

Revision of fossil lemmings (Lemminae) from Poland with special reference to the occurrence of *Synaptomys* in Eurasia

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Abstract. A description is given of abundant lemming remains from the Polish sites Zamkowa Dolna Cave and Kozi Grzbiet with an account of morphotype variation. Thanks to analysis of molar pattern the Late Villanyian – Biharian lemmings (Lemminae) from Poland, can be identified as *Lemmus kowalskii* CARLS et RABEDER, 1988. The range of molar pattern variation in the largest sample from Zamkowa Dolna Cave, unit C, and Kozi Grzbiet demonstrates the very gradual nature of the transition in tooth morphology of Eurasian lemmings from the first occurrence to the Recent, and clearly shows that there is no gap in the masticatory surface pattern between the species of “*Synaptomys*” described from Pliocene sites of Eurasia and the first *Lemmus* species. On the basis of the data obtained, the first lemmings from Eurasia are included as subgenus *Pliotomys* SUKHOV, 1976 into the genus *Lemmus* not *Synaptomys*. The evolution and taxonomy of Lemminae above the species level are discussed.

Key words: *Lemmus*, *Synaptomys*, Poland, Villanyian, Biharian, molar pattern.

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I. INTRODUCTION

Most taxonomists recognize the brown and bog lemmings as rootless voles belonging to a distinct subfamily Lemminae GRAY, 1825 (within Arvicolidae: Rodentia), distinguishing three genera *Lemmus* LINK, 1795, *Myopus* MILLER, 1910 and *Synaptomys* BAIRD, 1858. KOENIGSWALD and MARTIN (1984) are of the opinion that brown lemmings (tribe Lemmini) are represented by only one genus *Lemmus* (*Myopus* in their classification is a subgenus of *Lemmus*), while all North American bog lemmings are included in the separate tribe Synaptomyini with two genera: *Synapto-*

mys and *Mictomys* TRUE, 1894. Also CARLS and RABEDER (1988) synonymized *Myopus* under *Lemmus*. On the other hand, FEJFAR and REPENNING (1998) distinguished among the tribe Lemmini three genera: *Lemmus*, *Myopus* and *Pliotomys* SUKHOV, 1976 and among Synaptomyini: *Synaptomys*, *Mictomys* and a new genus with rooted molars – *Tobienia* FEJFAR et REPENNING, 1998.

The evolution of genus *Lemmus* has for a long time been a puzzle for scholars – first of all owing to the great stability of their dentition over a rather long period of time. The first who recognized that lemming teeth are subjected to variation in time was KOWALSKI (1977). He also proposed the first scheme of evolution of the group. During more than 20 years since that classical work, new material has been published and respective data accumulated. As a result, the new forms *Lemmus kowalskii* CARLS et RABEDER, 1988 and *Lemmus sheri* ABRAMSON, 1992 were described. However, interrelations between them are far from clear. Thus, a detailed description of rich *Lemmus* material from Late Cenozoic sites in Poland that was originally reported by KOWALSKI (1977) taking into account new characters involved have become necessary.

Moreover, some doubts have recently arisen (CARLS and RABEDER 1988; REPENNING and GRADY 1988; FEJFAR and REPENNING 1998) regarding the taxonomy and phylogenetic position of lemming remains from Eurasia which were referred to the genus *Synaptomys* (KOWALSKI 1977; SUKHOV 1976; SHER et al. 1977; DEVYATKIN and ZAZHIGIN 1974). The most intriguing fact concerning these forms is that, according to the geography of the records (Poland, South Ural, North Mongolia and North-East Siberia), their range in Late Pliocene (Villanyian) covered almost the whole territory of Eurasia. However, already from the beginning of Early Pleistocene (Biharian) these forms have completely disappeared from all this vast territory in Eurasia and are never recorded in the well-studied younger fauna. At the same time, the first remains of *Synaptomys* in North America appear slightly later than the mentioned forms in Eurasia, in the Late Pliocene (Blancan) fauna; its further evolution is connected exclusively with this continent, where several fossil and recent taxa occur.

Records of *Lemmus* of Villanyian and Biharian age have been reported from many sites in Europe and Siberia, but only in a few of them are these remains sufficiently abundant for the study of molar pattern variation. The sites from Poland are among them and Zamkowa Dolna Cave presents a unique case with the largest number of lemming remains in Europe, comparable only with those from some Late Pleistocene sites of the Urals and Siberia. This material makes it possible to analyse the range of intrapopulation variation.

The main objective of the present work is the revision of Lemminae remains from the Late Pliocene – Early Pleistocene (Villanyian – Biharian) sites of Poland including the type material of “*Synaptomys* (*Praesynaptomys*) *europaeus* KOWALSKI, 1977” and their comparison with the recently described forms from the Late Pliocene – Early Pleistocene of Eurasia.

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II. MATERIAL AND METHODS

According to KOWALSKI (1977), the first lemmings in Poland, described as *Synaptomys* (*Praesynaptomys*) *europaeus*, appeared in Rębielice Królewskie 1A and Rębielice Królewskie 2 and are of Early Villanyian age (MN 16). In Late Villanyian and Early Biharian lemming remains of the genus *Lemmus* are present in almost all localities (Kadzielnia, Kamyk, Kielniki 3A, Zalesiaki 1A) as

very rare elements; an exception is the sample from Zamkowa Dolna Cave (unit C) where *Lemmus* constitutes one of the predominant species (NADACHOWSKI 1990a, b). In Late Biharian relatively abundant remains are present in the Kozi Grzbiet assemblage (KOWALSKI 1977).

The material studied comes from the following localities:

1. Rębielice Królewskie 1A (MF/1558): left half of mandible with M_1 - M_2 (holotype), detached teeth: $8M_1$, $8M_2$, $5M_3$, $5M^1$, $8M^2$, $6M^3$.

R e m a r k s. The type locality of *Synaptomys* (*Praesynaptomys*) *europaeus* KOWALSKI, 1977 is of Early Villanyian age (MN 16) (NADACHOWSKI 1990a). Lemmings are accompanied by ca. 20 species of rodents, e.g. *Mimomys polonicus* KOWALSKI, 1960, *Stachomys trilobodon* KOWALSKI, 1960, and *Kowalskia polonica* FAHLBUSCH, 1969.

2. Rębielice Królewskie 2 (MF/1559): left half of mandible with M_1 - M_2 , detached teeth: $3M_1$, $1M_2$, $1M_3$, $7M^1$, $6M^2$.

R e m a r k s. The faunal composition of Rębielice Królewskie 2 (MN 16) is very similar to Rębielice Królewskie 1A, although rodents are not so diversified (ca. 13 species) (NADACHOWSKI 1990a).

3. Zamkowa Dolna Cave, unit C (MF/1566): 2 halves of mandibles with M_1 - M_2 , $94M_1$, $92M_2$, $62M_3$; $85M^1$, $73M^2$, $87M^3$

R e m a r k s. During archaeological excavations in Zamkowa Dolna Cave, a deep hollow filled with a loam sediment (=unit C) in the rocky bottom was discovered which contained very rich fauna of rodents. Most of the materials (more than 95%), probably including all remains of lemmings, belong to species of Villanyian age (MN16? – MN17) (NADACHOWSKI 1990a). The rest of the assemblage, however, is either of the Ruscinian or of Late Biharian age (NADACHOWSKI 1990b).

3. Kozi Grzbiet – layer 2c (MF/1572): $10M_1$, $6M_2$, $2M^1$, $5M^2$, $2M^3$; layers 2a+b+c (MF/1576): $3M_2$, $5M_3$, $5M^1$, $1M^2$, $3M^3$; all layers (MF/1577): $2M_1$, $5M_2$, $4M^1$, $9M^2$, $28M^3$.

R e m a r k s. A rich vertebrate and snail fauna was found in unit 2 in three layers: 2a, 2b and 2c, most probably of the same age (Late Biharian) (NADACHOWSKI 1985, 1990b).

In the present work the terminology for the parts of occlusal surface of lemming molars introduced by VAN DER MEULEN (1973, 1974) was followed: L – length of molar; W – width of molar; ACC – anteroconid complex, PL – posterior lobe; T1-T5 – dentine fields of occlusal surface of molars; BRA – buccal re-entrant angle; LRA – lingual re-entrant angle; BSA – buccal salient angle; LSA – lingual salient angle. Definition of M^3 morphotypes follows CARLS and RABEDER (1988, Abb. 69) with slight modifications (Fig. 2).

III. DESCRIPTION

The masticatory surface pattern in brown lemmings is relatively stable in time and space and its structure has been studied in detail in many earlier works, thus only distinguishing features of teeth in the studied material are described here. More details are given in the case of characters which have particular significance in the evolution of lemmings. These were used as key features for taxonomic decisions, especially with regard to the structure of M^3 . It was this structure which was the key point for the first scheme of evolution of the whole group (KOWALSKI 1977) and was one of five characters used in the cladogram by KOENIGSWALD and MARTIN (1984). There is no doubt concerning the highest importance of M^3 morphology for Lemminae taxonomy.

M_1 – The masticatory surface pattern of this tooth is relatively stable (Fig. 1). Some variation can be observed only in the general outline of the very simple anteroconid complex. In most cases it

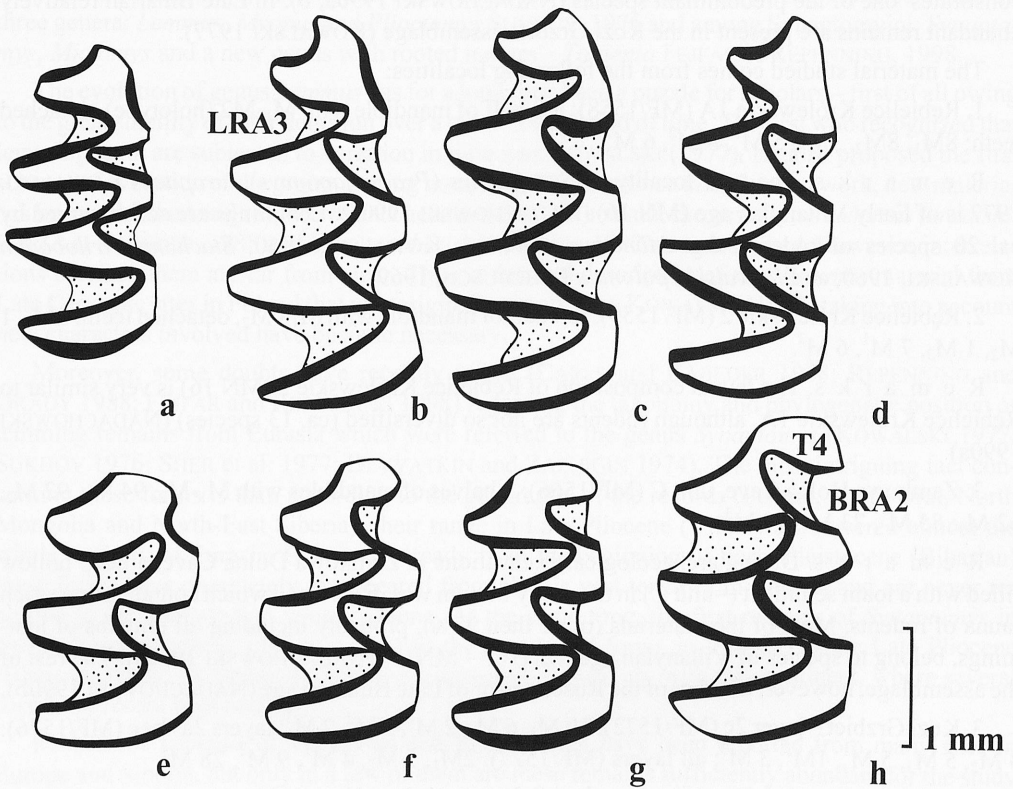


Fig. 1. Molar patterns of M_1 and M_2 in lemmings. a-d: right M_1 ; e-h: right M_2 . a, e: *Synaptomys cooperi* BAIRD, 1858, recent, Canada; b, f: "*Synaptomys (Praesynaptomys) europaeus*", Rębielice Królewskie 1A, MF/1558/1, holotype, reversed; c, g: *Lemmus* sp., Zamkowa Dolna Cave; d, h: *Lemmus* sp., Zamkowa Dolna Cave. See text for explanation.

has a form of romboïd, elongated forwards. The apices of the buccal and lingual re-entrant angles at the base of the anteroconid complex meet at the median line of the tooth. This character distinguishes the pattern of M_1 of all fossil and recent representatives of the brown lemmings (*Lemmus* – *Myopus*) from the representatives of bog lemmings (*Synaptomys*). In the latter group the anteroconid complex (ACC) is narrower in the anterior-posterior direction and shows almost the same lateral elongation as other loops (Fig. 1a). The apex of the LRA3 in *Synaptomys* is located opposite the posterior wall of the ACC. Such a morphotype is practically never observed in the samples from Recent populations of *Lemmus-Myopus* species, although some variations in the interlocation of buccal and lingual re-entrant angles do occur. Among M_1 in the sample from Zamkowa Dolna Cave, only one tooth ($n=94$) corresponds approximately to such a structure. Also in the sample from Kozi Grzbiet, in layer 2c, there is M_1 with the same structure.

M_2 – The masticatory surface pattern of this tooth is also very stable and in its main features shows no noticeable differences among the lemmings from Late Cenozoic sites of Eurasia and Recent *Lemmus* – *Myopus* (Fig. 1). At the same time, it differs distinctly from the structure present in both Recent and all fossil species of bog lemmings. The main difference is that in *Lemmus-Myopus* this tooth consists of 5 dentine fields and both the lingual and the buccal re-entrant angles are well developed (Fig. 1h). The T4 is small and rounded, the apex of the BRA2 connects with the very be-

ginning of the enamel wall of T4 and completely divides the dentine fields of T3 and T4. In recent bog lemmings (*Synaptomys*) the molar pattern of this tooth consists of four dentine fields. The first has the form of trapezium while BRA2 (if present) is strongly reduced (Fig. 1e). The T3 and T4 in fossil forms of bog lemmings [e.g. *Mictomys vetus* (WILSON, 1933) and *Mictomys landesi* HIBBARD, 1954] are broadly confluent. In the sample from Zamkowa Dolna Cave all M₂ (n=92) are of *Lemmus* – *Myopus* type. However, in the sample from Kozi Grzbiet, all teeth from layer 2c (n=6) correspond to the above mentioned pattern typical of fossil bog lemmings while the teeth from other layers show the *Lemmus-Myopus* pattern.

M₃ and M¹ – Both these teeth are considered to be unlike other ones. On the one hand, no serious qualitative difference in masticatory surface pattern of these teeth can be observed between brown and bog lemmings, while on the other, they show no essential variation in time and space. However, in the teeth from Zamkowa Dolna Cave the apices of all re-entrant angles are more strongly curved and located at more acute angle in relation to the mesial axis than in those of Recent lemmings, where they are oriented almost perpendicular to the tooth axis. The observed changes are difficult to measure and to estimate quantitatively, this phenomenon being also typical of other lemming teeth. CARLS and RABEDER (1988) introduced the term “revergency” to characterize these changes.

M² – In the structure of this tooth the gradual changes in the molar surface pattern could be observed only in relatively large samples. The noticed changes from Early Pleistocene to Recent times are of qualitative character and can be described in terms of two distinct morphotypes. In that typical of *Lemmus kowalskii* the T3 is of nearly triangular shape. The apex of the LRA2 is curved backwards and located near the beginning of the posterior buccal enamel wall of the next loop (CARLS and RABEDER 1988; Abb. 67; ABRAMSON 1992, Fig. 8,9). The morphotype typical of all Recent forms is characterized by the rectangular shape of the second lingual loop, the apex of the LRA2 being located opposite the wide dentine wall, so that T3 and T4 are divided by a broad dentine isthmus. All (n=72) of M² from Zamkowa Dolna Cave have the structure of *L. kowalskii* morphotype. In the sample from Kozi Grzbiet all five teeth from the layer 2c have the typical structure of *L. kowalskii* morphotype. Among the teeth from all layers (n=8) two teeth show such a structure, while that of the other six is close rather to the structure of Recent morphotype.

M³ – The character that was first considered by the cited authors is the mutual location of the apices of BRA2 and LRA2 (Fig. 2). The apices of these re-entrant angles may alter, while LRA2 may be (1) completely reduced – the structure typical of recent bog lemmings (*Synaptomys*, *Mictomys*); (2) slightly reduced – the structures typical of “*Synaptomys (Pliotomys) mimomiformis* SUKHOV, 1976”, “*Synaptomys (Praesynaptomys) europaeus* KOWALSKI, 1977”, and *Synaptomys rinkeri* HIBBARD, 1956). The apices of these re-entrant angles may be located opposite each other in the centre of the tooth (in recent *Lemmus* – *Myopus* species). Analysis of variation of this character in the largest sample from Zamkowa Dolna Cave (N=87) has shown that there are here all variants of the M³ structure listed above – from those typical of Recent bog lemmings to those of Recent brown lemmings. Thus, it is noteworthy that there exists a very smooth transition between these extremes and there is very little doubt that these teeth do not belong to one population (Figs 2 and 3). It can be seen that for Zamkowa Dolna Cave the number of teeth corresponding to the “*europaeus*” structure (morphotype e2) and to the recent *Lemmus-Myopus* structure (morphotype 11) is equal (13%).

Among other characters in the structure of this tooth that have taxonomic significance are the orientation of the BRA2 relative to tooth axis and the structure of the posterior loop. In Recent brown lemmings (*Lemmus* – *Myopus*) BRA2 is located almost transversal in relation to the median line of the tooth. In consequence, the next dentine loop has the shape of an elongated quadrangle. In the sample from Zamkowa Dolna Cave the number of teeth with molar pattern that closely corre-

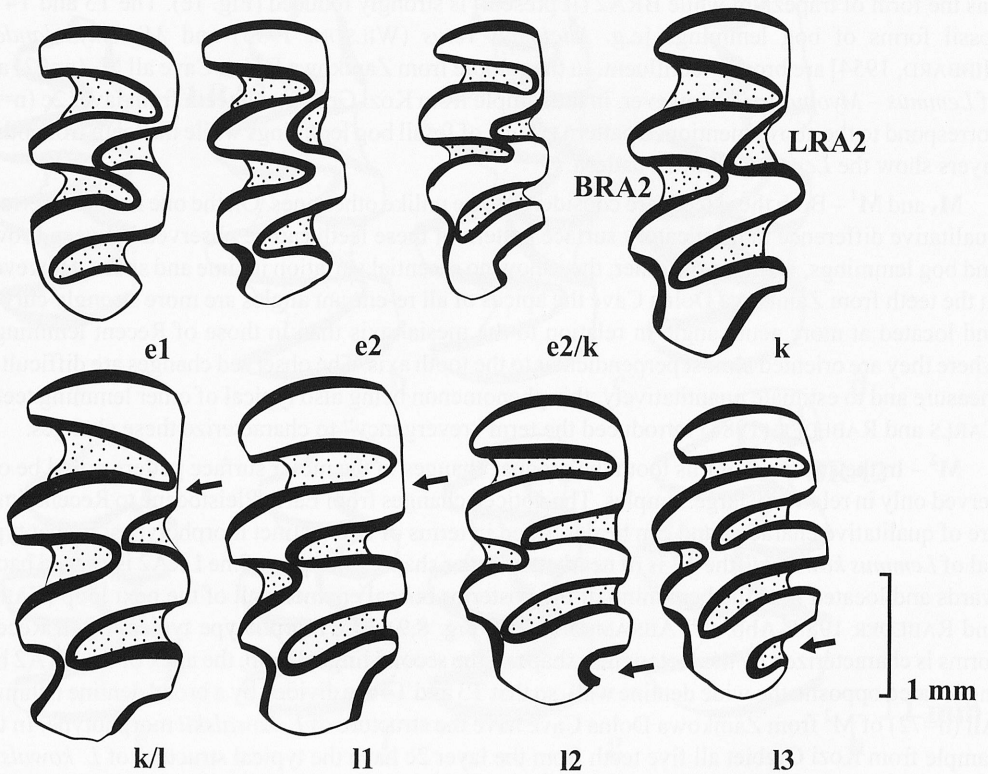


Fig. 2. Morphotypes of M^3 in lemmings. Designations are given after CARLS and RABEDER (1988) and VAN DER MEULEN (1973). Arrows indicate the most variable parts of the tooth. See text for explanation.

spond to the Recent lemming structure covers 13%. The tooth pattern in which the apex of BRA2 bends backward, the posterior cutting edge is located at an angle to the median line and the second dentine field has the shape of a triangle, was described for *Lemmus kowalskii* as morphotype "k" (CARLS and RABEDER 1988). In Zamkowa Dolna Cave it occurs with 49% frequency. The apices of BRA2 and LRA2 may be slightly shifted. The structure of the posterior loop in teeth of the discussed sample mainly has a simple oval shape, the lingual re-entrant angle at the posterior loop being either absent or very poorly pronounced (primarily in the morphotypes l1-l3).

Another sample sufficient for the study of molar pattern variation comes from Kozi Grzbiet. Practically all M^3 in this sample from all layers ($n=31$) clearly show the structure of Recent *Lemmus* species in all characters (morphotypes l1). However, one tooth from the layer 2c and one fragment correspond in all characteristics to the morphotype e1-e2.

IV. SIZE VARIATION

For Eurasian lemmings, the general tendency towards gradual size increase in time from the first records to the recent Arctic lemmings can be well followed and the significantly larger size may be

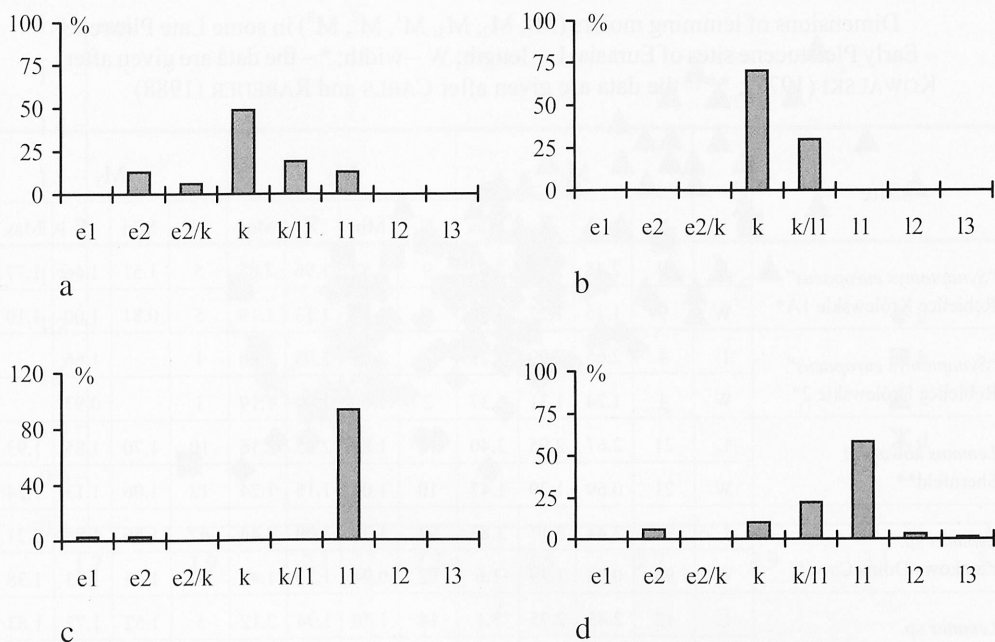


Fig. 3. Frequency distribution of M³ morphotypes in lemmings. a: *Lemmus* sp. – Zamkowa Dolna Cave, Poland; b: *Lemmus kowalskii* – Schenfeld, Germany; c: *Lemmus* sp. – Kozi Grzbiet, Poland; d: *Lemmus sheri* – Krestovka, north-eastern Siberia, Russia. Designation of morphotypes after CARLS and RABEDER (1988).

regarded as an apomorphic character. The dimensions of teeth from Zamkowa Dolna Cave and Kozi Grzbiet vary greatly (Table I). The dimensions of teeth of *L. kowalskii* from Shernfeld are within the limits of this variation, though on the average they are slightly smaller. Both *L. kowalskii* and lemmings of Zamkowa Dolna Cave and Kozi Grzbiet are significantly smaller than *L. sheri* from sites in North-Eastern Siberia which are of approximately Biharian age (Table I, Fig. 4).

A comparison of the dimensions of “*Synaptomys (Praesynaptomys) europaeus*” from Rębielice Królewskie 1A with *Lemmus kowalskii* from Shernfeld and lemmings from Zamkowa Dolna Cave and Kozi Grzbiet shows that the latter are larger. The difference in size between the Rębielice Królewskie 2 sample and other localities is not so significant. It should also be mentioned that the dimensions of M³ and M₁ of “*Synaptomys (Praesynaptomys) europaeus*” are within the range of size variation of lemming remains from Zamkowa Dolna Cave (Table I). The material which was described as “*Synaptomys (Pliotomys) mimomiformis*” by SUKHOV (1976) is too scarce to assess its size variation, it can only be stated that the measured teeth are within the size range of lemmings from Zamkowa Dolna Cave and Kozi Grzbiet.

V. COMPARISON AND DISCUSSION

Analyses of tooth structure in the largest sample from Zamkowa Dolna Cave have shown that this structure is very close to the morphological stage of *Lemmus kowalskii* from Shernfeld, or even somewhat more primitive. Among M³, the teeth that could be assigned to the morphotype k (CARLS and RABEDER 1988; p.220, Abb.69) comprise 49% (Fig. 3). The proportion of teeth that could be as-

Table I

Dimensions of lemming molars (M_1 , M_2 , M_3 , M^1 , M^2 , M^3) in some Late Pliocene – Early Pleistocene sites of Eurasia. L – length; W – width; * – the data are given after KOWALSKI (1977); ** – the data are given after CARLS and RABEDER (1988)

Site		M_1				M_2				M_3			
		N	Min	\bar{X}	Max	N	Min	\bar{X}	Max	N	Min	\bar{X}	Max
“ <i>Synaptomys europaeus</i> ” Rębielice Królewskie 1A*	L	9	2.48	2.74	2.91	9	1.82	1.96	2.05	5	1.51	1.66	1.77
	W	9	1.15	1.22	1.30	9	1.11	1.13	1.19	5	0.81	1.00	1.10
“ <i>Synaptomys europaeus</i> ” Rębielice Królewskie 2*	L	4	2.65	2.99	3.25	2	2.05	2.05	2.06	1		1.66	
	W	4	1.24	1.31	1.37	2	1.00	1.09	1.19	1		0.97	
<i>Lemmus kowalskii</i> Sternfeld**	L	21	2.67	2.95	3.40	10	1.89	2.05	2.16	10	1.70	1.85	1.93
	W	21	0.69	1.29	1.47	10	1.06	1.15	1.24	12	1.06	1.13	1.24
<i>Lemmus</i> sp. Zamkowa Dolna Cave C	L	94	2.44	3.17	3.83	92	1.73	2.09	2.44	62	1.56	1.88	2.21
	W	94	0.88	1.39	1.6	92	0.94	1.23	1.47	62	1.03	1.23	1.38
<i>Lemmus</i> sp. Kozi Grzbiet	L	12	2.45	2.75	3.1	14	1.70	1.94	2.12	5	1.52	1.72	1.83
	W	12	1.15	1.23	1.39	14	1.09	1.17	1.36	5	1.15	1.24	1.33
<i>Lemmus sheri</i> Krestovka	L	31	2.7	3.17	3.75	36	2.10	2.37	2.75	22	1.45	2.10	2.70
	W	31	1.10	1.42	1.95	36	1.25	1.44	1.75	22	1.25	1.49	1.85

Site		M^1				M^2				M^3			
		N	Min	\bar{X}	Max	N	Min	\bar{X}	Max	N	Min	\bar{X}	Max
“ <i>Synaptomys europaeus</i> ” Rębielice Królewskie 1A*	L	5	2.38	2.51	2.68	7	1.80	1.3	2.06	5	1.93	2.06	2.17
	W	5	0.95	1.00	1.08	7	0.87	1.01	1.07	5	0.84	0.96	1.06
“ <i>Synaptomys europaeus</i> ” Rębielice Królewskie 2*	L	7	2.61	2.70	2.85	5	2.02	2.09	2.23				
	W	7	0.93	1.01	1.11	6	1.00	1.06	1.10				
<i>Lemmus kowalskii</i> Sternfeld**	L	20	2.44	2.67	2.81	17	1.93	2.07	2.25	16	2.07	2.24	2.41
	W	20	1.01	1.10	1.20	17	1.01	1.10	1.20	18	0.94	1.05	1.12
<i>Lemmus</i> sp. Zamkowa Dolna Cave C	L	85	2.29	2.72	3.24	73	1.74	2.12	2.44	80	1.97	2.34	2.71
	W	85	1.0	1.34	1.58	73	0.88	1.14	1.29	87	0.91	1.15	1.35
<i>Lemmus</i> sp. Kozi Grzbiet	L	11	2.09	2.51	2.90	15	1.79	1.96	2.14	22	1.88	2.32	2.88
	W	11	1.21	1.3	1.45	15	0.94	1.07	1.18	32	0.92	1.27	1.45
<i>Lemmus sheri</i> Krestovka	L	78	2.55	2.94	3.70	28	1.85	2.32	2.75	26	2.20	2.53	3.20
	W	78	1.10	1.53	1.95	28	1.10	1.38	1.70	26	1.15	1.34	1.75

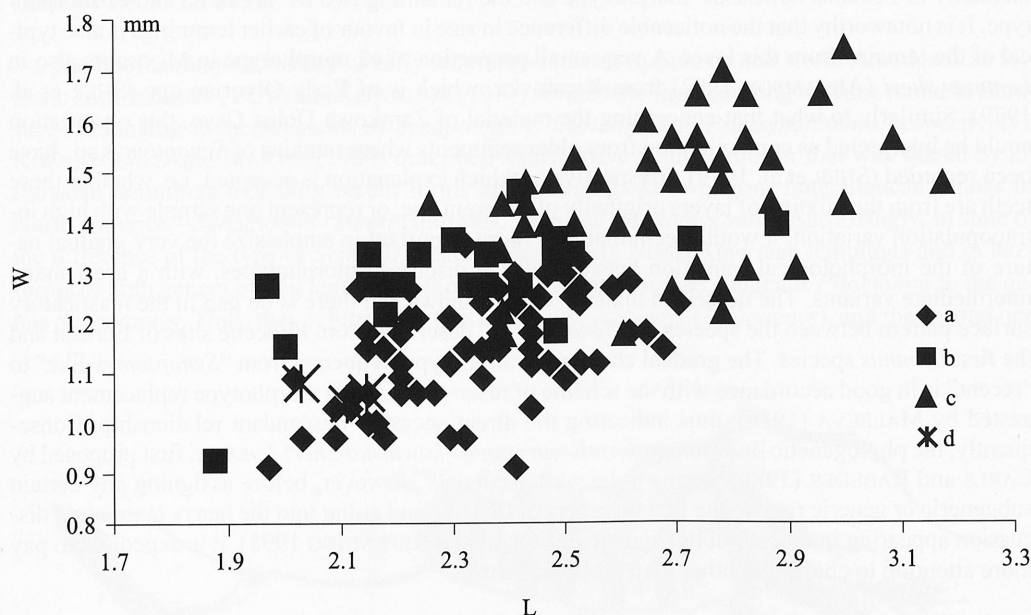


Fig. 4. Diagram of M^3 dimensions in lemmings. a: *Lemmus* sp. – Zamkowa Dolna Cave; b: *Lemmus* sp. – Kozi Grzbiet; c: *Lemmus sheri* – Krestovka; d: “*Synaptomys* (*Praesynaptomys*) *europaeus*” – Rebiełice Królewskie 1A.

signed to morphotype k/11 (CARLS and RABEDER 1988; p.220, Abb.69) is 19%. The teeth with advanced molar pattern (11) comparable with recent *Lemmus lemmus* (LINNAEUS, 1758) – *L. sibiricus* (KERR, 1792) comprise 13%. The teeth with the structure identical with “*Synaptomys* (*Pliotomys*) *mimomiformis*” and “*Synaptomys* (*Presynaptomys*) *europaeus*” (morphotype – e2) comprises 13%, while 6% of teeth show intermediate structure between k and e2 (morphotype e2/k). Other teeth in the sample from Zamkowa Dolna Cave, where distinct qualitative characteristics may be followed, (M^2) are clearly of *Lemmus kowalskii* structure. Thus, the bulk of the teeth from Zamkowa Dolna Cave, corresponds, according to its main characteristics, to *Lemmus kowalskii* described from Shernfeld. Both the wide range of variation and the presence in equal proportions of teeth with both primitive *Synaptomys*-like structure and the advanced recent *Lemmus* one can be explained by fact that, as was stated earlier (NADACHOWSKI 1990a, b), the main fauna is most probably of Villanyan age (MN 16? -MN 17), but some rodents suggest Ruscinian age (MN 15) and a very small part is correlated with Upper Biharian. More difficult to explain are the great dissimilarities in morphology of lemming teeth from different layers of Kozi Grzbiet. As far as is known, all layers (2a, 2b, 2c) of this site according to the faunistic assemblage are referred to Upper Biharian (NADACHOWSKI 1985, 1990a, b). Most of the lemming teeth known from sites of this age have a structure intermediate between *Lemmus kowalskii* and recent species, the stage described earlier as *Lemmus sheri* (ABRAMSON 1992). This, in general, is true also for teeth from Kozi Grzbiet, the sample from layers 2a+b+c and one sample from all layers. All M^3 (n=31) of these samples have the typical structure of Recent *Lemmus*; among M^2 (n=8) only two teeth may be assigned to *Lemmus kowalskii* morphotype, and six show the structure of Recent lemmings. Other proportions are observed in the layer 2c. Probably the most interesting is the occurrence here among M_1 (n=14) of teeth very close to the typical structure of Recent bog lemming (Fig. 1a). Even more surprising is the fact that all six M_2 are characterized by a structure similar to teeth in type material of “*Synaptomys* (*Praesynaptomys*) *eu-*

ropaeus” which show a broad confluence between T3 and T4 (Fig. 1). All M₂ (n=5) of this layer are distinctly of *Lemmus kowalskii* morphotype and the remaining two M³ are of e2 and e1 morphotype. It is noteworthy that the noticeable difference in size in favour of earlier lemmings is also typical of the remains from this layer. A very small proportion of e2 morphotype in M³ occurs also in *Lemmus sheri* (ABRAMSON 1992) from Krestovka, which is of Early Olyorian age (SHER et al. 1979). Similarly to what that concerning the material of Zamkowa Dolna Cave, this observation could be interpreted as contamination from older sediments where remains of *Synaptomys* sp. have been recorded (SHER et al. 1979). Irrespective of which explanation is accepted, i.e. whether these teeth are from the mixture of layers originally of different age, or represent one sample with high intrapopulation variation, it would seem that it is more important to emphasize the very gradual nature of the morphological transition between all the discussed morphotypes, with a great many intermediate variants. The described material clearly shows that there is no gap in the masticatory surface pattern between the species of “*Synaptomys*” described from Pliocene sites of Eurasia and the first *Lemmus* species. The gradual change in morphotype frequency from “*Synaptomys*-like” to “recent” is in good accordance with the scheme of reserve-dominant morphotype replacement suggested by MALEEVA (1976), thus indicating the direct ancestral-descendant relationship. Consequently, the phylogenetic line *mimomiformis-europaeus-kowalskii-sheri-lemmus*, first proposed by CARLS and RABEDER (1988), seems to be well grounded. However, before assigning any certain subgeneric or generic rank to the first members of this line and going into the heavy taxonomic discussion appearing in recent publications (e.g. FEJFAR and REPENNING 1998), it is expedient to pay more attention to characters other than molar pattern.

In all previous works where the evolution and phylogenetic relationships within the group were discussed (KOWALSKI 1977; KOENIGSWALD and MARTIN, 1984; CARLS and RABEDER 1988; REPENNING and GRADY, 1988; FEJFAR and REPENNING 1998), only the characters of molar pattern and the position of the end of the lower incisor relative to the toothrow were analyzed. The last character seems to be of little phylogenetic significance because of individual variation and very high probability of reversals (homoplasy). The rest of the regarded characters, with the exception of the enamel ultrastructure, may also be connected with this, though not to such an extent. However, a great difference occurs in the structure of the skull and jaws between both the Recent genera of bog lemmings (*Synaptomys*) and the brown lemmings (*Lemmus* – *Myopus*). The remains of the skull are very rare, but the evolution of the mandible structure can be followed. The ventral surface of the mandible in *Synaptomys* is flat, no pronounced ridge ascending to the coronoid processes being found, whereas in *Lemmus* and *Myopus* the well developed ridge as well as the deep fossa for the insertion of temporal muscle is present. As far as can be judged from the literature in *Mictomys vetus*, the oldest known North American bog lemming, “the ventral surface of the mandibular ramus is broad and fairly flat” (TOMIDA 1987, p.127). Thus, if the Eurasian origin of the first North American lemmings is accepted, then “*Synaptomys (Pliotomys) mimomiformis* – *Synaptomys (Praesynaptomys) europaeus*” as well as other lemmings from Mongolia and North-Eastern Siberia, currently referred to *Synaptomys* sp. (ZAZHIGIN 1997), should have the flattened structure of the mandible, without any marked strengthening of musculature. In this case we have to propose a dramatic morphological rearrangement in the mandible structure that might have taken place between Early and Late Villanyian on the background of very gradual, barely noticeable changes in the tooth structure. Two mandibles recovered from Zamkowa Dolna Cave have the mentioned ridge, though the strengthening of the musculature is less expressed than in recent forms of *Lemmus* (Fig. 5b). Unfortunately, the two fragments of mandibles recovered from Rębielice Królewskie 1A and 2 are not sufficient for a definite conclusion being made because the most important part is broken. However, mandible MF/1559 from Rębielice Królewskie 2 as compared with Zamkowa Dolna Cave clearly has less expressed temporal fossa and seemingly no signs of ascending ridge (Fig. 5a). Serious rearrangement of mandible structure during the mentioned time span would not seem to be too fantastic if it is taken into account that the main evolutionary trends in *Lemmus* – *Myopus* line from Early Bi-

harian to Recent were observed not in the dentition but in the skull and mandible structure (ABRAMSON 1992; 1993).

The brief taxonomic history of early lemmings remains in Eurasia and North America is as follows: both SUKHOV (1976) and KOWALSKI (1977) defined the first lemming remains found in Eurasia as belonging to the subgenus of *Synaptomys* (*Pliotomys* and *Praesynaptomys*, respectively). KOENIGSWALD and MARTIN (1984) described a distinctive Schmelzmuster that was shared by all Eurasian lemmings including recent forms and lemmings known from Late Blancan faunas of North America – *Synaptomys rinkeri* HIBBARD, 1956 and *Mictomys vetus*. Surprisingly, in spite of the difference of the type of Schmelzmuster in these early North American lemmings and in later forms of both genera of bog lemmings, those authors also assigned subgenus *Pliotomys* to the genus *Synaptomys*. Thus, they referred the first form to *Synaptomys* (*Pliotomys*), and the second one

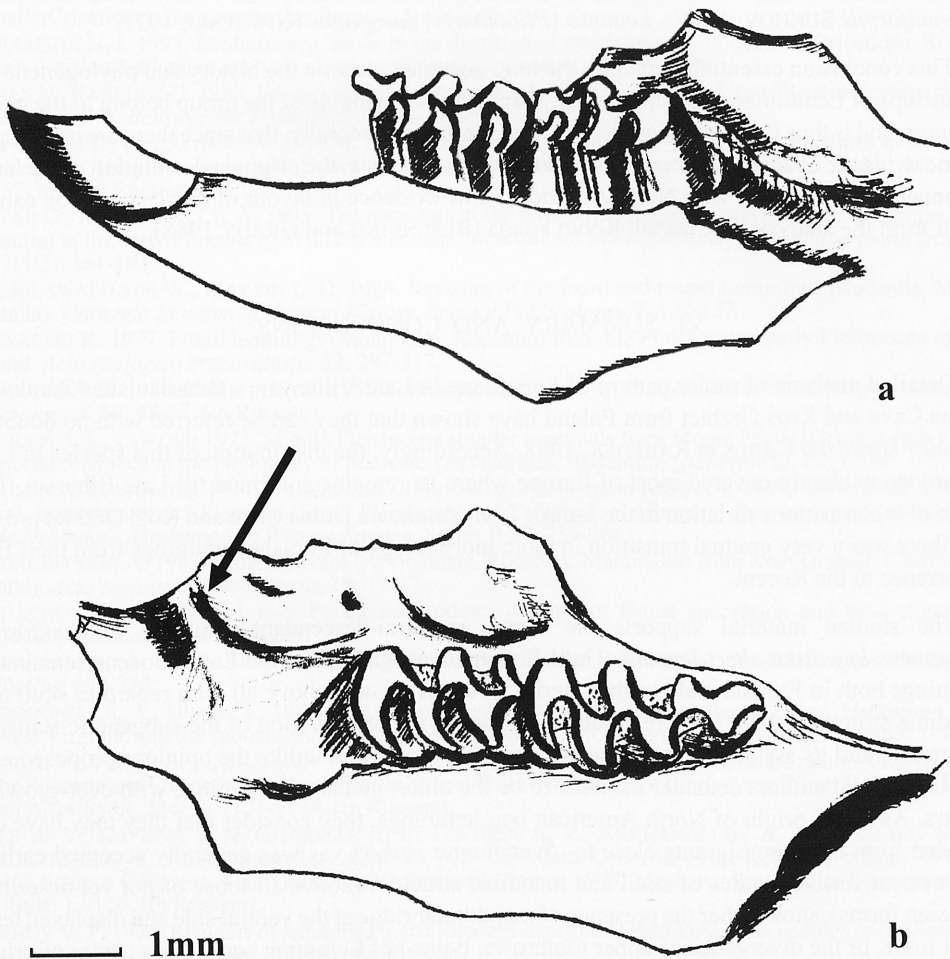


Fig. 5. The mandible structure in lemmings, medial view. a: Rębielice Królewskie 2, MF/1559/1; b: Zamkowa Dolna Cave. The arrow points to the ridge and temporal fossa. See text for explanation.

to *Mictomys* (*Metaxyomys*). REPENNING and GRADY (1988) demonstrated the origin of *Synaptomys* from a source other than *S. (Pliotomys) rinker* and raised subgenus *Pliotomys* to a full generic rank. Those authors also stressed that *Pliotomys* is not very different from the living genera of the Lemninae. In a later work (FEJFAR and REPENNING 1998: 180) it was definitely stated that “*Pliotomys* belongs to the tribe Lemmini, not to the tribe Synaptomyini”. The most radical viewpoint was presented by CARLS and RABEDER (1988) who assigned both “*Synaptomys (Pliotomys) mimomiformis*” and “*Synaptomys (Praesynaptomys) europaeus*” to the genus *Lemmus*, not distinguishing any subgeneric status. The data on the molar pattern variation set forth in the present paper are in accordance with the latter interpretation. However, taking into account the possible significant rearrangement of the mandible structure discussed above, before a comprehensive description of the lemming remains reported from Mongolia and Northeastern Siberia (ZAZHIGIN 1997) is given, it is reasonable to preserve the subgeneric status – *Pliotomys* SUKHOV, 1976 (= *Praesynaptomys* KOWALSKI, 1977) – for the first two forms of the line. Therefore, the present authors underline the important point in this transition, regarding the first Eurasian lemmings as *Lemmus (Pliotomys) mimomiformis* SUKHOV, 1976 – *Lemmus (Pliotomys) europaeus* KOWALSKI, 1977.

This conclusion essentially changes the long-accepted view on the history and phylogenetic relationships of Lemninae. It means, firstly, that the oldest remains of the group belong to the genus *Lemmus*, and is thus the most primitive genus in the group. Secondly, that since there are no remains and no evidence of any occurrence of bog lemmings in Eurasia, the origin and evolution of the latter is connected exclusively with North America. Some evidence in favour of this last opinion can be taken from the analysis of Cheetah Room Fauna (REPENNING and GRADY 1988).

VI. SUMMARY AND CONCLUSIONS

Detailed analysis of molar pattern of Lemninae in Late Villanyan – Biharian sites Zamkowa Dolna Cave and Kozi Grzbiet from Poland have shown that they can be referred with no doubt to *Lemmus kowalskii* CARLS et RABEDER, 1988. Accordingly, the distribution of this species in Late Villanyan evidently covered most of Europe where its remains are found till Late Biharian. The range of molar pattern variation in the sample from Zamkowa Dolna Cave and Kozi Grzbiet proves that there was a very gradual transition in tooth morphology of Eurasian lemmings from their first occurrence to the Recent.

The studied material supports the direct ancestral-descendant sequence *mimomiformis*–*europaeus*–*kowalskii*–*sheri*–*lemmus*. Until further investigations of the Late Pliocene remains of lemmings both in Eurasia and North America, are carried out (above all with regard to skull and mandible structure) there is more evidence favouring the preservation of the subgeneric status of *Pliotomys* and its assignation to the genus *Lemmus*. Therefore, unlike the opinions proposed earlier, the present authors consider *Lemmus* to be the oldest genus of Lemninae with ever-growing molars. As to the origin of North American bog lemmings, they consider that they may have descended from early immigrants close to *Synaptomys rinker*, as was generally accepted earlier. However, if further studies of skull and mandible structure (above all those of not yet described Eurasian forms), show either the presence of mandibular ridge at the ventral side and displayed temporal fossa, or the divergence of upper tooththrows, typical of Lemmini, some other centre of origin for bog lemmings will have to be considered. In the latter case a parallel development of tooth structure from cricetid ancestors, owing to similar food specialization, should not be excluded. It must be emphasized here that, unlike most of the discussed dental characters, reversals in characters connected with muscle strengthening should not be expected.

In Lemmini the main evolutionary trends are displayed in the skull and mandible structure rather than in the dentition, that shows very little change with time. The main apomorphic characters for Lemmini are progressive divergence of tooththrows, development of well-pronounced ridge at the ventral surface of mandible, temporal, and pterygoid fossa. The split of two recent genera of Lemmini, *Lemmus* and *Myopus*, cannot be traced in fossil record, because they are practically indistinguishable in all characteristics of the skull and dentition. However, since recent representatives of these genera differ dramatically in karyotype characteristics and biology, the generic rank for *Myopus schisticolor* (LILLJEBORG, 1844) should be retained, in spite of its having sometimes been included into genus *Lemmus* (KOENIGSWALD and MARTIN 1984; CARLS and RABEDER 1988).

REFERENCES

- ABRAMSON N. I. 1992. A new species of lemming from the Eopleistocene of North East Siberia (Mammalia: Cricetidae). *Zoosystematica Rossica*, **1**: 156-160.
- ABRAMSON N. I. 1993. Evolutionary trends in the dentition of true lemmings (Lemmini, Cricetidae, Rodentia): functional-adaptive analysis. *Journal of Zoology*, London, **230**: 687-699.
- CARLS N., RABEDER G. 1988. Die Arvicoliden (Rodentia, Mammalia) aus dem Ältest-Pleistozän von Schernfeld (Bayern). *Beiträge zur Paläontologie von Österreich*, **14**: 123-237.
- DEVYATKIN E. V., ZAZHIGIN V. S. 1974. Eopleistocene deposits and new mammalian localities in Northern Mongolia. [In:] *Mesozoic and Cenozoic Faunas and Biostratigraphy of Mongolia*. Nauka, Moscow: 357-363. (In Russian).
- FEJFAR O., REPENNING Ch. A. 1998. The ancestors of the lemmings (Lemmini, Arvicolinae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near Frankfurt am Main, Germany. *Senckenbergiana lethaea*, **77**(1/2): 161-193.
- KOENIGSWALD von W., MARTIN L. D. 1984. Revision of the fossil and recent Lemminae (Rodentia, Mammalia). *Carnegie Museum of Natural History, Special Publications*, **9**: 122-137.
- KOWALSKI K. 1977. Fossil lemmings (Mammalia, Rodentia) from the Pliocene and early Pleistocene of Poland. *Acta zoologica cracoviensia*, **22**: 297-317.
- MALEEVA A. G. 1976. On the microtine (Microtinae) teeth variability. *Proceedings of the Zoological Institute, Leningrad*, **66**: 48-57. (In Russian).
- MEULEN A. L. VAN DER 1973. Middle Pleistocene smaller mammals from Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria*, **17**: 1-144.
- MEULEN A. L. VAN DER 1974. On *Microtus (Allophaiomys) deucalion* KRETZOI, 1969 (Arvicolidae, Rodentia), from the upper Villanyian (lower Pleistocene) of Villany 5, S. Hungary. *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen, Series B* **77**: 259-266.
- NADACHOWSKI A. 1985. Biharian voles (Arvicolidae, Rodentia, Mammalia) from Kozi Grzbiet (Central Poland). *Acta zoologica cracoviensia*, **29**: 13-27.
- NADACHOWSKI A. 1990a. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. *Quaternary Palaeontology*, **8**: 215-223.
- NADACHOWSKI A. 1990b. Review of fossil Rodentia from Poland (Mammalia). *Senckenbergiana Biologica*, **70**(4/6): 229-250.
- REPENNING Ch. A., GRADY F. 1988. The microtine rodents of the Cheetach Room Fauna, Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys*. *U.S. Geological Survey Bulletin*, **1853**: 1-32.
- SHER A. V., VIRINA E. L., ZAZHIGIN V. S. 1977. The stratigraphy, paleomagnetism and mammalian fauna of the Pliocene and Lower Quaternary deposits around the lower reaches of the Kolyma River. *Doklady Akademii Nauk SSSR*, **234**(5): 1171-1174. (In Russian).
- SHER A. V., KAPLINA T. N., GITERMAN R. E., LOZHKIN A. V., ARKHANGELOV A. A., KISELYOV S. V., KOUZNETSOV Y. V., VIRINA E. L., ZAZHIGIN V. S. 1979. Late Cenozoic of the Kolyma lowland: XIV Pacific Science Congress, Tour Guide XI, Khabarovsk, August 1979. Moscow, Academy of Sciences of the USSR: 1-116. (In Russian).
- SUKHOV V. P. 1976. Remains of lemmings in the Pliocene deposits of Bashkiria. *Proceedings of the Zoological Institute, Leningrad*, **66**: 117-121. [In Russian].
- TOMIDA Y. 1987. Small mammal fossils and correlation of continental deposits, Safford and Duncan basins, Arizona, USA. National Science Museum, Tokyo, **IX**: 141.
- ZAZHIGIN V. S. 1997. Late Pliocene and Pleistocene rodent faunas in the Kolyma Lowland: possible correlations with North America. [In:] M. E. EDWARDS, A. V. SHER, R. D. GUTHRIE (eds) – *Terrestrial paleoenvironmental studies in Beringia*, University of Alaska, Fairbanks, 25-29.

