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Morphometric variability of dentition of the Late Pleistocene Voles *(Arvicolidae, Rodentia)* from Bacho Kiro Cave (Bulgaria)

[With 18 text-figs.]

Morfometryczna zmienność uzębienia późnoplejstoceńskich nornikowatych (*Arvicolidae, Rodentia*) z Jaskini Baczo Kiro (Bułgaria)*

Abstract. The paper comprises a description of the morphotypical variation in the dentition (chiefly M_1) and dimensions of seven arvicolid species. The frequency of particular morphotypes has been calculated and conclusions as to the microevolutionary changes in some species (e.g. *Microtus nivalis* and *Lagurus lagurus*) have been drawn. The method of analysis of morphotypes made it possible to treat the specimens described previously under the name of *Microtus* cf. *oeconomus* as extreme variants of *Microtus nivalis* and to include them in this last species. Two forms (*M. arvalis* and *M. agrestis*), described earlier as *M. arvalis*, have also been shown to be present in the fossil materials, although they could not be separated entirely on the basis of either morphology or measurements. In view of the well-established stratigraphy of the locality an analysis and discussion of changes in the length of M_1, occurring in particular species from the Early Würm up to the Holocene, have been carried out. These changes were not connected with climatic fluctuations and so they had been brought about by a selective factor other than climatic conditions.

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* Praca wykonana w ramach Problemu MR.II.3.

I. INTRODUCTION

An excavation was carried out in Bacho Kiro Cave in 1971—1975 and it provided fossil materials covering a relatively long period, from the beginning of the last glaciation (Würm) to the Holocene (KOZŁOWSKI, 1982). The significance of this locality lies above all in the finding of an assemblage of the Upper Pleistocene fauna in it, the richest, as regards its specific composition, in this part of Europe (108 species). Its rodential fauna has been described preliminarily in a complex work on Bacho Kiro (KOWALSKI & NADACHOWSKI, 1982). It includes descriptions of 7 species of voles with a detailed list of materials but lacks a morphological analysis comprehensive enough and teeth measurements. The present paper, containing a morphotypic analysis of the dentition and descriptions of variation in tooth measurements, partly fills this gap. Only first lower molars were examined (in some cases also M^3), because it is these teeth that are of essential taxonomic value in this group of rodents. The great abundance of materials and the well-established stratigraphy of the locality made the investigation of morphometric changes in dentition with time feasible.

The author wishes to express his thanks to Mrs Barbara MALCZEWSKA for the care and skill with which she has drawn the figures.

II. REMARKS ON STRATIGRAPHY

In respect on their lithology and stratigraphy the deposits of Bacho Kiro have been divided into 3 series (MADEYSKA, 1982; GINTER and KOZŁOWSKI, 1982):

A — lower series with rubble, typical of dry caves devoid of streams (Layers 14—11),

B — middle series, with only small amounts of rubble but with a marked admixture of sand in connection with intermittent flows of water in the cave (layers 10—3), and

C — upper series with a large amount of rubble and big rock blocks (layers 2 and 1).

Within these three main types of sediments the author distinguished subseries, chiefly on the basis of an analysis of the faunal assemblages representing various climatic phases. This procedure made it possible to investigate the changes occurring in the tooth size or those in the proportions of some of their parts and also to grasp the tendency of morphological transformations in the dentition in course of the period examined. The following subseries have been separated in the present work:

A I — layers 13/14, 13/13h, 13. This last layer has been C_{14} dated at above 47500 years BP, which places these deposits practically out of reach of the radioactive method. Layer 13 should most likely be referred to one of the interstadial of the Early Würm (Elevtheroupolis interstadial for the Balkan Peninsula) (see also fig. 12).

A II — layer 12. This subseries represents a period of maximum cold in series A. Its age, the first Würm pleniglacial, has been obtained by interpolation from the radiocarbon datings, but it may well be that it was one of the earlier fluctuations.

A III — layers 11, 11a. These deposits represent a period of somewhat milder and moister climate than that reflected by layer 12 and the radiocarbon dating of the first cultural horizon of layer 11 gives an age above 43000 years BP. This refers these deposits to the Heraclitus interstadial.

B I — layers 10, 9, 6c, 8, 6b, 7, 6a and 4b. This subseries is lithologically heterogeneous. A small number of faunal specimens present in layers 9 and 10, formed probably in a rather cold and dry climate, are included here. Layers 6c and 8, which provided somewhat more remains, may also be referred to the same climatic phase. The following group of deposits, i.e. layers 6b—7—6a—4b, was formed in a milder climate. Two C_{14} dates have been obtained here: for layer 6b (32 700 ± 300 years BP) and for layer 7 (29 150 ± 950 years BP), which attribute both these layers of deposits to a milder fluctuation of the Middle Würm, designed as the Krinides interstadial for the Balkan Peninsula. The next two layers, 6b and 4b, were still formed in a relatively mild climate (Krinides II).

B II — layers 4a, 5, 3a and 4. Starting from layer 4a the climate becomes cooler and dryer. Layer 5 represents a slightly milder fluctuation, whereas layer 3 a period of maximum cold (Pleniglacial II). A special situation exists in layer 2, which lithologically corresponds to Pleniglacial II but contains many forest elements from the overlying layer and this is due to the occurrence of fissures in the rubble, filled with humus and clay derived from layer 1. This situation inclined the author to include the fauna from layer 2 in series C.

C — layers 2 and 1. Layer 1 was formed in the Holocene, probably in the Atlantic or Sub-Boreal period and in view of the scarcity of fossil remains no subseries have been distinguished.

III. METHODS

Teeth of each species were divided with respect to their morphology into groups, referred to as morphotypes. In morphological descriptions the distinctive features of a given morphotype were characterized briefly and its percentage frequency in particular subseries or in the whole material was also calculated. Each morphotype is besides presented in a figure. The changes in the frequency of morphotypes in particular samples permit conclusions concerning the tendency prevailing in the morphological changes of teeth in particular species in course of time. The nomenclature introduced by HIBBARD (1950) and applied increasingly often by various European palaeontologists (e.g. MEULEN, 1973; RADULESCO & SAMSON, 1977; LOPEZ MARTINEZ, 1980) has been adopted in descriptions of the structure of teeth (Fig. 1).

The measuring of teeth in voles was based on the system proposed by VAN DER MEULEN (1973), with some of its designations and symbols modified. The lower first molars and, in the case of *Arvicola terrestris*, the upper third molars were measured. As many undamaged teeth as possible were used for measuring and in some cases also their fragments in which the anteroconid was well preserved. Measuring was done using a stereoscopic microscope with an eyepiece micrometer. The following

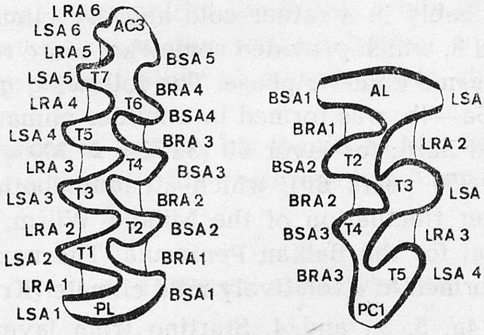

Fig. 1. Terminology used in the descriptions of M_1 and M^3: AC — anterior cap, AL — anterior lobe, BRA — buccal re-entrant angle, BSA — buccal salient angle, LRA — lingual re-entrant angle, LSA — lingual salient angle, PC — posterior cap, PL — posterior lobe, T — triangle

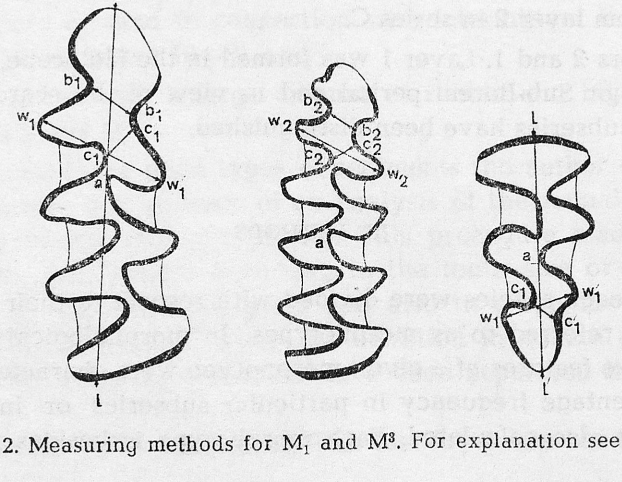

Fig. 2. Measuring methods for M_1 and M^3. For explanation see text

measurements were taken on M_1 and M^3 to an accuracy of 0.01 mm: L, A, W_1, W_2, B_1, B_2, C_1 and C_2 (Fig. 2). All these measurements were used to calculate the following indices: $A \times 100 : L = A/L$, $B_1 \times 100 : W_1 = B_1/ /W_1$, $C_1 \times 100 : W_1 = C_1/W_1$, $B_2 \times 100 : W_2 = B_2/W_2$, $C_2 \times 100 : W_2 = = C_2/W_2$.

The range of variation (Min. — Max.), mean ($\bar{x}$), standard deviation (SD), coefficient of variation (CV) and the number of specimens in the sample (N) are given for linear measurements and indices in the tables. If there are differences between the means, a variance analysis has been carried out and the significance of the differences between the means examined, using the new multiplex test of range (DUNCAN's test), which makes it possible to make comparisons between all the samples at the same time.

IV. ANALYSIS OF DENTITION OF PARTICULAR SPECIES

Clethrionomys glareolus (SCHREBER 1780)

Material. MF/1055/73 : 28 M_1

Morphology of M_1

Three morphotypes can be distinguished in the structure of the anteroconid (Fig. 3). Morphotype A is the commonest (85.7%). It is characterized by a broad connection between areas T4 and T5 as well as between T5 and T6. Morphotype B, with triangle T4 entirely isolated and T5 and T6 connected occurred in two specimens (7.1%) and morphotype C (maškii), with AC2 separated was also found in two specimens. Moreover, all the specimens had a broad connection between areas T1 and T2.

Measurements of M_1

	Min. — Max.	$\bar{x}$	SD	CV	N
Series A, L	: 2.26 — 2.60	2.430	0.096	3.9	16
Series B, L	: 2.18 — 2.56	2.376	0.154	6.5	5
Series C, L	: 2.25 — 2.43	3.350	0.092	3.9	3
Series A, A/L	: 38.1 — 46.0	42.47	2.02	4.8	16
Series B, A/L	: 39.6 — 43.2	41.62	1.33	3.2	5
Series C, A/L	: 38.3 — 44.4	41.07	3.10	7.5	3
Series A, B_1/W_1	: 7.4 — 44.0	23.78	7.64	32.1	19
Series B, B_1/W_1	: 6.7 — 34.6	26.74	11.64	43.5	5
Series C, B_1/W_1	: 22.2 — 26.0	24.27	1.71	7.0	4
Series A, C_1/W_1	: 11.2 — 30.0	17.38	5.22	30.0	19
Series B, C_1/W_1	: 7.8 — 18.4	13.76	4.65	33.8	5
Series C, C_1/W_1	: 7.8 — 18.4	12.80	4.42	34.5	4

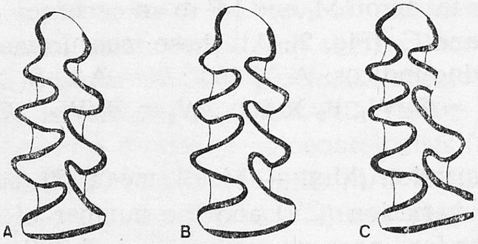

Fig. 3. *Clethrionomys glareolus*, M_1. A — layer 13, L = 2.48; B — layer 6a/7, L = 2.50; C — layer 12, L = 2.50

The length of the lower first molar varies with time, this measurement undergoing a reduction as we pass from the older layers to the younger ones. However, this tendency is rather poorly marked and, in addition, there is no information about a fairly long period in the Middle Würm. Only the difference between series A and C is statistically significant ($P < 0.05$). The differences shown in the index A/L are small and not significant, whereas the values of the indices B_1/W_1 and C_1/W_1 are apparently fairly high but this is due chiefly to the small number of specimens and these differences are hard to interpret.

Remarks

The teeth of the genus *Clethrionomys* show age variation as regards their grinding surface (ZEJDA, 1960), but at the same time this intraspecific variation is very similar in specimens from various geological periods. This brings about a situation in which the populations of earlier phases of the Pleistocene, often described under various names (e.g., HELLER, 1930, 1936; TOPACHEVSKI, 1965), little differ from the recent forms.

Arvicola terrestris (LINNAEUS 1758)

Material. MF/1052/73 : 41 M_1 and 25 M^3

Morphology of M_1

The first three morphotypes (A, B, C) have a very similar structure and they present typical arvicolid patterns (Fig. 4). They differ in the size and shape of AC2 and the structure of LSA5 and BSA4. Their frequency in the population from Bacho Kiro comes, respectively, to 66, 12.2 and 4%. The distinctive character of morphotype D is the developmental of a fold of enamel on the anterior edge of BSA3. This feature characterizes most extinct species of the genus *Mimomys* FORSYTH MAJOR 1902 and is referred to as the „*Mimomys* ridge". This archaic morphotype occurred in only one specimen from layer 3a/4. Morphotype E

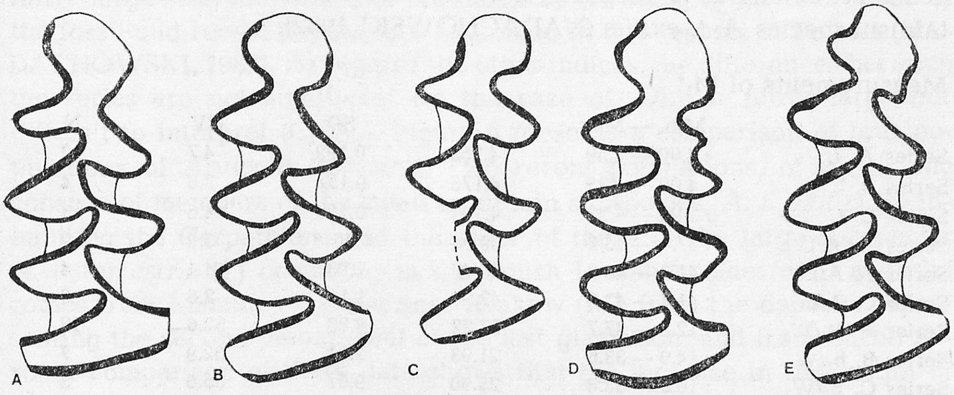

Fig. 4. *Arvicola terrestris*, M_1. A — layer 11, L = 4.12; B — layer 8, L = 4.24; C — layer 11, L = 4.14; D — layer 3a/4, L = 4.35; E — layer 2, L = 4.32

is distinguishable by a strong constriction between AC2 and the remaining part of the tooth, and the development of LRA5 and in some cases BRA4. This pattern was found in six specimens (14.5%). All the teeth from Bacho Kiro had a thick coat of enamel on the concave parts of the triangles, which is typical of *Arvicola terrestris* (KOENIGSWALD, 1973; HEINRICH, 1978).

Morphology of M^3

Five morphotypes can be singled out (Fig. 5), of which two, A and B, are marked by a weak development of LSA4 and the occurrence of a broad connection between T4 and PC1. The frenquency of their occurrence

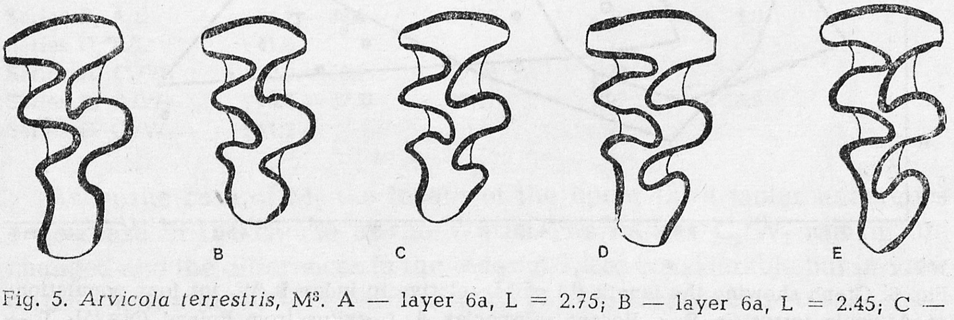

Fig. 5. *Arvicola terrestris*, M^3. A — layer 6a, L = 2.75; B — layer 6a, L = 2.45; C — layer 11, L = 2.58; D — layer 2, L = 2.74; E — layer 11, L = 2.82

is, respectively, 4 and 16%. These patterns may be included in the type „*terrestris*", since they are characteristic of the subspecies *A. t. terrestris* (NADACHOWSKI, 1982). The remaining morphotypes show a strong development of LSA4 and, successively, a tendency to close T4, which becomes accomplished in morphotype E. The frequency of these morphotypes is 20, 32 and 28%, respectively. They are characteristic of the mountain subspecies *A. t. exitus* (NADACHOWSKI 1982).

Measurements of M_1*

	Min. — Max.	$\bar{x}$	SD	CV	N
Series A, L	: 4.00 — 4.59	4.255	0.199	4.7	10
Series B, L	: 4.00 — 4.35	4.175	0.152	3.6	4
Series C, L	: 3.99 — 4.32	4.103	0.188	4.6	3
Series A, A/L	: 37.4 — 43.2	39.96	1.56	3.9	9
Series B, A/L	: 41.8 — 46.2	43.47	1.93	4.4	4
Series C, A/L	: 41.7 — 43.9	42.90	1.11	2.6	3
Series A, B_1/W_1	: 12.8 — 47.7	27.22	8.88	32.6	18
Series B, B_1/W_1	: 14.9 — 33.6	21.93	7.21	32.9	7
Series C, B_1/W_1	: 16.0 — 33.8	25.90	9.07	35.0	3
Series A, C_1/W_1	: 11.0 — 31.8	23.56	5.18	22.0	18
Series B, C_1/W_1	: 11.7 — 27.8	21.00	6.34	30.2	7
Series C, C_1/W_1	: 21.8 — 29.2	26.30	3.95	15.0	3

The range of length of M_1 observed in *Arvicola terrestris* is large compared with that in other arvicolid species. A fairly distinct decrease in the length of this tooth took place in the Würm, and the differences are significant ($p<0.05$). The population of Bacho Kiro is, generally, of

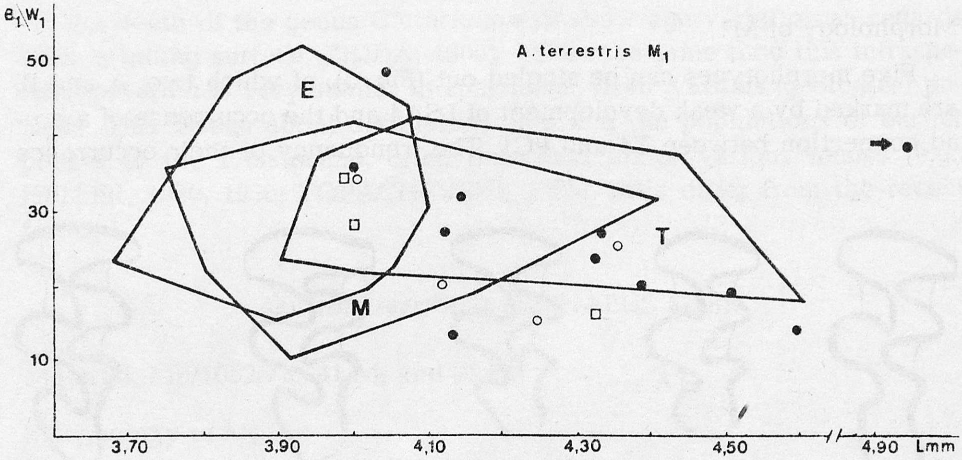

Fig. 6. Graph showing the length (L) of M_1 relative to index B_1/W_1 for four populations of *Arvicola terrestris*. E — Recent subspecies *A. t. exitus* from Poland (N=25); T — Recent subspecies *A. t. terrestris* from Poland (N=20); M — Late Pleistocene population (Pleniglacial II) from Mamutowa Cave in Poland (N=14), ● — Bacho Kiro, Series A (N=11), ○ — series B (N=4), □ — series C (N=3). The arrow indicates an exceptionally big specimen from layer 12 (L=4.96, B_1/W_1 = 39.7)

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* The M_1 specimen, the length of which L = 4.96, from layer 12 has not been included in the table.

fairly large size, the values of the index B_1/W_1 being lower than those of the fossil and recent populations examined in this respect in Poland (NADACHOWSKI, 1982). As regards the other indices, the differences between the series are not significant (in the case of A/L) or fairly large but difficult to interpret (C_1/W_1). Figure 6 presents a comparison of four populations of *Arvicola terrestris.* Two recent populations, of which one consists of members of the small mountain subspecies. *A. t. exitus* (E) inhabiting the Carpathians and the other of those of the large subspecies *A. t. terrestris* (T) occurring in the Polish lowlands. The fossil material comes from Mamutowa Cave near Kraków (M), from the deposits representing the second pleniglacial of the last glaciation, and from Bacho Kiro. A comparison of these data shows that the increase in the length of M_1, irrespective of the place and time of the accumulation of the material, is accompanied by a small decrease in the value of the index B_1/W_1. One specimen (indicated with an arrow) from layer 12 of Bacho Kiro, having very large dimensions and besides „abnormal" proportions of the anteroconid makes an exception. This tooth has all the typical characters of *Arvicola terrestris* and there is no doubt as to its membership in this species. This fact seems to be noteworthy, because it informs of the occasional occurrence of exceptionally large (or small) specimens in the fossil populations examined, such as do not lie within the normally observed range of variation.

Measurements of M^3

	Min. — Max.	$\bar{x}$	SD	CV	N
Series A, L	: 2.29 — 2.92	2.657	0.173	6.5	14
Series B, L	: 2.21 — 2.69	2.485	0.204	8.2	4
Series C, L	: 2.74				1
Series A, A/L	: 36.0 — 49.7	40.15	3.28	8.2	14
Series B, A/L	: 34.7 — 38.5	37.00	1.76	4.8	4
Series C, A/L	: 41.6				1
Series A, C_1/W_1	: 10.0 — 50.7	22.09	1.22	5.5	14
Series B, C_1/W_1	: 15.3 — 37.8	22.47	1.07	3.9	4
Series C, C_1/W_1	: 11.2				1

As in the case of M_1 the length of the upper third molar undergoes a decrease in the course of the Würm. The indices C_1/W_1 remain unchanged and the differences in the index A/L are considerable but in view of the small number of specimens may be of a fortuitous nature.

Remarks

On the basis of the measurements of M_1 the specimens from Bacho Kiro may be regarded as large ones, whereas in so far as its morphology is concerned do not differ much from the other Late Pleistocene populations (MALEEVA, 1975; MALEEVA & POPOVA, 1975; NADACHOWSKI, 1982). The analysis of variation of M^3 plays a fairly important part in the systematics of recent and fossil *Arvicola terrestris* (CAIS, 1974; NADACHOWSKI, 1982). Populations of cold periods and mountain subspecies show higher frequencies of morphotypes having a complex structure („*exitus*") and it is just this type of structure that is characteristic of the population from Bacho Kiro.

Pitymys subterraneus (DE SÉLYS-LONGCHAMPS 1836)

Material. MF/1041/73 : 585 M_1

Morphology of M_1

Five morphotypes can be distinguished in the structure of this tooth in the European pine vole (Fig. 7). Morphotype A (arvalid) has well-developed LSA6 and BSA5 and a broad connection between AC3 and the rest of the anteroconid. It is a dominant morphotype throughout the profile of deposits of Bacho Kiro (83.5%). Morphotype B is distinguishable by the complete separation of AC3 from the anteroconid and the term „maškii" is most often used for this pattern. It is relatively unfrequent (5.3%) and gradually vanishing in younger deposits. Its frequency comes nearly to 10% in series A, whereas it is only 5% in series B. Morphotype C is characterized by the distinct development of LSA6 and lack of BSA5 and its general morphology permits us to treat it as a variant of the arvalid pattern. Its specimens form 6.8%. In the following morphotype (D), LRA6 undergoes a development; this morphotype is represented in the population from Bacho Kiro by a small number of specimens (2.4%). Morphotype E is marked by the presence of an additional fold of enamel, which develops between BSA4 and BSA5 in the anteroconid, bringing also about the formation of an additional enamel valley. This pattern may be recognized as characteristic of the population from Bacho Kiro, because it occurs in nearly all the layers with fairly numerous teeth, although they are scarce in them (2%). Among the 585 M_1

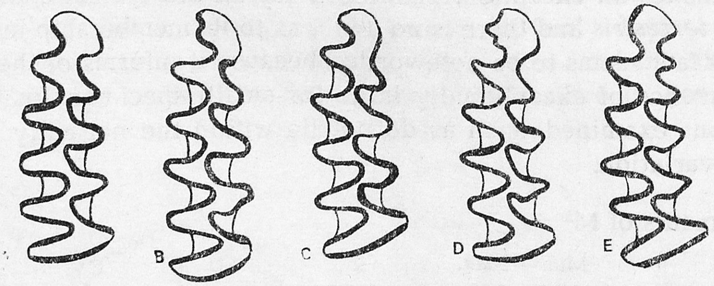

Fig. 7. *Pitymys subterraneus*, M_1. A — layer 7/6b, L = 2.76; B — layer 4b, L = 2.89; C — layer 11a, L = 2.68; D — layer 4b, L = 2.80; E — layer 4b, L = 2.78

examined there were 13 specimens (2.2%) with confluent areas T1 and T2 (Fig. 8).

Fig. 8. *Pitymys subterraneus*, M_1. Morphotype with broad connection between T1 and T2, layer 11, L = 2.59

Measurements of M_1

	Min. — Max	x̄	SD	CV	N
Series AI, L	: 2.40—2.95	2.622	0.123	4.7	47
Series AII, L	: 2.39—2.85	2.614	0.105	4.0	50
Series AIII, L	: 2.45—2.85	2.613	0.086	3.3	50
Series BI, L	: 2.42—2.88	2.630	0.115	4.4	50
Series BII, L	: 2.42—2.71	2.605	0.079	3,0	13
Series AI, A/L	: 47.1—54.1	50.87	1.445	2.8	47
Series AII, A/L	: 45.7—54.7	51.38	1.653	3.2	50
Series AIII, A/L	: 47.8—55.7	51.53	1.939	3.8	50
Series BI, A/L	: 49.1—55.4	51.93	1.510	2.9	50
Series BII, A/L	: 47.2—54.7	50.65	1.687	3.3	13
Series AI, B_2/W_2	: 13.5—60.0	35.62	8.955	25.1	47
Series AII, B_2/W_2	: 11.3—49.7	28.31	9.518	33.6	50
Series AIII, B_2/W_2	: 14.3—44.9	31.00	7.829	25.3	50
Series BI, B_2/W_2	: 9.0—44.1	26.52	7.825	29.5	50
Series BII, B_2/W_2	: 20.3—47.9	32.48	8.122	25.0	13

In the samples from particular series the mean value of L undergoes rather small changes and the differences observed are not significant. This indicates that the European pine vole lacks a tendency towards changes in size, which is also confirmed by small fluctuations in the index A/L. On the other hand, the changes in the index B_2/W_2 are pretty considerable, but it is hard to observe any distinct trend in these changes.

Remarks

The morphological variation of M_1 in *Pitymys subterraneus* is relatively poorly known, far more attention being given to the structure of M^3, since some more reliable characters that differentiate species can be found in this last tooth. As far as M_1 is concerned, the differences between populations of *Pitymys subterraneus* consist, above all, in different frequencies of the morphotype „maškii" (NADACHOWSKI, 1982). ANGERMANN (1974) observed geographical variation in this character in the recent European pine vole. There are also differences in the frequency of this character in the material from Bacho Kiro, which has been confirmed by the results of measurements. The present state of knowledge makes it however difficult to interpret these results more closely.

Microtus arvalis (PALLAS 1779) and *Microtus agrestis* (LINNAEUS, 1761)

Material. MF/1042/73 : 1394 M_1

In the first description of the rodents from Bacho Kiro only one species of the genus *Microtus* SCHRANK 1798 with the arvalid build of the anteroconid of M_1, i.e. *M. arvalis,* was given in the list of animals (KOWALSKI & NADACHOWSKI, 1982). However, the length measurements of M_1 suggest that we are concerned with two species. Theoretically, these materials can be included in the following four species: *Microtus guentheri,* DANFORD et ALSTON, 1880, *M. arvalis, M. epiroticus* ONDRIAS 1966 (= *M. subarvalis* MEYER, ORLOV et SCHOOL 1972) or *M. agrestis.* The first of them is out of the question, because this thermophilous species probably never passed Stara Planina Mts., particularly during Würm. As regards the remaining forms, the sibling species *M. arvalis* and *M. epiroticus* are indistinguishable on the basis of the morphological structure of dentition (MALYGIN, 1978) and so far the fossil materials have been traditionally included in *M. arvalis.* Therefore, it remains for us to consider *M. agrestis* whose morphological structure of M_1 is very similar to that of *M. arvalis.* These species however differ somewhat in the length of this tooth (NADACHOWSKI, 1982). It should be stressed out that there were no five-looped teeth M^2 characteristic of this species among the specimens from Bacho Kiro.

Morphology of M_1

At first an attempt was made to divide the material in respect of morphology by the method of analysis of morphotypes (Fig. 9). The build and occurrence of morphotypes were analysed separately in small specimens ($L<2.90$ mm), tentatively included in *M.* cf. *arvalis,* and separately in big specimens ($L>3.10$ mm), treated as *M.* cf. *agrestis* (see also the subsection on the measurements of M_1). Ten morphotypes of M_1 have been distinguished in the whole material. Morphotype A (gregalid) was found in only one specimen from layer 7; it is marked by the complete lack of BSA4 and only exceptionally met with in *Microtus arvalis* (JÁNOSSY & SCHMIDT, 1960, 1975; NADACHOWSKI, 1982). However, it may very well be that this tooth is an extreme morphological variant (ratticepid) of *Microtus nivalis,* as it has a relatively broad connection of T5 with T6. In a preceding paper (KOWALSKI & NADACHOWSKI,

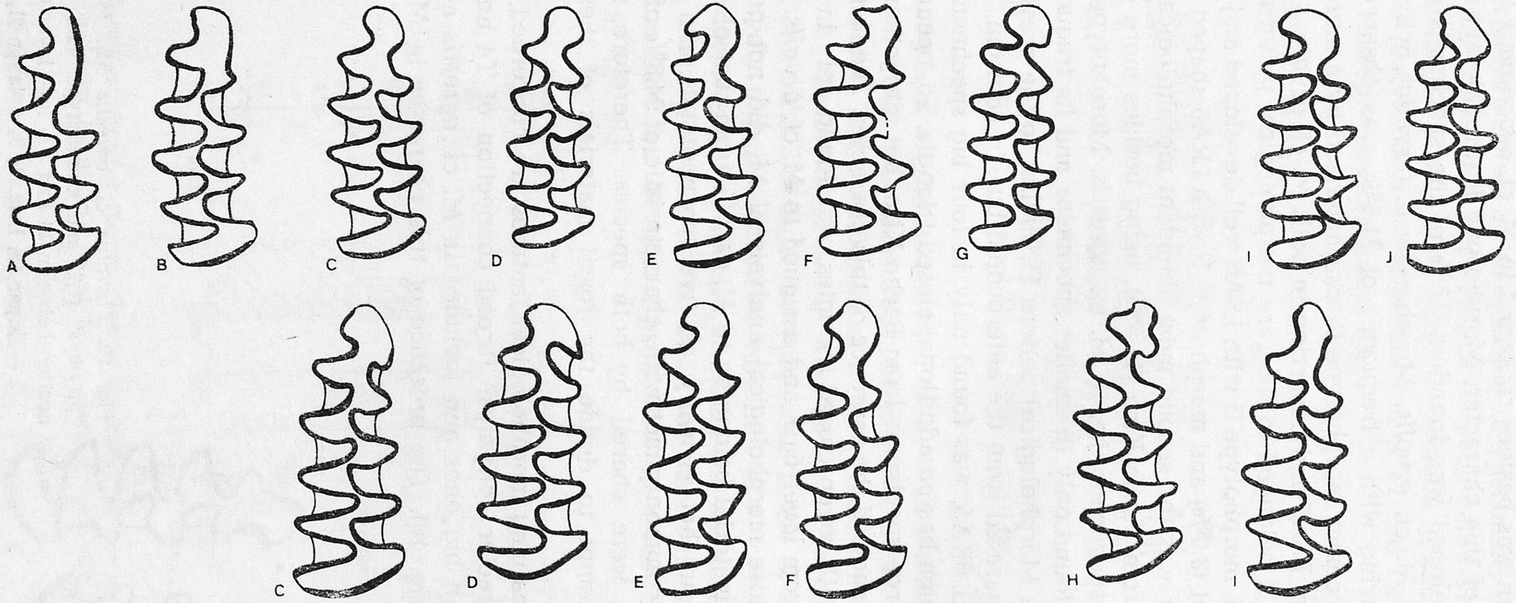

Fig. 9. Morphological variation of M_1 of *Microtus* cf. *arvalis* (upper row) and *Microtus* cf. *agrestis* (lower row). *Microtus* cf. *arvalis* — A — layer 7, L=2.98; B — layer 6a, L=2.92; C — layer 4b, L=2.86; D — layer 11a, L=2.80; E — layer 12, L=2.86; F — layer 11, L=2.82; G — layer 7/6b, L=2.82; I — layer 11a, L=2.84; J — layer 6a/7, L=2.97. *Microtus* cf. *agrestis* — C — layer 7, L=3.16; D — layer 6b, L=3.12; E — layer 11a, L=3.22; F — layer 6c, L=3.23; H — layer 13, L=3.12; I — layer 6a/7, L=3.25

1982) this specimen was besides reckoned in *M.* cf. *oeconomus* (Fig. 2(1)) just on the basis of this character. Morphotype B (gregalo-arvalid) with BSA4 poorly developed was found in 2.5% of the specimens and only those included in *M.* cf. *arvalis*. Morphotype C (arvalid), which is the commonest, occurring with a frequency of 71.6%, was observed in all size classes. Next comes morphotype D, characterized by a more conspicuous convexity of BSA5 and occurring in both *M.* cf. *arvalis* and *M.* cf. *agrestis* although it belonged to the rare morphological patterns (1.9%). On the other hand, morphotype E with LSA6 well developed and no BSA5 was more frequent (8.9%) and morphotype F with LRA6 shaped in a characteristic manner was the second most abundant morphological pattern in the materials from Bacho Kiro (11.5%), being besides more often encountered in big specimens, i.e. in *M.* cf. *agrestis*. Morphotype G, called „maškii", was found only in smaller specimens and its frequency was rather low (3.9%). Morphological pattern H, similar to the previous one, also with AC3 separated from the anteroconid but, in addition, with two valleys, LRA6 and BRA5, was found only in four big specimens (0.3%). Morphotype I, which has an additional closed triangle, T6, occurred both in small and in large specimens from Bacho Kiro, but altogether only 12 specimens (0.9%) showed the presence of this character. The last of these morphotypes, I, with seven closed triangles, was found only in one specimen, obtained from layer 6a/7 and assigned to *M.* cf. *arvalis*.

And so the close morphological analysis of M_1 did not permit the distinction of the material belonging to *M. arvalis* from that of *M. agrestis*, for it turned out that as many as five morphotypes, and what is more, those most commonly met with, characteristic of 94.8% of the specimens examined, were shared by both species. Therefore, it seems groundless to attempt to divide the fossil materials of these forms thoroughly.

As far the remaining morphological features are concerned, the presence of the character „*pitymys*" (broad connection of T4 and T5) in four specimens, all big ones and included in *M.* cf. *agrestis* at that, is worth noticing (Fig. 10). The presence of this character in *M. agrestis*

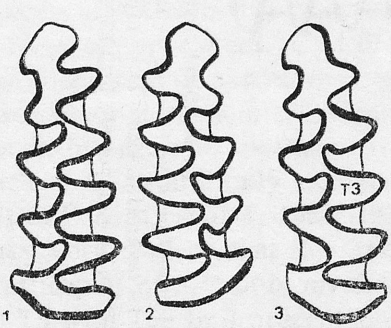

Fig. 10. *Microtus* cf. *agrestis* M_1. Morphotypes "*pitymys*" (1,2) and morphotype with broad connection between T1 and T2; 1 — layer 6b, L=3.17; 2 — layer 12, L=2.97; 3 — layer 11, L=3.15

has been corroborated by the finding of specimens of this type in the present-day populations from Poland (unpubl. data). This is an additional argument for the presence of *Microtus agrestis* in Bacho Kiro. Only five specimens (0.4%) has a broad connection of T1 and T2 and so fewer than in other vole species from Bacho Kiro.

Measurements of M_1*

	Min. — Max.	$\bar{x}$	SD	CV	N
Series AI, lay. 13/13 h, L	: 2.61—3.48	3.028	0.212	7.0	50
Series AI, lay. 12/13, 13, L	: 2.55—3.36	2.916	0.191	6.6	192
Series AII, L	: 2.42—3.46	2.932	0.167	5.7	82
Series AIII, L	: 2.58—3.32	2.962	0,179	6.0	235
Series BI, L	: 2.50—3.37	2.915	0.229	7.9	261
Series BII, L	: 2.55—3.15	2.839	0.145	5.1	27
Series C, L	: 2.56—2.98	2.759	0.133	4.9	14

The length of all the undamaged teeth from the whole profile of the deposits (N=861) was measured and the specimens were divided into 11 size classes. The distribution of teeth in particular classes resembles the normal distribution (Fig. 11), which in most cases suggests the presence of one form, but both the very wide range of this dimension and the relatively high coefficient of variation (CV = 7%) speak in support of the conception of two species, in which the measurements of M_1 overlap each other to a great extent. Thus, the discrimination of one of these forms from the other became a problem. Data from literature show that

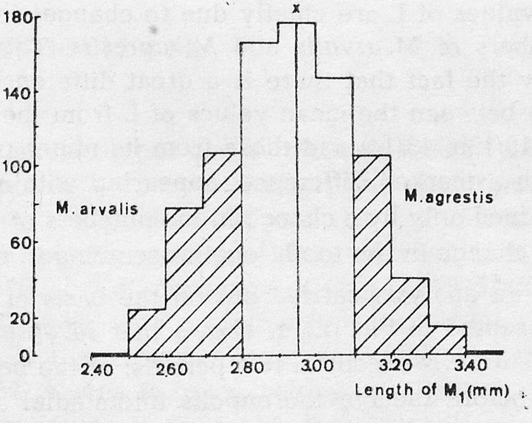

Fig. 11. Histogram showing the numbers of specimens of the *Microtus arvalis-agrestis* group in particular length classes of M_1. A detailed discussion included in the text

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* Only the length (L) of M_1 was measured.

the length of M_1 in recent *M. arvalis* most often lies within the limits of 2.40—2.90 mm (GROMOV & POLYAKOV, 1977; NADACHOWSKI, 1982, and others), whereas in recent *M. agrestis* between 2.75 and 3.40 mm. The measurements of M_1 taken by the author in the contemporary population of this last species, range from 2.73 to 3.42 mm (N=64) and they support the data obtained so far. It may be assumed on the basis of this information that the teeth less than 2.80 mm in length belonged in all probability, to *M. arvalis* and those exceeding 3.10 mm should mostly be numbered in the species *M. agrestis*. However, as regards specimens measuring 2.80—3.10 mm in length, the problem of identification remains unsolved. Virtually, it is impossible to include them in either species for certainty, although, naturally, it is much more likely to find *M. arvalis* in the 2.80—2.90 mm class than in the 3.00—3.10 mm class and, as regards *M. agrestis,* vice versa. An attempt was made on the basis of the above-mentioned, assumption to grasp the ratio of the number of *Microtus arvalis* to that of *M. agrestis* in particular series of deposits in Bacho Kiro. First the ratio of small specimens (below 2.80 mm in length) to big ones (above 3.10 mm) was calculated separately for each subseries and next, assuming that similar proportions also prevail between these species in the middle size classes (2.80—3.10 mm), the percentage occurrence of either species in them was calculated. The application of this sort of argumentation is however limited by 1) the small number of specimens examined and 2) the phenomenon of changes in tooth length with time. In the author's opinion, in the case of Bacho Kiro the material was sufficiently abundant (N=861), whereas as regards the second qualification, it was assumed for simplification (it is disputable whether justly) that the changes in size, if there were any, proceeded in a similar manner in both species. With this assumption, therefore, the changes observed in the mean values of L are chiefly due to changes in the relations between the numbers of *M. arvalis* and *M. agrestis*. This reasoning is supported, e.g., by the fact that there is a great difference (statistically highly significant) between the mean values of L from the lower part of series AI (layers 13/13h, 13/14) and those from its upper part (layer 13). It seems that such a marked difference, appearing within such a short time, can be explained only by a change in the numbers of these two species and not by a change in the tooth length occurring in one form.

The results of an analysis carried out on the basis of the foregoing reasoning are presented in Fig. 12. It shows that *M. agrestis* are fewer in number than *M. arvalis* except in two periods: at the beginning of the Würm glaciation before the Elevtheroupolis interstadial and in the period of the Middle Würm, before the Krinides interstadial. Moreover, in the first cold period (Pleniglacial I) the numerousness of *M. agrestis* fell dramatically to disappear definitively from the study area (Stara Planina Range) at the beginning of the second climatic

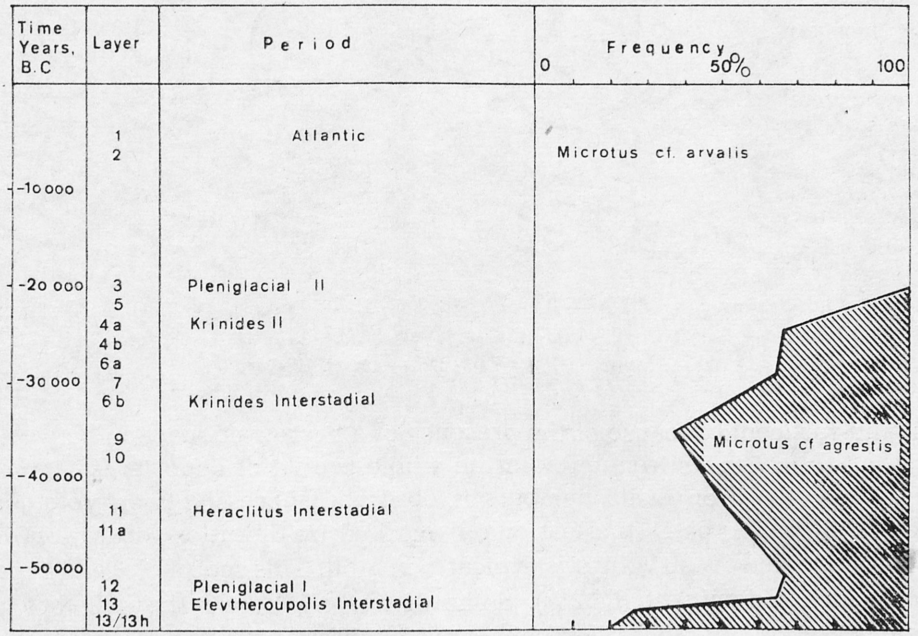

Fig. 12. Percentage relations of the numbers of remains of *Microtus* cf. *arvalis* and those of *Microtus* cf. *agrestis* in particular layers of deposits in Bacho Kiro. Discussion in text

minimum (Pleniglacial II). At present *Microtus agrestis* does not occur in Bulgaria.

Microtus nivalis (MARTINS 1842)

Material. MF/1043/73 : 298 M_1

Morphology of M_1

Four main morphotypes can be distinguished in the build of M_1 (Fig. 13). Morphotype A is characterized by the occurrence of a broad connection between areas T5 and T6 and the lack of BSA4 (ratticepid morphotype). Such specimens were earlier described from Bacho Kiro under the name of *Microtus* cf. *oeconomus* (PALLAS 1776) (KOWALSKI & NADACHOWSKI, 1982). Teeth of this type occurred in layer 7,7/6b and 11a, there being 4 specimens altogether (1.3%). The justification of their inclusion in *M. nivalis* is given below in „Remarks". The distinctive feature of morphotype B, for which the designation „gud" is used (ANGERMANN, 1974), is the development of BRA4 and BSA4. The frequency of this pattern in Bacho Kiro comes to 2.7% (8 specimens). In morphotype C LRA5 and BRA4 either disappear or are developed to a very small degree. BSA4 is always present. This morphotype may be defined as

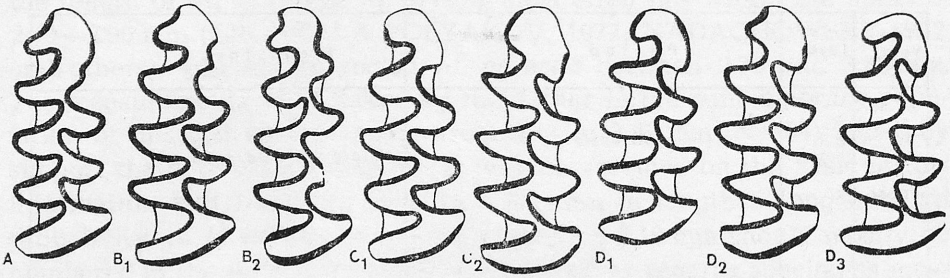

Fig. 13. *Microtus nivalis*, M_1. A — layer 7, L=2.94; B_1 — layer 13, L=2.98; B_2 — layer 12, L=2.95; C_1 — Layer 4b, L=2.93; C_2 — layer 12, L=3.10; D_1 — layer 12, L=2.85; D_2 — layer 6a/7, L=2.93; D_3 — layer 12, L=2.90

nivalid-ratticepid because of the presence of a narrow connection between areas T5 and T6. Its frequency in the whole profile of deposits is 11,8%, but a gradual drop in its numbers is observed successively in younger layers. Morphotype D, the last one, is marked by the utter separation of T5 from T6 and its structure is typically nivalid. This morphological type is decidedly dominant (84.2%). Some of the M_1 teeth show a broad connection of T1 with T2 (5 specimens, 1,7%) (Fig. 14).

Measurements of M_1

	Min. — **Max**	x̄	SD	CV	N
Series AI, L	: 2.75 — 3.35	3.023	0.165	5.5	21
Series AII, L	: 2.63 — 3.23	2.981	0.142	4.8	28
Series AIII, L	: 2.68 — 3.16	2.979	0.132	4.4	23
Series BI, L	: 2.55 — 3.24	2.940	0.160	5.4	45
Series BII, L	: 2.59 — 2.97	2.782	0.122	4.4	6
Series C, L	: 2.52 — 2.99	2.748	0.206	7.5	6
Series AI, A/L	: 43.5 — 51.6	47.08	1.90	4.0	21
Series AII, A/L	: 45.2 — 51.3	48.10	1.53	4.4	28
Series AIII, A/L	: 44.7 — 50.5	47.66	1.31	2.7	23
Series BI, A/L	: 45.1 — 52.3	47.48	1.73	3.6	45
Series BII, A/L	: 43.2 — 48.2	46.10	1.93	4.2	6
Series C, A/L	: 45.4 — 49.8	47.62	1.70	3.6	6
Series AI, B_1/W_1	: 1.8 — 22.5	11.16	5.34	47.8	26
Series AII, B_1/W_1	: 2.6 — 20.9	9.01	4.87	54.0	34
Series AIII, B_1/W_1	: 1.8 — 18.1	7.63	4.58	60.0	34
Series BI, B_1/W_1	: 1.0 — 23.8	6.70	5.08	75.8	53
Series BII, B_1/W_1	: 2.4 — 16.7	7.31	5.70	78.0	11
Series C, B_1/W_1	: 1.6 — 16.5	6.53	5.20	79.6	7

In the course of the period studied the tooth length underwent fairly marked changes (Fig. 15). A comparison of six samples from various parts of the profile of deposits shows that the populations of four deeper subseries (from AI to BI) are of similar size and the differences between the means of L are not significant. On the other hand, the differences between these samples and the samples from the upper portion of deposits

Fig. 14. *Microtus nivalis*, M_1. Morphotype with broad connection of T1 with T2, layer 12, L=3.11

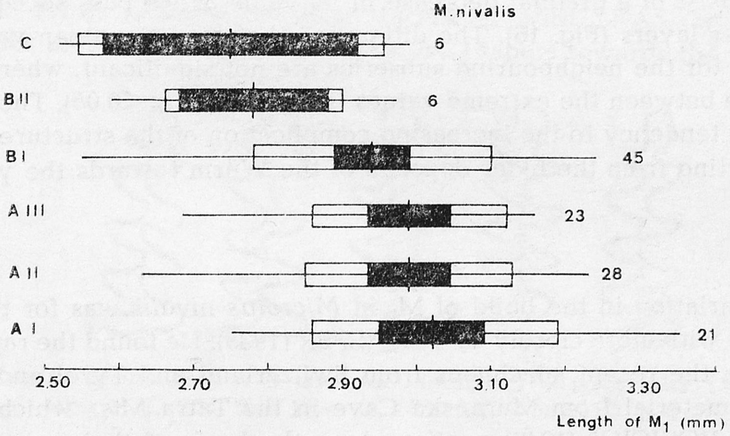

Fig. 15. Graph showing the changes in the length of M_1 in *Microtus nivalis* from particular series of deposits (AI—C). The horizontal lines represent the observed range of variation, the mean values are marked by vertical lines, the empty rectangle illustrate the standard deviations from the mean and the blackened rectangles the double standard error on both sides of the mean; the figures give the size of the samples

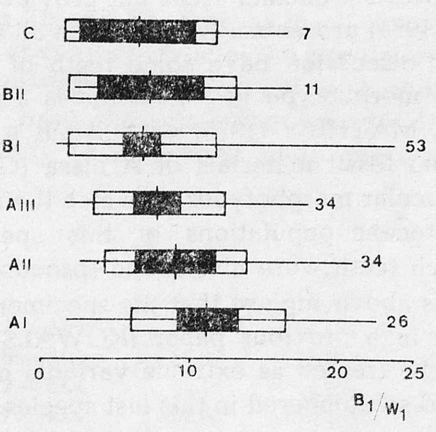

Fig. 16. Graph showing the changes in the value of index B_1/W_1 for *Microtus nivalis* (M_1) in particular series of deposits (AI—C). For explanation of symbols see Fig. 15

(subseries BII and C) are highly significant ($p<0.01$). And again the last two populations resemble each other very much in respect of the length of M_1. Generally speaking, in the period examined a gradual but distinct decrease in the length of the tooth in question took place. The mean values of the index A/L do not differ significantly from each other except the sample from BII ,which departs rather considerably from the remaining ones; this however can be explained by the small number of specimens and, consequently, a greater probability of this result being fortuitous. The index B_1/W_1, illustrating the degree of separation of the anterior part of the anteroconid, undergoes distinct though not large changes, which consist in a gradual decrease in its value as we pass successively to younger layers (Fig. 16). The differences between the mean values of the index for the neighbouring subseries are not significant, whereas the difference between the extreme values is significant ($p<0.05$). These data indicate a tendency to the increasing complication of the structure of this tooth starting from the older deposits of the Würm towards the younger ones.

Remarks

The variation in the build of M_1 in *Microtus nivalis* was for the first time dealt with more closely by SCHAEFER (1935). He found the ratticepid pattern in the recent specimens from Switzerland and Tyrol and in the subfossil material from Murańska Cave in the Tatra Mts., which HANZAK and ROSICKÝ (1949) confirmed on the basis of their present-day material. KRATOCHVIL (1956) and KOWALSKI (1957) examined the Tatra populations of *M. n. mirhanreini,* finding great variation in the morphology of M_1 in them and the presence of morphotypes similar in structure to the pattern in *M. oeconomus.* In his description of recent specimens of *M. nivalis* from Bulgaria PESHEV (1970) writes about the presence of teeth with six enamel areas but provides no drawings of M_1. SPITZENBERGER (1971) presents a list, in which all the recent subspecies of the form under discussion have some teeth of ratticepid type. The occurrence of this morphotype in *M. nivalis* is also observed by ANGERMANN (1974). MAYHEW (1978) carried out a close morphological analysis of M_1 from fossil materials of Arnissa (Greece) and gave the frequencies of particular morphotypes, of which the ratticepid one formed 7%. In Late Pleistocene populations of this species from Rumania (TERZEA 1972) such teeth were also found (pseudo-ratticepoid variant). All the descriptions above suggest that the specimens included in *Microtus* cf. *oeconomus* in a previous paper (KOWALSKI & NADACHOWSKI, 1982), should be treated as extreme variants of the morphology of M_1 in *M. nivalis* and so numbered in this last species.

Lagurus lagurus (PALLAS 1773)

Material. MF/1044/73 : 50 M_1

Morphology of M_1

With respect to their morphology the teeth have been included in five morphotypes (Fig 17). Morphotype A has not a developed LRA5 and LSA4 is also relatively weakly marked. This morphotype was observed only in one specimen from layer 6a/7. It is an archaic pattern, characteristic of the subspecies *Lagurodon* KRETZOI 1956, and in this connection it is referred to as a lagurodonid morphotype (MALEEVA & NORDSTREM, 1974). Morphotype B is furnished with LRA5, while BSA5 developes to the same extent as BSA4. AC3 tapers towards the top of the tooth. This morphological pattern is typical of *Lagurus transiens* JÁNOSSY 1962 (transiensid morphotype). Only two specimens from layers 6a/7a and 12/13 showed this pattern. Morphotype C was represented by the largest number of specimens ($84^0/_0$); it is a typical lagurid pattern in which BRA4 is better developed than LRA5. Morphotype D is distinguished by its additional closed triangle (T6), arising owing to the lack of a connection between T6 and T7, present in all the other morphotypes. It may be recognized as characteristic of the population from Bacho Kiro, as it occurs fairly frequently ($8^0/_0$). Morphotype E shows a tendency for AC3 to be separated from the remaining portion of the anteroconid, although this is not fully accomplished. Only one specimen from layer 12 bore this character.

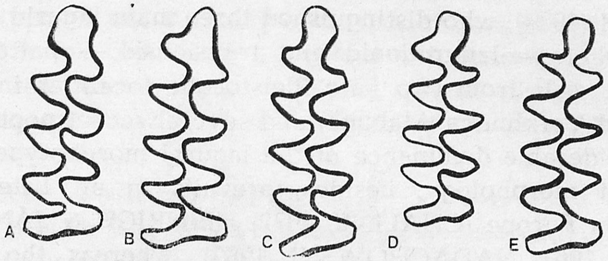

Fig. 17. *Lagurus lagurus*, M_1. A — layer 6a/7, L=2.58; B — layer 12/13, L=2.61; C — layer 5c, L=2.75; D — layer 12, L=2.37; E — layer 12, L=2.66

Measurements of M_1

	Min. — Max.	$\bar{x}$	SD	CV	N
Series A, L	: 2.37 — 2.66	2.562	0.087	3.4	13
Series B, L	: 2.43 — 2.80	2.631	0.131	5.0	13
Series A, A/L	: 52.8 — 55.3	53.85	0.932	1.7	13
Series B, A/L	: 51.2 — 57.4	54.18	3.251	6.0	13
Series A, B_2/W_2	: 14.1 — 41.6	32.96	7.13	21.6	13
Series B, B_2/W_2	: 16.2 — 75.8	32.65	14.11	43.2	13
Series A, C_2/W_2	: 9.5 — 44.7	31.39	9.69	30.9	13
Series B, C_2/W_2	: 23.5 — 45.9	31.84	6.81	21.4	13

Because of the small number of remains the populations of whole series A and B were compared. They differ clearly from each other in tooth length (L), the differences being highly significant and the specimens from series B bigger than those of the populations from early periods of the Würm. On the other hand, the mean values of particular indices show no statistically significant differences.

Remarks

The morphological variation in the dentition of the tribe *Lagurini* KRETZOI 1955 is relatively well known because of the importance and usefulness of this group of voles in the stratigraphy of the Pleistocene (ZAZHIGIN, 1970; MALEEVA, 1976; ALEKSANDROVA, 1976). The morphotypic variation of *Lagurus lagurus* was studied by MALEEVA and NORDSTREM (1974), who distinguished three main lagurid morphotypes and two archaic — lagurodonid and transiensid — patterns. Having analysed materials from two Late Pleistocene localities in Transuralia (Malkovo and Verkhnaya Alabuga) and several recent populations, they found a considerable dominance of the lagurid morphotypes (81—97%). This type of morphology, besides, prevails in all Late Pleistocene populations in Europe (CHALINE, 1972; HEINRICH & JÁNOSSY, 1978; KOWALSKI, 1967; NADACHOWSKI, 1982), whereas the lagurodonid morphotype (corresponding with morphotype A in the present work) was very rarely met with in the Transuralian populations (1—2%); only the recent subspecies *L. l. abacanicus* SEREBRENNIKOV 1929, which lives isolated from the main range (GROMOV & POLYAKOV, 1977), showed a higher frequency of this morphotype (7%). The other archaic (transiensid) morphotype was more frequent in the Transuralian populations (3—18%) than in the population from Bacho Kiro (4%). Morphotypes D and E, described in this paper, have been illustrated by LOZAN's (1971) drawing for Early Holocene *Lagurus lagurus* from Moldavia. In the light of the foregoing data it seems that the population from Bacho Kiro has its dentition exceptionally variable compared with other populations.

V. INTERPRETATION OF MORPHOMETRIC CHANGES IN DENTITION

Changes occurring with time in the morphology and size of mammalian dentition have been studied for many years; nevertheless, the interpretation of the phenomena observed is difficult and complex. The causes of these difficulties are various. One of them is the still poor knowledge of the intrapopulation variation of teeth morphology in many species. And so the recording — among other things — of rare morphotypes seems to be important for several reasons.

First, in some cases the rarely encountered morphological patterns, described from the fossil material of arvicolids as separate species, in fact constitute extreme morphological variants of another form. It is only the knowledge of the full range of variation that permits their correct classification. In this case it is necessary to depart from exclusively typological classification and to look at this problem from the population standpoint (NADACHOWSKI, 1982). In Bacho Kiro the rare ratticepid morphotype, numbered initially in *Microtus* cf. *oeconomus*, was eventually included on this basis in *Microtus nivalis.*

Second, the rare morphological patterns are sometimes archaic morphotypes (MALEEVA, 1976). which were characteristic of the ancestors of the species under study, and their recording provides some information as to the philogenesis of a given group. An example that well illustrates this phenomenon is the variation of M_1 in *Lagurus lagurus* from Bacho Kiro. Morphotypes A and B, rarely occurring, show a morphology typical of the extinct forms *Lagurodon* and *Lagurus transiens,* which seems to indicate their relationship with the recent species. Another case of this sort is the occurrence of the character „*Mimomys* ridge" in the population of *Arvicola terrestris.*

Third, in some cases the calculation of the frequency of particular morphotypes permits the observation of some morphological changes microevolutionary in nature. In *Microtus nivalis* from Bacho Kiro the frequency of the nivalid-ratticepid morphotype (C) decreased successively in younger layers. This process has been corroborated by suitable measurements which indicate an intensification of the tendency for the build of this tooth to become more complicated.

Fourth, some rare morphotypes may happen to be progressive characters, new ones, freshly acquired in the course of evolution. There seems however to be no adequate example of this in the material from Bacho Kiro.

The morphological changes with time are naturally followed also by changes in tooth dimensions. During the last glaciation the changes in the length of M_1 ran in a manner varying from species to species (Fig. 18). Three types of these changes can be distinguished: 1) successive decrease in length from the beginning of the Würm to the Holocene; changes of this sort are particularly distinct in *Microtus nivalis,* weaker in *Arvicola terrestris* and very slightly and less reliably marked in *Clethrionomys glareolus;* 2) lack of statistically significant changes in size during the study period (*Pitymys subterraneus*) and 3) the opposite phenomenon to that observed in the first group, i.e. an increase in measurements in the populations derived from younger periods (*Lagurus lagurus*). It is striking that there are no relations between the tooth size and the climatic conditions and, what is more, this is true of all the species examined. In other words, the observed trends in size changes do not agree with BERGMAN's rule.

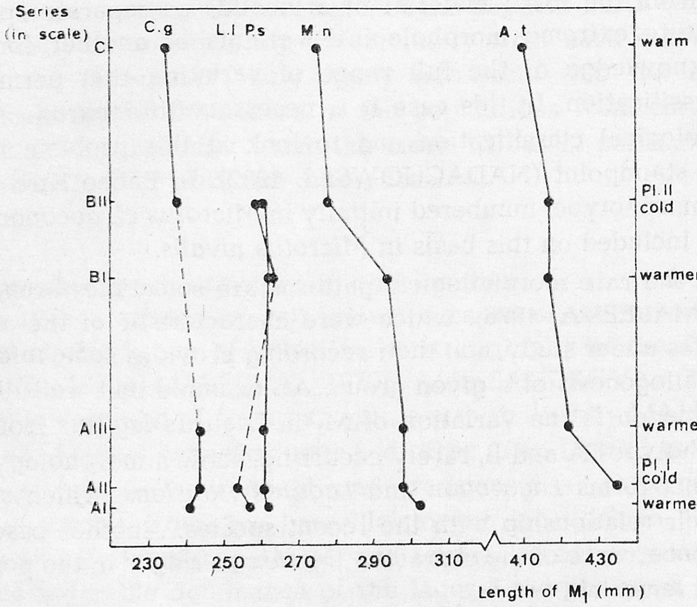

Fig. 18. Graph showing the changes in the mean length of M_1 from the beginning of the Würm to the Holocene in the following species from Bacho Kiro: *Clethrionomys glareolus* (C.g.), *Lagurus lagurus* (L.l.), *Pitymys subterraneus* (P.s.), *Microtus nivalis* (M.n.) and *Arvicola terrestris* (A.t.). The broken line indicates lack of data. A detailed interpretation of the graph to be found in the text (p. 171)

Connections between the length of the tooth-row or single teeth and climatic conditions were described in palaeontological literature, e.g. in *Cricetus* and *Allocricetus* (KÚRTEN, 1960) or in *Ondatra* (NELSON & SEMKEN, 1970), in which, in both cases, the teeth were shown to have grown in size in the glacial periods. The complexity of this problem is well illustrated by an example given by TCHERNOV (1979), who demonstrated tooth size changes occurring in accordance with BERGMAN's rule in three sympatric species of the genus *Apodemus (Sylvaemus)* from Israel. However, when in warmer periods *S. flavicollis* was missing, the size of teeth changed against that rule in the other two species (*S. sylvaticus* and *S. mystacinus*). The question arises what factor, if not climatic ones, caused the changes in the size of dentition observed in the voles from Bacho Kiro? This question is not easy to answer because adaptation to environment is a very complex phenomenon. It is manifested, above all, by the occurrence of a number of physiomorphological mechanisms (HAMILTON, 1961; SHVARZ, 1963; ROSENZWEIG, 1968, KENDEIGH, 1969; JAMES, 1970), of which the most important are adaptations involving the effective insulation of the body covering from environment, the regulation of the metabolic activity that controls heat generation and its dissipation, various behavioural adaptations influencing the thermoregulation and, finally, the variable body-size: surface ratio according to changing climatic factors (BERGMAN's rule). As can be seen from the foregoing, the tooth size changes, with which adequate changes in the body size are supposed to be correlated (which is often assumed by palaeontologists), need not at all be the most important factor of adaptation to changing climatic conditions. It also seems indispensable at this moment to attract attention to the fact that this correlation between the size of dentition and the size of body, on which the whole course of reasoning is based, is a very complex problem and not, as yet, fully solved and clear at the level of both individuals and populations (KÚRTEN, 1967; GOULD & GARWOOD, 1969;, GOULD, 1975; SYCH & SYCH, 1975; BARNETT, 1977; GINGERICH & WINKLER, 1979). Therefore, it may merely be stated that in the cases of tooth size changes described in this paper we are concerned with a selective factor other than climatic conditions, inconsistent with the trend of size changes occurring according to BERGMAN's rule.

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STRESZCZENIE

Praca zawiera opis zmienności morfotypowej uzębienia (głównie M_1) oraz zmienności wymiarów siedmiu następujących gatunków nornikowatych z późnego plejstocenu Jaskini Baczo Kiro w Bułgarii: *Clethrionomys glareolus, Arvicola terrestris, Pitymys subterraneus, Microtus arvalis, Microtus agrestis, Microtus nivalis* i *Lagurus lagurus*. Metoda analizy morfotypów pozwoliła na potraktowanie okazów opisanych poprzednio pod nazwą *Microtus oeconomus* jako skrajnych wariantów zmienności *Microtus nivalis* i włączenie ich do tego ostatniego gatunku. Wykazano również obecność dwóch form (*M. arvalis* i *M. agrestis*) w materiałach kopalnych opisanych wcześniej jako *M. arvalis*, choć ich całkowicie rozdzielenie nie było możliwe zarówno na podstawie morfologii, jak i pomiarów. Ponadto prześledzone zostały przemiany mikroewolucyjne w budowie M_1 dla *Microtus nivalis* i *Lagurus lagurus*. Dzięki dobrej stratygrafii stanowiska przeprowadzono analizę i przedyskutowano zmiany długości M_1 od wczesnego Würmu po holocen u poszczególnych gatunków. Zmiany te nie są związane z fluktuacjami klimatycznymi, a tym samym jest za nie odpowiedzialny jakiś czynnik selekcyjny inny niż warunki klimatyczne.

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