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Fossil Lemmings (*Mammalia, Rodentia*) from the Pliocene and Early Pleistocene of Poland *

[Pp. 297—318, with 6 text-figs.]

Kopalne lemingi (*Mammalia, Rodentia*) z pliocenu i wczesnego plejstocenu Polski

Abstract. *Synaptomys (Praesynaptomys) europaeus* subg. n. sp. n. from the fauna of the Middle Villafranchian of Rębielice Królewskie I and II is described. It is the oldest member of the genus, whose origin in the Palaearctic it indicates, and at the same time the oldest form of the *Arvicolidae* with rootless teeth in Europe. *Lemmus lemmus* (Linnaeus 1758) occurs in Poland from the beginning of the Pleistocene till the Mindel glaciation; it shows only a slight evolution in the pattern of molars and remarkable fluctuations in size. In the fauna of Kozi Grzbiet (Mindel I/Mindel II) the genus *Dicrostonyx*, represented by *D. simplicior* Fejfar 1966, appears for the first time in Poland. In addition to descriptions, measurements, and drawings of the forms under study, this paper contains a discussion of their systematic position, and, in the light of new finds, of the evolution of lemmings in the Holarctic.

INTRODUCTION

The occurrence of fossil remains of lemmings belonging to the genera *Dicrostonyx* Gloger 1841 and *Lemmus* Link 1795 in Europe was ascertained more than a hundred years ago (Hensel 1855, Sanford 1870) and they have been regarded as typical components of the cool fauna of the Pleistocene ever since. As the stratigraphy of the Quaternary was worked out, it appeared possible to refer all the older finds of these rodents to the last Pleistocene glaciation in Europe. It was also found that the European lemmings of that time belonged to the species that still live in the Arctic nowadays: *Dicrostonyx torquatus* (Pallas 1779) and *Lemmus lemmus* (Linnaeus 1758). Their southernmost

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

European range in the Pleistocene is given, among other authors, by JANOSSY (1954) and CHALINE (1973).

It is only recently that fairly numerous records of the occurrence of the genera *Lemmus* and *Dicrostonyx* in Europe during the older Pleistocene glaciations began to appear in literature. TERZEA (1972) give a list of *Lemmus* remains from the Early and Middle Pleistocene in Europe. Data concerning the oldest occurrence of the genus *Dicrostonyx* have been published by JANOSSY (1965), FEJFAR (1965, 1966), HELLER and BRUNNACKER (1966), BOURDIER, CHALINE and PUISSEGUR (1969), CHALINE (1972) and MEULEN and ZAGWIJN (1974).

The remains of the genus *Lemmus* from the older periods of the Pleistocene in Europe were either assigned to the present-day species *Lemmus lemmus* or referred to as *Lemmus* sp. Many authors emphasize also that because of the similarity in the structure of teeth between the genera *Lemmus* and *Myopus* MILLER 1910 it cannot be determined for certain which of them is represented by the fossil specimens found in Early Pleistocene deposits.

The remains of the genus *Dicrostonyx* of Middle and Lower Pleistocene age differ from the contemporary species and were assigned to the species *D. simplicior* FEJFAR 1966 and *D. antiquitatis* CHALINE 1972.

In the territory of the U. S. S. R. the remains of *Lemmus* of Early Pleistocene age are known from the western Ukraine (PIDOPLICHKO 1956) and Siberia (AGADJANIAN and MOTUZKO 1971, SHER 1971). Early Pleistocene remains of *Dicrostonyx* have been recorded from Siberia (SHER 1971, VANGENGEIM and ZAZHIGIN 1972, AGADJANIAN 1971, 1972, 1973, 1976). GUTHRIE and MATTHEWS (1971) described a new genus and species, *Praedicrostonyx hopkinsi*, from the Early Pleistocene Cape Deceit formation in Alaska and ascertained the presence of *Lemmus* there. In North America *Dicrostonyx* is known, in addition to Alaska, only from a few Late Pleistocene localities lying outside the present range of its occurrence (GUILDAY 1963). Out of Alaska, the fossil remains of *Lemmus* have been found nowhere in North America.

It follows that the genus *Dicrostonyx*, its ancestor *Praedicrostonyx* and the genus *Lemmus* are now known from numerous localities representing early periods of the Pleistocene in Europe, Asia and also in Alaska, althought the materials found are generally very scanty and, what is more, not all of them have been described (in many papers there are only remarks upon their occurrence).

Among the lemmings *(Lemmi)* we number also other two of now living genera. *Myopus* inhabits the boreal forests of Eurasia. Its remains are known exclusively from East Asia: from the period of penultimate glaciation of Japan (KOWALSKI and HASEGAWA 1976) and from the latest Pleistocene of eastern Siberia (VINOGRADOV 1922).

Synaptomys BAIRD 1857 is an ecological counterpart of the genus *Myopus* in North America. Numerous fossil species of this genus are known from North America, also from beyond its present range, as far in the south as Mexico (ZBYSZEWSKI 1972). REPENNING (1967) supposes that, although this genus lives only in America now, it comes from Eurasia. DEVIATKIN and ZAZHIGIN (1974) mention the occurrence of a form related to *Synaptomys* at Burial-Obo in Mongolia, but they do not give its description.

In the territory of Poland the occurrence of *Lemmus lemmus* and *Dicrostonyx torquatus* has been found at numerous localities referred to the last glaciation (Würm) and also those of Riss glaciation age. On the basis of information obtained from the author of the present paper TERZEA (1972) mentions the occurrence of *Lemmus lemmus* in the Lower Pleistocene fauna of Kamyk (Günz) and CHALINE (1973) writes about the presence of this species in the Pliocene (Middle Villafranchian) fauna of Rębielice Królewskie I.

A series of local faunae of small mammals, ranging in age from the Lower Pliocene to the Middle Pleistocene (Mindel), are known in Poland nowadays. Lemming remains have been discovered in eight out of these faunae (Rębielice Królewskie I and II, Zamkowa Dolna Cave, Kadzielnia, Kamyk, Kielniki, Zalesiaki and Kozi Grzbiet). KOWALSKI (1975) published a preliminary report on them and added the characteristics of the total faunae containing lemmings. In discussing the origin of the arctic mammal fauna, KOWALSKI (1977) mentioned the occurrence of the genus *Synaptomys* at Rębielice Królewskie.

The purpose of this paper is to present a description of the remains of lemmings occurring in the fossil faunae of Poland from the Pliocene (Middle Villafranchian) to the Mindel glaciation.

All the fossil materials described in this paper are in the possession of the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, in Cracow.

The author is very much indebted to Dr. Wighart von KOENIGSWALD from Tübingen for the comparative material of the genera *Dicrostonyx* and *Lemmus* from Canada and to Dr. Karl FREDGA from Lund for the specimens of *Myopus* from Sweden.

SYSTEMATIC PART

Family *Arvicolidae* GRAY 1821
Genus *Synaptomys* BAIRD 1857
Subgenus *Praesynaptomys* subg. nov.
Synaptomys (Praesynaptomys) europaeus sp. n.
(text-fig. 1)

Name derivation: *Praesynaptomys* — ancestor of *Synaptomys*; *europaeus* — occurring in Europe.

Holotype: left half of mandible with $M_1 - M_2$ from Rębielice Królewskie I in Poland (Middle Villafranchian), No. MF/1558/1.

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

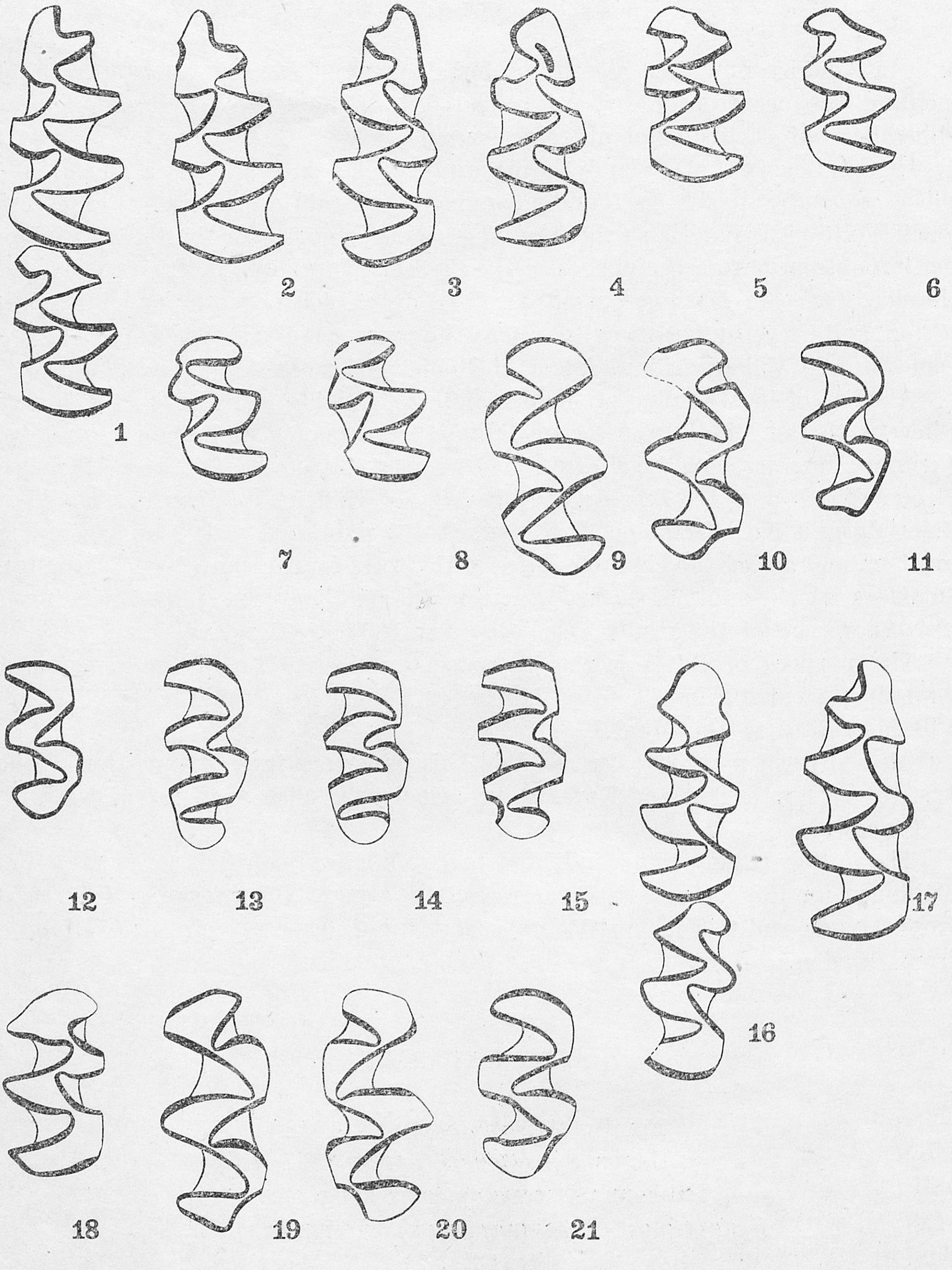

Fig. 1. *Synaptomys (Praesynaptomys) europaeus* subg. n. sp. n. 1—15 Rębielice Królewskie I, 16—21 — Rębielice Królewskie II. 1 — M_1 — M_2 (holotype), MF/1558/1, L = 4.7 mm; 2 — M_1, MF/1558/2, L = 2.85 mm; 3 — M_1, MF/1558/3, L = 2.9 mm; 4 — M_1, MF/1558/4, L = 2.8 mm; 5 — M_2, MF/1558/5, L = 1.9 mm; 6 — M_2, MF/1558/6, L = 1.85 mm; 7 — M_3, MF/1558/7, L = 1.65 mm; 8 — M_3, MF/1558/8, L = 1.7 mm; 9 — M^1, MF/1558/9, L = 2.7 mm; 10 — M^1, MF/1558/10, L = 2.4 mm; 11 — M^2, MF/1558/11, L = 1.95 mm; 12 — M^2, MF/1558/12, L = 1.8 mm; 13 — M^3, MF/1558/13, L = 2.2 mm; 14 — M^3, MF/1558/14, L = 2.2 mm; 15 — M^3, MF/1558/15, L = 2.1 mm; 16 — M_1 — M_2, MF/1559/1, L = 4.7 mm; 17 — M_1, MF/1559/2, L = 3.2 mm; 18 — M_2, MF/1559/3, L = 2.1 mm; 19 — M^1, MF/1559/4, L = 2.6 mm; 20 — M^1, MF/1559/5, L = 2.6 mm; 21 — M^2, MF/1559/6, L = 2.1 mm

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

Description. The incisor, situated over its whole length on the internal side of the mandible, reaches half-way along M_3. The molars are rootless. Cement is present in the re-entrant angles.

The M_1 consists of a posterior loop, three triangles and an anterior loop. On the internal side of the anterior loop there may be a well-developed re-entrant, sometimes filled with cement. In other specimens this re-entrant is shallow, devoid of cement, or hardly marked. On the external side of the anterior loop there is no re-entrant or only a slight depression. All the triangles are isolated and not confluent with the posterior and anterior loops. The tooth is slightly asymmetrical: the middle (external) triangle is smaller than the internal triangles. The enamel layer is of more or less the same thickness on the anterior and posterior walls of the triangles, being thinner at the bottom of the re-entrants. There is no enamel on the external surface of the anterior loop and on the external wall of the middle triangle and posterior loop. On the internal side the dentine tracks are usually visible at the tops of the triangles and at the projecting end of the anterior loop.

The M_2 is composed of an oval posterior loop, two closed triangles and an anterior loop, which is broadly confluent with the anterior internal triangle. Also the dentine tracks are distinct on the external side of this tooth.

The M_3 has an oval anterior loop, two triangles and a posterior loop.

The M^1 has its occlusal surface composed of five isolated dentine fields and the M^2 of four.

The M^3 consists of an anterior loop, three triangles and a posterior loop, which lacks enamel all over its external side. The antero-external triangle is closed or only slightly confluent with the external triangle, whereas the posterior triangle always fuses more or less extensively with the reduced internal triangle.

Dimensions: see Table I.

Discussion. The described remains belong undoubtedly to a lemming, because the incisor is situated on its entire length on the internal side of the mandible. The molar pattern brings them nearest to the genus *Synaptomys*. They differ from the genus *Dicrostonyx*, in addition to the completely different pattern of molars, in the presence of cement in the re-entrants. From the genera *Lemmus* and *Myopus* they differ in the structure of M^3 since in these last genera the two middle fields of dentine on this tooth are connected in the region of the tooth axis.

No doubt the subgenus *Praesynaptomys* is the most primitive in the genus *Synaptomys*, which is particularly well seen in the structure of M^3. The genus *Synaptomys* has an evolutionary tendency towards the increasing asymetry of molars and in this connection the external triangles of the lower molars and the internal triangles of the upper molars undergo a reduction. In the M^3 the reduction affects the middle triangle. In *Praesynaptomys* this triangle remains distinct, although it is smaller than the external ones. In the recent subgenera of *Synaptomys* the progressive reduction of this triangle brought about its disappearance and also the disappearance of the internal re-entrants. In consequence, the two external triangles form transverse fields of dentine, which extend all across the tooth and touch each other at its internal margin.

Table I

Dimensions of molars in *Synaptomys europaeus* (in mm)

		Rębielice Królewskie I				Rębielice Królewskie II			
		n	min	m	max	n	min	m	max
M_1	L	9	2.48	2.74	2.91	4	2.65	2.99	3.25
	W	9	1.15	1.22	1.30	4	1.24	1.31	1.37
M_2	L	9	1.82	1.96	2.05	2	2.05	2.055	2.06
	W	9	1.11	1.13	1.19	2	1.00	1.09	1.19
M_3	L	5	1.51	1.66	1.77	1	—	1.66	—
	W	5	0.81	1.00	1.10	1	—	0.97	—
M^1	L	5	2.38	2.51	2.68	7	2.61	2.70	2.85
	W	5	0.95	1.00	1.08	7	0.93	1.01	1.11
M^2	L	7	1.80	1.93	2.06	5	2.02	2.09	2.23
	W	7	0.87	1.01	1.07	6	1.00	1.06	1.10
M^3	L	5	1.93	2.06	2.17	—	—	—	—
	W	5	0.84	0.96	1.06	—	—	—	—

Out of three American subgenera of *Synaptomys*, the extinct subgenus *Metaxyomys* Zbyszewski 1972 is the most primitive. In its M^3 the vestigial internal triangle is still preserved, although it is broadly confluent with the two external triangles. This subgenus, in addition, shows a specialization leading to the confluence of the fields of dentine in the M_1. In the subgenus *Synaptomys* the external re-entrant of M^3, between two triangles, which have already the form of antero-posteriorly narrowed fields of dentine here, reaches nearly as far as the internal margin of the tooth. This process is best seen in the subgenus *Mictomys* True 1894, in which the external re-entrant reaches the margin of the tooth, and not a trace of the internal triangle has been preserved (Fig. 6).

The presence of *Synaptomys* at Rębielice is the oldest sign of the existence of this genus, which at the same time is the oldest member of the *Arvicolidae* with ever-growing rootless molars in Europe. It indicates that the genus *Synaptomys* — as Repenning supposed as early as 1967 — originated in the Palaearctic, whence it colonized North America later. In the Old World this genus was soon ousted by the genus *Lemmus*, which had appeared here at the beginning of the Pleistocene, whereas in North America it continued evolving and differentiating and has persisted up to now.

The specimens from Rębielice Królewskie II have somewhat larger dimensions than those from Rębielice Królewskie I (Table I). Unfortunately, lack of an M^3 at Rębielice Królewskie II makes it impossible to estimated which of the two populations is more primitive. There are no morphological differences between the remaining preserved teeth.

Genus *Lemmus* LINK 1795
Lemmus lemmus (LINNAEUS 1758)
(text-figs. 2—4)

Material: Zamkowa Dolna Cave, layer C (Late Middle Villafranchian) (MF/1566): 2 halves of mandibles with M_1 — M_2, 146 isolated M_1, a large number of other isolated molars and their fragments.

Kadzielnia (Upper Villafranchian) (MF/1567): fragmentary half of mandible with M_1, 1 M^1, 1 molar-fragment.

Kielniki (Günz) (MF/1568): 1 M_1, 1 M^2, 1 molar-fragment.

Kamyk (Günz) (MF/1569): 7 M_1 and other molars.

Rębielice Królewskie I (younger material, probably Cromerian) (MF/1570): 8 M_1 and other molars.

Zalesiaki (Cromerian?) (MF/1571): 2 halves of mandibles with M_1, 15 M_1 and other molars.

Kozi Grzbiet (Mindel I/Mindel II); layer 2c (MF/1572): 12 M_1 and other molars; layer 2b (MF/1573): 2 M_1 and other molars; layer 2a (MF/1574): 4 M_1 and other molars; layers 2b+c (MF/1575): 1 M_1 and other molars; layers 2a+b+c (MF/1576): 3 M_1 and other molars; material of undetermined stratigraphic position (MF/1577): 4 M_1 and other molars.

Description. The mandible and molars do not differ in structure from those of *Lemmus lemmus* from the Late Pleistocene of Poland and from the recent material of this species from Scandinavia, U. S. S. R. and Canada. The variability of the occlusal surface pattern of molars is conspicuous, but it corresponds with the variability observed in the above-mentioned comparative material. Only the population from Zamkowa Dolna Cave differs from all the other populations, namely, in that in M^3 the re-entrant angles are wider and more obtuse, the dentine-triangles more distinct and not so completely transformed into transverse dentine fields as they are in the younger materials.

Dimensions: see Table II and the diagram in text-fig. 4.

Discussion. The first known occurrence of *Lemmus lemmus* in the Polish fossil faunae is that in the layer C of Zamkowa Dolna Cave at Olsztyn near Częstochowa. This fauna is younger than the fauna of Rębielice Królewskie I and II and it points to a marked cooling of the climate. Except for *Lemmus lemmus* this fauna contains no voles with permanently growing teeth. CHALINE'S (1973) statement of the presence of *Lemmus lemmus* in the Middle Villafranchian fauna of Rębielice Królewskie I is a mistake caused by the occurrence of the previously unrecognized species *Synaptomys (Praesynaptomys) europaeus* sp. n.

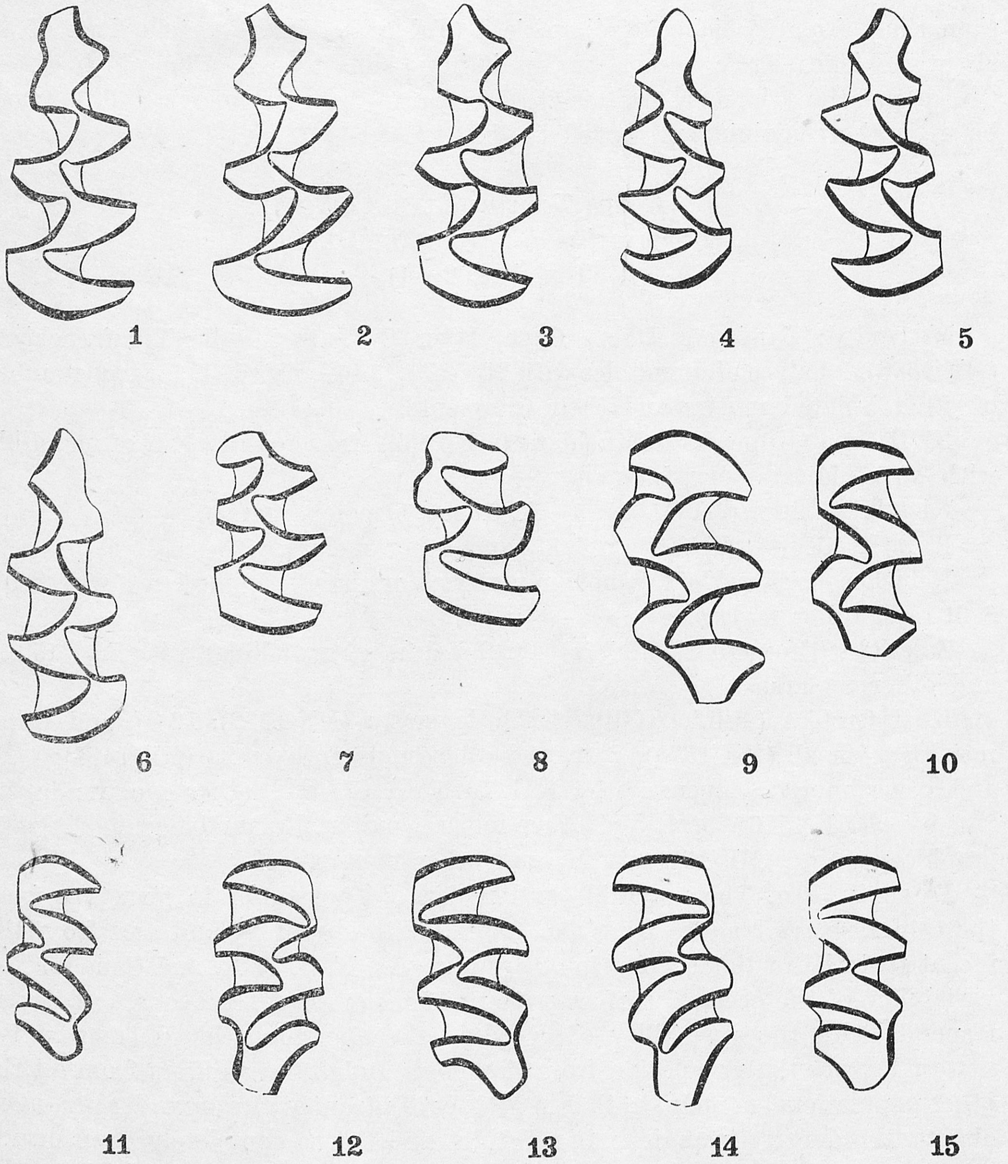

Fig. 2. *Lemmus lemmus*. Zamkowa Dolna Cave, layer C. 1 — M_1, MF/1566/1, L = 3.4 mm; 2 — M_1, MF/1566/2, L = 3.4 mm; 3 — M_1, MF/1566/3, L = 3.3 mm; 4 — M_1, MF/1566/4, L = 3.0 mm; 5 — M_1, MF/1566/5, L = 3.15 mm; 6 — M_1, MF/1566/6, L = 3.5 mm; 7 — M_2, MF/1566/7, L = 2.15 mm; 8 — M_3, MF/1566/8, L = 2.2 mm; 9 — M^1, MF/1566/9, L = 3.0 mm, 10 — M^2, MF/1566/10, L = 2.2 mm, 11 — M^3, MF/1566/11, L = 2.2 mm; 12 — M^3, MF/1566/12, L = 2.6 mm; 13 — M^3, MF/1566/13, L = 2.6 mm; 14 — M^3, MF/1566/14, L = 2.8 mm; 15 — M^3, MF/1566/15, L = 2.45 mm

at this locality and at the same time the occurrence of an admixture of a younger, probably Cromerian, fauna with *Lemmus lemmus*. This admixture comes from the layer of sand overlying the clay in which the fauna of Middle Villafranchian

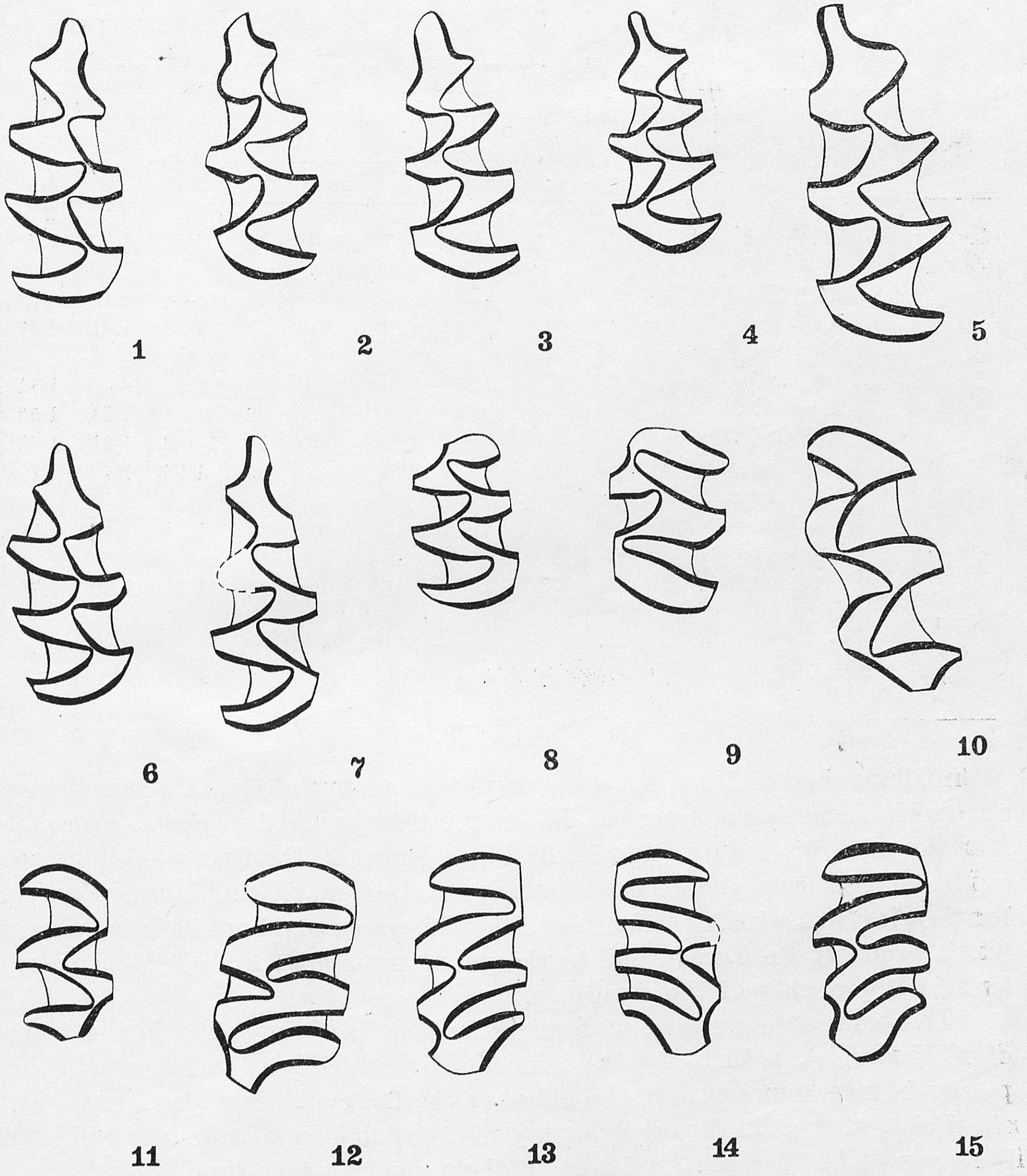

Fig. 3. *Lemmus lemmus*. 1 — Kamyk, 2 — Kielniki, 3—15 — Kozi Grzbiet. 1 — M_1, MF/1569/1, L = 3.2 mm, 2 — M_1, MF/1568/1, L = 3.0 mm; 3 — M_1, MF/1572/1, L = 3.1 mm; 4 — M_1, MF/1572/2, L = 3.0 mm; 5 — M_1, MF/1577/1, L = 3.8 mm; 6 — M_1, MF/1574/1, L = 2.95 mm, 7 — M_1, MF/1573/1, L = 3.2 mm; 8 — M_2, MF/1572/3, L = 2.0 mm; 9 — M_3, MF/1572/4; L = 2.1 mm; 10 — M^1, MF/1572/5, L = 3.0 mm, 11 — M^2, MF/1572/6, L = 2.0 mm; 12 — M^3, MF/1572/7, L = 2.5 mm; 13 — M^3, MF/1572/8, L = 2.4 mm; 14 — M^3, MF/1575/1, L = 2.3 mm 15 — M^3, MF /1577/1, L = 2.4 mm

age was found. Only *Synaptomys* occurs at Rębielice Królewskie II, which is situated in the neighbourhood of Rębielice Królewskie I and represents the same period as its main fauna.

Table II

Dimensions of M_1 in *Lemmus lemmus* and *Myopus schisticolor* (in mm)

Species	Locality	Length				Width			
		n	min	m	max	n	min	m	max
Lemmus lemmus	Zamkowa Dolna Cave	89	2.60	3.17	3.83	83	1.17	1.39	1.60
	Kadzielnia	1	—	3.92	—	1	—	1.30	—
	Kielniki	1	—	2.97	—	1	—	1.18	—
	Kamyk	3	2.98	3.23	3.63	3	1.34	1.41	1.47
	Rębielice Królewskie I (Cromerian material)	2	3.17	—	3.18	2	1.25	—	1.41
	Zalesiaki	8	2.75	3.08	3.37	7	1.31	1.24	1.55
	Kozi Grzbiet	10	2.90	3.12	3.80	10	1.12	1.31	1.62
	Raj Cave, Early Würm	65	2.69	3.25	3.92	65	1.06	1.45	1.70
	Mamutowa Cave, Late Würm	33	2.90	3.20	3.66	33	1.12	1.42	1.70
	Banks Is., Canada (Recent)	27	2.90	3.52	4.04	26	1.21	1.60	1.78
Myopus schisticolor	Sweden (Recent)	11	2.59	2.69	2.91	11	1.13	1.19	1.26

Small numbers of *Lemmus lemmus* occur in the fauna of Upper Villafranchian age (with *Mimomys pliocaenicus* F. Major 1902 and *Allophaiomys deucalion* Kretzoi 1959) from Kadzielnia at Kielce and next in the faunae of Günz age (with *Allophaiomys pliocaenicus* Kormos 1933) from Kielniki and Kamyk. Further, it is met with in the fauna of Zalesiaki, which could not be dated closely but is probably Cromerian, and in the younger material from Rębielice Królewskie I, probably of the same age.

The abundant occurrence of *Lemmus lemmus* has been found in the fauna of Kozi Grzbiet, referred to the Mindel I/Mindel II interstadial, where this species is most numerous in the oldest layer, 2c, containing also *Dicrostonyx simplicior*, whereas in the overlying layers it occurs in small numbers and even it may well be that the specimens in them come in fact from layer 2c.

Thus, *Lemmus lemmus* seems to have been a constant component of the faunae of small mammals in the territory of Poland from the beginning of the Pleistocene to the Mindel period and, moreover, it occurs in faunae which do not suggest an arctic environment but rather indicate a temperate climate with the presence of forest and steppe elements.

The population of Zamkowa Dolna Cave, geologically the oldest, has primitive characters, namely, the isolation of the triangles is better preserved in it, especially on M^3. However, on the whole, this species has been marked by very great conservatism and stability in morphology since the beginning of the Pleistocene, which has already been demonstrated in earlier papers. The dimensions of M_1 in the populations from the Early Pleistocene, differing from those of the Late Pleistocene and modern populations, have been regarded as its essential distinctive character (KOENIGSWALD 1970). It should be emphasized that the length and width of M_1 in *Lemmus lemmus* not only show very great individual variability but also change during its ontogenic development: young teeth are much smaller than the teeth of older specimens. Since the fossil population under study may comprise various proportions of young specimens, the differences in dimensions found (and even the means calculated from them) may be partly due to this factor. Attention has also been drawn to another character, i.e. the height of the tooth. Nevertheless, in fossil materials, in which we are as a rule concerned with detached teeth, whose thin walls of the lower part are more or less heavily crumbled, the height measured is always smaller than the actual height. In this connection rather the maximum values of the tooth height, and not the means and the minimum values, may be of systematic importance.

The dimensions of M_1 from the localities of the Early Pleistocene of Poland compared with those from the Late Pleistocene and recent materials are given in Table II and the diagram in Fig. 4. The height of M_1 is 3.4—5.5 mm, most frequently 4—5 mm, in the population from Zamkowa Dolna Cave, 3.2—5.0 mm in the specimens from Kozi Grzbiet, 3.5—6.5 mm (averaging 5.4 mm) in the recent *Lemmus lemmus* from Canada and 2.6—2.9 mm (averaging 2.7 mm) in *Myopus schisticolor* from Scandinavia.

As can be seen from Table II, the lemmings from Zamkowa Dolna Cave hardly differ in dimensions from those of the Late Pleistocene of Poland. The population from Kozi Grzbiet is distinctly smaller. The other series of specimens from the Early Pleistocene are too scanty to allow detailed characterization. The material from the Würm glaciation in Poland is somewhat larger than that from Kozi Grzbiet, but at the same time it is outsized markedly by the recent specimens of *Lemmus lemmus*. This indicates that the size of the population of *Lemmus lemmus* underwent cyclic changes of dimensions during the long periods of the Pleistocene in Europe, which was due to changes in the environment (e.g. those of the temperature) or perhaps also to the competition of other species. All the materials examined so far from both Poland and other European localities differ very much in size from the recent species *Myopus schisticolor* (LILLJEBORG 1844). The presence of the genus *Myopus* in the Pleistocene of Europe seems therefore hardly probable.

Both the morphological characters and dimensions permit the inclusion of all the materials of the genus *Lemmus* from Poland and other European countries in the modern species *Lemmus lemmus*, understood as comprising all the forms of this genus both from the Palaearctic and Nearctic. Although the study of variation in this species in the Pleistocene seems very interesting, the giving of separate systematic names to particular populations would not

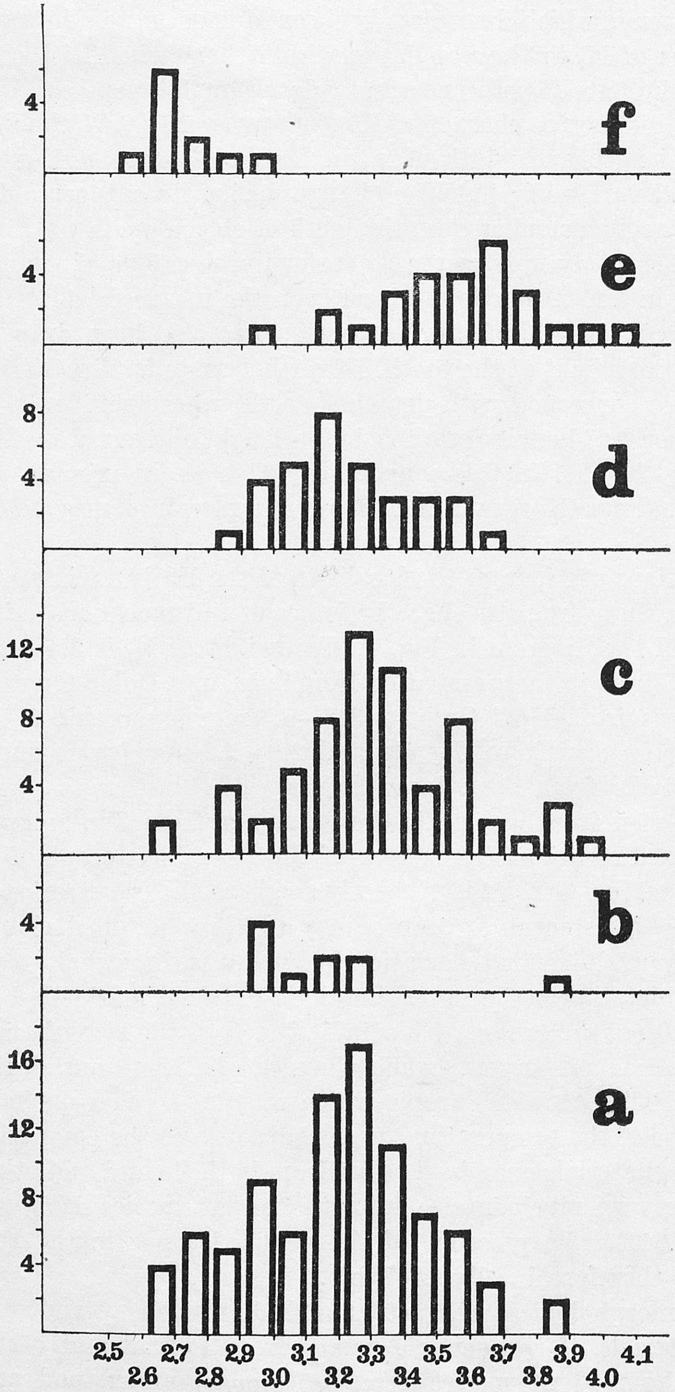

Fig. 4. Histograms showing length of M_1 in *Lemmus lemmus* (a-e) and *Myopus schisticolor* (f). a — Zamkowa Dolna Cave; b — Kozi Grzbiet; c — Raj Cave, Early Würm; d — Mamutowa Cave, Late Würm; e — Banks Is., Canada, Recent, f — *Myopus schisticolor*, Sweden, Recent. On the abscissa length of M_1 in mm, on the ordinate number of specimens

contribute anything to our knowledge of this variation, the more so since on account of the great conservatism of this species and its morphological uniformity it would not be possible to determine the membership of single specimens in the systematic units thus erected.

Genus *Dicrostonyx* GLOGER 1841
Dicrostonyx simplicior FEJFAR 1966
(text-fig. 5)

Material: Kozi Grzbiet (Mindel I/Mindel II), layer 2c (MF/1560): 2 fragments of mandibles with M_1, 10 M_1 and fragments of further 37 M_1, 14 M_2, 8 M_3, 9 M^1, 7 M^2, 21 M^3 or their fragments, numerous fragments of molars; layer 2b (MF/1561): 1 M_1, 2 M^2, 2 M^3; layer 2a (MF/1562): 1 M_1, 1 M_2, fragments of molars; layers 2b+c (MF/1563): 2 M_1, fragments of molars; layers 2a+b+c (MF/1564): 15 M_1 or their fragments, 3 M_2, 2 M_3, 5 M^1, 3 M^2, 6 M^3, numerous fragments of molars; material of undetermined stratigraphic position (MF/1565): 11 M_1, 5 M_2, 3 M_3, 3 M^2, 4 M^3.

Description. The whole incisor is situated on the lingual side of the mandible. The teeth are rootless and lack cement in the re-entrant angles. In the lower molars the enamel layer is considerably thicker on the anterior walls of the triangles than on the posterior, this situation being reversed in the upper teeth. Enamel is missing on the anterior wall of the anterior loop of M_1 and at the tops of all salient angles of molars.

The structure of the occlusal surface of molars is shown in Fig. 5. The M_1 consists of a posterior loop, seven distinctly alternating triangles and an anterior loop, which is usually simple and obliquely situated. The anterior loop has sometimes a more complicated structure (Fig. 5/4) or only slightly marked indent on either side (Fig. 5/5).

The M_2 much resembles the M^2 in structure, from which it can be distinguished by the more oblique position of the grinding surface in relation to the vertical tooth axis and by the somewhat arched lateral bend. This tooth consists of a posterior loop and four triangles, of which the anterior is the smallest. The anterior wall of the tooth lacks enamel. On the sides of the anterior loop of some specimens there are additional protrusions in the form of enamel ridges.

The M_3 has its grinding surface still more obliquely positioned in relation to the vertical tooth axis than has the M_2. It is composed of a posterior loop, three triangles, and a fourth rudimentary triangle in the front of the tooth.

The M^1 consists of a relatively narrow anterior loop and five triangles, of which the posterior is the smallest. At the end of the tooth, on the external side, there is, in addition, a sixth rudimentary triangle.

The M^2 is built of a broad anterior loop and four triangles, of which the posterior is the smallest. Moreover, there generally occurs the rudiment of a fifth field of dentine, oval in shape.

The M^3 is composed of an anterior loop, four triangles and a posterior loop,

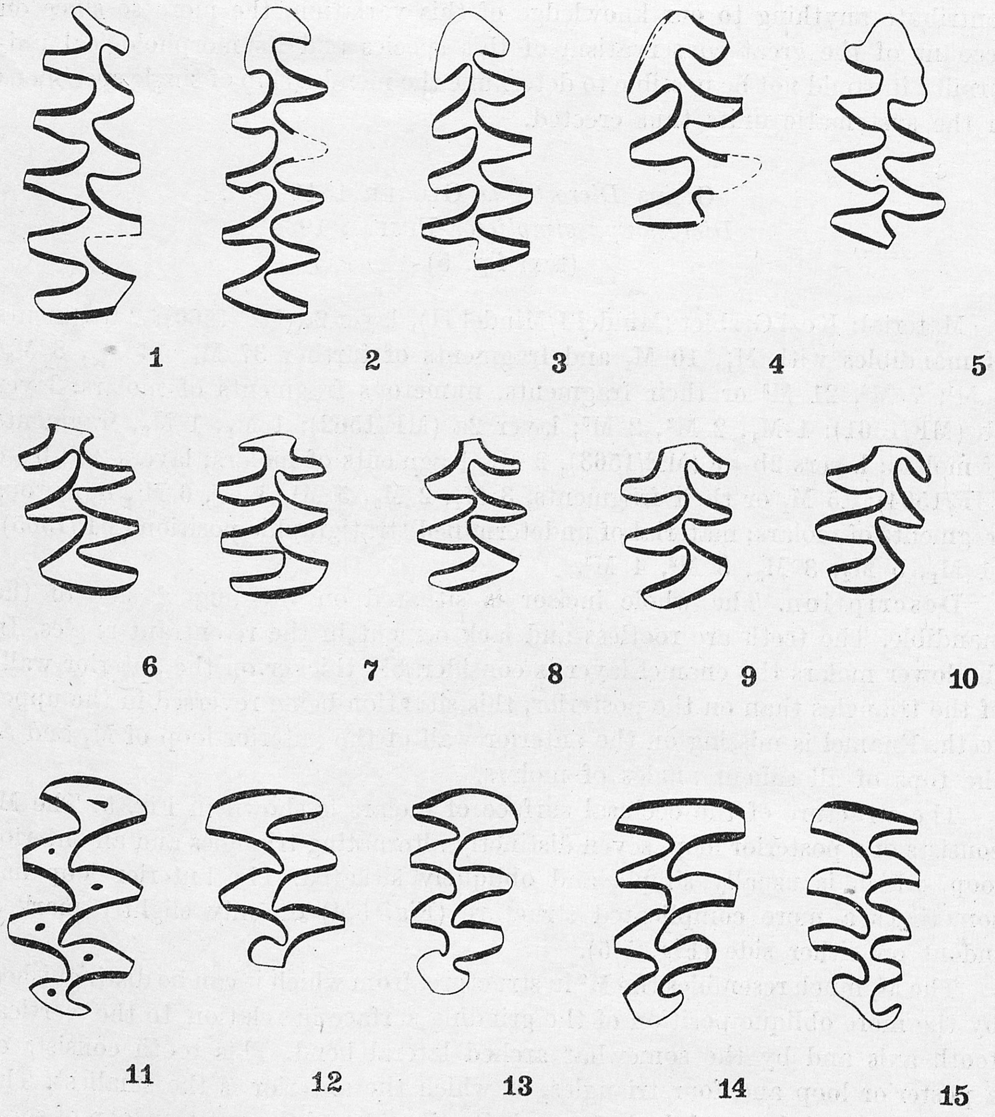

Fig. 5. *Dicrostonyx simplicior*, Kozi Grzbiet. 1 — M_1, MF/1564/1, L = 4.5 mm; 2 — M_1, MF/1565/1, L = 4.4 mm; 3 — M_1, MF/1560/1, L = 2.9 mm; 4 — M_1, MF/1560/2, L = 2.4 mm; 5 — M_1, MF/1564/2, L = 2.6 mm; 6 — M_2, MF/1560/3, L = 2.0 mm; 7 — M_2, MF/1560/4, L = 1.8 mm; 8 — M_2, MF/1560/5, L = 1.7 mm; 9 — M_3, MF/1560/6, L = 1.7 mm; 10 — M_3, MF/1560/7, L = 1.7 mm; 11 — M^1, MF/1560/8, L = 2.65 mm; 12 — M^2, MF/1560/9, L = 2.0 mm; 13 — M^3, MF/1560/10, L = 2.2 mm; 14 — M^3, MF/1560/11, L = 2.5 mm; 15 — M^3, MF/1564/3, L = 2.5 mm

the shape of this last being very variable. It may be very simple, round, or bent like a hook (Fig. 5/13—15).

Dimensions: see Table III.

Discussion. Most of the specimens described here from Kozi Grzbiet come from the lowest fossil-bearing layer of this locality, designated as 2c, or from the materials containing mixt bones from different layers, including layer 2c. A small number of specimens from layers 2b and 2a may in fact come also from layer 2c, for the lack of clear-cut boundary lines between the layers and their small thickness make the exact division of this material impossible. Anyhow, this species is most numerous in the bottom part of the profile, dating from the decline of the Mindel I glaciation.

Table III

Dimensions of molars in *Dicrostonyx simplicior* from Kozi Grzbiet (in mm)

Tooth	Length				Width			
	n	min	m	max	n	min	m	max
M_1	8	3.16	3.47	3.80	7	1.09	1.17	1.27
M_2	23	1.62	1.80	2.03	23	1.07	1.17	1.29
M_3	14	1.50	1.64	1.77	14	0.82	1.02	1.22
M^1	13	2.36	2.71	3.07	13	1.05	1.17	1.26
M^2	11	1.91	2.03	2.21	11	1.21	1.32	1.42
M^3	16	1.85	2.30	2.55	16	1.11	1.26	1.51

Table IV

Dimensions of first lower molar (m_1) in *Dicrostonyx* (in mm)

Locality	M_1							
	Length				Width			
	n	min	m	max	n	min	m	max
Dicrostonyx simplicior Kozi Grzbiet	8	3.16	3.47	3.80	7	1.09	1.17	1.27
Dicrostonyx torquatus, Koziarnia Cave, Poland Layer II (Late Würm)	50	3.13	3.61	3.95	50	1.07	1.31	1.45
Dicrostonyx torquatus, Banks Island, Canada Recent	30	3.04	3.38	3.78	30	1.08	1.21	1.39

The relatively simple structure of the teeth, in which the accessory elements on the anterior wall of the lower teeth and on the posterior wall of the upper ones are poorly developed, refers these specimens to the species *Dicrostonyx simplicior*. AGADJANIAN (1973, 1976) demonstrated that in the fossil and modern populations of *Dicrostonyx* there occur teeth showing different degrees of development of the accessory elements and that the proportion of particular types varies with geological age. The simplest teeth (AGADJANIAN'S types I and II) represent the whole of the population of Mindel age and the populations assigned by that author to the Riss period. Besides these teeth, simple in structure, the populations of the last glaciation (Würm) have also teeth marked by a more complex structure, whereas in the modern specimens of *Dicrostonyx torquatus* from the Palaearctic all the teeth have a complex structure, with the accessory elements present. On the other hand, *Dicrostonyx hudsonius* (PALLAS 1778) from Labrador has a simple structure of molars, very similar to that od *D. simplicior*.

The size of *D. simplicior* from Kozi Grzbiet is somewhat smaller than that of *D. torquatus* from the period of Würm glaciation in Poland and larger than the size of the recent specimens of *D. torquatus* from Canada (Table IV).

EVOLUTION OF LEMMINGS

The lemmings (tribe *Lemmini* SIMPSON 1945), which comprise the modern genera *Dicrostonyx*, *Synaptomys*, *Lemmus* and *Myopus* and the extinct genus *Praedicrostonyx*, are an artificial polyphyletic group. The only character that unites the genera *Praedicrostonyx* and *Dicrostonyx* with the genera *Synoptomys*, *Lemmus* and *Myopus* is the position of the lower incisor. In the *Lemmini* the whole of this tooth extends on the internal side of the mandible and it is relatively short, whereas in all the remaining *Arvicolidae* it passes under the row of lower molars on to the external side of the mandible, reaching as far as its ascending ramus. This character of lemmings was generally considered to be primitive. However, the position of the incisor in the lemmings must be regarded as secondary, because in the *Cricetidae*, which are undoubtedly ancestral to the *Arvicolidae*, this tooth passes under the row of molars on to the external side of the mandible. It may be supposed that the shortening of the incisor took place independently in the *Praedicrostonyx Dicrostonyx* group on the one hand and in the *Synaptomys-Lemmus-Myopus* group on the other. In both these groups it was connected with the lengthening of the molars and their attainment of faculty for permanent growth. In the other groups of the *Arvicolidae* this character developed in the Middle Pleistocene, and so considerably later and in a different way, without the shortening of the incisor. This very early attainement of the permanent growth of molars in both groups of lemmings may be thought to have been due to their adaptation to feeding on green plant tissue of low nutritional value in the arctic zone as early as the Pliocene. The ancestors of both these groups were primitive *Arvicolidae* as yet unknown, with the limited growth of molars and the incisor passing on to the external side of the mandible.

In the *Synaptomys-Lemmus-Myopus* group *Synaptomys (Praesynaptomys) europaeus* sp. n. from the Pliocene (Middle Villafranchian) of Poland is the oldest and most primitive form known. Its M^3 is built of distinctly alternating triangles, although the tendency to reduction of the internal triangle typical of *Synaptomys* is already noticeable. It may be supposed that the common ancestor of the genera *Synaptomys* and *Lemmus* had the M³ with a well-developed internal triangle of dentine (Fig. 6). In the further evolution of *Synaptomys*, in which the subgenera *Metaxyomys*, *Synaptomys* and *Mictomys* formed a conspicuous adaptive sequence, although they do not necessarily represented one and the same evolutionary line, the middle triangle of M³ underwent a complete reduction, as the assymmetry of this tooth developed. The development of the genus *Lemmus*, which undoubtedly form a sister group to the genus *Synaptomys*, proceeded in another way. Here, the middle triangle was not reduced but it fused with the posterior external triangle. The M³ is not asymetrical and the junction of two middle fields of dentine, which extend all across the tooth, is not situated at the internal edge of the tooth, as in *Synaptomys*, but near its axis. In the oldest members of the genus *Lemmus* (e.g. those from Zamkowa Dolna Cave) the internal triangle keeps a higher degree of independence and the junction of two middle fields of enamel often lies closer to the internal edge of the tooth.

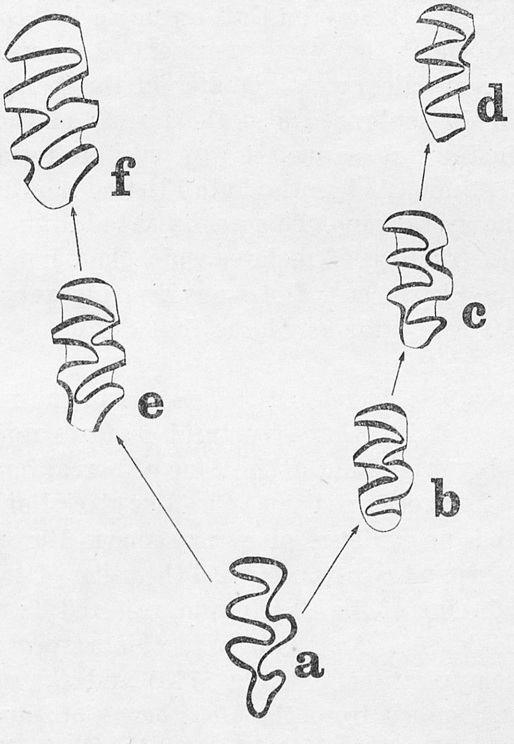

Fig. 6. Development of M³ — pattern in *Synaptomys* and *Lemmus* from the hypothetical common ancestor (a). b — *Synaptomys (Praesynaptomys) europaeus* subg. n. sp. n.; c — *S. (Metaxyomys) landesi* HIBBARD 1949; d — *S. (Synaptomys) cooperi* BAIRD 1857; e — *Lemmus lemmus*, Zamkowa Dolna Cave; f — *Lemmus lemmus*, Canada, Recent

The genus *Synaptomys*, which in the Pliocene of Europe was the first member of the *Arvicolidae* that had ever-growing teeth, had originated in the Palaearctic, from where it soon disappeared, perhaps ousted by *Lemmus*. It is however present in North America,where the genus *Lemmus* (except for Alaska) arrived very late, probably not before the postglacial period.

The genus *Lemmus* probably took origin in the western Palaearctic, where it tourned up around the bondary between the Pliocene and Pleistocene, being still the only arvicolid with permanently growing molars then. It seems to be always associated with relatively humid environment and so is completely lacking from the typical steppe faunae of the Early Pleistocene of Eastern Europe and Central Asia. It may be that owing to less competition shown by other *Arvicolidae*, which at that time represented a lower evolutionary stage of molars, its ecological valency was greater in the Early Pleistocene than it is to-day and no doubt embraced also the forests of the temperate zone or rather open areas in the forest-zone. It was only after the origin of the voles with ever-growing teeth, not before the Late Pleistocene, that the genus *Lemmus* was restricted to the arctic zone. This genus, in addition, exhibited enormous conservatism in the structure of molars, which had not undergone a change since the outset of the Pleistocene. The genus *Lemmus* spread along the northern margin of Asia as far eastwards as Alaska, but did not get beyond the ice-cap of North America.

The genus *Myopus*, closely related to *Lemmus* in the morphology of molars though differing from it in other structural features and in the number of chromosomes, probably originated in the zone of boreal forests of Eastern Asia, where it is known to have occurred since the Riss glaciation. It has never passed to America and there is no evidence of its presence in Europe in the Pleistocene. Probably it did not expand westwards until the zone of taiga, which has been disrupted at the beginning of the Pleistocene, restored its continuous extension in Eurasia in the Holocene. An analogy in this respect is observed in such species as *Clethrionomys rutilus* (PALLAS 1779) and *C. rufocanus* (SUNDEVALL 1846), which are not known from the Pleistocene of Europe either and now constitute an element of the fauna of boreal forests in its northern part.

The evolution of the group *Praedicrostonyx-Dicrostonyx*, which shows a number of similarities to the genera *Lagurus* GLOGER 1841 and *Pliolemmus* HIBBARD 1938, present itself in a different way. The genus *Praedicrostonyx* probably took rise in the dry area of Beringia. In Europe it arrived later than did the genus *Lemmus* and was always more closely associated with the arctic environment. In the Pleistocene this group showed a marked evolution towards the increasing complication of the molars, although populations with a relatively primitive structure of these teeth have persisted in isolated areas (Labrador).

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STRESZCZENIE

W faunach kopalnych drobnych ssaków Polski z okresu od górnego pliocenu (środkowy wilafransz) po zlodowacenie Mindel stwierdzono obecność 3 gatunków lemingów. *Synaptomys (Praesynaptomys) europaeus* subg. n. sp. n. występuje w Rębielicach Królewskich I i II, których wiek określa się na środkowy wilafransz. Od początku plejstocenu (Jaskinia Zamkowa Dolna) po okres Mindel I występuje *Lemmus lemmus* (Linnaeus 1758), przy czym najstarsze populacje wykazują obecność prymitywnych cech w budowie M^3. Gatunek ten, zachowując ustalony typ budowy zębów, podlega cyklicznym zmianom rozmiarów w poszczególnych okresach plejstocenu. W faunie Koziego Grzbietu (Mindel I — Mindel II) stwierdzono obecność *Dicrostonyx simplicior* Fejfar 1966.

W świetle nowych znalezisk autor przedstawia ewolucję lemingów. Wspólną cechą tej grupy jest obecność krótkiego dolnego siekacza, który nie przechodzi na zewnętrzną stronę żuchwy. Jest to cecha wtórna, gdyż u przodków *Arvicolidae*, którymi są *Cricetidae*, siekacz ten jest długi i przechodzi pod szeregiem molarów na zewnętrzną stronę żuchwy. Cecha ta powstała niezależnie u grupy *Praedicrostonyx-Dicrostonyx* z jednej strony i u grupy *Synaptomys-Lemmus-Myopus* z drugiej, w rezultacie wydłużania się zębów trzonowych i uzyskania przez nie stałego wzrostu, co było adaptacją do odżywiania się zielonymi częściami roślin w środowisku arktycznym. Grupa lemingów jest więc polifiletyczna.

W grupie *Synaptomys-Lemmus-Myopus* najpierwotniejszą formą jest *Synaptomys (Praesynaptomys) europaeus* sp. n. z najmłodszego pliocenu Polski. Zaznacza się u niego redukcja wewnętrznego trójkąta M^3, co jest charakterystyczne dla *Synaptomys*, ale zachowuje on jeszcze swoją odrębność. U innych znanych podrodzajów *Synaptomys* występujących w faunie plejstoceńskiej

i współczesnej Ameryki Pn. trójkąt wewnętrzny M^3 zanika, a dwa trójkąty zewnętrzne tworzą poprzeczne pola łączące się przy wewnętrznym brzegu zęba. Rodzaj *Synaptomys* powstał w Palearktyce, gdzie jednak wkrótce wyginął, by zachować się jedynie w Nowym Świecie.

W rodzaju *Lemmus* wewnętrzny trójkąt M^3 nie ulega redukcji, lecz zlewa się z tylnym trójkątem zewnętrznym tworząc wraz z nim poprzeczne pole. Pole to łączy się w pobliżu osi zęba z przednim polem poprzecznym utworzonym przez przedni trójkąt zewnętrzny. Rodzaj *Lemmus* pojawia się w Palearktyce na początku plejstocenu i w czasie całej swojej ewolucji zachowuje prawie niezmienną budowę zębów trzonowych. Związany jest ze środowiskiem wilgotnym, arktycznym i borealnym i nie występuje w faunach kopalnych o wyraźnie stepowym charakterze.

Rodzaj *Myopus*, w budowie zębów podobny do *Lemmus*, powstał w strefie lasów borealnych wschodniej Palearktyki. Do Europy przedostał się prawdopodobnie dopiero w postglacjale, z chwilą utworzenia się ciągłej strefy tajgi w Eurazji. Nie ma żadnych danych o jego występowaniu w plejstocenie Europy.

Grupa *Praedicrostonyx-Dicrostonyx* powstała w suchym, arktycznym środowisku Beringii na początku plejstocenu. Dalsza jej ewolucja przebiegała w całości w strefie arktycznej i wyrażała się postępującą komplikacją zębów trzonowych.

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