isle of Rhodes (the locality Maritsa). Initially this material was described under the name *Apodemus* aff. *jeanteti* Michaux, 1967 (De Bruijn *et al.* 1970). This short review of the Pliocene findings of the genus shows that it evolved in south and southeastern Europe. The main evolutionary trend is the increase of size and hypsodonty. The latest form, *Rh. frequens athensis*, is the largest one and has higher crowned molars. Therefore, it can be supposed that the forms of this phyletic lineage have stratigraphical significance for the Pliocene and the early Pleistocene.

The teeth from Muselievo are larger than these of the Greek population of *Rhagapodemus hautimagnensis*. In this respect, they are similar with *Rh. hautimagnensis* from its type locality (Mein & Michaux 1970) as well as with *Rh. wandeweerdi*. On the other hand, the molars available are smaller than the molars of the latter forms (*Rh. frequens* [Sulimski 1964] and *Rh. frequens athensis*). It appears that the *Rhagapodemus*-assemblage under consideration shows an intermediate evolutionary stage.

Although similar in size, the molars from Muselievo differs from *Rhagapodemus wandeweerdi* (cf. De Bruijn & Van der Meulen 1975) by: 1) having an oval posterior labial accessory cusp (c1) on m1, which fuses quickly with the hypoconid; 2) a poor or lacking posterior accessory cusp on m2; and 3) a large distance between the *t1* and *t3* on M2. In these features the material is similar with *Rh. hautimagnensis* and *Rh. frequens*. Therefore, if one considers these species as evolutionary stages of one phyletic lineage, the population from Muselievo provides a link between them. The material is tentatively referred to the first species on the basis of the similarity in size.

Although some small molars of *Rhagapodemus* are reminiscent at first glance of that of *Sylvaemus* they are readily distinguishable by their hypsodonty and occlusal pattern. In *Rhagapodemus*, the crowns of molars are high and the wear surfaces of the cusps and the ridges all lie in about the same (horizontal) plane. In contrast, in *Sylvaemus*, these surfaces are oblique to the horizontal plane and the ridges between cusps are lower (Van de Weerd 1979).

Rhagapodemus sp.
(Fig. 27I, J)

MATERIAL EXAMINED. — 3 M1 (Ms301, 302, 303).

MEASUREMENTS. — M1 (L × W) = 1.92 × 1.15; 1.90 × 1.20.

DESCRIPTION

Small first upper molars with structural details of occlusal surface, level of hypsodonty and wearing pattern entirely correspond to the characteristics of genus *Rhagapodemus*.

REMARKS

These three molars strongly resemble the M1 of the above species, however they are definitely smaller. In the same time, they are larger than the respective molars of *Rhagapodemus ballesioi* Mein & Michaux, 1970, but are nearly identical with *Rh.* cf. *ballesioi* from Gundersheim-4 (Germany), (Fejfar & Storch 1990). The length and width of the teeth available fall near to the lower limit of variability of *Rhagapodemus hautimagnensis* from the early Ruscinian of Greece (Van de Weerd 1979). Since the material available is too limited, I refrain from a closer specific assignment.

Genus *Sylvaemus* Ognev, 1923

Sylvaemus dominans (Kretzoi, 1962)
(Figs 28; 29)

Apodemus dominans Kretzoi, 1959: 243 (*nomen nudum*); 1962: 311, 357, pls IV, V. — De Bruijn *et al.* 1970: 544, 545, pl. I, figs 7-11. — Pasquier 1974: 42-44, pl. II, figs 4-7. — De Bruijn & Van der

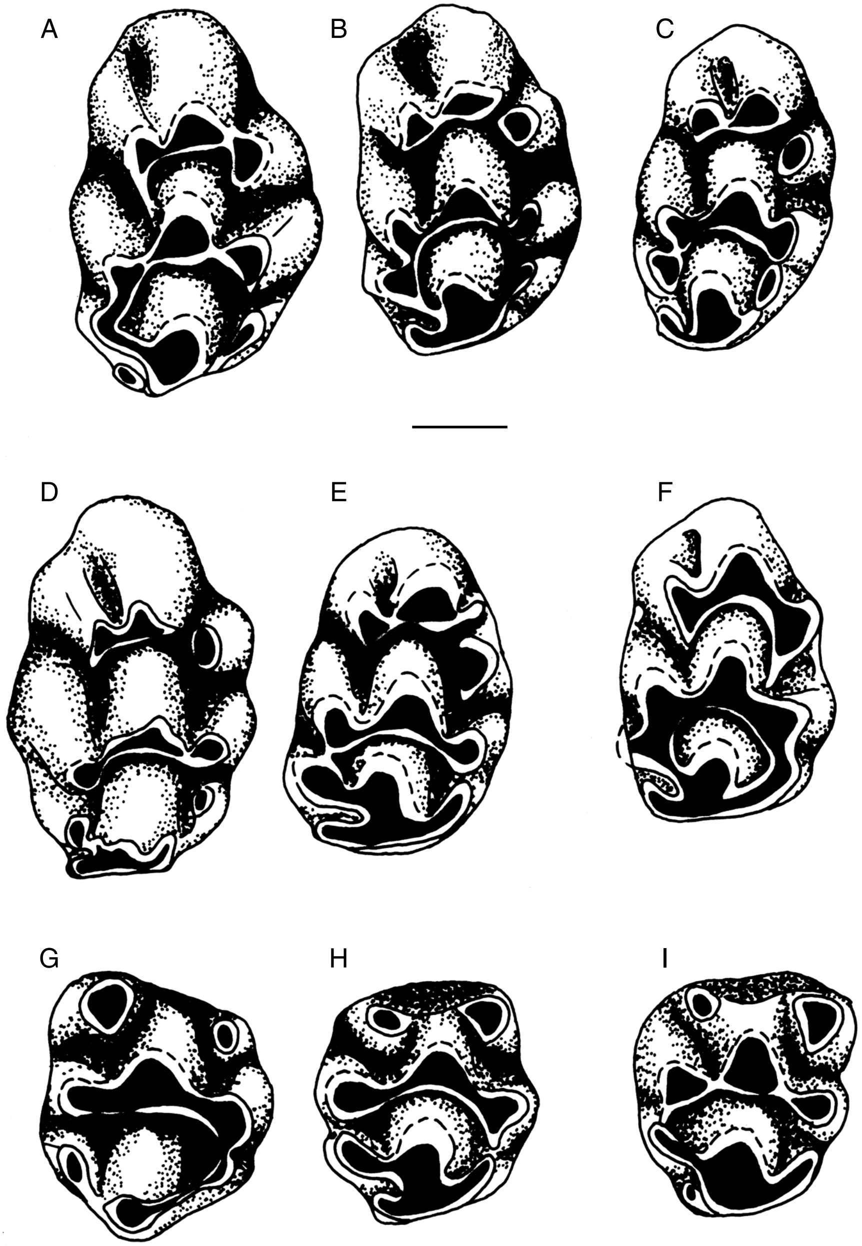

FIG. 28. — *Sylvaemus dominans* (Kretzoi, 1962), upper molars in occlusal view; **A**, right M1, Ms265; **B**, right M1, Ms266; **C**, right M1, Ms267; **D**, right M1, Ms268; **E**, right M1, Ms269; **F**, right M1, Ms272; **G**, left M2, Ms297; **H**, right M2, Ms298; **I**, right M2, Ms294. Scale bar: 1 mm.

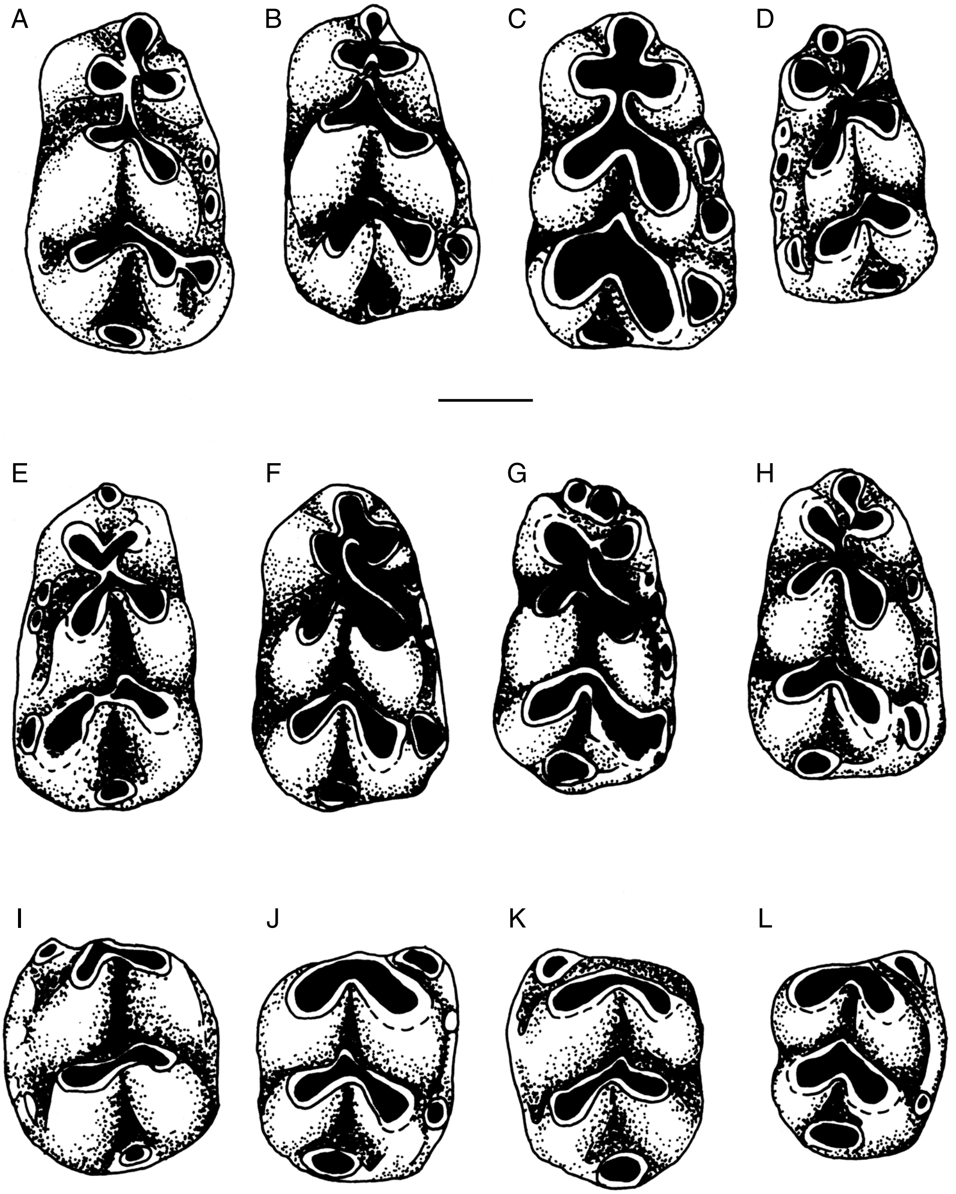

FIG. 29. — *Sylvaemus dominans* (Kretzoi, 1962), lower molars in occlusal view; **A**, right m1, Ms269; **B**, right m1, Ms284; **C**, right m1, Ms277; **D**, left m1, Ms281; **E**, left m1, Ms279; **F**, right m1, Ms278; **G**, right m1, Ms276; **H**, right m1, Ms280; **I**, left m2, Ms292; **J**, right m2, Ms287; **K**, left m2, Ms288; **L**, right m2, Ms290. Scale bar: 1 mm.

TABLE 10. — Molar measurements (mm) of *Sylvaemus dominans* (Kretzoi, 1962) from Muselievo. For abbreviations see Material and methods.

	Lower molars						**Upper molars**				
	N	**Min**	**M**	**Max**	**SD**		**N**	**Min**	**M**	**Max**	**SD**
Lm1	31	1.60	1.86	2.07	0.107	LM1	32	1.75	2.00	2.25	0.142
Wm1	31	0.95	1.13	1.27	0.077	WM1	31	1.15	1.30	1.60	0.101
Lm2	12	1.17	1.31	1.40	0.070	LM2	17	1.20	1.38	1.55	0.095
Wm2	12	1.02	1.14	1.22	0.050	WM2	17	1.22	1.31	1.42	0.061
Lm3	2	1.30	-	1.32	-	LM3	-	-	-	-	-
Wm3	2	1.20	-	1.32	-	WM3	-	-	-	-	-

Meulen 1975: 315-317, pl. 4, figs 1-8. — Van de Weerd 1979: 138-140, pl. 2, figs 1-9.

Apodemus occitanus Pasquier, 1974: 41, 42, pl. 2.

Sylvaemus dominans – Dahlmann 2001: 79, 81.

MATERIAL EXAMINED. — 33 m1 (Ms275-286), 12 m2 (Ms287-293), 2 m3 (Ms304-305), 34 M1 (Ms265-274, 301-303), 19 M2 (Ms294-300).

MEASUREMENTS. — See Table 10.

DESCRIPTION

M1: this tooth is three rooted. Only one specimen possesses four roots. In some young specimens the *t1* is shifted backward and is separated from the *t2*. Accessory small cusps *t1*-bis and *t2*-bis practically absent. Rarely, some specimens have a short backward directed spur on *t3*. The *t4* is situated slightly anteriorly than the *t6*. The *t4* and the *t7* are disconnected. They fuse at latter stages of wear. The posterior cingulum (*t12*) is well developed.

M2: the number of roots is three (6 specimens) or four (2 specimens). Both *t9* and *t12* are well developed.

m1: the anterocentral cusp is well developed and sometimes isolated in unworn teeth, but it quickly connects to the posterior lamina with further wear. The anterior and the middle pairs of cusps are connected by a short sagittal ridge. The labial accessory tubercles are variable in size, shape and number. The posterior one, being the largest, is separated from the hypoconid in some specimens or fused with this tubercle in others. The other two or three add cusps are weak buds on a low cingular ridge. The terminal hell is of medium size.

m2: the anterolabial cusp is continuing posteriorly by a more or less complete labial ridge which may bear one or two small tubercles.

REMARKS

The overlap in dental morphology (size, occlusal pattern) in the two closely related recent species, *Sylvaemus sylvaticus* (Linnaeus, 1758) and *S. flavicollis* (Melchior, 1834), is such that individual specimens are often indeterminable. As in recent forms, the determination of sympatric fossil species of the genus, based on dental features alone, meets with considerable difficulties.

According to the size, the available molars are larger than those of *S. atavus* Heller, 1936 from Gundersheim-4 (Fejfar & Storch 1990). They belong to a medium sized form. Based on some primitive characters (M1 and M2 with three roots and a well developed posterior cingulum, a posterior shifting of the *t1* on M1, etc.), one may distinguish the older medium sized forms, characteristic for the Pliocene and early Pleistocene, from the advanced forms of the Late Quaternary (Pasquier 1974; De Bruijn & Van der Meulen 1975).

According to Pasquier (1974), two European allopatric species occupied the lower evolutionary level – *Sylvaemus occitanus* (Pasquier, 1974) (western Europe) and *S. dominans* (Kretzoi, 1959) (Central and Eastern Europe). The differences between these forms are not impressive and concern the frequency of some details in the structure of the molars. It appears that the variation found between these species has the same range within species. According to De Bruijn & Van der Meulen (1975), the use of two specific names complicates the taxonomy unnecessarily. The available material confirms this point of view. The pattern of upper molars corresponds to *Sylvaemus occitanus*, while the lower ones are similar to *S. dominans*.

The presence of four roots in some M2s shows that the population from Muselievo is somewat more advanced, in comparison, for instance, with the form from Maritsa (De Bruijn *et al.* 1970). The larger size of the molars from Muselievo in comparison with these of *S. dominans* from the early Ruscinian in Greece (Van de Weerd 1979) should also be interpreted in this direction.

Family CRICETIDAE Murray, 1866
Genus *Allocricetus* Schaub, 1930

Allocricetus bursae Schaub, 1930
(Fig. 24D-G)

Allocricetus bursae Schaub, 1930: 33.

MATERIAL EXAMINED. — 2 M1 (Ms311, 313), 2 m1 (Ms309-310).

MEASUREMENTS (L × W). — M1 = 1.82 × 1. 30; 1.95 × 1.29; m1 = 2.00 × 1.22; 1.97 × 1.27.

DESCRIPTION

m1: the anteroconid consists of two poorly individualized cusps, which are either in close connection (unworn specimen) or widely associated but with separated dentine fields (slightly worn specimen). Although there is a short spur on the anterolophid, directed postero-labially, the anterosinusid remains open. The anterolophulid is single. The main tubercles alternate. The mesolophid is lacking. The posterolophid is well developed but it does not close the posterosinusid.

M1: the anterocone is bicuspide but its parts are closely situated, so, in some cases, their anterior parts connect and form an anterior pit. The main cusps are opposite and the inner parts of the respective labial valleys soon become reduced by the conversion of their inner portions into enamel pits. The posterior cingulum is well developed.

REMARKS

The early evolutionary stages of small hamsters of modern type, such as *Allocricetus*, *Cricetulus* Milne-Edwards, 1867, *Tscherkia* Ognev, 1914, and *Cricetinus* Zdansky, 1928 are poorly known. Four forms, *Cricetulus* sp. I, *Cricetulus* sp. II, *Cricetinus europaeus* Kretzoi, 1959 and *Cricetinus beremendensis* Hir, 1994, similar in size to the material from Muselievo, are known from some Vallesian (Sumeg, MN10) and Pliocene (Osztramos 1, Csarnóta, Beremend 15, MN14-16) localities of Hungary (Kordos 1987; Hir 1994). These forms differ from the population under study in having an undivided anteroconid on m1. This feature may be considered as a primitive one. More over *Cricetinus europaeus* from Csarnóta-2 shows a double anterolophulid on this tooth. On the other hand, the occlusal pattern of M1 of *C. europaeus* is very similar to the material from Muselievo and to the Pleistocene populations of *Allocricetus bursae*. The Far East Pleistocene species *Cricetinus varians* Zdansky (Fejfar 1970; Vorontsov 1982) differs from the Hungarian species by having mesolophid on the lower molars.

The material from the late Pliocene locality Maritsa (the isle of Rhodes, Greece), described as ?*Cricetulus* sp. (De Bruijn *et al.* 1970) is similar in size with the specimens from Muselievo but it differs in the presence of a short mesolophid on m1. According to Sen (1977), these specimens should be referred to *Mesocricetus primitivus* De Bruijn, Dawson & Mein, 1970, described from the same locality.

The teeth from the Slovakian locality Ivanovce (MN15), described as *Allocricetus* cf. *bursae*, are smaller than the specimens from Muselievo. In this respect, they differ also from the comparative material of *A. bursae* from Zirany and Hundsheim (Fejfar 1970). Moreover nearly all M1s from Ivanovce show undivided anterocone, while this tubercle is clearly divided in the material from Muselievo.

The available teeth are similar in size and overall occlusal pattern to the Pleistocene populations of *Allocricetus bursae* from Bulgaria. Although the anteroconid of the m1s from Muselievo is clearly divided, both parts are closely set, giving in this way a more primitive appearance of the population under consideration. However, this feature occurs also in some Pleistocene samples of *Allocricetus bursae* from Bulgaria (Varbeshnitsa, Morovitsa) (Popov 1988, 1989). These comparisons suggest that the teeth from Muselievo most probably belong to a primitive form of *Allocricetus bursae*.

Allocricetus ehiki Schaub, 1930
(Fig. 30)

Allocricetus ehiki Schaub, 1930: 34.

MATERIAL EXAMINED. — 3 M1 (Ms312, 314, 315), 1 M3 (Ms319), 3 m1 (Ms306-308), 3 m2 (Ms316-318).

MEASUREMENTS (L × W). — M1 = 2.35 × 1.65; 2.25 × 1.54; 2.10 × 1.44; M3 = 1.40 × 1.25; m1 = 2.09 × 1.42; 2.04 × 1.29; 2.16 × 1.37; m2 = 1.66 × 1.34; 1.70 × 1.40; 1.70 × 1.29.

DESCRIPTION

m1: the anteroconid is separated in two small cusps. One aberrant specimen (Ms308) possesses an extra cuspule between these cusps and they are practically connected. The anterolophulid is single, connected with the anterior part of the metaconid. There is no mesolophid. The protosinusid and the sinusid are closed by low cingula. The posterolophid does not reach the base of the entoconid.

m2: the lingual branch of the anterior cingulum is short, while the labial one is well developed. There is no mesolophid.

M1: during the early stages of wear, the inner part of the valleys between the main opposite tubercles become pits. The valley between the two parts of the anterocone opens anteriorly.

M3: both branches of the anteroloph are well developed. There are two pits between the opposite main cusps.

REMARKS

The simplified occlusal pattern distinguishes the material from the Pliocene hamsters of comparable size. In the same time, the available teeth are similar to the latest Pliocene and early Pleistocene populations of *Allocricetus ehiki* from Poland (Pradel 1988). The studied m2s lack a mesolophid, differing in this way from *Mesocricetus primitivus* (De Bruijn *et al.* 1970).

Family ARVICOLIDAE Gray, 1821
Subfamily ARVICOLINAE Gray, 1821
Genus *Propliomys* Kretzoi, 1959

Propliomys cf. ***hungaricus*** Kormos, 1934
(Figs 31B-F; 32)

MATERIAL EXAMINED. — 2 m1 (Ms43-44) and 4 fragmentary m1 (Ms45-48), 3 M3 (Ms49-56).

MEASUREMENTS. — Lm1 = 2.75; 3.05; Wm1 = 1.05; 1.15; LM3 = 1.45; 1.75; 1.70.

DESCRIPTION

The molars lack crown-cementum. Most m1s have enamel lightly differentiated, somewhat thicker on the anterior sides of the triangles. The anterolingual enamel-free area (*anterosinuid*) is relatively high. Two m1 fragments bear a *Mimomys*-ridge and a prismfold but these elements are not very prominent on the occlusal surface; the prismfold is wide and shallow while the relatively weak *Mimomys*-ridge is shifted anteriorly. On the lateral side of the crown, these elements are poorly pronounced on the uppermost part of the wall only, and probably vanish quickly with tooth wear.

M3: the second reentrant angle (BRA2) is rather shallow. In contrast, the second lingual reentrant angle (LRA2) and BRA2 are deep and separate the occlusal surface in three dentine fields; the second buccal salient angle (BSA2) is incipient; the posterior loop (PC1) is short and simple; two roots; the dentine trucks are not developed (but see specimen Ms50, which shows enamel interruptions); there are no enamel islets.

REMARKS

The m1 material from Muselievo is similar to *Propliomys hungaricus* (Kormos, 1934) a species, which is common in many European Pliocene

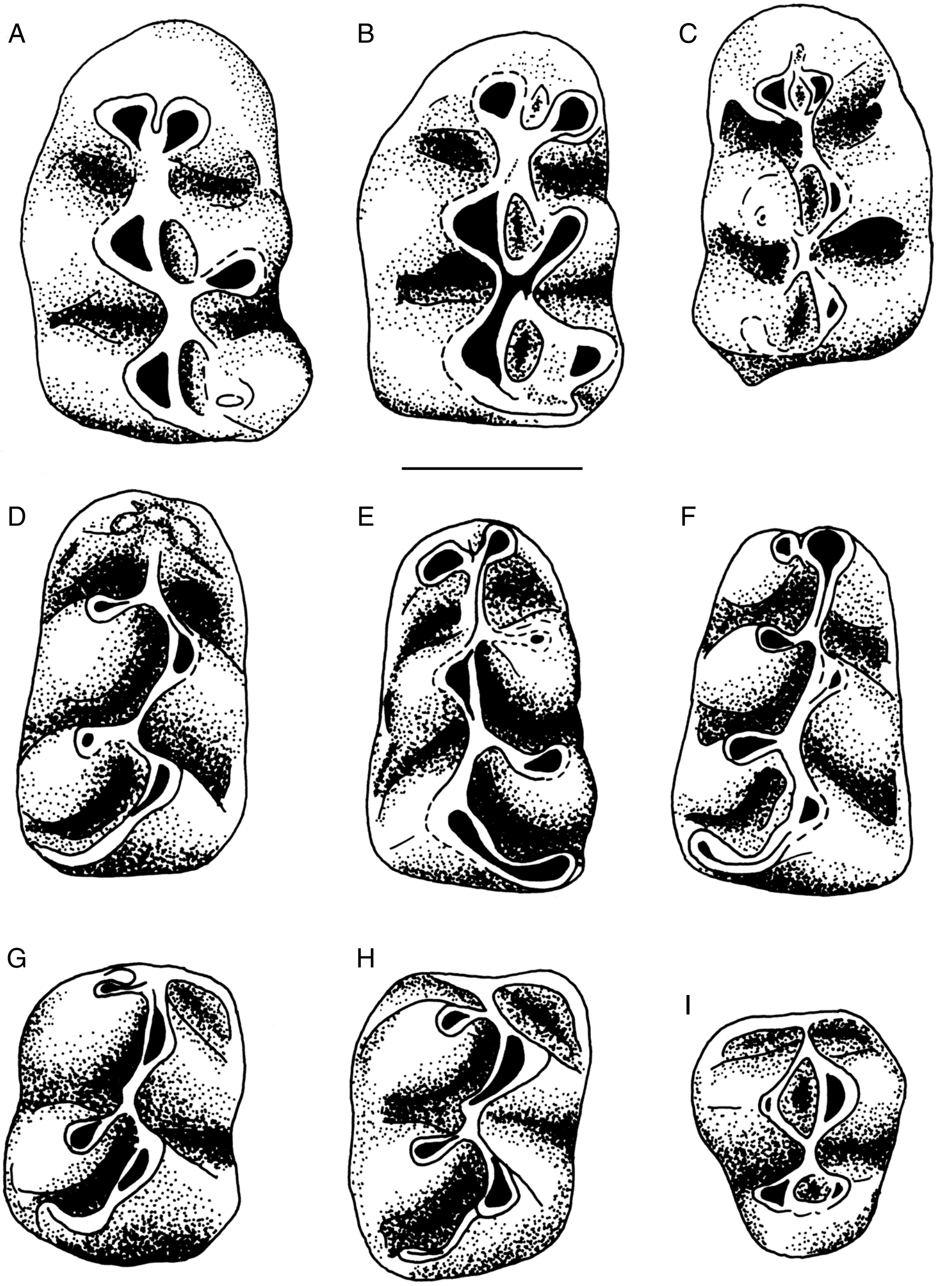

FIG. 30. — *Allocricetus ehiki* Schaub, 1930, molars in occlusal view; **A**, left M1, Ms314; **B**, left M1, Ms315; **C**, right M1, Ms312; **D**, right m1, Ms308; **E**, left m1, Ms307; **F**, right m1, Ms306; **G**, right m2, Ms318; **H**, right m2, Ms316; **I**, right M3, Ms319. Scale bar: 1 mm.

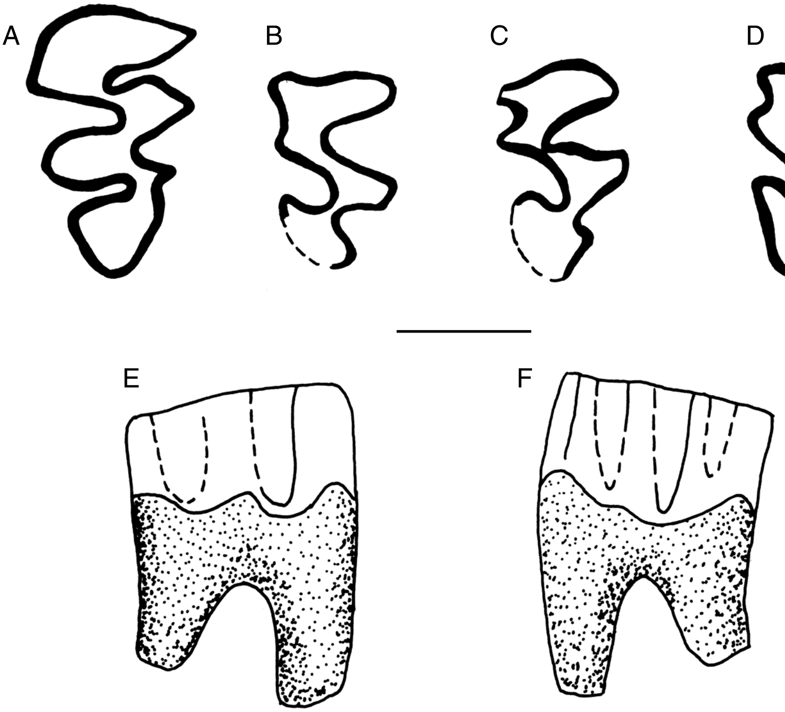

FIG. 31. — **A**, *Dolomys* cf. *nehringi* Kretzoi, 1959, left M3, Ms41, occlusal view; **B**-**F**, *Propliomys* cf. *hungaricus* Kormos, 1934; **B**, left M3, Ms49, occlusal view; **C**, left M3, Ms56, occlusal view; **D**, left M3, Ms51, occlusal view; **E**, left M3, Ms51, buccal view; **F**, left M3, Ms51, lingual view. Scale bar: 1 mm.

faunas (Kormos 1934b: fig. 46; De Bruijn & Van der Meulen 1975: pl. 1, figs 5, 6; Fejfar & Storch 1990). However, it differs from this species (De Bruijn & Van der Meulen 1975: pl. 2, fig. 10) by the structure of M3. The M3 in *Propliomys hungaricus* shows three roots, a posterior enamel islet (but see also Rabeder 1981: abb. 164, 6) and a large confluence between the T3 and the elongated posterior loop (Kowalski 1960: 471; De Bruijn & Van der Meulen 1975; Topachevsky & Nesin 1989). The small M3 sample from Muselievo is similar with *Pliomys graecus* De Bruijn & Van der Meulen, 1975 (Tourkobounia 1, Greece, lower Villanyian) in having two-rooted M3s and a reduced posterior loop. On the other hand, the hypsodonty as well as the height of the enamel free areas of some of the m1s (Ms43, 47) distinguish the form from Muselievo from *P. graecus*. In these respects, the available m1s are similar with *P. hungaricus* from Csarnóta-1. The scarce remains from Muselievo do not permit detailed comparisons, so the determination remains tentative until a more complete material will be known.

Genus *Dolomys* Nehring, 1898

Dolomys occitanus (Thaler, 1955)
(Figs 33-35)

Mimomys occitanus Thaler, 1955: 1255-1257. — Chaline 1974: 343-353, figs 3-8, 9 5,6. — Terzea 1981: 119-124, figs 2, 3, 4A-D, 5A, B. — Chaline *et al.* 1981: 821-826.

Mimomys hassiacus atavus Fejfar, 1961b: 57-60, taf. 18, figs 5, 6; abb. 5a, c, 6d.

Mimomys stehlini – Chaline & Michaux 1975: 749-757, pl. I, text-fig. 1.

Dolomys odessanus – Topachevsky & Nesin 1989: 49, fig. 18.

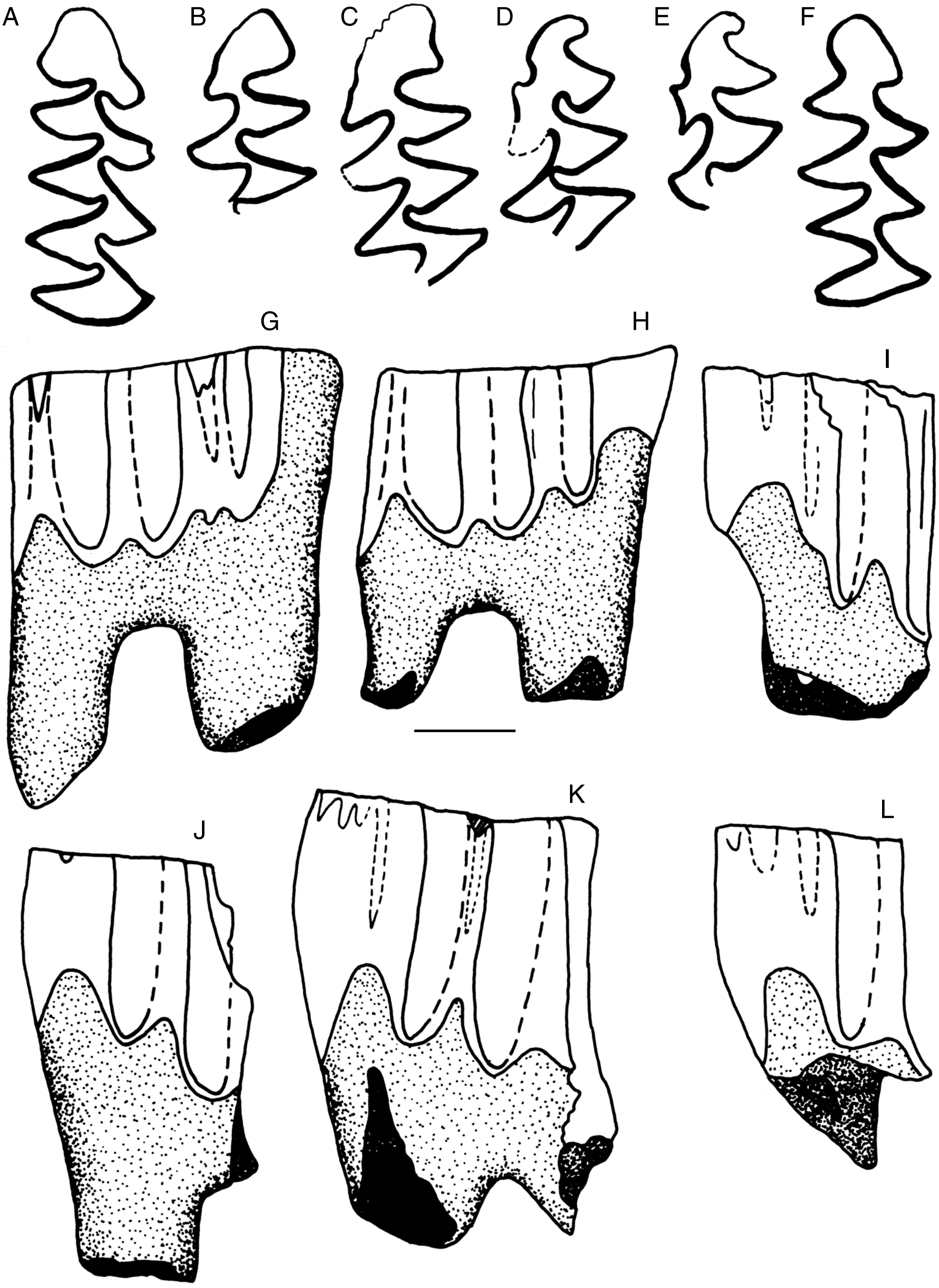

FIG. 32. — *Propliomys* cf. *hungaricus* Kormos, 1934, first lower molars; **A**, right, Ms43, occlusal view; **B**, left fragment, Ms47, occlusal view; **C**, left fragment, Ms45, occlusal view; **D**, left fragment, Ms46, occlusal view; **E**, left fragment, Ms48, occlusal view; **F**, right, Ms44, occlusal view; **G**, right, Ms43, buccal view; **H**, right, Ms44, buccal view; **I**, left, Ms46, buccal view; **J**, left, Ms47, buccal view; **K**, left, Ms45, buccal view; **L**, left, Ms48, buccal view. Scale bar: 1 mm.

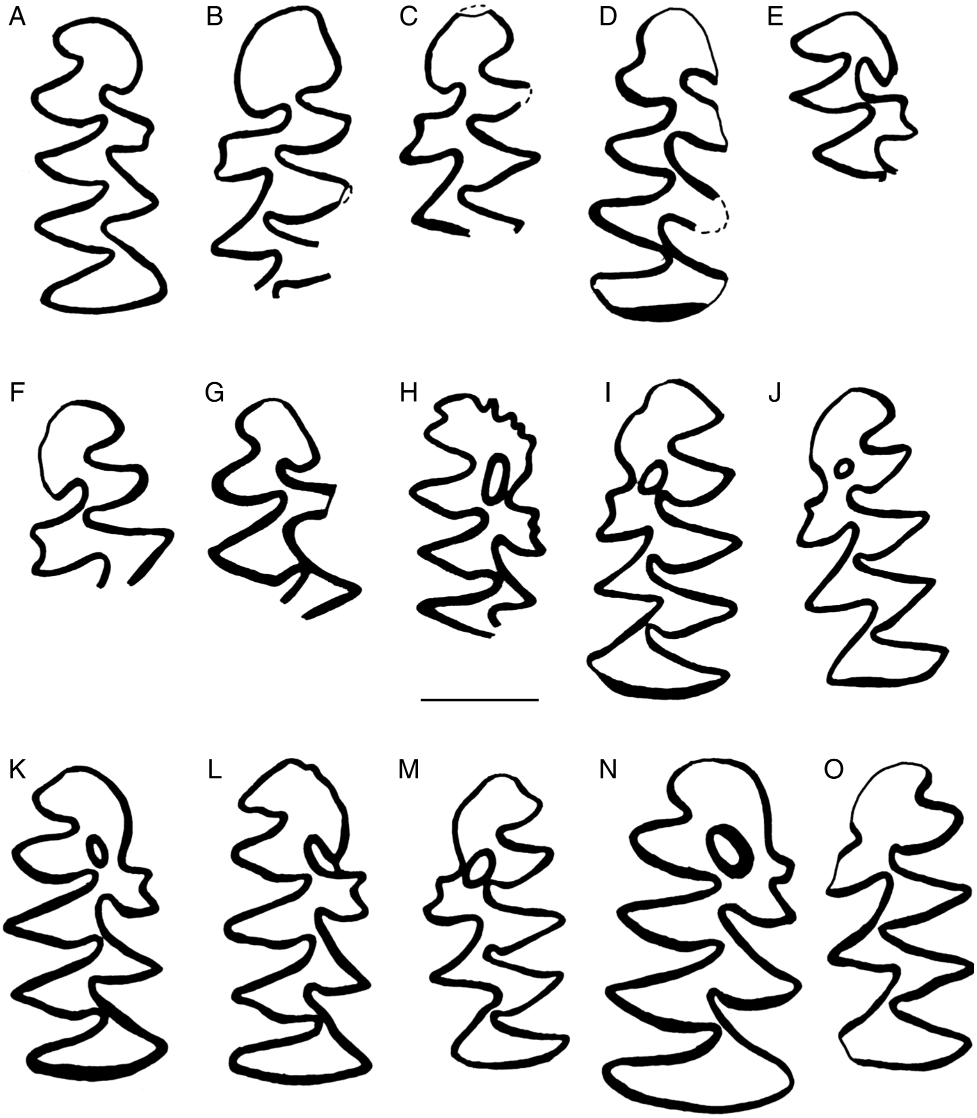

FIG. 33. — *Dolomys occitanus* (Thaler, 1955), first lower molars in occlusal view; **A**, right, Ms42; **B**, left, Ms1; **C**, left, Ms2; **D**, right, Ms3; **E**, right fragment, Ms5; **F**, left fragment, Ms6; **G**, right fragment, Ms4; **H**, right fragment, Ms7; **I**, left, Ms8; **J**, right, Ms9; **K**, right, Ms10; **L**, right, Ms11; **M**, left, Ms12; **N**, right, Ms13; **O**, left, Ms14. Scale bar: 1 mm.

Promimomys konstantinovae – Topachevsky & Nesin 1989: 82-86, fig. 31.

Dolomys occitanus – Maul 1996: 348. — Fejfar & Reppening 1998: 163, abb. 3, 5. — Dahlmann 2001: 73, abb. 20: 37-52

MATERIAL EXAMINED. — 23 m1: morphotype "*Mimomys*": 17 m1 (9 fragments, 8 intact [Ms7-14]; morphotype "*Dolomys*": 6 m1 [Ms1-6, 42], 19 M3 [Ms23-40]).

MEASUREMENTS (Min-M-Max, SD, N). — Lm1 = 2.67-2.91-3.20, 0.169, 8; am1 = 1.00-1.26-1.37, 0.163, 7; Wm1 = 1.07-1.23-1.65, 0.191, 8; LM3 = 1.50-1.76-2.00, 0.127, 17.

DESCRIPTION

There is no crown-cementum in the side folds of the molars. In most specimens, the enamel is not differentiated, but in some teeth it is slightly thinner on the tips of the salient angles. The crown is moderately high but the dentine tracks of the *linaea sinuosa* are low.

m1: the variable shape of occlusal surface can be classified into two morphotypes, called "*Dolomys*"- and "*Mimomys*"-morphotypes. The "*Dolomys*"-morphotype (Fig. 33A-G) is characterized by an open isle fold. The Sb3-wall is in a low position. The "*Mimomys*"-morphotype bears *Mimomys*-ridge, prism-fold and isle-fold or enamel islet (Fig. 33H-O).

M3: in unworn or slightly worn specimens, the BRA1 and LSA3 are deep, but after some wear they become reduced by insulation. The anterior islet vanishes quickly with further wear, while the posterior one is a long persistent structure, presented even in some worn teeth (Ms40). The clear relationship between the stage of wear and the number of islets indicates that all teeth belong to one species. Most teeth bear two roots. The anterior root is a compound structure, formed by the fusion of two roots. In some specimens the anterior fangs, although partially fused, are still clearly visible (Ms23, 25, 26, 35, 37-39). One tooth shows a very small third root (Ms23).

REMARKS

There is a great controversy regarding the taxonomic status of the "*Dolomys*" and "*Mimomys*" morphotypes of m1s referred to this species. Sulimski (1964) described them as two separate species – *Dolomys* cf. *hungaricus* and *Mimomys* cf. *stehlini* Kormos, 1931. Chaline (1974) found in the large assemblage from Sète that these types are connected by intermediate forms, depending mainly on the stage of wear (see also Van de Weerd 1979: table 9), and he therefore regarded the whole material as one highly variable species, *Mimomys occitanus.* It is a primitive, more or less mesodont form with a relatively high share of specimens in which the isle-fold remains open even in the advanced stages of crown wear – the so called "*Dolomys*"-morphotype. According to Chaline (1974) and Chaline & Michaux (1975) two evolutionary lineages derived from this variable species: one leading through *Mimomis stehlini* Kormos, 1931, *M. polonicus* Kowalski, 1960, *M. pliocaenicus* (Forsyth Major, 1889), and *M. savini* Hinton, 1910 to *Arvicola mosbachensis* (Schmidtgen, 1911), the other one through *Propliomys hungaricus* and *Pliomys episcopalis* Méhely, 1914 to *P. lenki* (Heller, 1930) [= *P. coronensis* (Méhely, 1914)]. The former phyletic sequence is referred to the "*Mimomys*"-lineage, the later one to the "*Dolomys*"-lineage. In fact, the second lineage represents the evolution of *Propliomys-Pliomys* Méhely, 1914 (Kretzoi 1955, 1962; De Bruijn & Van der Meulen 1975; Chaline 1975). This disagreement in the nomenclature within the second lineage reflects the similarity in teeth morphology of the earliest forms of these related genera (*Dolomys* and *Propliomys-Pliomys*) (Nehring 1898; Méhely 1914; Hinton 1926; Kormos 1934b). On the other hand the co-occurrence of the "ancestral" ("*Dolomys*"-morphotype of *M. occitanus*) and the derived forms (typical *Propliomys* with relatively high enamel free areas on m1) in Muselievo does not confirm that they belong to the same phyletic lineage. The lineage *Propliomys-Pliomys* apparently constitutes an early specialized branch of the evolution of voles and cannot be regarded to derive from *Mimomys occitanus* as though by Chaline & Michaux (1975).

According to Van de Weerd (1979), *M. occitanus* is an intermediate stage of evolution from *Promimomys* Kretzoi, 1955 to the advanced forms of *Mimomys* Forsyth Major, 1902. During this

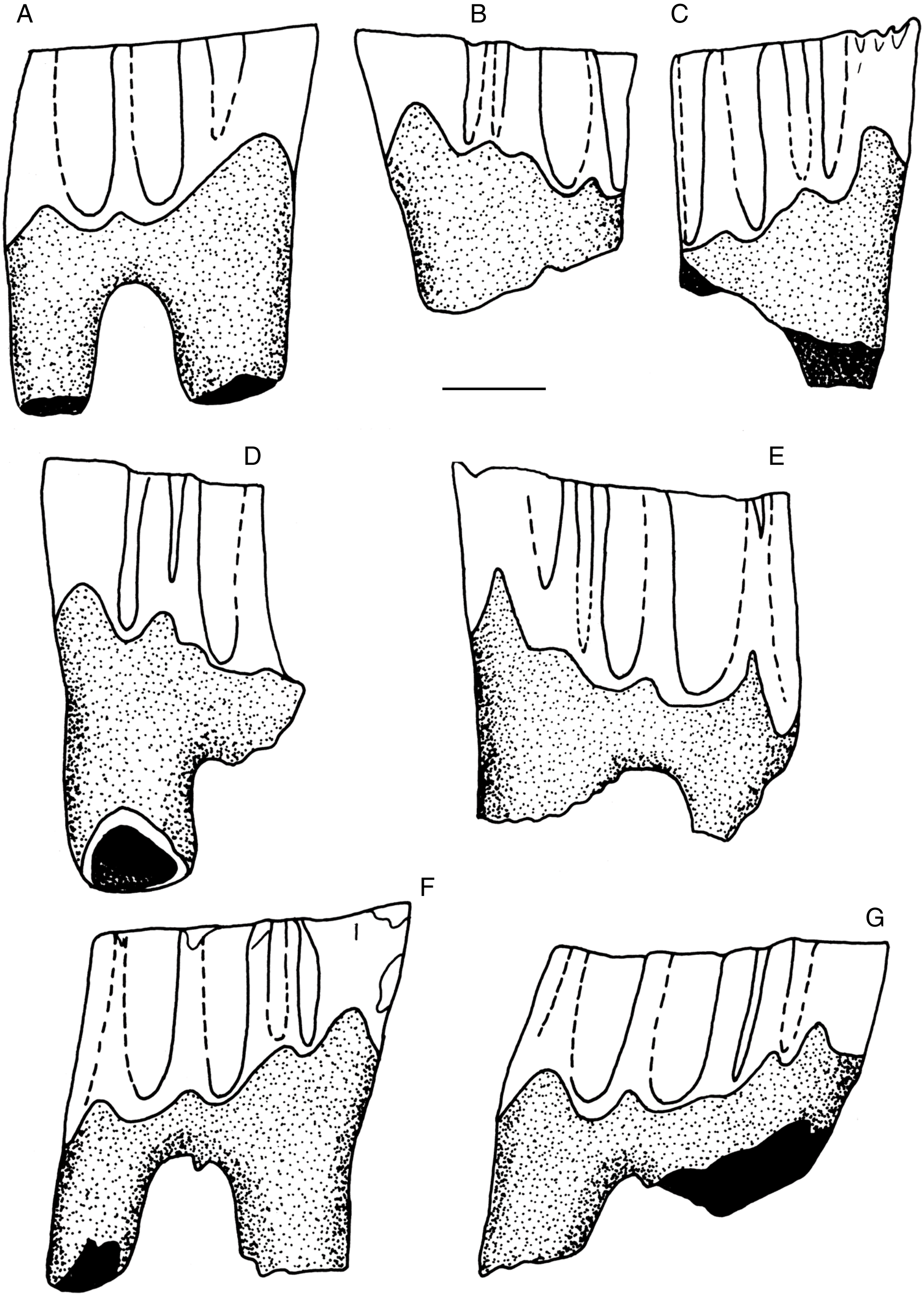

FIG. 34. — *Dolomys occitanus* (Thaler, 1955), first lower molars in buccal view; **A**, right, Ms42; **B**, left fragment, Ms1; **C**, right fragment, Ms7; **D**, left fragment, Ms2; **E**, left fragment, Ms8; **F**, right fragment, Ms11; **G**, right fragment, Ms13. Scale bar: 1 mm.

evolution, morphological changes of m1 with a variable direction have been proposed: from forms with an isolated islet (*Promimomys* and *Mimomys davakosi* Van de Weerd, 1979) through an open islet (most specimens in *M. occitanus*) to an isolated islet again (*M. stehlini*) (Van de Weerd 1979). This variable trend however seems unlikely, having in mind that the direction of an evolutionary change is usually irreversible.

The analysis of the detailed morphology of the enamel islet in the anteroconid of the m1 of *Dolomys*, *Promimomys* and *Mimomys* presented by Maul (1996) provides a new perspective for the solution of this evolutionary and taxonomic problem. Maul (1996) found that *M. occitanus* differs from the earliest members of the genera *Promimomys* and *Mimomys* in having a low positioned wall of the *Mimomys*-isle (Sb3-wall). This feature is considered a derived one, leading to an evolutionary trend toward lowering of the wall. With the decrease in the height of the wall more *Dolomys*-morphotypes appear in a population which have greater functional advantage because of their longer cutting edges. In this context, it seems likely that *M. occitanus* is an ancestral species to forms with a lower Sb3-wall like *Dolomys nehringi* and does not belong to the *Promimomys-Mimomys* evolutionary lineage comprising voles with a higher Sb3-wall (Maul 1996). For the time being, this hypothesis is the best solution of the problem and the attribution of the species "*occitanus*" to the genus *Dolomys* is followed here. According to Fejfar (2001), in contrast to the previous views (Chaline 1974; Chaline & Michaux 1975; Van de Weerd 1979), the evolutionary chain leading to *M. stehlini* is as follows: *M. davakosi* Van de Weerd, 1979-*M. gracilis* (Kretzoi, 1959)-*M. stehlini*.

According to the structure of M3, the genus *Dolomys* is rather specific and comprises such large species as *D. milleri* Nehring, 1898 and *D. nehringi* Kretzoi, 1959 (Chaline 1975). The occlusal pattern of m1 of these species (see for example Kretzoi 1962: abb. 4; Rabeder 1981: abb. 182) is quite different from the "*Dolomys*"-morphotypes of *Dolomys occitanus*. In this context the opinion of Maul (1996) that *D. occitanus* is an ancestor of *D. nehringi* seems unlikely. The occurrence of M3 in the locality very similar to *D. nehringi* confirms this opinion.

The same line of reasoning can be developed against the Chaline's hypothesis that *Dolomys*-morphotypes of *D. occitanus* represent an ancestral form for *Propliomys hungaricus*. The "*Dolomys*"-morphotype is quite different from the m1s of the true *Propliomys hungaricus* from Csarnóta-1 (Kormos 1934b: fig. 46; Terzea 1981: fig. 5s, d) and their co-occurrence in Muselievo (see above) indicates that this genus cannot be considered as a derivate of *D. occitanus*. For the time being, it can be said only that the ondatrine taxa, occurring in the European Pliocene [*Dolomys occitanus* (Thaler, 1955), *Dolomys milleri* (Nehring, 1898), *Dolomys nehringi* Kretzoi, 1962, *Dolomys adroveri* (Fejfar, Mein & Moissenet, 1990), and *Propliomys hungaricus* (Kormos, 1934)], represent a mosaic of species related to *D. occitanus*, which radiated quickly during the Ruscinian and early Villanyian (MN14-16-zones) (Fejfar & Repenning 1998).

As a whole, the population from Muselievo corresponds to the variability of *Dolomys occitanus* from the type locality (Grotte 1 de Sète) (Chaline 1974). In the scatter diagram composed for Lm1 and Em1 (Chaline 1974: fig. 2) the specimens from Muselievo would occupy the upper half of the cluster of the population from Sète. Hence, the material under study represents a slightly more advanced form. The m1s from Muselievo resemble also *D. occitanus* from Ciuperceni-2 in both size and morphology (Terzea 1981, 1997; and pers. comm.) and differ only in having somewhat higher dentine tracks. Most probably the material from the nearby Romanian locality Dranic, determined as *Mimomys moldavicus* (Radulescu & Samson 1996) belongs to *D. occitanus* too, having in mind that *M. moldavicus* (Kormos, 1932) is a rather primitive form with extremely low dentine tracks, referable to *Promimomys* (Fejfar *et al.* 1990).

In general, the material from Muselievo is very similar to m1 and M3 sample of *Dolomys occitanus* from Wölfersheim (Germany) (Fejfar & Repenning 1998; Dahlmann 2001). The differ-

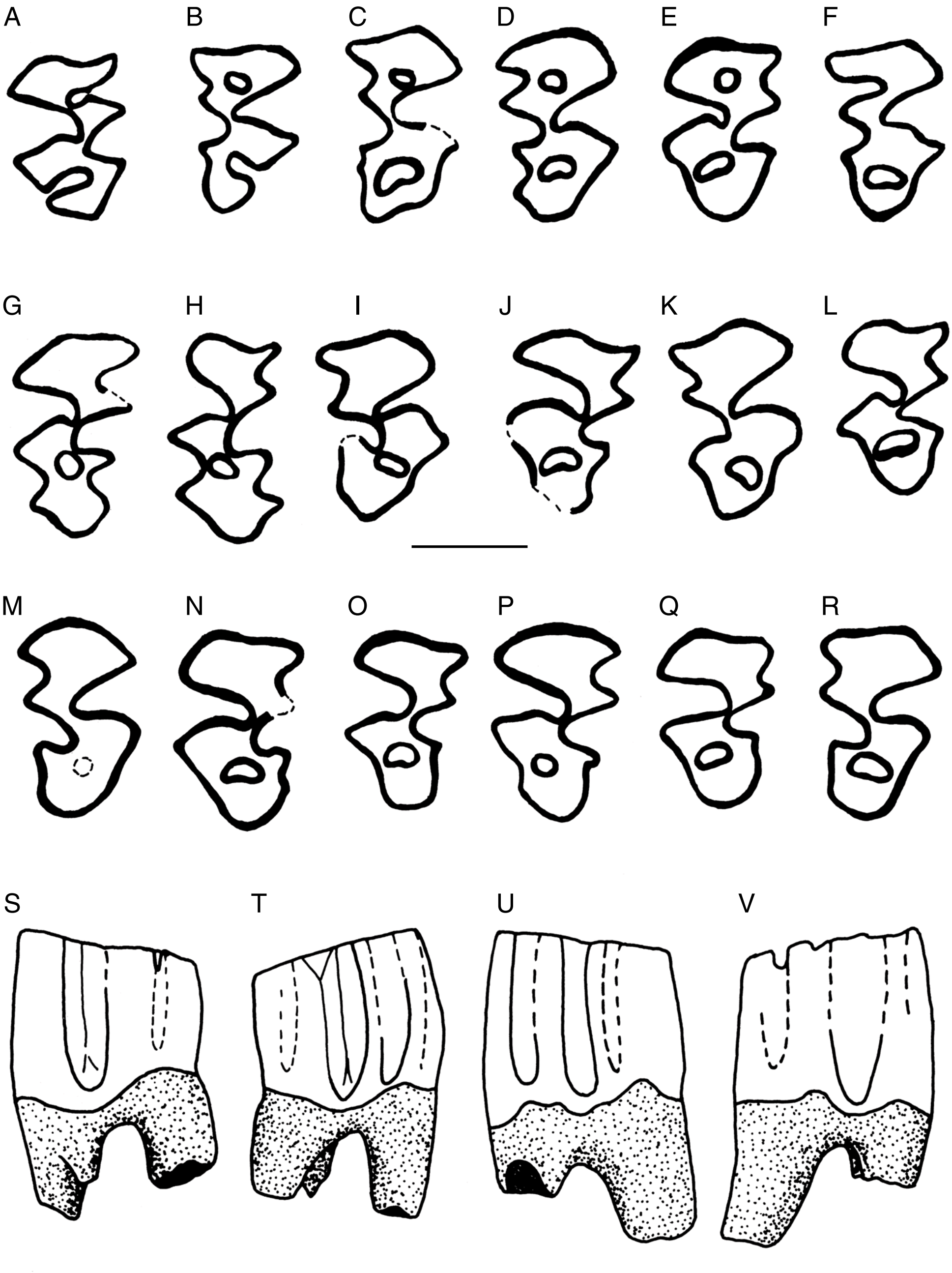

FIG. 35. — *Dolomys occitanus* (Thaler, 1955), third upper molars; **A**, left, Ms23, occlusal view; **B**, right, Ms24, occlusal view; **C**, right, Ms25, occlusal view; **D**, right, Ms26, occlusal view; **E**, left, Ms27, occlusal view; **F**, right, Ms28, occlusal view; **G**, left, Ms29, occlusal view; **H**, left, Ms30, occlusal view; **I**, right, Ms31, occlusal view; **J**, left, Ms32, occlusal view; **K**, right, Ms33, occlusal view; **L**, left, Ms34, occlusal view; **M**, right, Ms35, occlusal view; **N**, left, Ms36, occlusal view; **O**, left, Ms37, occlusal view; **P**, left, Ms38, occlusal view; **Q**, left, Ms39, occlusal view; **R**, right, Ms40, occlusal view; **S**, left, Ms23, lingual view; **T**, the same, buccal view; **U**, right, Ms24, lingual view; **V**, the same buccal view. Scale bar: 1 mm.

ence concerns only the somewhat longer m1 and the hyposinusids slightly lower in the sample from Muselievo.

The "*Mimomys*" morphotypes of *D. occitanus* are superficially similar to *M. davakosi* but differ in having higher dentine tracks (Van de Weerd 1979). This difference is clearly visible in relation to the material from Ptolemais 3, the type locality of *M. davakosi*, especially in respect to the anterosinuid. Moreover, *M. davakosi*, being a typical member of the *Mimomys* lineage, shows a higher position of the Sb3-wall (cf. Maul 1996: fig. 3).

Dolomys cf. ***nehringi*** Kretzoi, 1959
(Fig. 31A)

MATERIAL EXAMINED. — 1 M3 (Ms41); LM3 = 2.02.

DESCRIPTION

M3 bears three salient angles on each side. Except BSA3, all are well developed. The BRA1 and LRA3 are deep and narrow. They persist as normal folds throughout the crown instead of being subject to reduction by insulation. The enamel is not differentiated. There are not dentine tracks. Number of roots is two.

REMARKS

According to size, the tooth is smaller than the respective molars of the type species of the genus, *Dolomys milleri* (Nehring, 1898) (Méhely 1914). On the other hand, it resembles *Dolomys nehringi* from Csarnóta-2 both in general size (although slightly smaller) and occlusal pattern, judging from the Kretzoi's (1959: abb. 4) illustration. The molars of this species were however not described in detail by this author. This circumstance, as well as the scarce material from Muselievo (e.g., only one M3), makes the conclusive determination difficult.

Arvicolinae gen. et sp. indet.
(Fig. 36)

MATERIAL EXAMINED. — The vole molars, other than m1 and M3, indeterminable at species level, are described as if derived from a homogeneous sample. Having in mind the parallel evolution within particular vole lineages, the description of these molars may contribute in evaluating the overall evolutionary level of the vole assemblage in the locality. On the other hand, because the majority of the determinable molars belong to *Dolomys occitanus*, it can be supposed that the same is true for the other teeth. Hence, the descriptions presented below most probably should be referred to this species.

DESCRIPTION

All vole teeth lack crown-cementum and enamel differentiation.

M1: most teeth possess three roots. The enamel free areas at the sides of the crown are well pronounced, but they are low. The posterior dentine track is the highest. The occlusal surface consists of five, alternating and relatively well isolated dentine fields.

M2: the teeth have three roots. The occlusal surface consists of four dentine fields, anterior loop and three alternating triangles, of which the anterior two are more or less confluent with each other. The dentine tracks are low.

m2: the teeth possess two roots. The posterior one is concave in its lowermost part, indicating that it lies partly on the inner and partly on the outer side of the incisor (morphotype "*acrorhiza*"). The enamel free areas are generally low; the anterior one is the highest. The occlusal surface shows four alternating triangles, forming two pairs of largely confluent dentine fields (T4-T3 and T2-T1). The posterior loop is well separated.

m3: two roots and low dentine tracks. The occlusal surface consists of three dentine fields. The two anterior ones represent two pairs of opposite and widely communicating triangles (T4-T3 and T2-T1). The posterior root is also isolated.

ARVICOLIDAE *incertae sedis*
Genus *Bjornkurtenia* Kowalski, 1992

Bjornkurtenia canterranensis (Michaux, 1976)
(Fig. 37A-C)

Trilophomys canterranensis Michaux, 1976: 166-168.

"*Trilophomys*" *canterranensis* – Agadjanian & Kowalski 1978: 31.

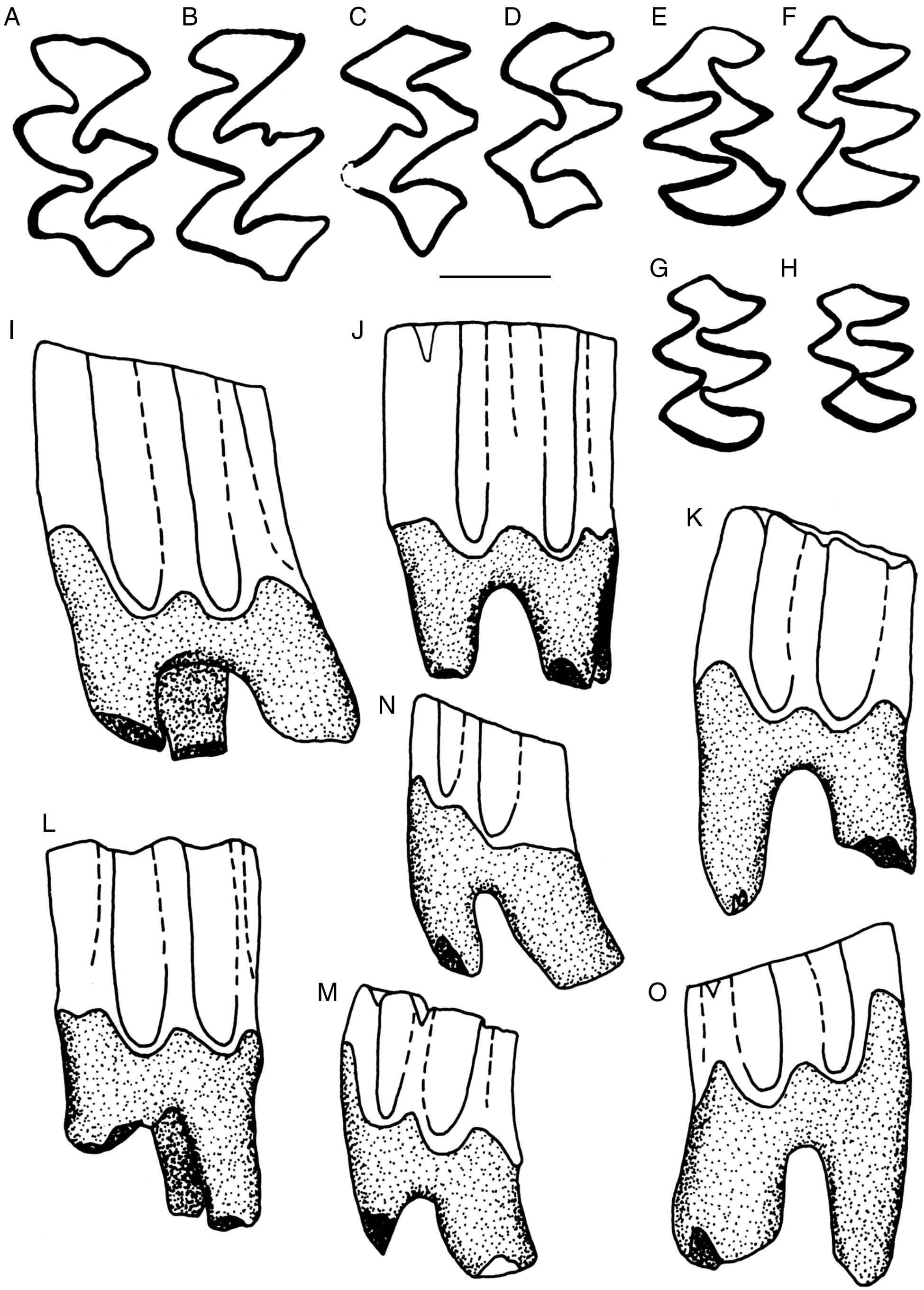

FIG. 36. — Arvicolidae; **A**, left M1, Ms19, occlusal view; **B**, left M1, Ms20, occlusal view; **C**, right M2, Ms21, occlusal view; **D**, right M2, Ms22, occlusal view; **E**, right m2, Ms15, occlusal view; **F**, left m2, Ms16, occlusal view; **G**, left m3, Ms17, occlusal view; **H**, left m3, Ms18, occlusal view; **I**, left M1, Ms19, buccal view; **J**, right M2, Ms22, lingual view; **K**, left m2, Ms16, buccal view; **L**, right M2, Ms21, lingual view; **M**, left m3, Ms17, buccal view; **N**, left m3, Ms18, buccal view; **O**, right m2, Ms15, buccal view. Scale bar: 1 mm.

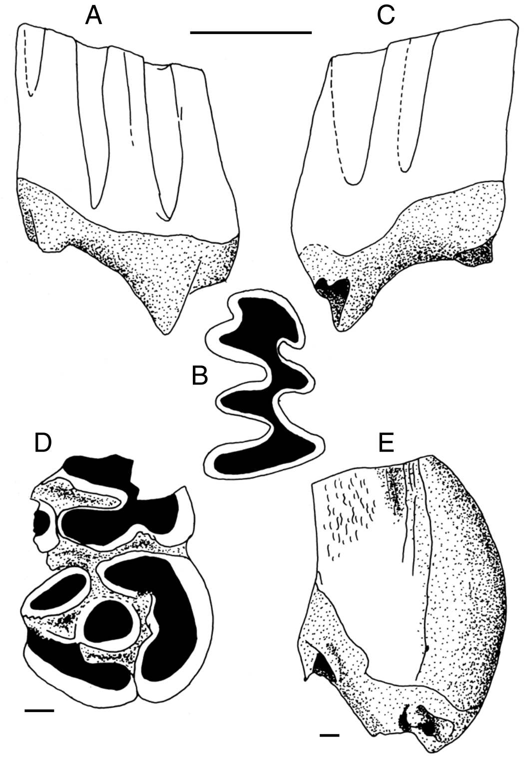

FIG. 37. — **A**-**C**, *Bjornkurtenia canterranensis* (Michaux, 1976); **A**, right m1, Ms52-1, lingual view; **B**, the same, occlusal view; **C**, the same, buccal view; **D**, **E**, *Hystrix* sp.; **D**, right P4, Ms396, occlusal view; **E**, the same, posterior view. Scale bars: 1 mm.

Bjornkurtenia canteranensis – Kowalski 1992: 321-327.

MATERIAL EXAMINED. — 1 m1 (Ms52-1); (L × W) = 1.62 × 1.05.

DESCRIPTION

The tooth is two-rooted. The occlusal surface is simple, consisting of a posterior loop, three alternating triangles and an anterior cap, situated obliquely to the sagital axis. The dentine field of the anterior cap is widely connected with the triangle behind it. The enamel is thick and uneven. There are no dentine tracks.

REMARKS

The available molar is slightly shorter than the original material from Terrats (Roussillon, France), described as *Trilophomys canterranensis*. It differs from *Trilophomys depereti* Fejfar, 1961, from Muselievo (see below) by having alternating triangles and by lacking dentine tracks. These features are characteristic for the genus *Bjornkurtenia* Kowalski, 1992, comprising the materials from Terrats and Podlesice (MN14, Poland), previously referred to *Trilophomys* Depéret, 1892. The species is also known from Gundesheim-4, MN15b (Germany) (Fejfar & Storch 1990). According to Kowalski (1992), *Bjornkurtenia* is one of the most primitive voles in the family Arvicolidae.

The available tooth is similar to the imperfect m1 from Osztramos 9, described as *Promimomys microdon* Janossy, 1974, but it has a narrow dentine isthmus between the third triangle and the anterior cap. In this respect, it is very similar to *Baranomys longidens* (Kowalski, 1960). However, because the Hungarian specimen is damaged in its anterior part, for the time being, it is impossible to ascertain whether this difference has systematic value or not. Since the structure of the mandible is not known, the systematic position of the genus and species within the family Arvicolidae cannot be adjusted (Kowalski 1992).

Family TRILOPHOMYIDAE Kretzoi, 1969
Genus *Trilophomys* Depéret, 1892

Trilophomys depereti Fejfar, 1961
(Fig. 38)

Trilophomys depereti Fejfar, 1961b: 71-73, abb. 10, b, e. — Brandy 1979: 107, 110-112, fig. 17f, g.

MATERIAL EXAMINED. — 1 m1 (Ms52), 2 m2 (Ms53-54), 1 m3 (Ms55), 1 M1 (Ms56), 2 M2 (Ms57, Ms58), 1 M3 (Ms140).

MEASUREMENTS (maximal length at the base of the crown). — Lm1 = 2.05; 1.85; Lm2 = 1.65; 1.67; Lm3 = 1.10; LM1 = 1.85; LM2 = 1.55; LM3 = 1.47.

DESCRIPTION

m1: the tooth is two-rooted, the crown is high, and the enamel free areas are moderately high. The occlusal surface comprises a posterior loop, two opposite triangles and a rhomboidal anterior

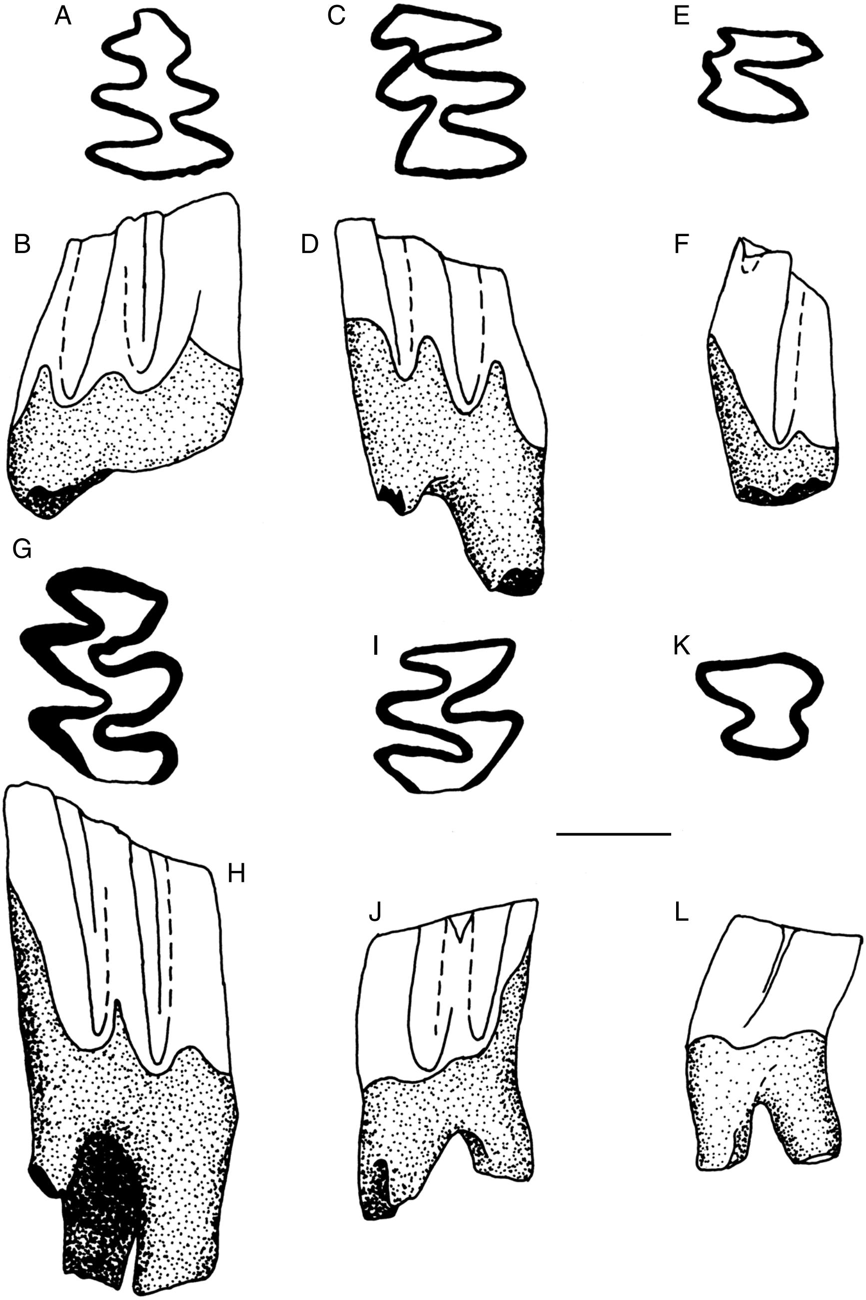

FIG. 38. — *Trilophomys depereti* Fejfar, 1961; **A**, right m1, Ms52, occlusal view; **B**, the same, labial view; **C**, left m2, Ms53, occlusal view; **D**, the same, buccal view; **E**, left m3, Ms55, occlusal view; **F**, the same, buccal view; **G**, left M1, Ms56, occlusal view; **H**, the same, buccal view; **I**, left M2, Ms57, occlusal view; **J**, the same, buccal view; **K**, left M3, Ms140, occlusal view; **L**, the same, buccal view. Scale bar: 1 mm.

cap. There is a well pronounced but shallow antero-lingual reentrant fold. The enamel is not differentiated.

m2: two roots. The dentine tracks at the sides of the crown, although not very high are well pronounced. The occlusal surface consists of three more or less rhomboidal dentine fields, well separated one from the other by deep opposite reentrant angles. The triangles are clearly asymmetrical – the lingual ones are larger than the labial ones.

m3: this tooth has two roots, which are nearly coalescent. The anterior dentine track is high. There is a shallow and ephemeral anterolabial infold, which would vanish quickly with further wear. The lingual reentrant fold is well pronounced transversely, while the postero-labial one is shallow. These folds separate the occlusal surface in two rhomboidal dentinal spaces, which are more or less isolated from each other.

M1: the tooth is with three roots, of which the anterior is larger. The posterior dentine track is rather high, reaching the occlusal surface even in a relatively early stage of wear. The irregular triangles, situated behind the anterior dentine field are distinctly alternating. The posterior two triangles are in relatively wide confluence while the remaining ones are more or less well separated.

M2: the tooth possesses three roots. The anterolingual is the larger one and consists of two completely fused though clearly recognizable elements, which in turn tend to fuse with the anterolabial root. The posterior dentine track is high. The triangles are alternate and more or less confluent.

M3: the occlusal surface is simple, consisting of two largely confluenting dentine fields, separated by two, lingual and labial, shallow reentrant angles.

REMARKS

The genus *Trilophomys* introduced by Depéret in 1892 from Perpignan (France) is later found in many other early Pliocene MN14-15 localities in Europe (Fejfar & Repenning 1998). Up to now the following species have been described: *Trilophomys pyrenaicus* (Depéret, 1892), *T. depereti* Fejfar, 1961, *T. schaubi* Fejfar, 1961, and *T. vandeweedi* Brandy, 1979. Sulimski (1964) synonymizes *T. schaubi*, *T. depereti*, and *T. pyrenaicus*, and refers the material from Weze 1 to the last species. The synonymy of *T. schaubi* and *T. pyrenaicus* is also confirmed by Brandy (1979). In his analysis, based mainly on the degree of hypsodonty, he recognized two evolutionary lineages of *Trilophomys*. The first lineage represents the evolution from *T. pyrenaicus* to *T. vandeweerdi*. The last species is the most advanced form, particularly the populations from Layna, Balaruc II and IV, Seynes (France), and Wölfersheim (Germany) (Fejfar & Repenning 1998). The second lineage, with relatively high dentine tracks, is poorly known and includes some chronopopulations (Ivanovce, Weze) of *T. depereti*. Brandy (1979) regards the dental pattern of the specimen from Weze 1, illustrated on figure 14 in Sulimski (1964: 192) to be different from *T. pyrenaicus* and belonging to the second evolutionary lineage. It is more evolved (more hypsodont with higher enamel-free areas) in comparison with the material of *T. depereti* from Ivanovce. Brandy (1979) designates the population from Weze 1 as *Trilophomys* cf. *depereti* (see also Nadachowski 1990). The available m1 from Muselievo is more primitive than the tooth from Weze 1 (Sulimski 1964: fig. 14) in its lower dentine tracks. It fits with the material of *T. depereti* from Ivanovce in having a comparable level of hypsodonty. It can be assumed that the geological age of the remains from Muselievo is closer to that of Ivanovce. However, the m1 from Muselievo has more elaborated anterior part (the presence of a shallow antero-lingual reentrant angle), being more similar with the type specimen of *T. schaubi* from Ivanovce and with the specimen from Weze 1, illustrated by Sulimski (1964) on figure 14a. However, Sulimski (1964), by a series of sections, showed that the pattern of the occlusal surface varies with the attrition of the crown, argumenting in this way the synonymy of *T. shaubi* with *T. depereti*. Hence, the determination of the material from Muselievo is based mainly on the level of hypsodonty. In accordance with the evolutionary scheme proposed by Brandy (1979), I assign the material from Muselievo to *T. depereti*.

Family SPALACIDAE Gray, 1821
Subfamily SPALACINAE Gray, 1821
Genus *Pliospalax* Kormos, 1932

Pliospalax* cf. *macoveii (Simionescu, 1930)
(Fig. 39)

MATERIAL EXAMINED. — 2 M1 (Ms114, 115), 2 M2 (Ms116, 117), 1 M3 (Ms118), 2 m1 (Ms120, 121), 1 m3 (Ms119).

MEASUREMENTS (L × W). — M1 = 2.37 × 2.05; 2.37 × 2.05; M2 = 2.00 × 2.00; 1.87 × 2.00; M3 = 1.60 × 1.57; m1 = 2.02 × 1.57; 2.00 × 1.70; m3 = 1.75 × 1.87.

DESCRIPTION

M1: both teeth available possess a mesocone (mesoloph) and a more or less well developed posterior cingulum. The postero-labial reentrant fold is an ephemeral feature, which becomes rapidly narrower and shallower as it descends, until it is represented be a mere groove, which may or may not persist in the worn tooth. In the slightly worn specimen, both the paracone and the metacone are still separated from the mesocone and the hypocone, respectively. The anterior loop is oblique in relation to the mesial axis of the occlusal surface. The teeth are three-rooted.

M2: in the younger stage of wear, the antero-lingual and postero-lingual valleys are closed labially. In the other, adult, tooth the posterior islet had already vanished. The tooth possesses three roots.

M3: the tooth belongs to a young specimen with the pulp-cavities still open below. The occlusal surface is e-shaped, due to a nearly crescent shaped reentrant fold.

m1: the teeth available belong to individuals of advanced ontogenetic age, as they are considerably worn. The occlusal surface is simple, elongated antero-posteriorly, S-shaped with two reentrant folds (one lingual and one labial), and an enamel island which corresponds to the postero-lingual reentrant fold, separating the entoconid from the posterior cingulum. The lingual sinus is obliquely directed forward, while the posterior one is more or less transversal in relation to the sagital axis of the occlusal surface. Two roots.

m3: the occlusal surface is nearly S-shaped but at this stage of attrition the posterior loop is shut off from the anterior part.

REMARKS

The determination of isolated molars of spalacids is difficult because the occlusal pattern is relatively simple and uniform within the genera but varies considerably with crown wear (De Bruijn & Van der Meulen 1975; Sen 1977). As a result, similar morphotypes may occur in the related species. According to the structure of the occlusal surface, the available M1s show some similarities with the most primitive species within the genus, *Pliospalax compositidontus*: small size, occurrence of a mesocone, a well pronounced posterior cingulum and a postero-lingual reentrant fold, three roots. These peculiarities differentiate the specimens from the latter species, *Pliospalax macoveii* (Simionescu, 1930) and *P. odessanus* (Topacevsky, 1969) (Topachevsky 1969). In particular, *P. macoveii* and *P. odessanus* have more simplified occlusal surface of upper molars, a reduced number of roots, and larger size, which, according to Topachevsky (1969), is a result of an evolutionary trend whitin this evolutionary branch. On the other hand, a latter form from the early Pleistocene of Greece (Tourkobounia-1, Athens), described as *Pliospalax tourkobounensis* De Bruijn & Van der Meulen, 1975, does not fit within this trend. According to De Bruijn & Van der Meulen (1975) "the stratigraphically youngest of these three species [*P. macovei*, *P. sotirisi*], *P. tourkobounensis*, is morphologically more archaic having relatively low-crowned cheek teeth and a mesoloph and posterior cingulum in M1". It is remarkable that some of the first upper molars from Çalta (Sen 1977: pl. XIII: 1, 3a), initially attributed to *Pliospalax compositidontus*, are also very similar to these of *P. tourkobounensis* and to the M1s from Muselievo in having a mesocone and a postero labial reentrant forld. According to Sen (1998), these molars should also be referred to *Pliospalax macoveii*. It should be mentioned that these three forms (Tourkoubonia 1, Çalta,

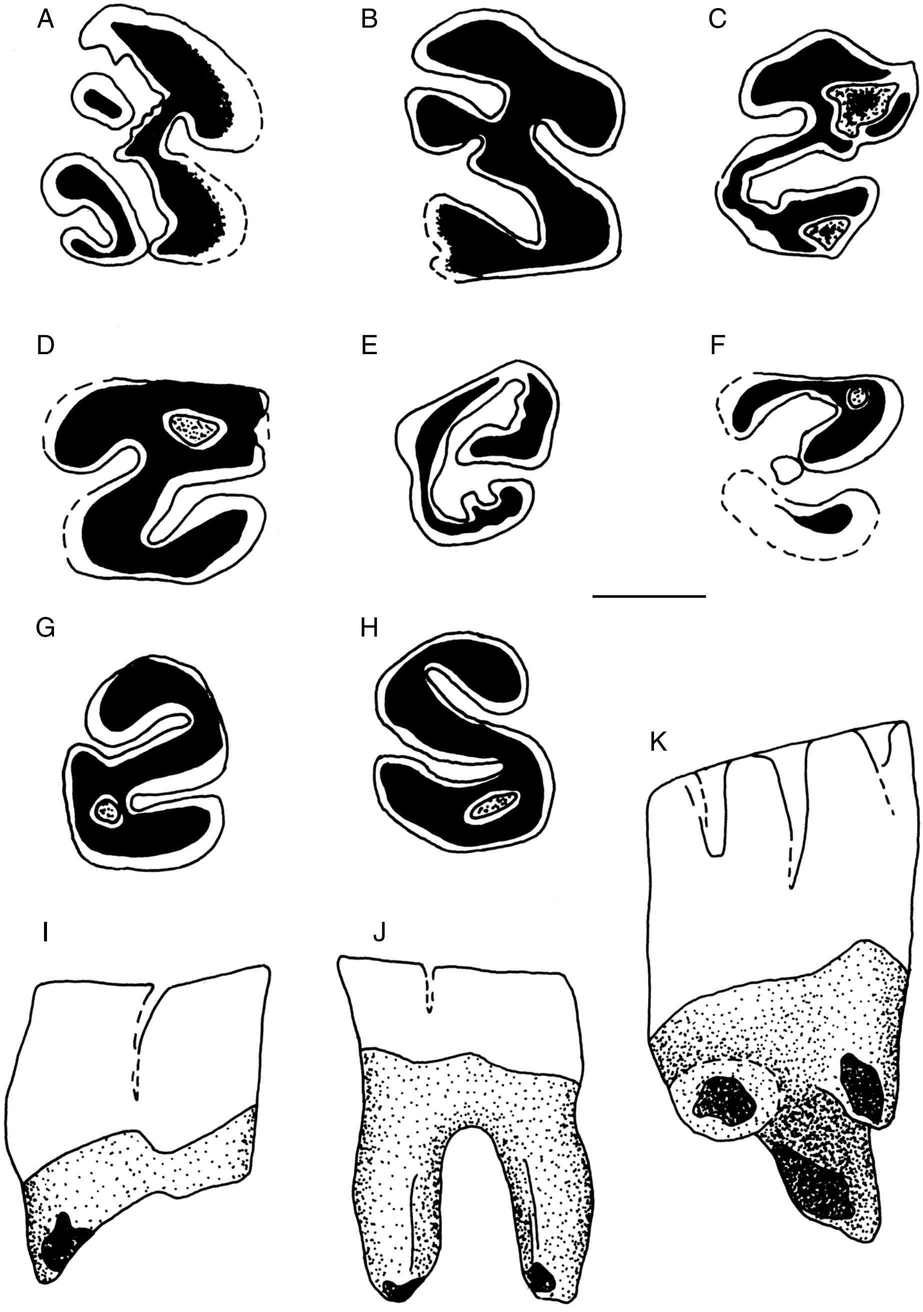

FIG. 39. — *Pliospalax* cf. *macoveii* (Simionescu, 1930); **A**, left M1, Ms114, occlusal view; **K**, the same, labial view; **B**, left M1, Ms115, occlusal view; **C**, right M2, Ms116, occlusal view; **D**, right M2, Ms117, occlusal view; **E**, right M3, Ms118, occlusal view; **F**, right m3, Ms119, occlusal view; **G**, right m1, Ms120, occlusal view; **J**, the same, lingual view; **H**, left m1, Ms121, occlusal view; **I**, the same, lingual view. Scale bar: 1 mm.

and Muselievo) have relatively small molars, similar to these of *Pliospalax compositidontus*, but considerably smaller than the molars of *Pliospalax macoveii* and *P. odessanus* (Topachevsky 1969).

In contrast to the upper molars, the first lower molars from Tourkobounia 1 (*P. tourkobounensis*), Çalta (*P. macoveii*), and especially these from Muselievo have a simplified occlusal pattern, quite different from the respective teeth of *Pliospalax compositidontus*, as figured in Topachevsky (1969: 18, fig. 6). In this respect they are similar to the first lower molars of *Pliospalax macoveii* and *P. odessanus* (Topachevsky 1969; De Bruijn 1984), but, as in the case of the upper molars, they are smaller. As concern the first lower molars from Muselievo, it must be emphasized that they are rather worn, which prevents more detailed comparisons.

The mole rate from Maritsa (isle of Rhodes), initially described as *Spalax sotirisi* De Bruijn, Dawson & Mein, 1970, is considered by the latter authors (De Bruijn & Van der Meulen 1975; Sen 1977) to belong to *Pliospalax macoveii.* This form shows a simplified occlusal pattern of M1.

The material from Muselievo, the above comparisons and discussion match the opinion of De Bruijn & Van der Meulen (1975) that "the relationship among the *Pliospalax* species may be rather complex" and, no doubt, the available materials from the southern part of Russian plain, Balkan Peninsula, and Asia Minor need a comprehensive revision. For the time being I refer tentatively the material from Muselievo to *P. macoveii* on the basis of its overall similarity to the sample from Çalta.

Family HYSTRICIDAE Fischer, 1817
Genus *Hystrix* Linnaeus, 1758

Hystrix sp.
(Fig. 37D, E)

MATERIAL EXAMINED. — Fragment of right P4 (Ms396).

DESCRIPTION AND COMPARISON

The available premolar shows relatively high crown, higher than in *Hystrix primigenia* Wagner, 1848. In this respect it is comparable with the porcupine materials from Perpignan and Weze, which for the time being should be designated as *Hystrix* cf. *primigenia* (Sen pers. comm.).

GENERAL DISCUSSION

AGE OF THE FAUNA

The small mammal assemblage from Muselievo comprises some genera, which appear during the late Turolian or earliest Ruscinian and whose time ranges cover the entire Pliocene (Ruscinian-MN14 and MN15-zone, and Villanyian, MN16 and MN17-zone): *Trilophomys*, *Deinsdorfia*, *Mafia*, *Blarinoides*. Some species have more restricted time ranges allowing precise correlations. The presence of *Glis minor*, indicates that the locality should be referred to the earlier part of the Pliocene – between MN14 and MN16-zones. The occurrence of *Dryomimus eliomyoides* is indicative for MN15-MN16-zones. *Dolomys occitanus* and *Deinsdorfia kordosi* were only reported from the upper part of MN15-zone, i.e. from MN15b-subzone. More exactly, having in mind that, as it was shown above, the studied population of *D. occitanus* is somewhat more advanced than the population from Sète (France), Muselievo should be younger than this locality. On the other hand, the population from Muselievo seems slightly more primitive than the form from Wölfersheim and it can be supposed that the studied locality is older. On the basis of the arvicolids, Wölfersheim was referred to the early Villanyian, MN16a-zone (Fejfar 2001). According to Dahlmann (2001), however, this locality falls within the uppermost part of MN15-zone, being synchronous with Csarnóta-2 and Layna (*c.* 3.4 my). It can be supposed that the age of Muselievo is intermediate between Sète and Wölfersheim and can be correlated with Gundersheim-4 (Findling) and Ivanovce. The similarity of the populations of

Trilophomys depereti from Muselievo and Ivanovce confirms this interpretation. The occurrence of a form similar to *Propliomys hungaricus* in Muselievo and the absence of representatives of the genera *Borsodia* and *Villanyia* that are very numerous in latter faunas in this part of Europe (Fejfar 2001) confirms the attribution of the studied locality to the MN15b. According to the stratigraphical chart, proposed by Fejfar (2001), the following European localities fall within this zone: Ivanovce A, Weze, Gundersheim (Tobien), Malusteni, Beresti, Csarnóta-2, Osztramos 9, 13, etc. The opinions concerning the age of some of these localities (Beresti, Malusteni, Weze, Csarnóta-2) are however controversial.

For instance, according to Terzea (1997) the Romanian localities Beresti and Malusteni belong to the upper part of MN14b and the lowermost part of MN15a, respectively. This is confirmed by the fact that *Trischizolagus dumitrescuae* from Muselievo seems more progressive than the form from these Romanian localities.

According to Van der Meulen & Van Kolfschoten (1986) the South Hungarian locality Csarnóta-2 should be referred to the lower part of MN16a-zone on the basis of the presence of *Mimomys gracilis* (Kretzoi, 1959). This species is slightly more advanced than *Mimomys proseki* Fejfar, 1961, which is associated with *Dolomys occitanus* in Weze 1, Ivanovce B, and Wölfersheim, belonging to MN15b (Van der Meulen & Van Kolfschoten 1986). Terzea (1997) also attributed Csarnóta-2 to MN16a-zone and placed Weze 1 at the boundary between MN15b and MN16a. According to Nadachowski (1990), the assemblage from Weze 1 is of the late Ruscinian age (MN15-zone) while the assemblage from Weze 2 is of an intermediate age between Ruscinian and Villanyian (MN15/16-zones).

The fauna from Sète is though to be 2.8 my old (Chaline & Laurin 1984). On the other hand Aguilar & Michaux (1984) consider the locality to be below the date of 3.3 my. The last opinion has latter been followed by various scholars (De Bruijn *et al.* 1992; Dahlmann 2001, etc.). Recently, Opdyke *et al.* (1997), in studying the magnetic stratigraphy of several sections in Spain bearing mammalian localities, have found that the MN15/MN16 boundary corresponds to the Gilbert/Gauss boundary at 3.58 my. Thus, the fauna from Muselievo, according to the above biostratigraphic considerations, should be slightly older than this date. According to Terzea (1997) Muselievo is younger than Ivanovce B and Sète, older than Apolakkia 2, Weze, and Csarnóta-2 and has an age of *c.* 3.75 my.

In summary, the fauna from Muselievo should be referred to MN15b-subzone with an absolute age between 3.8 and 3.6 my.

PALEOECOLOGY

As a rule the small mammal species have rather specific ecological requirements and if their fossils are found, it can be inferred that respective conditions prevailed in that place in the past, assuming that the animals originally lived near to the site of deposition. However, when we interpret a fossil assemblage in this respect, we must first be aware of taphonomic biases. Therefore, we must infer the factors responsible for bone accumulation as a first step towards interpretation of a fossil small mammal assemblage from paleoecological point of view.

The morphology of the karstic hollow is of particular importance in this respect. Based on the actual exposure, it is difficult to reconstruct the morphology of the ancient cave. According to its location on the slope of the river valley, however, it can be supposed that it was similar to the recent nearby cave "Nanin Kamak". This cave is located about 300 m apart and at the same altitude of about 50 m above the local base of erosion (the Osam River bed). It represents a system of small horizontal galleries and some relatively large sales. The first sale has a vertical chimney opened on the plateau. The cave is dry and the floor is covered with clay and bat guano. A large summer bat colony inhabits regularly the cave.

Likewise, it can be supposed that the ancient cave had a vertical shaft, opened on the plateau and formed a pitfall trap for animals. Since the bone concentration of large and small mammals is not great (except bats), it can be supposed that they belong to victims of accidental entrapment. The identity of the other vertebrate remains and their low concentration confirm the above assumption. The large mammals are represented by rather fragmentary remains of cervids, caprids, suids (*Sus minor* Depéret, 1890), primates (*Dolichopitecus* sp.), and small carnivores (*Lynx* sp.). Beside mammals some bones of birds (*Accipiter* sp., *Falco* sp., *Lagopus* cf. *atavus* Janossy, 1974, *Pavo bravardi* (Gervais, 1849) (Boev 2001), amphibians, and reptiles have been collected. Based on these considerations, it can be supposed that the fossil assemblage of the terrestrial small mammals represents the immediate surroundings of the locality.

The bones and teeth of bats were the most numerous fossils in the sediment. It can be supposed that the ancient cave was inhabited by a bat colony. It is remarkable that the species composition of the fossil bat assemblage is quite similar to the composition of the present day bat colony. The recent bats inhabiting the nearby cave are: *Rhinolophus ferrumequinum*, *Rh. hipposiderus*, *Rh. mehelyi*, *Rh. euryale*, *Miniopterus schreibersii*, *Myotis blythii*, *M. myotis*, and *Myotis capaccinii*. Thus, the fossil bat assemblage is comparable, from ecological point of view, with the bat colony in the nearby recent cave.

Fossil small mammal associations are often used for paleoenvironmental interpretations, according to the inferred ecological requirements of the species. Usually a particular taxon is considered indicative for a certain type of environment on the basis of actualistic extrapolations founded on functional morphology and similarity with related extant forms (Van Dam & Weltje 1999). Associated fossils and facies of the sediments may also be helpful in this respect (Reumer 1984). However, this approach allows only for gross distinctions to be made and very often conflicting hypotheses concerning the ecological tolerance and habitat preference of some extinct species have been proposed (Andrews 1995; Van Kolfschoten 1995). While conclusions of such analyses may be correct, it is difficult to effectively evaluate results since the reasoning presented often appears to contain a considerable degree of circularity. It may be expected that a more complex approach, based on an analysis of the general patterns of coincidence of several taxa along spatial environmental gradients may be helpful in revealing the species/environmental relationships, having in mind that the distribution of the extinct species was affected by climatic and environmental factors in the same way as it is done for the extant small mammals. Ordination techniques are especially useful in revealing such patterns. These analyses are especially helpful in studying assemblages composed predominantly by extinct species because they do not begin with any assumptions for the species' palaeoecological preferences. Instead, these techniques extract some internal structure directly from the data which allow to generate hypotheses about the species/environmental relationships.

In this context, in order to reveal the effect of particular palaeoenvironmental spatial gradients on the distribution of the fossil terrestrial small mammals and to depict in a parsimonious manner the biogeographical position of the Muselievo assemblage, eight Pliocene small mammal assemblages (lipotyphlans and rodents) from Europe and the Mediterranean coast of Asia Minor were analyzed by means of correspondence analysis (CA). The selected localities are fissure fillings and it can be supposed that they differ from the faunas that originally lived in the area in the same way. Thus, it may be expected that the differences between them result primarily from the regional faunal composition and in a lesser extent from the local landscape peculiarities. Six out of the eight selected fossil assemblages were approximately time-equivalent, belonging to the middle and upper Ruscinian stages (MN15b-MN16a-zones). One locality (Maritsa, the isle of Rhodos) belonged to the lower Ruscinian stage (lower part of the MN14-zone) and another one (Tourkoubounia 1) was referred to the Lower Villanyian stage (lower part of the MN16b-zone) (Van der Meulen & Van Kolfschoten 1986).

In order to avoid the appearance of rare species restricted to species-poor sites, which may distort the ordination results, the analysis was carried out on generic level. The study includes 70 genera of lipotyphlans and rodents. Within the data set, however, the majority of the genera (77%) comprise only one species. The database for this analysis is provided by faunal lists summarized in Dahlmann (2001), supplemented by the lists presented in Van der Meulen & Van Kolfschoten (1986). "? *Cricetulus* sp." from Maritsa (de Brujin *et al.* 1970) is considered as *Mesocricetus* (Sen 1977).

Having in mind that quantitative representation of a taxon depends primarily of taphonomy and local conditions, the rates of the taxa were considered less important at the selected scale of analysis than their actual presence. So, the ordination was based on qualitative data only. The data matrix consisted of 1 and 0, representing presence and absence, respectively, of each genus in each of the eight sites. Since only data for rodents were available for the assemblage from Tourkoubounia 1 it was included in the analysis as a passive sample (Ter Braak 1987).

The ordination was based on CA because the preliminary analyses showed that the first underlying gradient is relatively long, 3.85 SD, indicating that the generic distribution along this gradient is unimodal (Ter Braak 1987). Accordingly, the generic score is a weighted mean of the sample scores and can be interpreted as a center ("optimum") of this distribution.

The "spatial niche bread" of a genus is evaluated as a number of occurrences, while the diversity of the assemblages was estimated by the number of genera (Fig. 40). The last measure is strongly affected by the sample size. However, taking into account that the assemblage from Maritsa, having a low diversity, is based on a large sample, consisting of more than 1600 determinable teeth (de Brujin *et al.* 1970), it can be supposed that, within the data set, the effect of this factor was not very important. More over according to the diagram showing the relation between the number of rodent specimens and the number of species, presented by Van de Weerd & Daams (1978), the minimal sample size needed to establish a more or less complete sample of the taxonomic composition of a rodent fossil assemblage appears to be between 100 and 150 specimens.

Evidently, the number of the selected sites is too small to represent in detail the generic distributional patterns. As a result, the inferred environmental characteristic of a particular genus may differ from the "theoretical" tolerance, which can be recognized on the basis of the total distributional range. This is especially true having in mind the lack of suitable data from fissure fillings from Eastern Europe. Thus, within the context of

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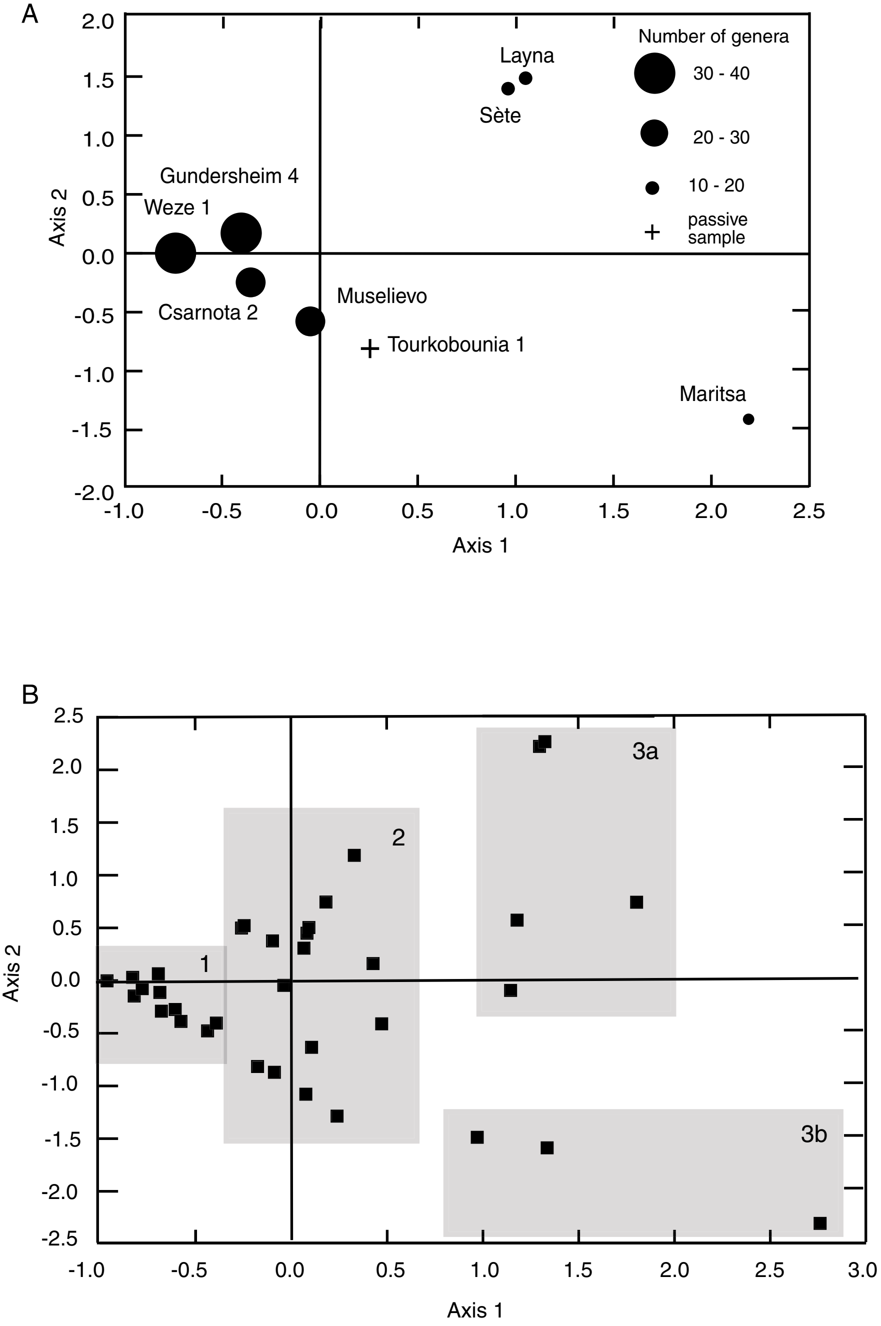
FIG. 40. — Correspondence analysis of the generic distributional patterns (presence/absence data) across eight Pliocene (MN14-MN16) small mammal assemblages (lipotyphlans and rodents) from Europe and the Mediterranean coast of Asia Minor; **A**, ordination of assemblages; **B**, ordination of genera. Identification of the genera, within each group denoted on the diagram, the genera are arranged according to their projection on the first ordination axis, from left to right:

Group 1, *Condylura* Illiger, 1811, *Scaptonix* Milne-Edwards, 1872, *Ungaromys* Kormos, 1932, "*Scalopoides*" Wilson, 1960, *Trogontherium* Fischer von Waldheim, 1809, *Parapodemus* Schaub, 1938, *Democricetodon* Fahlbusch, 1964, *Galemys* Kaup, 1829, *Germanomys* Heller, 1936, *Blackia* Mein, 1970, *Sulimskia* Reumer, 1984, *Stachomys* Kowalski, 1960, *Sminthozapus* Sulimski, 1962, *Pliopetes* Kretzoi, 1959, *Zelceina* Sulimski, 1962, *Muscardinus* Kaup, 1829, *Micromys* Dehne, 1841, *Sorex* Linnaeus, 1758, *Baranomys* Kormos, 1933, *Beremendia* Kormos, 1934, *Petenyia* Kormos, 1934, *Kowalskia* Fahlbusch, 1969, *Glirulus* Thomas, 1906, *Promimomys* Kretzoi, 1955, *Desmana* Gueldenstaedt, 1777, *Tamias* Illiger, 1811, *Propliomys* Kretzoi, 1959, *Blarinoides* Sulimski, 1959, *Deinsdorfia* Heller, 1963, *Talpa* Linnaeus, 1758, *Pliopetaurista* Kretzoi, 1962, *Mafia* Reumer, 1984, *Glis* Brisson, 1762, *Bjornkurtenia* Kowalski, 1992;

Group 2, *Prospalax* Méhely, 1908, *Erinaceus* Linnaeus, 1758, *Paenelimnoecus* Baudelot, 1972, *Dryomimus* Kretzoi, 1959, *Dolomys* Nehring, 1898, *Spermophilus* Cuvier, 1825, *Sciurus* Linnaeus, 1758, *Rhagapodemus* Kretzoi, 1959, *Hystrix* Linnaeus, 1758, *Mimomys* Forsyth Major, 1902, *Alloblarinella* Storch, 1995, *Trilophomys* Depéret, 1892, *Dryomys* Thomas, 1906, *Orientalomys* De Bruijn & Van der Meulen, 1975, *Archaeodesmana* Topachevskij & Pashkov, 1983, *Asoriculus* Kretzoi, 1959, *Sylvaemus* Ognev, 1923;

Group 3a, *Cricetus* Leske, 1779, *Eliomys* Wagner, 1840, *Myosorex* Gray, 1838, *Blancomys* Van de Weerd, Adrover, Mein & Soria, 1977, *Ruscinomys* Depéret, 1890, *Stephanomys* Schaub, 1938, *Paraethomys* Petter, 1968, *Castyllomys* Michaux, 1969, *Occitanomys* Michaux, 1969;

Group 3b, *Pliospalax* Kormos, 1932, *Myomimus* Ognev, 1924, *Allocricetus* Schaub, 1930, *Calomyscus* Thomas, 1905, *Pseudomeriones* Schaub, 1934, *Mesocricetus* Nehring, 1898, *Pelomys* Peters, 1852, *Spermophilinus* De Bruijn & Mein, 1968, *Keramidomys* Hartenberger, 1966, *Atlantoxerus* Forsyth Major, 1893.


A
Number of genera
30 - 40
20 - 30
10 - 20
+ passive sample
Layna
Sète
Gundersheim 4
Weze 1
Csarnota 2
Muselievo
Tourkobounia 1
Maritsa
Axis 2
Axis 1
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
B
1
2
3a
3b
Axis 2
Axis 1
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0

the still incomplete and fragmentary nature of the paleofaunistic and taxonomic knowledge, the present analysis is best viewed primarily as a preliminary, rough, and illustrative example and not as a definite study of the distribution of the Pliocene terrestrial small mammals. Nevertheless, taking into account that the sites are scattered across a wide range of conditions, it may be expected that the revealed patterns mirror the general distributional trends and the respective groups of genera (see below) could be broadly related to the environmental spatial gradients and physiographic conditions during this time.

The interpretation of the results of this analysis is based on evidences that the modern physiography of this region has been established since the earliest Pliocene (Robertson *et al.* 1991; Suc *et al.* 1995). Accordingly, it may be expected that, as today, the distribution of terrestrial small mammals was primarily determined by climate and/or habitat, while the effect of physiographic barriers was of secondary importance, more pronounced in the southern part of the region under consideration. In this context, it can be supposed that, as today, the only source of humidity was the Atlantic air mass and that the summer drought increased southward in parallel with increasing temperatures (Suc 1989). Therefore, the role of mesophilous or humid forest was greater in the western part of the continent than in the southern and eastern parts.

The results of CA are shown on Figure 40. The first four axes have eigenvalues of 0.59, 0.43, 0.38, and 0.18. The eigenvalue is a measure of importance of the ordination axis. Values over 0.40 denote a good separation of the taxa along the axis (Ter Braak 1987). As the eigenvalues of the third and fourth axes were smaller, they were ignored and it is expected that the first two axes display biologically relevant information. Together the first two axes explain 52.3% of the total variation of the distribution of the genera among localities. The first ordination axis, explaining 30.1% of the variance, identifies a gradient from north to south (Fig. 40A). The sites with a relatively northern location (Poland, Germany, Hungary) lay in the left part of the diagram and the southern ones (Spain, southern France, east Mediterranean) are located in the right part. Muselievo and Tourkoubounia 1 occupy an intermediate position along this axis. It can be supposed that this axis reflects the latitudinal gradient of temperature and the associated gradient of wetness/dryness (see above). The second axis, explaining 22.2% of variance, separates the southern sites in two groups according to their location along the northern border of the Mediterranean basin (Fig. 40A). The west Mediterranean sites, are in the upper part of the diagram while the east Mediterranean ones are located in its lower part.

Evidently, the obtained ordination results represent the main lines of biogeographical differentiation of Europe during the studied time interval, suggesting that it was caused primarily by the combined effect of temperature and humidity, while the role of physiography was of a secondary importance, affecting the Mediterranean part of the region. Most probably, the differences between east and west Mediterranean faunas can be attributed to the physiographic barriers such as Aegean, Adriatic and Tyrrhenian seas, and the southern slopes of the Alps.

From the data presented on the ordination diagram (Fig. 40A), it is apparent that the diversity is much higher in the assemblages in the left half of the diagram than in the right half; axis 1 is negatively correlated with the number of genera ($R = -0.86$, $P < 0.05$). According to the above interpretation of the first ordination axis, this relationship can be ascribed to the increasingly more arid environment. However, a time component may also contribute to this result, having in mind the age of Maritsa, one of the poorest assemblages. According to Sen & Leduc (1996), the generic diversity progressively decreases from the middle Turolian until the late Ruscinian in the Aegean area.

According to the ordination results (Fig. 40B), the genera can be separated in three rough groups based on the projections of their distributional “optima” on the first ordination axis. The third group can be further subdivided into two subgroups along the second ordination axis

(Fig. 40B). Having in mind the above interpretation of the first ordination axis, it can be supposed that each of the tree groups characterizes a particular type of climate rather than a particular biotope. However, it should be taking into account that the climatic type determines the range of the available biotopes, their territorial dominance (spatial structure) as well as their inherent environmental peculiarities in comparison with similar biotopes existing under other climatic types. For instance, open habitats under oceanic climate are more humid than steppe habitats under continental climate. Accordingly, the small mammals inhabiting each of these two types of open habitats will be different. Moreover, the climatic types may affect the habitat requirements of the small mammals. For instance, as today, under humid climate the terrestrial mesophilous small mammals may be very versatile and may inhabit a wide range of habitats, while under dry climate they become restricted to humid habitats only. So, the obtained groups, although not indicative for a concrete biotope, can be considered as a suitable starting point for palaeoenvironmental reconstructions based on small mammal assemblages, composed by extinct species. In the following considerations, they are regarded as ecogeographical groups.

The first ecogeographical group (Fig. 40B) can be considered as indicative for an even and humid climate and a wide occurrence of forests and wet habitats. Indeed, it consists predominantly of genera reported in the literature to be associated with "wet", "damp" or "forested" habitats (Van de Weerd & Daams 1978; Skoczen 1980; Reumer 1984; Van der Meulen & Van Kolfschoten 1986; Popov 2001, 2003). Although some of the soricids have been considered as species with unknown ecological preference (*Zelceina* Sulimski, 1962), ubiquitous (*Beremendia* Kormos, 1934, *Petenyia* Kormos, 1934, *Blarinoides*) or even open country dwellers (*Mafia*) (Reumer 1984, 1998), in general, the Pliocene and early Pleistocene shrews with pigmented teeth can be regarded as adapted to mild and humid climate (Reumer 1989). The great percentage and diversity of both soricids and talpids confirms the interpretation of this group as indicative for a relatively humid climate. On the other hand, some of the genera belonging to this group (*Germanomys* Heller, 1936, *Ungaromys* Kormos, 1932, *Baranomys* Kormos, 1933, *Stachomys* Kowalski, 1960, *Promimomys* Kretzoi, 1955, *Bjornkurtenia*, etc.) are usually considered as open country dwellers (Van de Weerd 1979; Kowalski 1989). This fact at first glance contradicts to the above generalization. However, it can be supposed that, like their recent relative or morphologically similar species *Prometheomys schaposchnikovi* Satunin, 1901, the members of these genera were mesophilous species inhabiting wet open sites such as meadows and moors (Gromov & Poljakov 1992). Repenning (1967b) and Michaux (1971) suggested an aquatique biotope for *Promimomys*. The northern distribution of the majority of the taxa within group 1 may be indicative of cooler conditions. In the light of these considerations, the genera from Muselievo belonging to this group should be regarded as characteristic for wet forested habitat (*Tamias*, *Deinsdorfia*, *Pliopetaurista*, *Glis*) or mesophilous open terrain (*Balrinoides*, *Mafia*, *Propliomys*, *Bjornkurtenia*). This group covers 54.5% of the genera of the terrestrial small mammals in Muselievo.

The distributional "optima" of the genera belonging to the second ecogeographical group occur in the central part of the ordination diagram (Fig. 40B) indicating that they comprise species with a wide distribution in the studied region and were little affected by the revealed gradients. Most probably, they include species with relatively wide tolerances, adapted to a wide range of biotopes under more continental and arid climate. Under such conditions, the forest occurs as scattered patches increasing in this way the spatial importance of the "ecotone" habitats. As a result, many of the species in these genera inhabited edge habitats such as dry open forests, bushes, dry meadows, etc. (Janossy 1972; Van de Weerd 1979; Van der Meulen & Van Kolfschoten 1986). About 32% of the genera from Muselievo belong to this group, representing the occurrence of more or less dry forest and thicket (*Dryomimus*, *Sciurus*, *Rhagapodemus*, *Asoriculus*, *Sylvaemus*, *Hystrix*), as well as open terrains (*Trilophomys*, *Spermophilus*). *Dolomys occitanus* was possibly associated with more or less wet conditions (Dahlmann 2001). Its great relative abundance in the studied assemblage may be attributed to the proximity of the river.

The majority of the genera within the third ecogeographical group are usually regarded as characteristic for "dry", "open" habitat. Nearly all of the genera within the group 3a are considered as dry savanna dwellers (Van de Weerd & Daams 1978). The same is true for the group 3b (De Bruijn *et al.* 1970; Sen 1977; Van de Weerd 1979, etc.). Only *Keramidomys* Hartenberger, 1967 is considered as related to forests (Van der Meulen & Van Kolfschoten 1986). In Muselievo, the genera belonging to this group (*Myomimus*, and *Allocricetus*) constitute 13.6% of the total number of genera. They represent the occurrence of dry open habitats in the surroundings of the locality.

The comparisons of the percentages of each of the above-defined ecogeographical groups of genera among localities may help to further clarify the environment in Muselievo (Fig. 41).

The Pliocene faunas from Central and Western Europe contain a large proportion (more than 70%) of mesophilous species (ecogeographical group 1). In contrast, the genera of this group are poorly presented in, or absent from the Mediterranean localities, while the genera from the third ecogeographical group predominate. As pointed out above, most probably, these differences reflect the climatic differentiation during this time – the cooler and humid climate in the northern parts of Central Europe in contrast to the warmer and arid climate in the Mediterranean area. The assemblage from Muselievo occupies an intermediate position in this respect. Although similar to the Central European faunas, it differs in the presence of genera, characteristic for dry open habitats (ecogeographical group 3b), showing a southeastern Mediterranean influence. In accordance with the geographical location of the locality, however, their rate is not so great as in Maritsa, for instance. The proportion of the rodent genera belonging to the ecogeographical group 1 in Muselievo is greater than in Tourkoubounia 1 (Fig. 41B), indicating somewhat more humid and cooler climate in the studied area.

The composition of bat and lagomorph assemblages, not included in the above analyses, may contribute further to the above palaeoenvironmental reconstructions.

The high representation or presence of bats, closely related to or identical with the extant termophilous species such as *Rhinolophus* spp., *Myotis blythii* and *Miniopterus schreibersii*, occurring in the area today, indicate a moderate climate, similar to the recent one. The absence of medium-sized horseshoe bats in Weze 1 (Woloszyn 1989) indicates that the climate in this part of Europe was cooler than in the area of Muselievo. However, it can be supposed that the climatic differences were less pronounced than today, having in mind the occurrence of *Hystrix* in both localities as well as the presence in Weze 1 of vertebrates contemporarily confined to the warmer regions of Europe (terrestrial tortoise, sand viper, glass snake, etc.) (Kowalski 1989).

The predominance of a relatively dry climate and the occurrence of wide territories occupied by light forests, shrubs and savanna-steppe is also supported by the great share of lagomorhs in the assemblage from Muselievo. *Hypolagus beremendensis* is usually regarded as a forest dweller since the species of the genus are usually associated with taphocoenoses with well pronounced wet- and woodland aspects (Erbaeva 1996; Fladerer & Reiner 1996). *Pliopentalagus* may also be considered as a forest dweller in analogy with its recent relative *Pentalagus furnessi*. Nevertheless, their occurrence in the central, eastern, and southeastern parts of Europe indicates that probably they were characteristic for relatively dry forests and bushes. According to Erbaeva (1985), the conditions of dry and hot climate in the middle and late Pliocene and the vast territories of savanna-steppes were favorable for pikas, such as *O. csarotanus*, which is quite numerous in the studied locality.

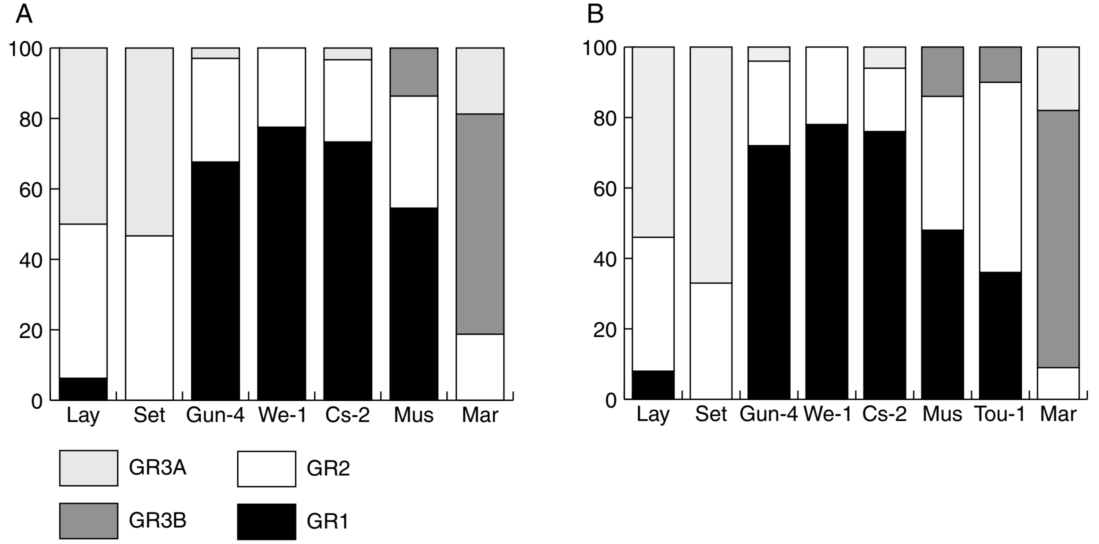


FIG. 41. — Percentage of the generic distributional groups (GR1-GR3A), identified by correspondence analysis in the studied assemblages; **A**, Lypotyphlans and rodents; **B**, rodents only. Assemblages: **Lay**, Layna; **Set**, Sète; **Gun-4**, Gundersheim 4; **We-1**, Weze 1; **Cs-2**, Csarnóta-2; **Mus**, Muselievo; **Tou-1**, Tourkobounia 1; **Mar**, Maritsa.

According to Van der Meulen & Van Kolfschoten (1986) the relative abundance of the murids and the arvicolids, may be considered as a measure of the humidity/aridity of the local climate. The percentages of both groups in Muselievo are nearly equal: 51.3% for Muridae (3 spp.) versus 48.6% for Arvicolidae (4 spp.). The percentages are based on the number of first and second upper and lower molars (N = 335). According to these data, the assemblage corresponds to the “wet” assemblages in karst fissure fillings in Greece, characteristic for the relatively humid climate (Van der Meulen & Van Kolfschoten 1986). The ratio between Muridae and Arvicolidae in the Hungarian locality Csarnóta-2 is 61% versus 26% (Van de Weerd & Daams 1978) showing dryer environment than in Muselievo. On the other hand, the diversity of arvicolids in Muselievo is limited in comparison to the situation in Central and Northwestern Europe, being similar in this respect to the Mediterranean assemblages during middle and late Ruscinian. This low number of arvicolid species in the Mediterranean Ruscinian is presumably related to the fact that climate was too warm for the voles (Van der Meulen & Van Kolfschoten 1986). The existence of a relatively warm and dry climate in the area of Muselievo is also confirmed by the low quantity of the shrews, generally considered as more or less mesophilous species. Most probably the great rate of voles in the studied locality may be attributed to the local landscape peculiarities related the proximity of the river, having in mind the inferred habitat preference of the dominant vole, *Dolomys occitanus*. In Weze, the murid/arvicolid ratio is 12% versus 46% thus indicating more humid environment.

Based on these considerations, the predominance of moderately continental climate can be supposed for the area of Muselievo during the time of deposition. Most probably tall forests, fresh meadows and reed occupied the bottom of the river valley. Rock exposures and xeric shrubs were distributed on the slopes of the valley and under the cliffs. Light forests and steppe patches covered large territories on the plain.

The above analyses reveal an environment very similar to the recent one in this part of Northern Bulgaria. The great difference in the taxonomic composition between the present day fauna of terrestrial small mammals and the Pliocene assemblage is a result of the Pleistocene glaciations. The ancient terrestrial small mammals progressively disappeared from Europe without returning because of several west-east oriented physiographic barriers, such as Pyrenees, the Alps, Mediterranean Sea, etc. In contrast, the bat fauna was less affected by the glaciations because these flying mammals had the possibility to overcome the barriers and to migrate south and north according to the climatic fluctuations.

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