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Fossil hamsters (*Cricetinae, Rodentia*) from the Pliocene and Quaternary of Poland

[With 12 Text-figs. and Plates VIII—XI]

Kopalne chomiki (*Cricetinae, Rodentia*) pliocenu i czwartorzędu Polski

Abstract. This paper comprises descriptions of 1630 molars found at 20 Polish localities representing a period from the Miocene/Pliocene boundary to the end of the Pleistocene, including a small addition of Holocene specimens. Only 16 teeth from the whole of the material could not be referred to any of the known species: the differences in size and morphology suggest that they perhaps belonged to four different species not described yet. In the Pliocene localities they were accompanied by *Kowalskia polonica* and *K. magna*. *Allocricetus bursae*, *A. ehiki* and *Cricetus runtonensis* occurred in the Villanyian and Biharian, while remains of *Cricetulus migratorius* and *Cricetus cricetus* were found in the deposits of the Upper Pleistocene.

The final part of the paper presents certain biometrical relationships within the dentition of the *Cricetinae*.

CONTENTS

I. INTRODUCTION

Inasmuch as the members of the subfamily *Cricetinae* are represented by large numbers of specimens belonging to numerous species in the Miocene of Europe, they have been found in smaller numbers and besides no in all localities referred to the Pliocene and Pleistocene. The phylogenetic relationships of the

Plio- and Pleistocene hamsters with their Miocene ancestors, on the one hand, and with the Recent species, on the other, are still obscure. These problems have been dealt with in more or less detail by many authors, e.g. SCHAUB 1930, WERTH 1936, VOGEL 1940, KURTÉN 1960, FAHLBUSCH 1969, 1976, FAHLBUSCH in KOENIGSWALD 1970, STORCH 1974 and VORONTSOV 1982.

The first record of hamster remains from the territory of Poland appeared in literature relatively early, namely, in RÖMER'S (1883) work *Cricetus frumentarius* PALL. (= *C. cricetus*) is reported from the sediments of Nietoperzowa Cave. Next, hamsters are mentioned in two works by NIEZABITOWSKI (1932, 1933). In 1932 NIEZABITOWSKI discussed the material gathered by KOZŁOWSKI in his excavations and described the remains of *C. cricetus* from Mamutowa Cave. In 1933 he cited *C. c. cricetus* L. from the caves of Ojców in general, but we are certainly concerned here with Mamutowa Cave (KOWALSKI 1959). ZOTZ (1939) mentions *C. cricetus* L. from Cisowe Rock-shelter I and *C. c. major* sensu WOLDŘICH (1880) from Cisowe Rock-shelter II. KOWALSKI (1954, 1959) described the same material from Cisowe Rock-shelter II as *C. cricetus* L. Since the publication of KOWALSKI'S (1958, 1961) two works, which constitute a turning point in the study of remains of small Pleistocene mammals, hamsters have been mentioned in many papers, the most important of which is that by FAHLBUSCH (1969).

Here I wish to thank Prof. K. KOWALSKI for giving me access to the material used in this study and to extensive literature of the subject. I am also indebted to him for his valuable suggestions made during my study and preparation of this paper.

II. METHOD AND GENERAL REMARKS

The study of material consisted of an analysis of the morphology of molar crowns and measurement of their size, which permitted the determination of their specific membership. The length and width of detached molars and the length of tooth-rows were measured to an accuracy of 0.01 mm, using a measuring microscope. The anterior width of upper teeth was measured at the protocone-paracone height and that of lower teeth at the protoconid-metaconid height. The posterior width of upper teeth was measured at the hypocone-metacone height and that of lower teeth at the hypoconid-entoconid height. The length of mandible was measured to an accuracy of 0.1 mm from the tip of the condylar process to the posterosuperomedian margin of the incisor alveolus. This measuring point in the alveolus was chosen in view of the fact that this region is relatively often preserved undamaged in fossil material. If the data thus obtained are to be used in compari-ons with the results of other authors, the method of measuring should be kept in mind, since different scientists choose different measuring points.

The following letter symbols are used in text as well as in the captions of tables, figures and plates:

L — length, e.g. LM^1 — length of first upper molar, LM_1 — length of third lower molar

LM^{1-3}, (LM_{1-3}) — length of upper (lower) tooth-row at the height of crowns

LM^{1+2+3}, (LM_{1+2+3}) — sum of lengths of successive molars forming a given row

Wf — anterior width of tooth

Wb — posterior width of tooth

N — number

$\bar{x}$ — arithmetic mean

SD — standard deviation

V — coefficient of variation

$\frac{LM^1 - LM^2 = 1 - LM^3}{LM_1 - LM_2 = 1 - LM_3}$ — relative length of molars in comparison with length of M2 assumed as unit.

$\frac{LM1-3.100}{LM1+2+3}$ — index of overlap of teeth (index of occlusion), showing the length of a row as the percentage of the sum of the lengths of particular teeth in the row.

In the description of the axes in the diagrams only the symbol W is used, without information whether it is Wf or Wb, because it was always the greater value (W_{max}) that was used to construct diagrams.

Differences between the numbers of teeth given in general quantitative specifications and the values of N, i.e. the numbers of specimens used to calculate the means, result from the fact that some teeth could not be measured because they were damaged.

In the explanation of plates illustrating the morphology of teeth the measurements of particular specimens are given and these measurements are binding. Tooth measurements that can be taken from the photographs would be charged with an error as a result of slight deformations of their shapes in photographs taken with a wide-angle lens and work connected with preparing the plates.

The value of x is given with a greater accuracy than that accepted for measurements, keeping in mind the possibility of its being used by other authors for comparative purposes.

III. LOCALITIES AND MATERIAL

The complete assemblage of fossil remains of the *Cricetinae* in the collection of the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, in Cracow is described in this paper. Part of the material (108 molars, 7 of which not determined to specific level) obtained from 5 localities was studied by V. Fahlbusch (1969). On its basis Fahlbusch erected two new species within a new genus and signalled the possibility of existence of 4 other

Table I

A list of localities and species found in them

The stratigraphy of the localities of the last glaciation is presented in detail in Table XIV

Europe: Mammal ages	Europe: Local classification	Localities \ Species	*Cricetinae* indet.	*Kowalskia polonica*	*Kowalskia magna*	*Allocricetus bursae*	*Allocricetus ehiki*	*Cricetus runtonensis*	*Cricetulus migratorius*	*Cricetus cricetus*
Toringian	Weichselian (Würm)	Zalas							+	+
		Witkowice								+
		Sąspowska Z. Cave								+
		Bramka Rock-shelter								+
		R.-s. above Niedostępna Cave								+
		Żytnia Skała Rock-shelters								+
		Mamutowa Cave							+	+
		Koziarnia Cave								+
		Nietoperzowa Cave							+	+
		Raj Cave							+	+

Upper Biharian	Elsterian (Mindel I/II)	Kozi Grzbiet				+	+	+		
	Cromerian	Zalesiaki 1, fauna A				+	+	+		
		Rębielice Kr. 1, fauna B				+		+		
Lower Biharian	Menapian (Günz II)	Kielniki 3A				+	+			
	Eburonian (Günz I)	Kamyk				+	+			
Villanyan	Tiglian	Kadzielnia				+	+	+		(+)
		Zamkowa Dolna Cave, fauna A				+	+	+		
Upper Villafranchian	Praetiglian	Rębielice Królewskie 2	+							
		Rębielice Kr. 1, fauna A	+	+						
Lower Villafranchian	Praetiglian/Reuverian	Zalesiaki 1, fauna B			+					
		Zamkowa Dolna Cave, fauna B		+	+					
Csarnotan	Reuverian	Węże 1	+							
Ruscinian	Brunssumian	Podlesice	+	+	+					

new species. Since that time the material has increased markedly in amount. Now it comprises 1646 molars from 20 localities representing the period from the Miocene-Pliocene transition throughout the Pleistocene with some, possibly Holocene, admixtures (Table I). Most of the teeth (1630) belong to 7 known species, the remaining ones (16 including 7 described by FAHLBUSCH in 1969) still remain undetermined.

Detached molars prevail in the material, only a few of them being set in fragmentary maxillae and mandibles, 1, 2 or 3 in each. Undamaged mandibular branches were found only in few cases. There was no complete skull.

A. Localities in the Częstochowa and Kielce regions

1. Podlesice near Kroczyce (50°34′N, 19°32′E)

K. KOWALSKI found some vertebrate remains in the karst filling of Jurassic limestones and he was the first to describe them (KOWALSKI 1951b, 1956). The breccia found there was rich in animal remains, accumulated in the cave below a bat colony. The composition of the fauna suggests a Mediterranean-like climate, differentiated distinctly into summer and winter seasons and the occurrence of 2 types of vegetation in that region, i.e. representative of forests and of open areas. The geological age of the find was determined only on the basis of the fauna, first as early Pleistocene (KOWALSKI 1956), later as Lower Pliocene (KOWALSKI 1969).

Material: *Kowalskia polonica* FAHLBUSCH, 1969: 138 teeth
Kowalskia magna FAHLBUSCH, 1969: 35 teeth
Cricetus sp.: 10 teeth

2. Węże 1 near Działoszyn (51°07N, 18°49′E)

The deposits of this cave contained a rich fauna of amphibians, reptiles and mammals. At first the material was referred to the Upper Pliocene; however, it has been established recently that the fauna of this locality is younger than that of Podlesice but older than the faunae from Rębielice Królewskie 1 and 2.

Material: FAHLBUSCH (1969) mentions 1 left M_2 from this locality, described by him as *Copemys (Democricetodon)* sp. nov. No new materials has been found.

9. Rębielice Królewskie 1 near Kłobuck (50°59N, 18°50′E)

Animal bones occurred in the red clay filling of a fissure in Jurassic limestones. The materials found here come from both the Upper Villafranchian and Upper Biharian.

Material: Rębielice Królewskie 1 (fauna A) — Upper Villafranchian
Kowalskia polonica: 1 tooth
Cricetus sp.: 3 teeth
Rębielice Królewskie 1 (fauna B) — Upper Biharian
Allocricetus bursae SCHAUB 1930: 2 teeth
Cricetus runtonensis NEWTON 1909: 2 teeth

4. Rębielice Królewskie 2 (50°59′N, 18°50′E)

This locality is situated c. 800 m NW of Rębielice Królewskie 1. It is a fissure in Jusassic limestones filled with weathered dark-red clay, abounding in animal bones. The fauna occurring here is referred to the Upper Villafranchian and in respect of age corresponds to fauna A from Rębielice Królewskie 1.
Material: ?*Cricetus* sp.: 1 M^1
?*Copemys* sp., ?*Kowalskia* sp.: 1M^2

5. Zamkowa Dolna Cave, Olsztyn near Częstochowa (50°45′N, 19°10′E)

As regards stratigraphy, the locality is very heterogeneous. Out of the seven layers dinstinguished here, five upper ones were secondarily intermixed in historic times. KOWALSKI (1977) determines the age of this site as early Villafranchian, but in his earlier work (KOWALSKI 1975) he wrote that some of the specimens found here, even those showing the same colouration as the others, might represent an earlier period. Simultaneously, NADACHOWSKI (1982) and SZYNDLAR (1984) described assemblages of rodents and snakes from the same locality, assuming their age to be upper pleniglacial of the last glaciation.
Material: Zamkowa Dolna Zave, fauna A — Villanyian
Allocricetus bursae: 32 teeth
Allocricetus ehiki: 7 teeth
Cricetus runtonensis: 5 teeth
Zamkowa Dolna Cave, fauna B — Lower Villafranchian
Kowalskia polonica: 2 teeth
Kowalskia magna: 1 M_3

6. Kadzielnia, in the area of Kielce (50°52′N, 20°37′E)

Material obtained from a karst depression in Upper Devonian limestones filled with clay. The locality was referred to various periods, recently to the Villanyian.
Material: *Allocricetus bursae*: 10 teeth
Allocricetus ehiki: 4 teeth
Cricetus runtonensis: 2 teeth
Cricetus cricetus L. — well-preserved right mandible with a row of molars. This is certainly the mandible of an early-Holocene specimen, the occurrence of which in the material was accidental.

7. Kamyk near Częstochowa (50°54′N, 19°01′E)

A locality found and described by MOSSOCZY (1959). It was a karst depression filled with clay with small numbers of vertebrate remains. Its poor fauna of reptiles, lack of the red colouration of the clay, and the distinct increase in the size of the leporid *Hypolagus brachygnathus* suggest that the climate was much cooler than at Kadzielnia. Recently, this find has been described as coming from Lower Biharian times.

Material: *Allocricetus bursae*: 11 teeth
Allocricetus ehiki: 19 teeth

8. Kielniki 3A, near Częstochowa (50°44′N, 19°24′E)

This locality was discovered in the course of rock working in the southern wall of the Kielniki quarry. Some vertebrate remains were found in dark-red clay occurring in Jurassic limestones. It has been assumed that the locality represents the Lower Biharian.

Material: *Allocricetus bursae*: 11 teeth
Allocricetus ehiki: 1 M^2

9. Zalesiaki 1, near Działoszyn (51°05′N, 18°54′E)

This locality is situated in the neighbourhood of the already known localities at Węże. It was discovered and, at the same time, heavily spoilt in the process of rock working in the quarry. Two faunal assemblages have been found here: Cromerian (fauna A) and the considerably older fauna B from the Lower Villafranchian.

Material: Zalesiaki 1, fauna A
Allocricetus bursae: M^2
Allocricetus ehiki: damaged M^2
Cricetus runtonensis: 25 teeth
Zalesiaki 1, fauna B
Kowalskia magna: M_1

10. Kozi Grzebiet near Kielce (50°51′N, 20°27′E)

This is an old cave in Devonian limestones, filled with red-brown clay containing numerous bony remains. In the course of study a number of layers were distinguished, of which only layer "2", divided into sublayers a, b and c, comprised palaeozoological material. Unluckily, the material got partly mixed so that it was in addition necessary to consider the samples combined together: a + b + c and b + c. A sample was also taken from the talus cone referred to as the "damp". Close descriptions of the locality and its stratigraphy are given in papers by GŁAZEK et al. (1976, 1977a, 1977b). The authors of these papers arrive at the conclusion that whole layer "2" represents the warm phase preceding the Mindel II glaciation and layer 2b corresponds with the climatic optimum of this phase.

Material: *Allocricetus bursae*: 889 teeth
Allocricetus ehiki: 42 teeth
Cricetus runtonensis 164 teeth

11. Raj Cave at Szewce in the Kielce Province (50°50′N, 20°30′E).

The cave is situated in the slope of Malik Hill. Eleven layers were distinguished in the profile of deposits in the process of excavation, the oldest of them coming from the final period of the climatic optimum of the last interglacial. The remains of a hamster were found in layer 11a built of Holocene sands. This layer contained a mixed fauna: bones of postglacial animals lighter in colour and darker bones of Pleistocene animals. The remains of Pleistocene animals were sporadically met with also in Holocene humus (Kowalski 1972).
Material: *Cricetulus migratorius*: dark-coloured mandible with a row of molars.

B. Caves and rock-shleters in the Ojców region
(± 50°12′—50°14′N, 19°45′—19°50′E)

12. Nietoperzowa Cave (= Jerzmanowicka Cave)

A detailed description of the cave and a history as well as the results of the investigation carried out in it are given in Kowalski's monograph (1951a, item no. 153) and in a work by Kubasiewicz (1957). Sixteen layers have been distinguished in the deposits and the fauna contained in them illustrates climatic changes starting from the decline of the Saalian glaciation (layers 16—15) through the Eemian interglacial (14—12), Weichselian glaciation I (11—9), Weichselian interstadial I/II (8—6) to Weichselian glaciation II (5—3).
Material: *Cricetus cricetus*: right M_1 from layer 14
Cricetulus migratorius: right M^1 from layers 9/10.

13. Koziarnia Cave, in the village of Sąspów

The cave is situated in the Ojców National Park, in the eastern slope of Koziarnia Valley The deposits of this cave have been repeatedly excavated. Twenty-one layers corresponding with the succession of the Eemian interglacial, Weichselian glaciations I and II and the Holocene were recognized here during a study carried out by Chmielewski et al. (1967).
Material: *Cricetus cricetus*: right M^2 from layer 12 deposited in the lower pleniglacial of the Weichselian glaciation.

14. Mamutowa Cave (= Wierzchowska Dolna Cave) at Wierzchowie

The cave is situated in the left-hand side of the valley of the Kluczwoda Brook. A detailed description of the cave and investigations made in it as well as their results are presented by Kowalski (1951a, 1959) and Nadachowski (1976). Nadachowski (1976, 1982) gives a detailed description of the fauna collected in it. The remains of hamsters come from layers, 2, 2 g, 1 of excavation I, situated near the entrance of the cave. Layer 2 was whole formed of loess and deposited in the upper pleniglacial of the last glaciation, whereas layer 1 was built of Holocene humus.

Material: *Cricetus cricetus*: 6 teeth from layer 2 and 2 teeth from layer 1.
Cricetulus migratorius: 2 right maxillary bones with rows of molars from layer 2 and ioslated M_1 from layer 2 g.

15. Żytnia Skała Rock-shelters at Będło

These are two rock-shelters, Małe and Wysokie, lying just beside each other in the Żytnia Skała, isolated sock in the village of Będło. In the past they were probably protected by a common overhang. Two excavations were made: one outside the entrance of the rock-shelters and the other inside Wysokie Rock-shelter. A number of layers were distingusihed in both excavations but they could not be related stratigraphically. A detailed description of these layers and climatic changes taking place during their formation is given by KOWALSKI et al. (1967). Remains of hamsters were found in both excavations. It may be assumed that they are of early Holocene age.

Material: *Cricetus cricetus*: 16 molars.

16. A Rock-shelter above Niedostępna Cave at Sąspów

This rock-shelter is situated in the Ojców National Park, about 25 m above the floor of the Koziarnia ravine in the village of Sąspów. Six layers illustrating climatic changes from the early Weichselian (layer 1) to the Holocene (layer 6) were distinguished in the course of excavation in 1968 and 1969. A general account of the study carried out in the rock-shelter is given by MADEYSKA (1972). Some remains of hamsters were found in layers 4 and 4k, corresponding with the final phase of the Weichselian.

Material: *Cricetus cricetus*: 11 teeth.

17. Bramka Rock-shelter in the Ojców National Park

The rock-shelter of Bramka is situated on the left-hand bank of the stream Sąspówka. Six layers, illustrating climatic changes in the early Holocene, have been distinguished in the profile of deposits.

Material: *Cricetus cricetus*: M_3 and heavily damaged M_1 from layer 4, M_1, M_2 and M_3 from layer 5a.

18. Sąspowska Cave at Sąspów

The entrance of the cave is located in the left-hand slope of the stream in Sąspówka valley. Six layers were uncovered at the time of excavation. Large numbers of big hamsters occurred in layer 3 from the Pleistocene-Holocene

transition. Numerous mandibles, mostly in a good state of preservation, fragmentary skulls with teeth in situ and also some bones of the skeleton have been found at this locality. These remains have been described in a separate paper (PRADEL 1981b), only the results of that study being summarized here.
Material: *Cricetus cricetus*: 165 molars including 13 M^1, 16 M^2, 17 M^3, 33 M_1, 44 M_2 and 40 M_3.

C. Other localities of the Cracow region

19. Witkowice (50°06′N, 19°57′E)

In 1957 K. KOWALSKI found a mandible of *C. cricetus* in a good state of preservation in the village of Witkowice, bordering upon Cracow. No investigation has been carried out in this place. The loess deposits in which the mandible was found come probably from the final phase of the last glaciation. The mandible may be the same age or it may have got into them from the overlying Holocene stratum.
Material: *Cricetus cricetus*: right mandible with incisor and set of molars.

20. Zalas (50°06′N, 19°38°E)

This locality was discovered during the construction of the Cracow—Katowice motorway. Twenty-five stratigraphically undetermined samples were taken. Many data indicate the Pleistocene-Holocene age of the deposits, which do not extend back further than the climatic optimum of the last interstadial of the Weichselian glaciation (BOCHEŃSKI et al. 1985).
Material: *Cricetus cricetus*: sample 4: M^3, M_1, M_2 M_3
sample 6: M_2, M_3, M^1, M^2
sample 9: M^1 with its back portion broken off

Cricetulus migratorius: sample 16: mandible with its complete dentition

Remarks. A close analysis of the cave deposits and of their mutual relations is comprised in NADACHOWSKI'S (1982) work, in which its results are given in a table containing data concerning the age, the mean July temperature and the plant communities. In his analysis NADACHOWSKI included 17 localities, nine of which are discussed in the present paper. These are: Raj Cave, Zamkowa Dolna Cave, Sąspowska Cave, Bramka Rock-shelter, rock-shelter above Nietoperzowa Cave, Żytnia Skała Rock-shelter, Nietoperzowa Cave, Mamutowa Cave and Koziarnia Cave.

BOCHEŃSKI (1974) gives a similar table in his paper. SZYNDLAR (1984) presents the situation, stratigraphy and literature of 26 Polish localitiss in comparison with the stratigraphy of other European localities.

IV. SYSTEMATIC PART

A. Pliocene hamsters

Specimens unidentifiable to species

Fahlbusch (1969) discusses 7 teeth from 3 Pliocene localities, which he failed to number in any of the known species and which because of their small number could not make the basis for the erection of new species. Recently another 9 teeth of this type have been found.

Table II

Undetermined cricetids. Numbers of particular molars

	M^1	M^2	M^3	M_1	M_2	M_3	Total
Podlesice;							
Fahlbusch 1969,							
Cricetus sp. 1, MF/824	—	1	—	1	—	1	3
Cricetus sp. 2, MF/825	—	—	—	—	—	1	1
New material, MF/1685	1	—	—	2	—	—	3
Cricetus sp. 2, MF/825	—	—	—	—	—	1	1
MF/1712	—	—	—	3	—	—	3
Węże 1, Fahlbusch 1969, MF/834							
Copemys/Democricetodon ? sp.	—	—	—	—	1	—	1
Rębielice Królewskie 1;							
Fahlbusch 1969,							
Cricetus sp. 3 MF/827	1	1	—	—			2
New material MF/1713	—	—	—	1	—	—	1
Rębielice Królewskie 2; MF/1715	1	1	—	—		—	2
Total	3	3	—	7	1	2	16

The measurements of particular specimens are given in the descriptions of the plates illustrating their morphology (Pl. VIII, figs. 1—15 and Pl. IX, fig. 14). They differ from other well-defined species not only in morphology but also in size. To bring out the differences, the measurements are shown in a collective diagram and not in separate L/W diagrams, text-fig. 1a, b and c gives the lengths and widths of consecutive molars in some fossil and recent hamsters.

Cricetus sp. 1, FAHLBUSCH 1969

FAHLBUSCH used this provisional name for 3 teeth from Podlesice: $1M_1$, fragmentary M^2, and $1M_3$ (MF/824/1—3), in the present paper shown in Pl. VIII, figs. 10, 11 and 12. In their description FAHLBUSCH emphasizes the fact that they correspond with the teeth of the modern *C. cricetus* in measurements (Text-fig. 1a, b and c), but at the same time the lobularly developed anteroconid of M_1 makes them similar to the teeth of *Kowalskia*. Three other teeth of this type — $1M^1$ and $2M_1$ (MF/1685/1—3, Pl. VIII, Figs. 13, 14 and 15) — have been found in the new material from Podlesice. They agree with the description of *Cricetus* sp. 1 both in size and in morphology.

Cricetus sp. 2, FAHLBUSCH 1969

This designation has been applied for a left M_3 (MF/825) from Podlesice (Pl. IX, fig. 17). FAHLBUSCH draws attention to the fact that its anterior width is somewhat larger than in M_3 of the recent *C. cricetus* and also to many additional elements which bring it close to *Cricetus major* sensu FAHLBUSCH 1976 from Petersbuch 1.

It seems, however, that this tooth may have belonged to the form *Cricetus* sp. 1, whose teeth compared with those of the recent *C. cricetus*, are also a little wider relative to their length. This tooth differs considerably from the corresponding tooth of *C. major* and the additional grooves are of no taxonomic importance here. The morphology of the third molars of hamsters is variable: the metacone and entoconid are subject to changes in size, the roots vary in development and some additional elements very often appear in them. These additional elements occur in *C. runtonensis* (see Pl. X, figs. 5—7, 10, 11 and 17), *C. cricetus* from the Weichselian (Pl. XI, figs. 7—10) as well as in the recent *Cricetulus migratorius* from Syria (PRADEL 1981). They have also been described from Pleistocene materials by other authors (e.g. FAHLBUSCH 1976, p. 77). As I have shown in my work on the dentition of the modern *C. cricetus* from Poland (PRADEL, 1985), numerous additonal elements of its teeth appear in the course of development, just before their eruption. The tooth under discussion belonged to a very young animal, which is evidenced by its roots, not quite developed yet, and enamel, showing no traces of wear. For these reasons the tooth in question cannot be identified on the basis of its dimensions and morphology; at the most, it can be tentatively assigned to the species from which it does not depárt in measurements and together with which it was found. This would be probably the form *Cricetus* sp. 1.

Cricetus sp. 3, FAHLBUSCH 1969

FAHLBUSCH used this designation for 2 teeth — $1M^2$ and $1M^1$ (MF/827/1—2) — from Rębielice Królewskie 1 (Pl. VIII, figs. 1 and 2). In their description he states that it is impossible to assign them on the basis of their measurements and morphology to any of the Plio-Pleistocene species known *(C. kormosi, C. nanus, C. praeglacialis)*. Two other teeth, which perhaps belong to this form, have been obtained from Rębielice Królewskie 1 and 2.

Rębielice Królewskie 1: right M_1 (MF/1713, Pl. VIII, fig. 3). As regards measurements, this tooth is inferior to M_1 of the recent *C. cricetus*. Morphologically it differs from this last species in the shape of the anteroconid, two cusps of which lie very close to each other and are separated by a narrow groove. In consequence, the outline of the anterior portion of the tooth is narrow and rounded, whereas in *C. cricetus* it is broad and flattened (see Pl. X, figs. 11 and 12, and Pl. XI, fig. 8).

Fig. 1a

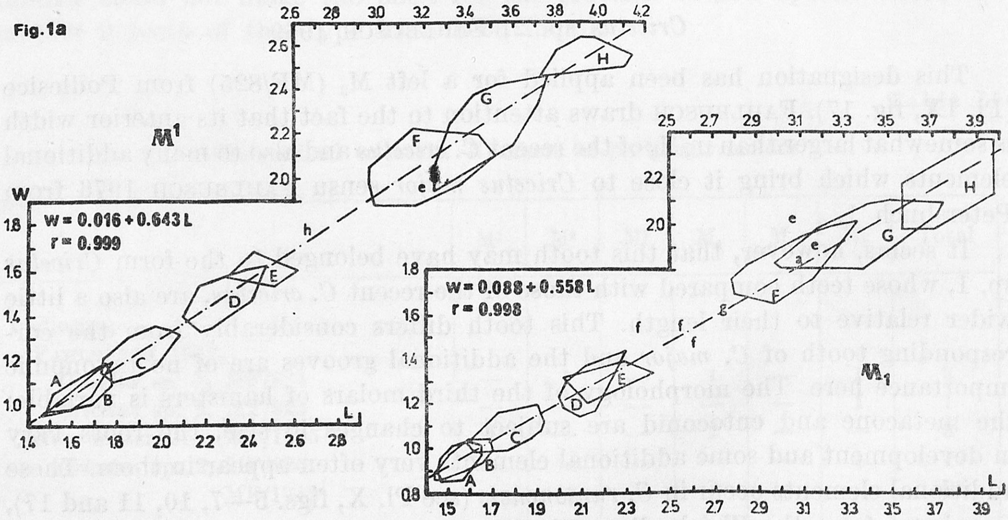
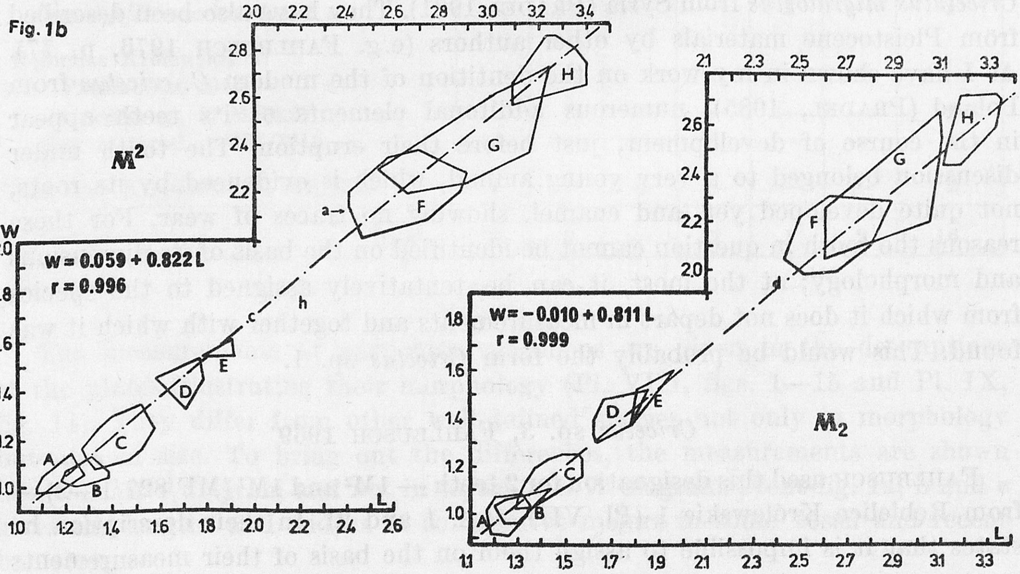


Fig. 1b



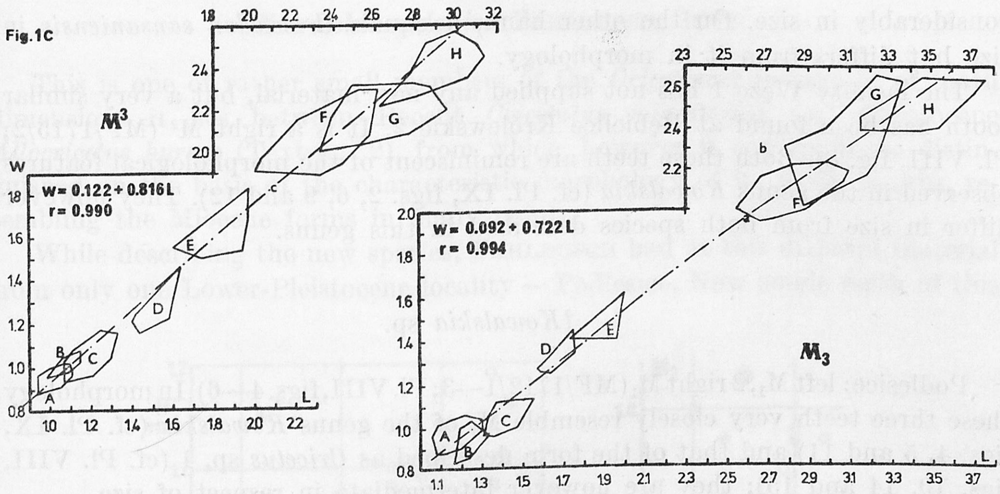


Fig. 1a, b, c. Cumulative L/W diagram of molars for several fossil and living species of hamsters. A — *Cricetulus migratorius*, recent, Syria (Pradel 1981a); B — *Kowalskia polonica* (present paper); C — *Allocricetus bursae* (present paper); D — *A. ehiki* (present paper); E — *Kowalskia magna* (present paper); F — *Cricetus c. cricetus*, recent, Poland (Pradel 1985); G — *C. runtonensis* (present paper); H — *C. major* sensu Fahlbusch 1976, Pleistocene, Petersbuch 1. The diagram does not include the data concerning *Cricetus cricetus* and *Cricetulus migratorius* from the Polish last glaciation localities discussed in the present paper. They are presented in Text-figs. 9 and 10. a — *Cricetus* sp. 1, Podlesice (see Pl. VIII, figs. 10—12); b — *Cricetus* sp. 2, Podlesice (Pl. IX, fig. 14); c — *Cricetus* sp. 3, Rębielice Królewskie 1 (Pl. VIII, figs. 1—2); d — *Copemys (Democricetodon)* ?, Węże 1 (Pl. VIII, fig. 9); e — ?*Cricetus* sp., Podlesice (Pl. VIII, figs 13—15); f — ?*Cricetus* sp., Podlesice (Pl. VIII, figs. 4—6); g — ?*Cricetus* sp., Rębielice Królewskie 1 (Pl. VIII, fig. 3); h — ?*Cricetus* sp., Rębielice Królewskie 2 (Pl. VIII, figs. 7—8). The regression equation has been calculated on the basis of the mean lengths and widths of teeth of 10 populations belonging to 8 species of fossil and recent *Cricetinae*. Data from present paper: *K. polonica*, *K. magna*, *A. bursae*, *A. ehiki*, *C. runtonensis*, *C. cricetus* (last glaciation, Poland). Data from literature: *C. cricetus*, recent, Germany and *C. major* s. Fahlbusch (Fahlbusch 1976), *C. migratorius*, recent, Syria (Pradel 1981a), *C. c. cricetus*, recent, Poland (Pradel, 1985)

Rębielice Królewskie 2: right M^1 (MF/1715; Pl. VIII, fig. 7). As regards measurements, this specimen lies in the upper zone of the length range of M^1 of *C. kormosi* but differs from it in the oval outline of the crown, the presence of the well-developed anterior branch of the metacone as well as in the occurrence of distinct ridges descending from both cusps of the anterocone and forming a junction with the anterior branch of the protocone in the shape of the letter Y.

Copemys (Democricetodon) sp., Fahlbusch 1969

Fahlbusch (1969) applies this designation for left M_2 from Węże 1 (MF/834; Pl. VIII, fig. 9). In the description he compares its morphology to that of *Copemys (Democricetodon) gaillardi* from Sansan, from which it however differs considerably in size. On the other hand, it equals *Cricetodon sansaniensis* in size but differs from it in morphology.

The locality Węże 1 has not supplied any new material, but a very similar tooth has been found at Rębielice Królewskie 2. It is a right M^2 (MF/1715/2; Pl. VIII, fig. 8). Both these teeth are reminiscent of the morphological features observed in the genus *Kowalskia* (cf. Pl. IX, figs. 2, 6, 9 and 12). They however differ in size from both species described in this genus.

?*Kowalskia* sp.

Podlesice: left M_1, 2 right M_1 (MF/1712/1—3; Pl. VIII, figs. 4—6). In morphology these three teeth very closely resemble M_1 of the genus *Kowalskia* (cf. Pl. IX, figs. 4, 5 and 11) and that of the form described as *Cricetus* sp. 1 (cf. Pl. VIII, figs. 10, 14 and 15); they are however intermediate in respect of size.

The foregoing discussion suggests that there are several (at least 4) new species to be described from Pliocene localities. For the time being they are referred to as forms:

Cricetus sp. 1, ?*Kowalskia* sp. — Podlesice, Lower Pliocene. Characters of these teeth: the build of the anterior portion of M_1 and the presence of the merolophid more resemble the morphology observed in the genus *Kowalskia* than that of *Cricetus*.

Copemys (Democricetodon) sp. — Węże, Rębielice Królewskie 2. It has many characters in common with *Kowalskia*.

Cricetus sp. 3 — Rębielice Królewskie 1 and 2 (Upper Pliocene) — stands closer to *Cricetus* than to *Kowalskia*.

It may be stated that here we are concerned with very interesting material which illustrates evolutionary changes almost in statu nascendi. The genus *Kowalskia*, still partly resembling the Miocene forms, occurs in these localities, but in the Uper Pliocene there are already forms more closely related to *Cricetus* (*Cricetus* sp. 3). This statement is however very hypothetical and the explanation of the problem must be put off until a greater number of similar teeth have been found. We cannot expect to get more materials from Węże 1, Rębielice Królewskie 1 and 2, but there are chances to obtain more new material from Podlesice, where the bone breccia has not been exploited thoroughly.

Genus: *Kowalskia* Fahlbusch, 1969

Fahlbusch (1969) described 50 small and 17 somewhat larger teeth from Podlesice, sharing a number of common morphological features, which differ them from all the known species. He regarded them as two new species belonging to the new genus *Kowalskia*.

The material concerning these species has been enriched with further molars from Podlesice and also a few specimens from other localities.

Kowalskia polonica Fahlbusch, 1969

This is one of rather small members of the *Cricetinae*; in respect of tooth dimensions it lies between Recent *Cricetulus migratorius* and Pleistocene *Allocricetus bursae* (Text-fig. 2), from which however it can easily be distinguished on the basis of the characteristic morphology of its tooth crowns, resembling the Miocene forms in many points.

While describing the new species, Fahlbusch had at this disposal material from only one Lower-Pleistocene locality — Podlesice. Now single teeth of this

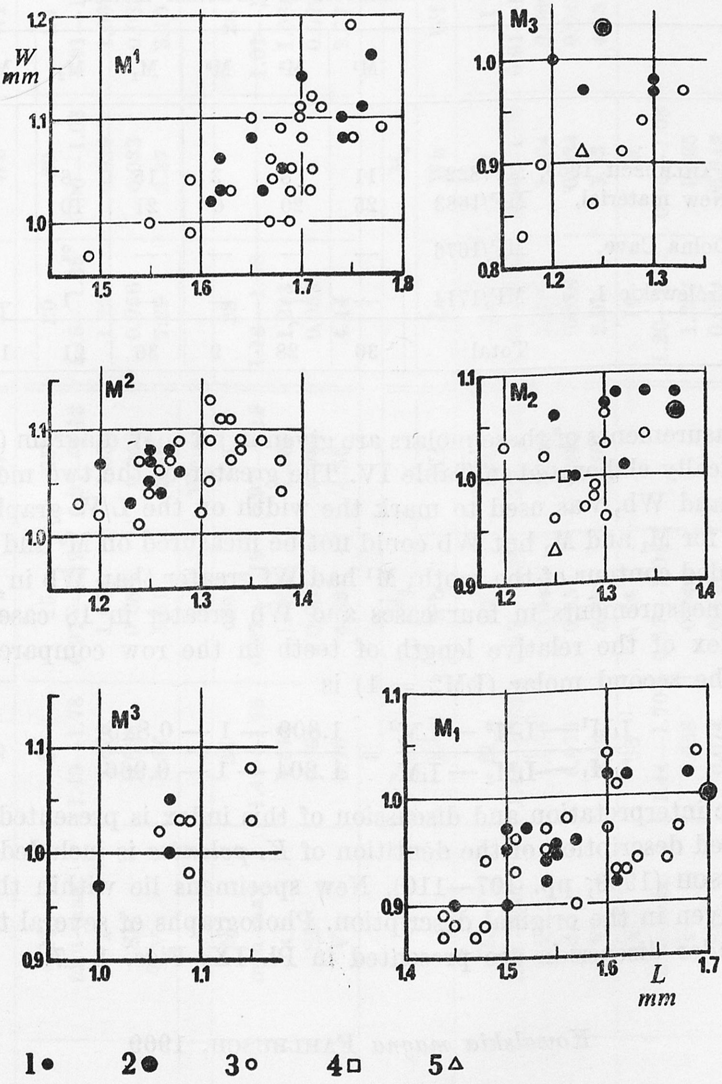


Fig. 2. *Kowalskia polonica*. L/W diagram of molars. 1, 2 — after Fahlbusch (1969), Podlesice (2 — holotype). New material: 3 — Podlesice, 4 — Rębielice Królewskie, 5 — Zamkowa Dolna Cave

species have been found at Rębielice Królewskie 1 and Zamkowa Dolna Cave (fauna B). *K. polonica* is a Pliocene species and the finding of teeth of this species in Zamkowa Cave supports the earlier observations (e.g. KOWALSKI 1975) about the heterogeneity of material collected there.

The whole of material, unfortunately restricted to only detached molars, is presented in Table III.

Table III

Kowalskia polonica. Numbers of particular molars

		M^1	M^2	M^3	M_1	M_2	M_3	Total
Podlesice;								
FAHLBUSCH 1969,	MF/822	11	8	3	15	8	5	50
New material,	MF/1683	25	20	6	21	10	6	88
Zamkowa Dolna Cave,	MF/1676	—	—	—	—	2	1	2
Rębielice Królewskie 1,	MF/1714	—	—	—	—	1	—	1
	Total	36	28	9	36	21	12	141

The measurements of these molars are given in an L/W diagram (Text-fig. 2) and statistically elaborated in Table IV. The greater of the two measurements taken, Wf and Wb, was used to mark the width on the L/W graph. This was always Wb for M_1 and M_2 but Wb could not be measured on M^3 and M_3 because of the rounded contour of the tooth; M^1 had Wf greater than Wb in three cases, the equal measurements in four cases and Wb greater in 18 cases.

The index of the relative length of teeth in the row compared with the length of the second molar (LM2 = 1) is

$$\frac{\overline{LM}^1 - \overline{LM}^2 - \overline{LM}^3}{\overline{LM}_1 - \overline{LM}_2 - \overline{LM}_3} = \frac{1.309 - 1 - 0.845}{1.204 - 1 - 0.966}$$

The graphic interpretation and discussion of this index is presented on p. 289.

A detailed description of the dentition of *K. polonica* is included in a paper by FAHLBUSCH (1969, pp. 107—110). New specimens lie within the range of variation given in the original description. Photographs of several teeth of the material under discussion are presented in Pl. IX, Figs. 1—7.

Kowalskia magna FAHLBUSCH, 1969

This is a medium-sized Pleistocene hamster, the teeth of which have been so far, found always together with remains of *K. polonica*. The measurements of these teeth overlap the upper range of L/W variation of teeth of *Allocricetus*

Table IV

Kowalskia polonica. Dimensions of detached molars, in mm

		M^1 L	M^1 Wb	M^1 Wf	M^2 L	M^2 Wb	M^2 Wf	M^3 L	M^3 Wf
A	N	25	25	25	20	20	20	6	6
	min-max	1.49—1.78	0.97—1.19	0.97—1.13	1.18—1.38	0.90—1.03	1.01—1.13	1.06—1.15	0.98—1.08
	$\bar{x}$	1.676	1.057	1.034	1.297	0.988	1.067	1.103	1.028
	SD	0.064	0.053	0.040	0.056	0.033	0.033	0.038	0.032
	V	3.84	5.01	3.86	7.29	3.37	3.10	7.42	3.10
				Wmax					
B	N	36	36	36	28		28	9	9
	min-max	1.49—1.78	0.97—1.19	0.97—1.19	1.18—1.38		1.01—1.13	1.00—1.15	0.97—1.08
	$\bar{x}$	1.679	1.064	1.066	1.283		1.065	1.084	1.021
	SD	0.062	0.051	0.049	0.053		0.029	0.046	0.034
	V	3.70	4.82	4.56	4.14		2.77	4.23	3.34

		M_1 L	M_1 Wb	M_1 Wf	M_2 L	M_2 Wb	M_2 Wf	M_3 L	M_3 Wf
A	N	21	21	21	11	11	11	7	7
	min-max	1.44—1.69	0.87—1.04	0.77—0.93	1.20—1.34	0.96—1.06	0.91—1.04	1.17—1.33	0.83—0.97
	$\bar{x}$	1.556	0.942	0.842	1.277	1.004	0.969	1.246	0.903
	SD	0.078	0.051	0.044	0.038	0.034	0.047	0.056	0.047
	V	5.02	5.38	5.20	2.95	3.43	4.83	4.49	5.18
B	N	36	36		19	19		12	12
	min-max	1.44—1.70	0.87—1.04		1.20—1.37	0.96—1.08		1.17—1.33	0.83—1.03
	$\bar{x}$	1.558	0.949		1.294	1.025		1.250	0.939
	SD	0.074	0.047		0.044	0.042		0.049	0.059
	V	4.72	4.96		3.38	4.07		3.95	6.25

A — data concerning the new material from Podlesice, Zamkowa Dolna Cave (one left M_3: L = 1.23, Wf = 0.91) and Rębielice Królewskie 1 (one right M_2: L = 1.26, Wb = 1.00, Wf = 0.96). B — data concerning the new material from Podlesice, Zamkowa Dolna Cave and Rębielice Królewskie 1, together with those from Fahlbusch (1969).

Table V

Kowalskia magna. Measurements of teeth, in mm

	M^1			M^2			M^3		M_1			M_2			M_3	
	L	Wb	Wf	L	Wb	Wf	L	Wf	L	Wb	Wf	L	Wb	Wf	L	Wf
Podlesice	2.30	1.57	1.44	1.90	1.54	1.61	1.74	1.50	2.43	1.34	1.24	1.78	1.38	1.38	1.88	1.45
FAHLBUSCH 1969	2.40	1.60	1.60	1.89	1.41	1.54	1.60	1.55	2.13	1.20	1.09	1.80	1.52	1.52	1.97	1.48
MF/823/1—17	2.62	1.60	1.55				1.97	1.82	2.29	1.39	1.29				2.00	1.62
	2.51	1.60	1.58													
New material	2.51	1.54	1.53	1.80	1.50	1.55	1.94	1.53	2.26	1.29	1.19	1.85	1.47	1.43	1.73	1.41
MF/1684/1—18	2.42	1.68	1.61	1.91	1.44	1.54	1.70	1.61	2.02	1.31	1.22	1.96	1.60	1.57	1.96	1.41
	2.49	1.55	1.57	1.78	1.50	1.54	1.97	1.68				1.80	1.43	1.45		
	2.35	1.61	1.49				1.97	1.65								
Zamkowa D. Cave MF/1677															1.79	1.46
Zalesiaki 1 MF/1667									2.16	1.27	1.20					
N	8	8	8	5	5	5	7	7	6	6	6	5	5	5	6	6
$\bar{x}$	2.45	1.59	1.53	1.86	1.48	1.56	1.84	1.62	2.22	1.30	1.19	1.84	1.48	1.47	1.89	1.47
SD	.103	.043	.053	.061	.052	.030	.157	.109	.143	.064	.074	.073	.085	.075	.109	.078
V	2.19	2.72	3.43	3.29	3.53	1.96	8.53	6.76	6.45	4.96	6.26	3.97	5.71	5.11	5.76	5.29

ehiki (Text-fig. 1a, b, c). They also lie within the range of variation of *Cricetus kormosi* SCHAUB 1930, but differ from these species in morphology. *K. magna* was described by FAHLBUSCH (1969) on the basis of 17 detached molars found at Podlesice. In the description he gives a close analysis of the elements in which this species differs from other fossil and recent hamsters.

Since the description of the species the material has been enriched with some other molars found at Podlesice and one specimen from Zamkowa Dolna Cave and one from Zalesiaki 1, where these teeth constituted a slight admixture coming from the Lower Villafranchian (fauna B).

Now the collection of teeth of *K. magna* consists of 37 molars. Unluckily they are all detached teeth. Their kind, place of derivation and measurements are presented in Table V.

All the new-found specimens agree with the description given by FAHLBUSCH (1969, pp. 112—113) in respect of both morphology (Pl. IX, Figs. 8—13) and dimensions (Table V and Text-fig. 3).

The index of relative lengths of teeth in the row is: $\frac{1.32 - 1 - 0.99}{1.21 - 1 - 1.03}$ (see also p. 289).

General remarks

The materials discussed above, i.e. *K. polonica*, *K. magna* and the forms not specifically determined, come mostly from Pliocene localities. (Table I). These are Podlesice, Węże 1 and Rębielice Królewskie 1 and 2. No other members of the subfamily *Cricetinae* occur as a rule in these localities. Rębielice Królewskie 1 is an exception, for here 2 teeth of *Allocricetus bursae* and 2 of *Cricetus runtonensis* have been found in addition to the dominant fauna (fauna A) of Upper Villafranchian (Praetiglian) age. This locality is known, as the only one of the Pliocene localities, to contain an admixture of Pleistocene species (KOWALSKI 1977). The above-mentioned four teeth undoubtedly make up such an admixture, which is referred to the Upper Biharian and designated as Rębielice Królewskie 1 fauna B.

On the other hand, as regards the Pleistocene sites, teeth belonging to *K. polonica* and *K. magna* have been found merely at two of them, namely, the only ones at which other authors (KOWALSKI 1975, 1979; RZEBIK-KOWALSKA 1976; MŁYNARSKI 1977) previously proved the presence of admixtures of older materials: Zamkowa Dolna Cave (fauna B) and Zalesiaki 1 (fauna B).

This observation confirms the stratigraphic usefulness of the species under discussion. Their occurrence at a locality indicates its Lower and Middle Pliocene age or at least the existence of an admixture of a fauna of that age. These species appear as late as the Upper Villafranchian but do not occur longer in the upmost Pliocene (Villanyian).

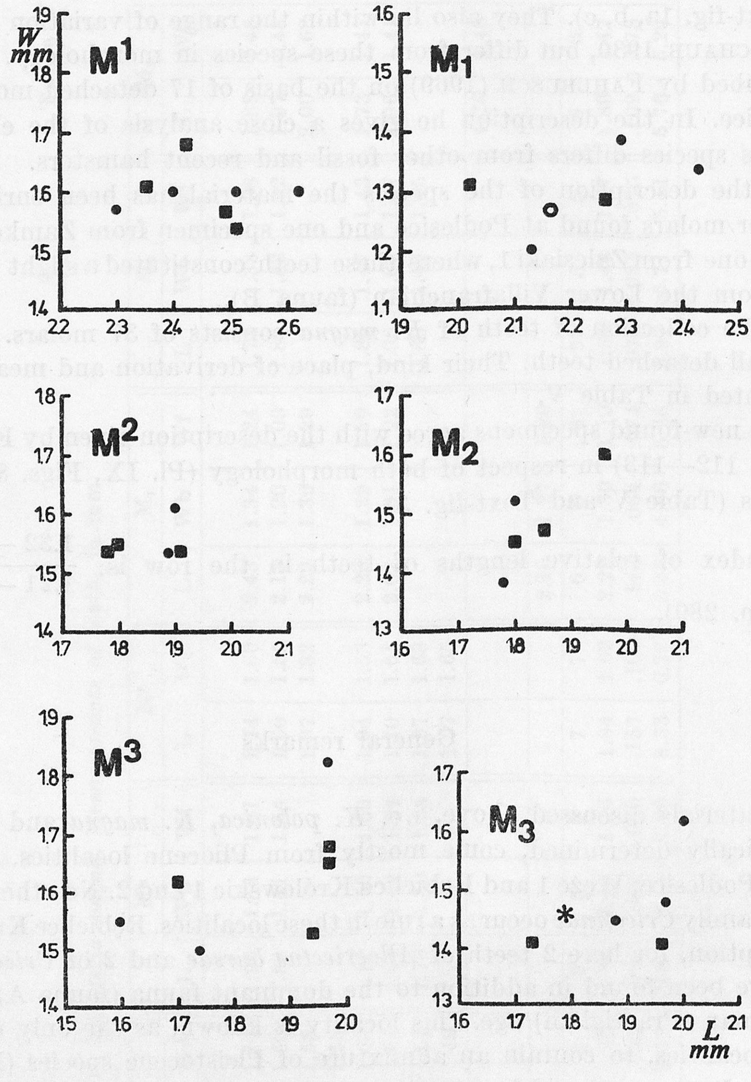


Fig. 3. *Kowalskia magna.* L/W diagram of molars. 1 — after FAHLBUSCH (1969), Podlesice. New material: 2 — Podlesice; 3 — Zalesiaki 1; 4 — Zamkowa Dolna Cave

B. Upper Pliocene (Villanyian) and Quaternary Hamsters

Remains of the *Cricetinae* from Villanyian and Quaternary of Poland have been found in 15 localities, but their appearance is distinctly split into two periods. Five localities are referred to the Biharian (Table I) and the materials collected in them give a survey of faunas over a period from the Eburonian to the Elsterian. A time gap, about 0.4 million years long, stretches startin from this period until the Eemian interglacial. There are no materials concerning the *Crictetinae* in Poland from that period, which, however, is no evidence of the absence of hamsters from the territory of this country at that time, but results from lack of finds.

The remaining 10 localities cover a period of about 70.000 years and various phases of the Weichselian glaciation. They are for the most part localities of the Ojców region (Table XIV).

In view of the foregoing, while discussing the remains of the *Cricetinae* obtained from these localities, I divide them into two groups: Late Pliocene and Early Pleistocene species and Late Pleistocene ones. The first group includes *Allocricetus bursae*, *A. ehiki* and *Cricetus runtonensis*, the second — *Cricetulus migratorius* and *Cricetus cricetus*.

Remarks on systematics

The systematic position of Quaternary hamsters is not fixed definitively and it is still subject to controversy.

Heller (1930) referred to all the small hamsters from Sackdillinger Höhle as *Cricetulus* sp. *fossilis*, laying stress only on differences from *Cricetulus phaeus fossilis*.

Schaub (1930, pp. 32—35) quoted Heller's work and, basing himself on some of his measurements, created a new genus for these forms, *Allocricetus*, which, according to him, comprises *A. bursae* and somewhat larger *A. ehiki*. He based his diagnosis on differences in the build of the skull and remarked that in the morphology of tooth crowns the new genus does not differ from the now living genera *Mesocricetus* and *Cricetulus*.

Kretzoi (1941, p, 318) numbered *A. ehiki* in the genus *Rhinocricetus* erected by him, but the justification of its erection on the basis of cranial characters is unsatisfactory. It is very probable that he did not allow for the marked variability of the skull shape in particular individuals or changes in their build connected with the age of the given animal.

Kurtén (1968, pp. 211—212) used the name *Cricetulus bursae* for *A. bursae* and stated that originally this species belonged to the genus *Allocricetus* but next appeared identical with *Tscherskia*, the subgenus of *Cricetulus*.

Also the systematics of big Pleistocene hamsters is still disputable.

Liebe (1879) wrote that the lengths of the lower tooth-rows of the big hamster from Vypustek were 9.8 and 10.1 mm and identified it as *Cricetus frumentarius* (= *C. cricetus*).

Woldřich (1880) used the name *Cricetus cricetus major* for a skull from Vypustek, in which the length over the alveoli of the molars is 9.5 mm and the condylobasal length (Cb) 56 mm.

Nehring (1894) stated that Woldřich did not show the specifity of the skull from Vypustek well enough to justify its new name and himself placed it in the subspecies *C. vulgaris fossilis*, newly established by him.

From the Forest Bed series in Norfolk NEWTON (1909) described a specimen of the right maxilla in which the length over the alveoli is 10.3 mm and that of the tooth-row preserved 9.3 mm. He named this specimen *C. vulgaris runtonensis* (= *C. c. runtonensis*).

SCHAUB (1930) used the name *C. c. praeglacialis* for both these forms.

HELLER (1933) was of the opinion that the differences in morphology and size between the dentition of the present-day *C. cricetus* and that of *C. c. runtonensis* are great enough to entitle him to introduce a new species, *C. runtonensis* (see also HELLER 1930, 1936 and 1958).

KURTÉN (1960, 1968) was convinced that the length of tooth-rows depends on climatic factors (BERGMANN'S rule). In the big subspecies *C. c. major* sensu WOLDŘICH he saw the ancestor of the modern *C. cricetus*, whereas he treated older *C. runtonensis* as a separate species.

FAHLBUSCH (in KOENIGSWALD 1970 and FAHLBUSCH 1976) was of the opinion that the name *C. c. runtonensis* NEWTON, 1909 is a later synonym of *C. c. major* sensu WOLDŘICH 1880 and recognized the big form of the hamster from the Middle Pleistocene (Petersbuch 1) as *C. major*, excluding the possibility of its being the ancestor of the present-day *C. cricetus* (the question of big hamsters is discussed in more detail in another paper — PRADEL 1985).

The foregoing consideration only partly illustrates the existing situation. Even a close analysis of the data and arguments produced by the above-mentioned and other authors does not permit the elucidation of the existing obscurities.

Keeping those remarks in mind, I abide by the names *Allocricetus bursae*, *Allocricetus ehiki* and *Cricetus runtonensis* for the hamsters from the Villanyan and Lower Pleistocene and the names *Cricetulus migratorius* and *Cricetus cricetus* for the Late Pleistocene (Weichselian) species.

In the descriptions of *A. bursae*, *A. ehiki* and *C. migratorius* I shall not discuss the changes in the morphology of tooth crowns. I have already given a close description of the morphology of molars of the modern *C. migratorius* from Syria and discussed its variability (PRADEL 1981a). All the phenomena described there, i.e. the disappearance of the connections between cusps, the appearance of additional grooves and ridges, and the changes in the number and shape of roots are identical with those observed sporadically in the genus *Allocricetus*.

1. Early Pleistocene Hamsters

Genus: *Allocricetus* SCHAUB, 1930

Allocricetus bursae SCHAUB, 1930

FAHLBUSCH (1969) mentions 16 molars of this species from 2 Early Pleistocene localities; Kamyk (6 teeth) and Kadzielnia (8), and from one Pliocene locality, Rębielice Królewskie 1 fauna B (2 teeth). Out of these teeth however one M^1

Table VI

Allocricetus bursae. Dimensions of molars found at Kozi Grzbiet, in mm

	M^1			M^2			M^3	
	L	Wb	Wf	L	Wb	Wf	L	Wf
N	230	230	231	146	146	146	52	52
min-max	1.73—2.05	1.10—1.36	1.07—1.33	1.27—1.55	1.01—1.29	1.10—1.31	1.07—1.33	0.94—1.17
$\overline{x}$	1.896	1.240	1.193	1.407	1.142	1.193	1.193	1.047
SD	0.067	0.053	0.050	0.060	0.053	0.048	0.069	0.050
V	3.54	4.24	4.19	4.23	4.63	4.04	5.83	4.74

	M_1			M_2			M_3	
	L	Wb	Wf	L	Wb	Wf	L	Wf
N	207	210	211	163	163	162	84	84
min-max	1.58—1.93	0.98—1.20	0.88—1.09	1.29—1.56	0.99—1.25	1.31—1.50	1.31—1.50	0.96—1.13
$\overline{x}$	1.766	1.091	0.981	1.427	1.120	1.133	1.399	1.039
SD	0.069	0.048	0.043	0.054	0.048	0.047	0.046	0.039
V	3.88	4.41	4.38	3.76	4.25	4.13	3.29	3.72

	Wmax
N	162
min-max	1.02—1.25
$\overline{x}$	1.140
SD	0.045
V	3.94

Table VII

Allocricetus bursae. Dimensions of molars obtained from various localites, in mm

		M¹			M²			M³		M_1			M_2			M_3	
		L	Wb	Wf	L	Wb	Wf	L	Wf	L	Wb	Wf	L	Wb	Wf	L	Wf
Zamkowa Dolna Cave		2.04	1.30	1.16	1.53	1.30	1.29	1.17	1.06	1.75	1.05	0.96	1.57	1.16	1.14	1.52	1.08
		1.95	1.33	1.21	1.57	1.23	1.25						1.50	1.24	1.24	1.46	1.04
		1.99	1.26	1.23	1.52	1.22	1.34						1.53	1.23	1.23		
		1.96	1.22	1.17	1.49	1.19	1.28						1.57	1.24	1.24		
		1.79	1.18	1.12	1.43	1.10	1.20	1.10	1.05	1.52	0.97	0.95	1.33	1.10	1.07	1.31	1.03
		1.78	1.22	1.20	1.33	1.04	1.08			1.60	0.97	0.87	1.34	1.01	1.04	1.33	1.00
		1.77	1.13	1.05	1.41	1.09	1.14										
		1.80	1.21	1.25													
		1.77	1.18	1.12													
		1.79	1.12	1.11													
Kadzielnia					1.47	1.15	1.27			1.95	1.15	1.05					
Kielniki		2.02	1.28	1.30	1.52	1.23	1.30	1.23	1.15	1.91	1.18	1.13	1.51	1.17	1.18	1.55	1.13
		2.04	1.25	1.23	1.49	1.15	1.25			1.89	1.14	1.03	1.54	1.20	1.23		
		1.82	1.14	1.13													
Kamyk		broken															
Zalesiaki					1.48	1.23	1.28										
Kozi Grzbiet	min	1.73	1.10	1.07	1.27	1.01	1.10	1.07	0.94	1.58	0.98	0.88	1.29	0.99	1.00	1.31	0.96
	$\overline{x}$	1.90	1.24	1.19	1.41	1.14	1.19	1.19	1.05	1.77	1.09	0.98	1.43	1.12	1.13	1.40	1.04
	max	2.05	1.36	1.33	1.55	1.29	1.31	1.33	1.17	1.93	1.20	1.09	1.56	1.25	1.25	1.50	1.13

Table VIII

Allocricetus bursae. Data used to describe the relationships within tooth-rows, in mm

		LM^1	LM^2	LM^3	LM^{1+2+3}	LM^{1-3}	$\frac{LM^{1-3} \cdot 100}{LM^{1+2+3}}$	$LM^1 : LM^2$	$LM^3 : LM^2$
Kozi	min-max	1.82—1.96	1.30—1.52	1.09—1.25	4.22—4.71	4.15—4.50	95.33—99.09	1.283—1.423	0.816—0.899
Grzbiet	$\bar{x}$	1.890	1.381	1.190	4.467	4.377	98.013	1.370	0.862
N = 7	SD	0.061	0.076	0.063	0.177	0.142	1.337	0.048	0.031
	V	3.25	5.50	5.27	3.97	3.25	1.36	3.52	3.57
Kielniki		2.02	1.52	1.23	7.77	4.69	98.32	1.329	0.809

		LM_1	LM_2	LM_3	LM_{1+2+3}	LM_{1-3}	$\frac{LM_{1-3} \cdot 100}{LM_{1+2+3}}$	$LM_1 : LM_2$	$LM_3 : LM_2$
Kozi	min-max	1.67—1.85	1.35—1.52	1.34—1.49	4.42—4.80	4.27—4.68	93.91—99.57	1.194—1.314	0.907—1.052
Grzbiet	$\bar{x}$	1.779	1.430	1.388	4.597	4.486	97.600	1.245	0.972
N = 20	SD	0.060	0.047	0.038	0.113	0.114	1.115	0.034	0.041
	V	3.39	3.32	2.76	2.46	2.55	1.14	2.73	4.26
Zamkowa Dolna Cave		1.60	1.34	1.33	4.27	4.07	95.32	1.194	0.993

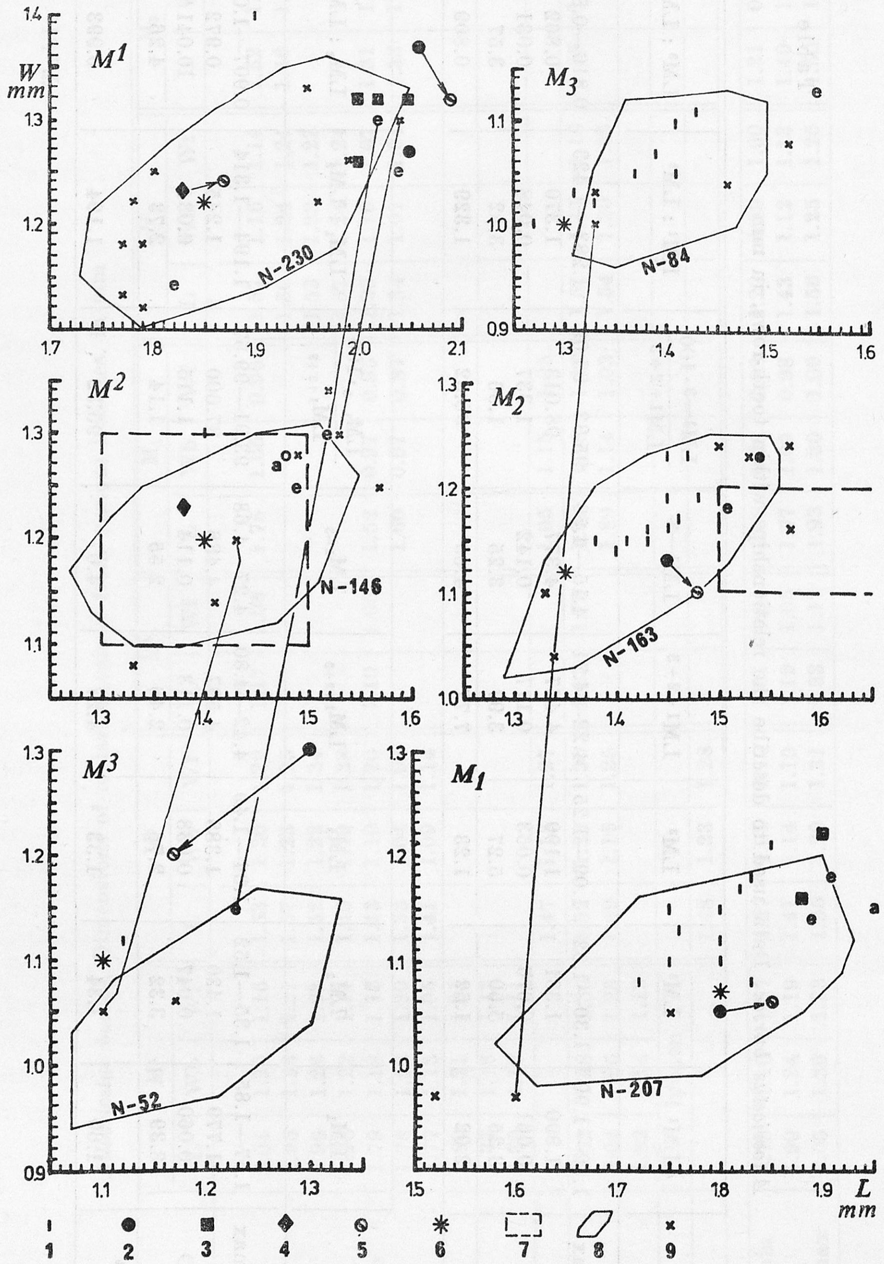


Fig. 4. *Allocricetus bursae.* L/W diagram of molars. After FAHLBUSCH (1969); 1 — Hundsheim (KORMOS 1937); 2 — Kamyk; 3 — Kadzielnia; 4 — Rębielice Królewskie 1; 5 — the same teeth, present author's measurements; 6 — after SCHAUB (1930. Pl. 1, fig. 7); 7 — after SCHAUB (1930, p. 33). New material: 8 — Kozi Grzbiet; 9 — Zamkowa Dolna Cave; a — Kadzielnia; e — Kielniki 3A; c — Zalesiaki 1

from Kamyk (MF/831/4) and two M_1 from Kadzielnia (MF/829/2 and 4) appeared to belong to *A. ehiki*.

As has already been mentioned the fauna found at Rębielice Królewskie 1 is not homogeneous (KOWALSKI 1977). The teeth of *Allocricetus bursae* found there confirm this observation: they constitute a Pleistocene admixture of the fauna of that locality.

The new material of *Allocricetus bursae* comes from 6 localities, in which the teeth of this species occurred in very various numbers, from 1 to 889 (cf. Tables VI and VII). The specimens described by FAHLBUSCH have been included together with the new ones in the L/W diagram in Text-fig. 4.

Altogether 936 teeth were studied; they were mostly detached, only some of them set in mandibular and maxillary remains, 2 or 3 teeth in each. The material from Kozi Grzbiet constituted a big sample, suitable for comparisons with specimens from other localities.

The lengths and widths of the teeth from different localities lie well within the range of variation noted for the population from Kozi Grzbiet. A few points which are outside this range represent the teeth from Zamkowa Dolna Cave, Kadzielnia and Kielniki 3A and so from the localities much older than Kozi Grzbiet. The points representing the teeth described by FAHLBUSCH (1969) as *A. bursae* (M^1, $2M_1$) but belonging to *A. ehiki* are distant from the range.

In addition to these data, the values obtained for *A. bursae* from literature have been plotted in Text-fig. 4. As regards the dimensions of the lower teeth, the specimens from Hundsheim (KORMOS 1937 in FAHLBUSCH 1969) lie well within the range of variation found at Kozi Grzbiet, but they differ somewhat in singular data concerning the upper teeth. The L and W values given in the description of the species by SCHAUB (1930, p. 33, in text) and the values obtained by FAHLBUSCH (1969) by measuring the illustrations presented in SCHAUB'S (1930) paper have also been plotted. And so have been the dimensions of the teeth from the Polish localities described by FAHLBUSCH (1969). All these data correspond fairly well with each other *.

Length of tooth-rows

Eight complete upper tooth-rows (7 from Kozi Grzbiet and one from Kielniki 3A) and 21 lower tooth-rows (20 from Kozi Grzbiet and one from Zamkowa Dolna Cave) have been collected (Table VIII). The tooth-rows from Kielniki 3A and Zamkowa Dolna Cave have not been included in calculations, for although the dimensions of particular teeth which make them up lie within the range of variation of the dimensions of the molars from Kozi Grzbiet (see the L/W graph), their inclusion would considerably change the results of calculations.

Table VIII shows the interrelations found within the tooth-rows. These values resemble the results of analogous calculations carried out for the pre-

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* I re-measured all the specimens described from Poland previously. In some cases the results obtained differ from the values given by FAHLBUSCH (1969). This is appropriately marked in Text-fig. 7. For further notes see the conclusions concerning *A. bursae* and *A. ehiki* on p. 271.

sent-day *Cricetulus migratorius* from Syria (PRADEL 1981a). Also in *Allocricetus bursae* the upper tooth-rows are shorter and form 97.5% of the length of the lower tooth-rows (in *C. migratorius* from Syria: 96.6%). The degree of overlap of the teeth in a row, defined by an index in which the length of a tooth-row (LM 1—3) is expressed in percentage of the sum of the lengths of particular teeth in this row (LM 1+2+3), is also similar, being 98.0% for the upper teeth (in Syria: 97.4%, N = 57) and 97.6% for the lower teeth (in Syria: 96.8%, N = 92). Both in *Allocricetus bursae* and in *C. migratorius* the lower teeth overlap each other to a greater degree. The ascertainment of these relationships permitted me (PRADEL 1981a) to point out false data in STORCH'S (1974) paper, in which the sum of the lengths of successive teeth in a row (even allowing for the roundings-off, most expedient for STORCH'S purposes) is smaller than the given lengths of the rows. This would imply that *Cricetulus migratorius* from Bastam has gaps between the molars set in a row. Nothing like that has been found in the dentition of the *Cricetinae.* The successive teeth bear distinct marks of occlusion. Also the fact that the upper tooth-rows are shorter than the lower ones, which I observed while studying *C. cricetus* from Sąspowska Cave and in the specimens of the modern hamster from Poland, allowed me to demonstrate the errors in MILLER'S (1912) work (PRADEL 1981b). The results obtained for the tooth-rows of *Allocricetus bursae* from Kozi Grzbiet confirms my earlier observations.

Table VIII gives also the values of the index of proportion for the lengths of successive teeth in a row, calculated only on the basis of the molars found in complete tooth-rows. They differ slightly from the quotients of the mean molar lengths, which are $\frac{1.35 — 1 — 0.85}{1.24 — 1 — 0.98}$. In my previous papers (PRADEL 1981a, b) I gave comparisons illustrating the differences between the anterior and posterior widths of molars (Wf-Wb) and suggested the possibility of their application for veryfying the differences between the species of identical morphology and similar dimensions of the molars. This comparison was possible thanks to the finding of numerous teeth of *A. bursae* at Kozi Grzbiet. It shows (Text-fig. 5) a certain difference in the proportions of the teeth of *A. bursae* compared with those in the modern *Cricetulus migratorius*. In order to make the comparison possible, the different numbers of teeth (*A. bursae*: $M^1 = 230$, $M^2 = 146$, $M_1 = 210$, $M_2 = 162$; *Cricetulus migratorius*: $M^1 = 96$, $M^2 = 87$, $M_1 = 152$, $M_2 = 136$) cave been reduced to their percentage values. The dimensions of the teeth of the recent *C. migratorius* are smaller than the corresponding measurements in *A. bursae* (cf. Text-fig. 1a, b, c). If the proportions within the crown outlines of the teeth were to be the same in both species, the differences between Wf and Wb would be expected to be larger in the teeth of the bigger species. However, in smaller *C. migratorius* they are larger than (e.g. M^2 and M_2) or at least equal to these differences observed in *A. bursae.* This means that while the ratio of the tooth length to its greatest width remains unchanged, the other width of the teeth in *C. migratorius* is relatively smaller and consequently the teeth are rather trapezoidal in shape. This difference is small, hardly perceptible; it does not become visible until a large number of teeth have been measured and a histogram constructed. It should be emphasized that in this series Wf has never been found equal to Wb in M^2 of *C. migratorius*, in which the front of the teeth is always broader; this is not the rule as regards M^2 of *A. bursae*. Also only 2 in 96 first upper molars of *C. migratorius* had Wf = Wb but never was Wf greater than Wb.

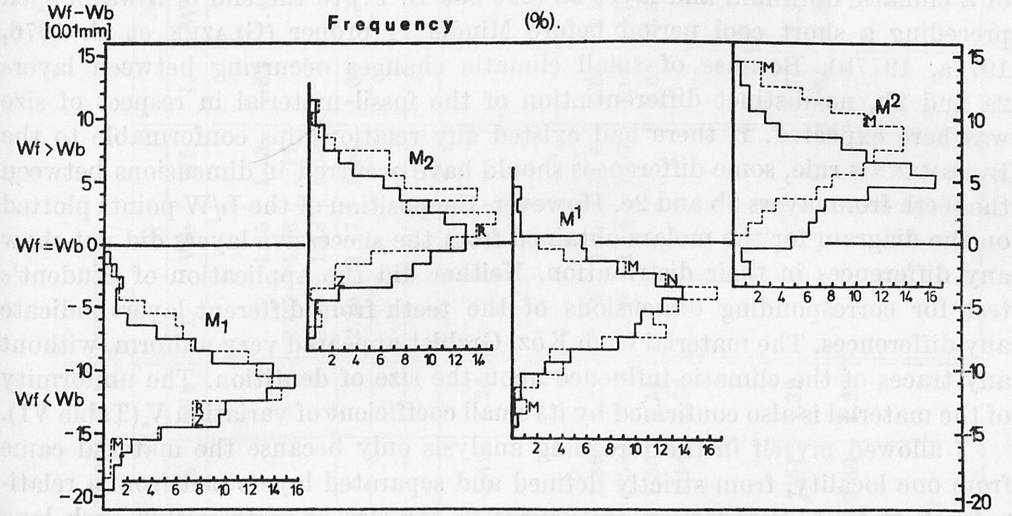

Fig. 5. A comparison of the differences betweer the anterior and posterior widths of M^1, M^2, M_1 and M_2 in *Allocricetus bursae* and the living *Cricetulus migratorius*. Solid line — *A. bursae*, Kozi Grzbiet, N = 889; broken line — *C. migratorius*, recent, Syria, N = 653 (Pradel 1981a). Single letters indicate the differences observed on the teeth of *C. migratorius* from the last glaciation of Poland: M — Mamutowa Cave, R — Raj Cave, Z — Zalas, N — Nietoperzowa Cave

The demonstration of this difference should restrict the fairly arbitrary use of these two names for fossil materials. In addition to the small difference in size, these species differ also in the outline of the crown. It is an open question whether the difference found refers to species or subspecies. Unfortunately, there are no such juxtapositions, e.g., for well-defined present-day species and subspecies and so it is impossible for the time being to establish the significance of this difference for systematic diagnostics.

Basing himself on the length of tooth-rows, Kurtén (1960, 1968) put forward the opinion that the changes in the size of teeth within a species are correlated with climatic changes, i.e. they are conformable to the Bergmann's rule. This rule has been repeatedly discussed. James (1970, p. 387) formulates the "Neo-Bergmannian Rule" as follows: "Intraspecific size variation in homeotherms is related to a combination of climatic variables that include temperature and moisture. Small size associated with hot humid conditions, larger size with cooler or drier conditions".

The abundant dental material of *Allocricetus bursae* from Kozi Grzbiet, permitting the application of statistical analysis, encouraged me to check if in this species we can find any relationships consistent with the BERGMANN'S rule.

Layers 2a, b and c, distinguished at Kozi Grzbiet are referred to the interstadial Mindel I/II (Cracovian I/II), layer 2c (620 000 to 615 000 B. P.) corresponding to a cool period, layer 2b (615 000 610 000 B. P.) to the period of a climatic optimum and layer 2a (610 000 B. P.) to the end of a warm spell preceding a short cool period before Mindel II proper (GŁAZEK et al. 1976, 1977a, 1977b). Because of small climatic changes occurring between layers 2a and 2b, no distinct differentiation of the fossil material in respect of size was here expected. If there had existed any relationships conformable to the BERGMANN'S rule, some differences should have occurred in dimensions between the teeth from layers 2b and 2c. However, the position of the L/W points plotted on the diagram for the molars obtained from the successive layers did not show any differences in their distribution. Neither did the application of Student's test for corresponding dimensions of the teeth from different layers indicate any differences. The material from Kozi Grzbiet appeared very uniform, without any traces of the climatic influence upon the size of dentition. The uniformity of the material is also confirmed by its small coefficient of variation V (Table VI).

I allowed myself in the foregoing analysis only because the material came from one locality, from strictly defined and separated layers and from a relatively short time. Comparison of changes in the size of teeth within such long periods as in KURTÉN (all through the Pleistocene) seems to me unjustified, for the possible adaptations of the species to the climatic conditions may be superimposed on by its evolutionary changes.

The morphology of the dentition is illustrated by the photographs of the upper and lower tooth-rows in Pl. IX, figs. 15 and 16.

Allocricetus ehiki SCHAUB, 1930

From among the Polish materials FAHLBUSCH (1969) identified 21 molars as belonging to *Allocricetus ehiki*: 2 from Kadzielnia and 19 from Kamyk. Three teeth: 1M^1 (MF/831/4) and 2M$_1$ (MF/829/2, 7), referred by him to *A. bursae*, should also be numbered in this species. Now teeth of this species have been found in 5 Early Pleistocene localities. They occurred mostly in small numbers except for Kozi Grzbiet, where their number was somewhat larger.

The new specimens of molars of *A. ehiki* are smaller than or equal in size to those described earlier, but they are all decidedly larger than the teeth of *A. bursae* occurring together with them in the same localities. On account of the scanty and differentiated material obtained from localities distant from each other in time and space, the results of direct measurements are given in Table IX. The statistical analysis given in Table X, which includes the measurements taken on both the new and the previously described material, should

Table IX

Allocricetus ehiki. Dimensions of molars, in mm

		M^1			M^2			M^3		M_1			M_2			M_3	
		L	Wb	Wf	L	Wb	Wf	L	Wb	L	Wb	Wf	L	Wb	Wf	L	Wf
Zamkowa Dolna Cave		2.23	1.42	1.28	1.65	1.30	1.39			?	1.25	1.13	1.62	1.40	1.33	1.57	1.27
		2.16	1.38	1.36						2.00	1.23	1.11					
										2.07	1.18	1.09					
Kadzielnia										2.16	1.17	1.06	1.62	1.34	1.27		
Kielniki 3A					1.69	1.37	1.40										
Zalesiaki 1					?	1.35	1.48										
Kozi Grzbiet	2a I				1.71	1.30	1.32										
	2a II	2.11	1.41	1.31	1.65	1.32	1.47	1.42	1.24								
	2b	2.33	1.47	1.44													
		2.20	1.37	1.33													
		2.18	1.33	1.28													
	2c I	2.37	1.55	1.48	1.65	1.38	1.46	1.40	1.21	2.04	1.26	1.14	1.65	1.31	1.30	1.59	1.26
		2.20	1.45	1.43	1.77	1.49	1.53	1.58	1.20	2.09	1.14	1.00	1.68	1.32	1.34		
		?	?	1.42	1.61	1.37	1.45	1.55	1.31				1.69	1.39	1.37		
		2.13	1.44	1.36				1.44	1.16								
		2.13	1.46	1.36													
		2.23	1.35	1.28													
		2.15	1.44	1.41													
	2b + c	2.17	1.53	1.45	1.60	1.34	1.46	1.51	1.32				1.71	1.35	1.37	1.76	1.35
	2a + b + c				1.58	1.37	1.45						1.64	1.38	1.41	1.63	1.25
	Dump	2.20	1.51	1.40	1.69	1.30	1.42	1.49	1.23								
		2.14	1.46	1.40													
		2.10	1.40	1.30													
		2.15	1.35	1.32													
		2.19	1.47	1.39													

be treated as tentative. The values of the coefficient of variation (V > 5) confirm the heterogeneity of the material.

An L/W diagram of the molars is given in Text-fig. 6. It covers the whole of the Polish material and also some comparative data. The measurements of the specimens from Poland correspond fairly well with the comparative material.

Table X

Allocricetus ehiki. Statistical analysis of the dimensions of molars. The data used in these calculations come from Table IX and from FAHLBUSCH, 1969

	M^1		M^2		M^3	
	L	Wb=Wmax	L	Wf=Wmax	L	Wf
N	23	23	12	13	7	7
min-max	2.10—2.50	1.33—1.62	1.58—1.78	1.32—1.53	1.40—1.58	1.16—1.32
$\bar{x}$	2.243	1.461	1.673	1.438	1.484	1.239
SD	0.125	0.081	0.063	0.051	0.068	0.058
V	5.59	5.56	3.74	3.53	4.55	4.69

	M_1		M_2		M_3	
	L	Wb=Wmax	L	Wmax	L	Wf
N	12	13	12	12	5	5
min-max	2.00—2.30	1.14—1.44	1.62—1.85	1.30—1.52	1.57—1.76	1.25—1.45
$\bar{x}$	2.101	1.256	1.690	1.389	1.660	1.316
SD	0.079	0.090	0.071	0.074	0.089	0.085
V	3.76	7.14	4.23	5.36	5.39	6.44

The measurements of the only complete upper tooth-row (from Kozi Grzbiet) found in the material are: $LM^{1-3} = 5.0$ mm, $LM^1 = 2.11$ mm, $LM^2 = 1.65$, $LM^3 = 1.42$ mm and the resulting relationships: $LM^{1+2+3} = 5.18$ mm, the index of overlap of the teeth — 97.7%, $LM^1 : LM^2 = 1.28$, $LM^3 : LM^2 = 0.86$. A photograph of this specimen is given in Pl. IX, fig. 17. The index of proportion of the teeth in the row calculated on the basis of the mean values from Table IX is $\frac{1.32 — 1 — 0.89}{1.25 — 1 — 0.99}$, but if this index is calculated exclusively for the teeth from Kozi Grzbiet, only the value $LM_1 : LM_2$ changes, being 1.23 here. The diagram showing this index and its interpretation are given in the final section. The morphology of the teeth is illustrated in the photographs in Pl. IX, figs. 17 and 18, and their description, bringing out essential details, was presented

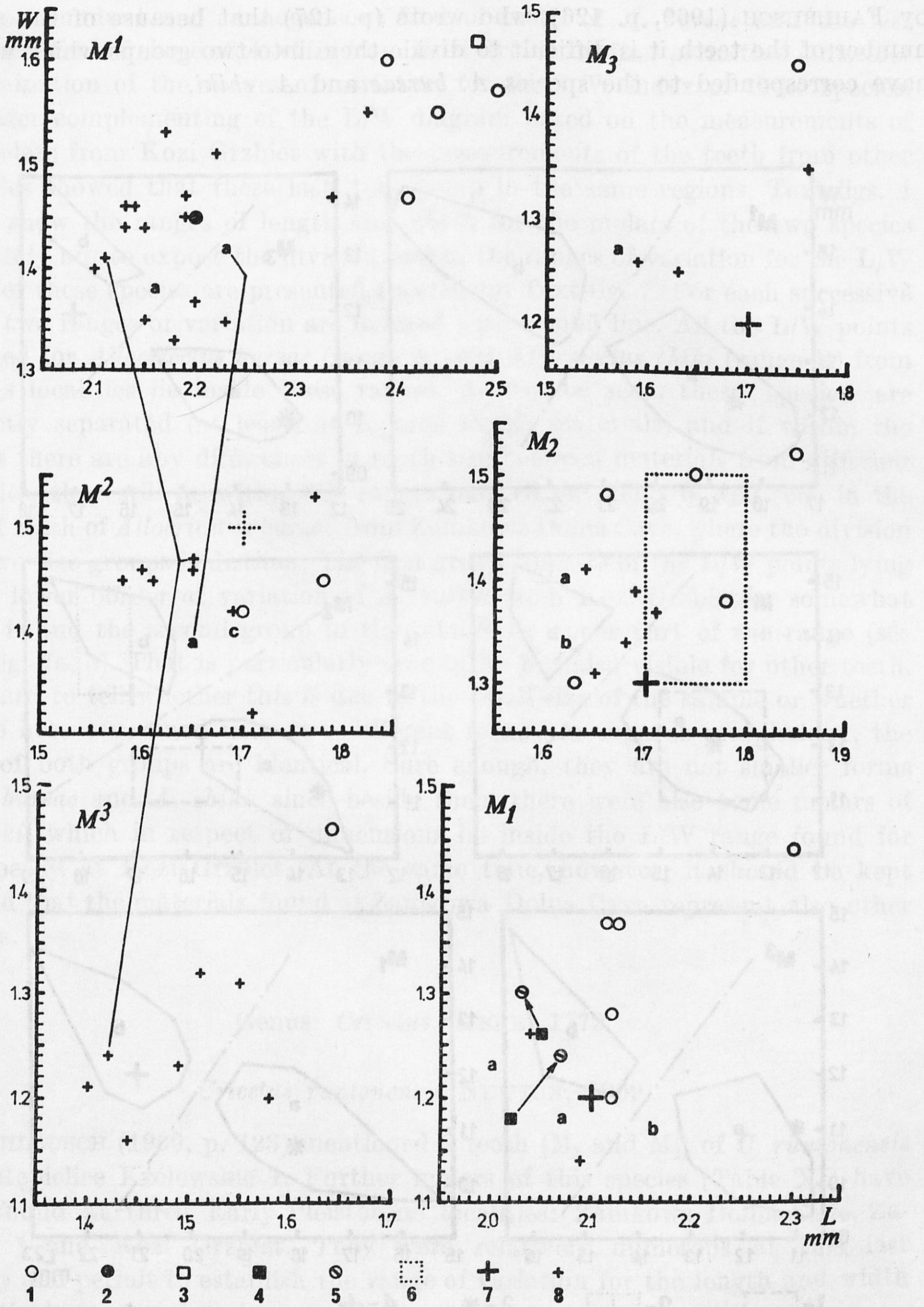

Fig. 6. *Allocricetus ehiki.* L/W diagram of molars. After FAHLBUSCH (1969): 1 — Kamyk; 2 — Kamyk, identified by FAHLBUSCH (1969) as *A. bursae*; 3 — Kadzielnia; 4 — Kadzielnia, identified by FAHLBUSCH (1969) as *A. bursae*; 5 — the same teeth, present author's measurements; 6 — *A. ehiki*, after SCHAUB (1930, pp. 33—35); 7 — *A. ehiki*, after SCHAUB (1930, Pl. 1, fig. 10). New material: 8 — Kozi Grzbiet; a — Zamkowa Dolna Cave; b — Kadzielnia; c — Kielniki 3A

by Fahlbusch (1969, p. 126), who wrote (p. 127) that because of the small number of the teeth it is difficult to divide them into two groups which would have corresponded to the species *A. bursae* and *A. ehiki*.

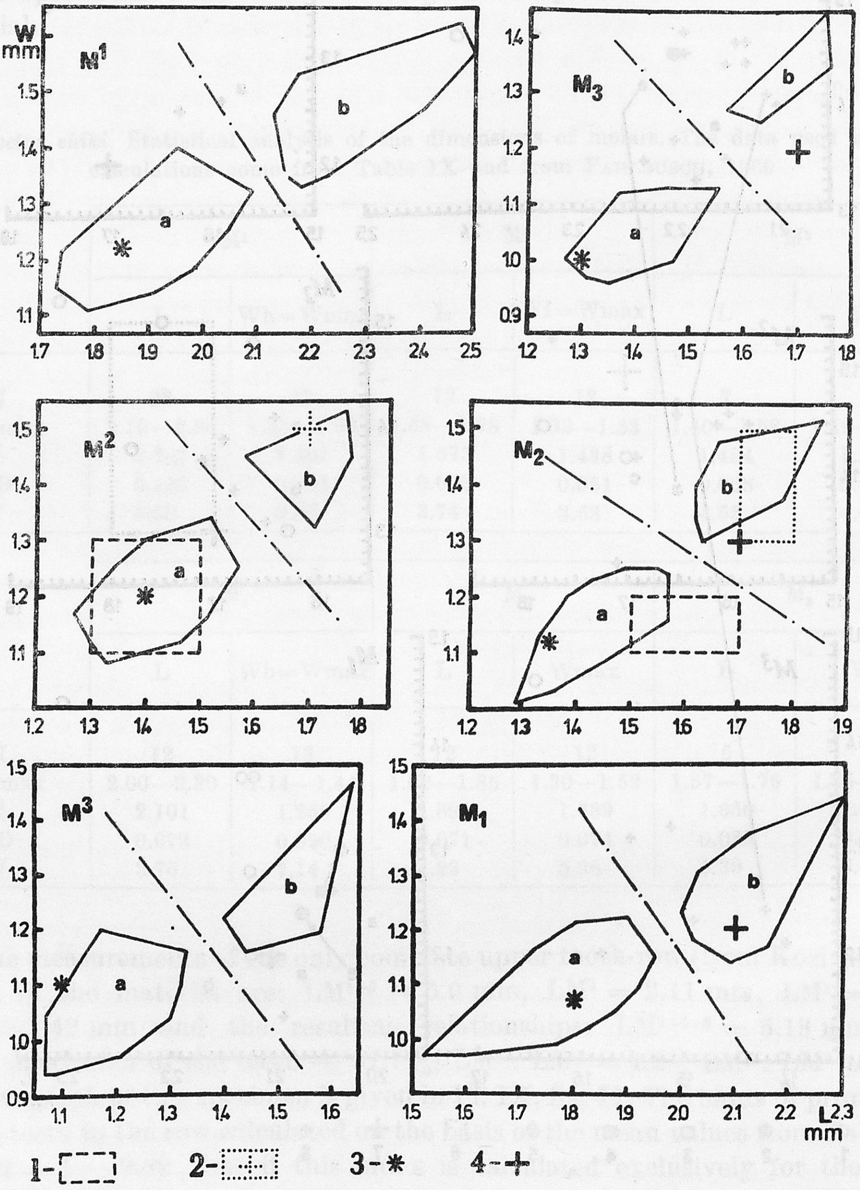

Fig. 7. Division of the ranges of variation for the lengths and widths of molars between a — *Allocricetus bursae* and b — *A. ehiki*. 1 — *A. bursae*, after Schaub (1930, p. 33); 2 — *A. ehiki*, after Schaub (1930, pp. 34—35); 3 — *A. bursae*, after Schaub (1930, Pl. 1, figs 7 and 9); 4 — *A. ehiki*, after Schaub (1930, pl. I, fig. 10). The ranges of variation a and b, marked with a solid line, refer only to the specimens from Poland described in this paper

The abundant and homogeneous find of teeth of *A. bursae* and the less abundant find of those of *A. ehiki* from Kozi Grzbiet at first permitted a distinct discrimination of the ranges of variation for the L/W index of these species. The later complementing of the L/W diagram based on the measurements of the molars from Kozi Grzbiet with the measurements of the teeth from other localities showed that these last, too, group in the same regions. Text-figs. 4 and 6 show the ranges of length and width for the molars of the two species separately but to expose the division better, the ranges of variation for the L/W index of these species are presented together in Text-fig. 7. For each successive molar two ranges of variation are marked with a solid line. All the L/W points obtained for *Allocricetus bursae* (range A) and *Allocricetus ehiki* (range B) from various localities lie inside these ranges. As can be seen, these species are distinctly separated (at least, as regards Polish materials) and if within the species there are any differences in tooth size between materials from different localities, they still lie within the ranges marked out. This is well seen in the case of teeth of *Allocricetus bursae* from Zamkowa Dolna Cave, where the division into two size groups is distinct. The first group consists of the L/W points lying at the lower border of variation of *A. bursae* from Kozi Grzbiet or somewhat below it and the second group in the middle or upper part of the range (see Text-fig. 7a, b). That is particularly true of M^1 but also visible for other teeth. It is hard to tell whether this is due to the small size of the sample or whether we are here concerned with two different forms. As regards morphology, the teeth of both groups are identical. Sure enough, they are not smaller forms of *A. bursae* and *A. ehiki*, since beside them there were also some molars of *A. ehiki*, which in respect of dimensions lie inside the L/W range found for this species at Kozi Grzbiet. At the same time, however, it should be kept in mind that the materials found at Zamkowa Dolna Cave represent also other periods.

Genus: *Cricetus* Leske, 1779

Cricetus runtonensis Newton, 1909

Fahlbusch (1969, p. 123) mentioned 2 teeth (M_1 and M_2) of *C. runtonensis* from Rębielice Królewskie 1. Further molars of this species (Table XI) have been found at three Early Pleistocene localities: Zamkowa Dolna Cave, Zalesiaki 1 and Kozi Grzbiet. They were relatively numerous at this last locality and permit to establish the range of variation for the length and width of particular sorts of molars.

The teeth of *C. runtonensis* appear more differentiated in respect of dimensions than the molars of *A. bursae* accompanying them at the same locality. Sometimes particular L/W points differ considerably from the mean value and enter the range of variation for *C. major* sensu Fahlbusch 1976 from Petersbuch 1 (Text-fig. 8); this variation however shows no connection with the derivation

Table XI

Cricetus runtonensis. Dimensions of molars from Zamkowa Dolna Cave and Zalesiaki 1 compared with the means of the material from Kozi Grzbiet, in mm

		M^1			M^2			M^3		M_1			M_2			M_3	
		L	Wb	Wf	L	Wb	Wf	L	Wf	L	Wb	Wf	L	Wb	Wf	L	Wf
Zalesiaki 1		3.39	2.25	2.23	2.65	2.05	2.20	2.47	2.11	3.47	1.89	1.84	2.60	2.05	1.99	3.22	2.39
		3.40	2.28	2.20	2.83	2.04	2.25	2.49	2.06	3.64	2.04	1.92	2.93	2.28	2.34	3.08	2.33
		3.25	?	2.05	2.70	2.13	2.24	2.54	2.04	2.98	1.82	1.62	2.77	2.14	2.13	2.92	2.19
		3.71	2.33	2.32	2.80	2.01	2.28	2.40	2.04								
		3.60	2.20	2.20				2.45	2.21								
		3.30	2.14	2.03													
		3.60	2.15	2.12													
Zamkowa Dolna Cave		3.32	2.20	2.13	2.88	2.14	2.28	2.54	2.17	3.20	1.85	1.74					
					2.62	2.16	2.25										
Kozi Grzbiet	min	3.25	1.92	1.94	2.52	2.03	2.24	2.33	2.00	3.01	1.80	1.65	2.60	2.07	2.10	2.79	2.02
	$\bar{x}$	3.48	2.27	2.22	2.92	2.24	2.43	2.63	2.19	3.35	1.94	1.82	2.84	2.24	2.26	3.04	2.33
	max	3.75	2.46	2.44	3.24	2.53	2.73	2.96	2.33	2.74	2.10	2.05	3.09	2.55	2.66	3.36	2.66

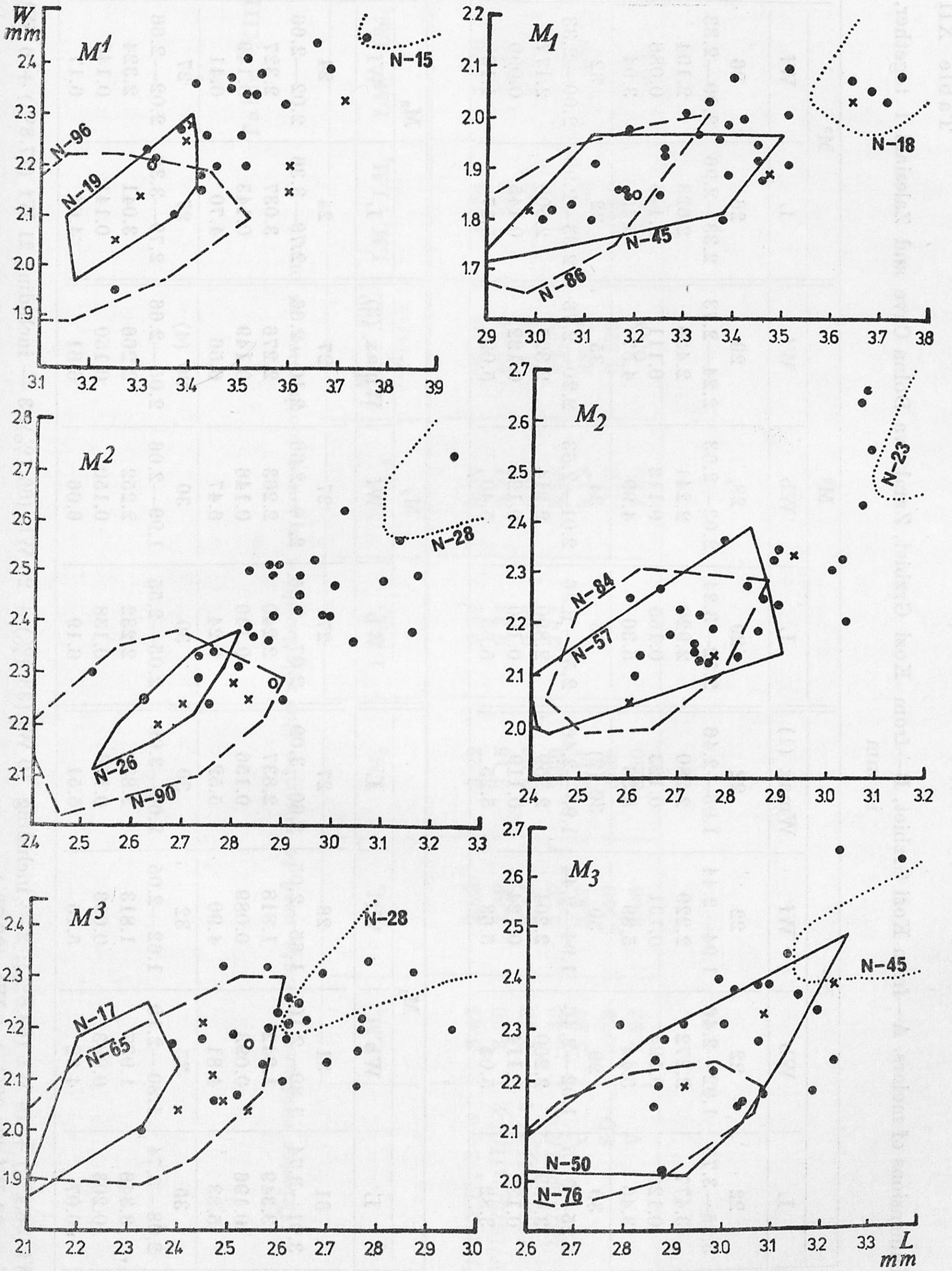

Fig. 8. *Cricetus runtonensis*. L/W diagram of morals. Dost — Kozi Grzbiet; crosses — Zalesiaki 1; circles — Zamkowa Dolna Cave; solid line — *Cricetus cricetus*, last glaciation, Poland; dashed line — recent *C. cricetus* from Poland (Pradel 1985); dotted line — approximate lower boundaries of variation of the lengths and widths of morals in *C. major* s. Fahlbusch 1976 on the basis of Fig. 1 and Table 1 in Fahlbusch's paper (1976)

Table XII

Cricetus runtonensis. Dimensions of molars. A—from Kozi Grzbiet, B—from Kozi Grzbiet, Zamkowa Dolna Cave and Zalesiaki 1 together, in mm

		M^1				M^2			M^3	
		L	Wb	Wf	Wmax (1)	L	Wb	Wf	L	Wf
A	N	22	22	22	22	29	28	29	26	26
	min-max	3.25—3.75	1.92—2.46	1.94—2.44	1.95—2.46	2.52—3.24	2.03—2.53	2.24—2.73	2.33—2.96	2.00—2.33
	$\bar{x}$	3.477	2.272	2.220	2.280	2.920	2.241	2.428	2.628	2.194
	SD	0.120	0.124	0.131	0.123	0.155	0.112	0.111	0.146	0.086
	V	3.46	5.44	5.89	5.38	5.30	4.99	4.57	5.55	3.94
B	N	30	29	30	30 (2)	35	34	35	32	32
	min-max	3.25—3.75	1.92—2.46	1.94—2.44	1.95—2.46	2.52—2.46	2.01—2.53	2.20—2.73	2.33—2.96	2.00—2.33
	$\bar{x}$	3.469	2.260	2.204	2.259	2.890	2.214	2.397	2.600	2.177
	SD	0.132	0.114	0.124	0.119	0.160	0.120	0.122	0.145	0.090
	V	3.82	5.04	5.63	5.25	5.55	5.40	5.09	5.57	4.13

		M_1			M_2				M_3	
		L	Wb	Wf	L	Wb	Wf	Wmax (3)	L	Wf
A	N	31	31	28	27	27	27	27	24	24
	min-max	3.01—3.74	1.80—2.10	1.65—2.05	2.60—3.09	2.07—2.55	2.10—2.66	2.10—2.66	2.79—3.36	2.02—2.66
	$\bar{x}$	3.349	1.942	1.818	2.837	2.240	2.263	2.276	3.037	2.327
	SD	0.196	0.093	0.089	0.156	0.140	0.146	0.149	0.143	0.149
	V	5.83	4.81	4.90	5.52	6.24	6.47	6.56	4.70	6.41
B	N	35	35	32	30	30	30	30 (4)	27	27
	min-max	2.98—3.74	1.80—2.10	1.62—2.05	2.60—3.09	2.05—2.55	1.99—2.66	2.05—2.66	2.79—3.36	2.02—2.66
	$\bar{x}$	3.346	1.937	1.813	2.830	2.232	2.252	2.266	3.041	2.324
	SD	0.203	0.093	0.093	0.156	0.138	0.150	0.150	0.141	0.143
	V	6.07	4.82	5.15	5.51	6.19	6.66	6.61	4.64	6.17

1 — including 8 Wf (36.4%) + 14 Wb (63.6%); 2 — including 10 Wf (33.3%) + 20 Wb (66.7%); 3 — including 21 Wf (77.8%) + 6 Wb (22.2%); 4 — including 22 Wf (73.3%) + 8 Wb (26.7%).

Table XIII

Cricetus runtonensis. Data used to describe the relationships in lower tooth-rows, in mm

	LM_1	LM_2	LM_3	LM_{1+2+3}	LM_{1-3}	$\frac{LM_{1-3} \cdot 100}{LM_{1+2+3}}$	$LM_1 : LM_2$	$LM_1 : LM_2$
Zalesiaki 1, MF/1665/79, 2—4	3.47	2.93	3.22	9.62	9.37	97.40	1.184	1.009
Kozi Grzbiet, MF/1675/2aII/V-2	3.30	2.89	3.15	9.34	9.11	97.54	1.142	1.090
1675/2cII/H-7	3.33	2.86	3.07	9.26	9.04	97.62	1.164	1.073
1675/2cII/J-6	3.39	2.79	2.99	9.17	8.98	97.93	1.215	1.072
$\bar{x}$	3.37	2.87	3.11		9.13	97.62	1.176	1.084
SD	.075	.059	.099		.172	0.223	0.031	0.013
V	2.22	2.06	3.20		1.88	0.23	2.64	1.22

of the specimens from particular layers. The range of dimensions of detached molars of *C. runtonensis* lies between the ranges of variation of L/W for the modern *Cricetus cricetus* from Poland and *C. major* sensu FAHLBUSCH 1976 from Petersbuch 1 and overlaps them respectively at the upper and lower borders. The dimensions of the molars of *C. runtonensis* from Zalesiaki 1 and Zamkowa Dolna Cave lie well within the range of variation marked out for the specimens from Kozi Grzbiet. In Table XI they are however given separately because of age differences (Zamkowa Dolna Cave, fauna A — Villanyian, Zalesiaki 1, fauna A — Cromerian, Kozi Grzbiet — Esterian). A statistical analysis of the measurements of molars of *C. runtonensis* from Kozi Grzbiet is presented in part A of Table XII, while part B covers the specimens from all three localities together. Both in part A and in part B the coefficients of variation V of particular dimensions generally exceed the value 5 (9.8—6.7) and indicate their great variability, but if a correction for small numbers (N = 22—35) has been applied, they do not differ much from the values of V found for the teeth of the living *C. cricetus* from Poland, where the range of variation is 9.34—5.17 with the numbers of specimens (N) from 65 to 97.

Only 4 complete lower tooth-rows have been found in the whole of material, composed mostly of detached molars. Their dimensions and the relationships resulting from the lengths of successive teeth are presented in Table XIII. These tooth-rows differ from the recent form in size: $LM_{1+3} = 9.13$ mm (N = 4), while in the present-day hamster from Poland: $LM_{1+3} = 8.09$ (N = 75); on the other hand, the relationships between dimensions resemble those in other big *Cricetinae*. A photograph of one of these rows is given in Pl. X, fig. 11. The index of proportion of the teeth in the row calculated from the means presented in Table XIIB is $\frac{1.20 — 1 — 0.90}{1.18 — 1 — 1.07}$.

In addition to the size of tooth-rows, both *C. c. runtonensis* sensu NEWTON 1909 and *C. c. major* sensu WOLDŘICH 1880 differ from the modern *C. cricetus* also in some morphological characters, notably in a greater width of the anterocone of M^1 and its displacement towards the buccal side, resulting in a characteristic outline of the crown. In *Cricetus major* sensu FAHLBUSCH 1976 this character is distinct and, besides, its 2nd and especially 3rd molars bear numerous additional ridges. These additional elements on the teeth of fossil hamsters were also mentioned by other authors, though they did not occur on so many teeth and so abundantly as in the form from Petersbuch 1 (FAHLBUSCH 1976). Having compared my material of *C. runtonensis* in respect of these characters, I may state that: 1) the greater width and the displacement of the anterior pair of cusps on M^1 occur also in other specimens discussed from all these localities, although here they vary in degree. In the principle, the larger the tooth, the more conspicuous is this character, but there are exceptions. 2) On M2 and M3 the additional elements occur relatively frequently, but not on all teeth and their intensity is lower than in the hamster from Petersbuch 1. Some of the 2nd and 3rd molars, although they belonged to larger specimens

Table XIV

The occurrence of hamsters in the Upper-Pleistocene localities. C — *Cricetus cricetus*, M — *Cricetulus migratorius*

Age	Age / Locality				Raj Cave	Nietoperzowa Cave	Koziarnia Cave	Mamutowa Cave	Żytnia Skała Rock-shelters	Rock-shelter above Niedostępna Cave	Bramka Rock-shelter	Sąspowska Cave	Witkowice	Zalas	Kadzielnia
10 000	Holocene														C
15 000	Pleistocene	Weichselian (Würm)	Late Glacial						C	C	C	C	C	CM	
29 000			Pleniglacial	Upper				CM							
39 000				Interstadial Paudorf											
				Middle	M				C						
50 000				Interstadial Moershoofd											
60 000				Lower		M	C								
			Early Glacial	Interstadial Brørup											
70 000				Prae-Brørup											
		Interglacial (Eemian)				C									

and in their L/W dimensions overlapped the range of variation for the teeth of the hamster from Petersbuch 1, had no such elements and looked like most teeth of the present-day *C. cricetus* from Poland, whereas some other teeth, much smaller, had them in large numbers (see Pl. X, figs. 1—14).

2. Late-Pleistocene Hamsters

After a long period starting from the Upper Biharian (Mindel I/II) and void of any finds, hamsters did not reappear in the Polish fossil materials until various phases of the last glaciation. They were mostly found in the caves of the Ojców region (7 sites) and at 2 sites near Cracow and two in the Kielce region. The hamsters found at these sites belonged to two species: *Cricetulus migratorius* and *Cricetus cricetus*. The molars of *C. migratorius* occurred in a small number and the remains of *C. cricetus* were also limited to single detached teeth at the most of localities. Only in Sąspowska Cave the molars of *C. cricetus* were found in a large number; they have already been described in another paper (PRADEL 1981b). Table XIV shows all the localities and species occurring in them against the stratigraphy of the Late Pleistocene.

Genus: *Cricetulus* MILNE-EDWARDS, 1867

Cricetulus migratorius PALLAS, 1773

Living hamsters, small and yet varying in size, are included in the genus *Cricetulus*, divided into three subgenera: *Cricetulus* MILNE-EDWARDS, 1867, *Allocricetulus* ARGYROPULO, 1933 and *Tscherskia*, OGNEV 1914. These subgenera comprise 11 species (among them 2 incertae sedis) with 37 subspecies. In one species only, *Cricetulus migratorius* PALLAS, 1773, as many as 13 subspecies have been distinguished (ELLERMAN and MORRISON-SCOTT 1951, pp. 621—627). This diversity of forms of modern hamsters certainly results from a long process of evolution. A similar diversity of forms most probably existed in the Late Pleistocene.

The present-day species of hamsters are discriminated chiefly on the basis of external characters and the build of the skull. Unfortunately, there is no close study of the morphology and dimensions of their dentition, to provide data for comparisons with fossil materials, the bulk of which consists of detached teeth. For this reason I qualify the teeth of small hamsters from the Polish Late-Pleistocene localities only as belonging to *Cricetulus migratorius* PALLAS, 1773. Most of the comparisons carried out in this paper include the present-day *Cricetulus migratorius* cf. *cinerascens* WAGNER, 1848 from Syria (PRADEL 191a).

Teeth of *Cricetulus migratorius* were found at 4 localities. They consist of 2 upper and 2 lower tooth-rows and two detached M^1 and M_1.

Table XV

Cricetulus migratorius. Dimensions of detached molars, lengths of tooth-rows and relationships within them in mm

	M_1			M_2			M_3		LM_{1+2+3}	LM_{1-3}	$\frac{LM_{1-3} \cdot 100}{LM_{1+2+3}}$	$LM_1:LM_2$	$LM_3:LM_2$
	L	Wb	Wf	L	Wb	Wf	L	Wf					
Mamutowa Cave	1.71	1.07	0.91										
Raj Cave	1.61	1.01	0.88	1.30	1.03	1.04	1.08	0.95	3.99	3.94	98.75	1.238	0.831
	1.65	1.05	0.91	1.33	1.13	1.10	1.16	1.03	4.14	4.06	98.07	1.241	0.872
									$\bar{x}$ =	4.00	98.41	1.239	0.851

	M^1			M^2			M^3		LM^{1+2+3}	LM^{1-3}	$\frac{LM^{1-3} \cdot 100}{LM^{1-2-3}}$	$LM^1:LM^2$	$LM^3:LM^2$
	L	Wb	Wf	L	Wb	Wf	L	Wf					
Nietoperzowa Cave	1.71	1.14	1.11										
Mamutowa Cave	1.86	1.22	1.09	1.36	1.08	1.18	1.14	1.02	4.36	4.27	97.94	1.368	0.838
	1.74	1.11	1.09	1.25	0.98	1.12	1.01	0.93	4.00	3.95	98.75	1.392	0.808
									$\bar{x}$ =	4.11	98.34	1.379	0.823

The dimensions of particular teeth are given in Table XV, whereas in the L/W graph (Text-fig. 9) these dimensions are presented in comparison with the data concerning the modern hamster from Syria, the Middle-Pleistocene *C. migratorius* from hios I. in the Aegean Sea (STORCH 1975) and *Allocricetus*

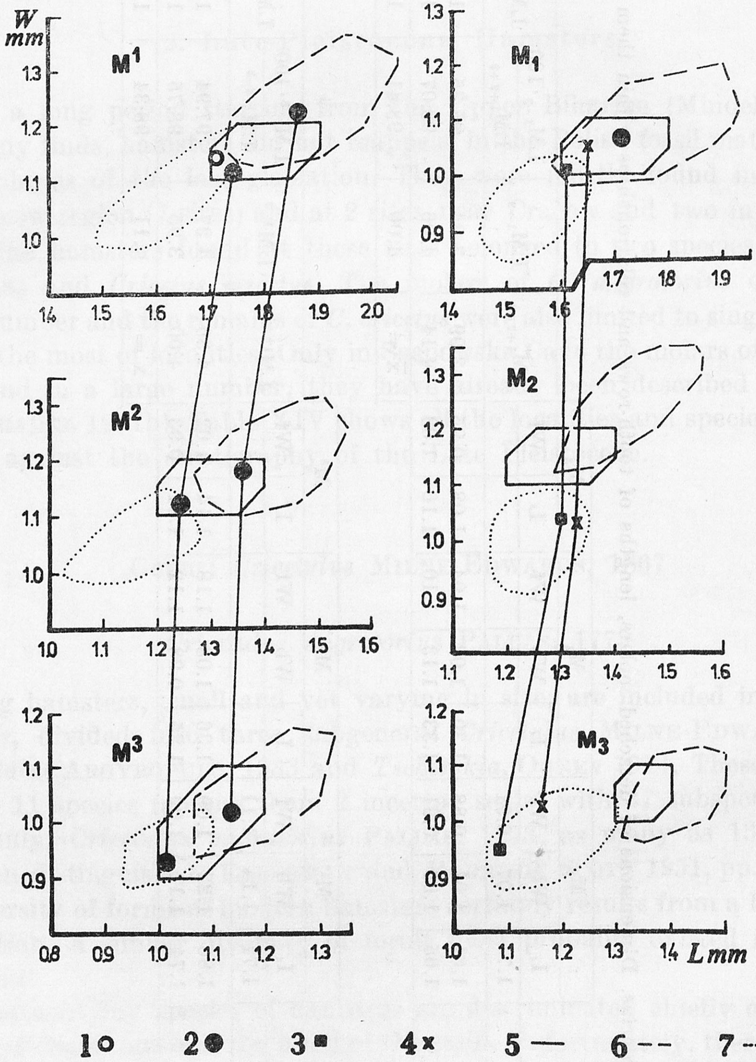

Fig. 9. *Cricetulus migratorius*. L/W diagram of molars. 1 — Nietoperzowa Cave; 2 — Mamutowa Cave; 3 — Raj Cave; 4 — Zalas; 5 — *C. migratorius*, Khios I. (STORCH 1975); 6 — *A. bursae*, Kozi Grzbiet; 7 — *C. migratorius*, recent, Syria (PRADEL 1981a)

bursae from Kozi Grzbiet. Compared with all these three forms the molars from the Weichselian of Poland show some similarities and differences. The teeth of one of the upper rows from Mamutowa Cave (Pl. XI, fig. 1) resemble the corresponding teeth of *A. bursae* and *C. migratorius* from Khios in dimensions, whereas the measurements of the teeth of the second row from the same locality agree exactly with those of the teeth of the modern *C. migratorius* from Syria and the Middle Pleistocene one from Khios. The teeth of the lower rows from Raj Cave and Zalas are similar to each other and, as a rule, already correspond with the molars of the present-day *C. migratorius* from Syria, although, in relation to M_1 and M_2, M_3 is shorter. In respect of dimensions their M_1 lies within the ranges of variation of all the three forms under comparison. Detached M_1 from Nietoperzowa Cave quite agrees with the modern *C. migratorius* from Syria, but it still lies in the lower portion of the range of variation of *C. migratorius* from Khios. As regards dimensions, these teeth summarily show a mosaic of characters of all the forms being compared and they come very close to the modern *C. migratorius* from Syria, although they are not identical. Here we may be concerned with a subspecies other than *C. c. cinerascens*. Further similarities and differences between *C. migratorius* from the last glaciation of Poland and the modern *C. migratorius* from Syria can be found in the lengths of the whole tooth-rows and relationships inside them, presented in Table XV. The dimensions of detached teeth and their rows are equal to or somewhat greater than the corresponding data for the modern *C. migratorius*. The upper tooth-rows of the modern hamster from Syria are 3.43—3.72 — 4.00 mm long (N = 57). One of the tooth-rows from Mamutowa Cave (LM^{1-3} = 3.95 mm) lies in this respect in the upper portion of the range, while the other one is distinctly longer (LM^{1-3} = 4.27 mm). The lower tooth-rows compare similarly. In the hamster from Syria LM_{1-3} is 3.61—3.85—4.01 mm (N = 98) and the row of molars from Raj Cave (3.94 mm) lies within this range, but the tooth-row from Zalas is slightly longer (4.06 mm). The overlap of teeth also shows a small difference. In the material from Syria the length of tooth-row is 94.5—96.8—98,3 % of the sum of the lengths of the three successive molars of which it is made up (N = 98) and the value of this index for the tooth-row from Zalas still lies within this range, but it is somewhat greater, 98.7 %, for the tooth-row from Raj Cave, which means that the teeth overlap each other to a somewhat smaller degree in this row than in the present-day *C. migratorius*.

Only the tooth-row from Zalas was set in the mandible, which despite its generally bad state of preservation retained the essential measuring points: the posterior edge of the alveolus of the incisor and the condylar process. Its length was 14.5 mm, which lies within the range of variation of the mandible length in the modern hamster from Syria: 11.50 — 13.74 — 15.75 m (N = 117). However, two groups of mandibles have been distinguished in the material from Syria: group A — young specimens and group B — old specimens, with their respective length equal to 11.50 — 12.94 — 14.00 mm (N = 27) and 12.50 — 19.99 — 15.75 mm (N = 90).

Taking into consideration the "massiveness" of the bone and the degree of wear of the teeth, I should decidedly number the mandible from Zalas in the group of younger specimens and consequently it is larger than the mandibles from Syria.

The differences between the measurements Wf and Wb, marked with the letters M, N. R and Z, are plotted in Text-fig. 5 in the context of differences found in *A. bursae* and *C. migratorius* from Syria. The small number of data does not permit any far-reaching inferences.

Genus: *Cricetus* LESKE, 1779

Cricetus cricetus (LINNAEUS, 1758)

A total of 221 teeth of this species have been collected. The homogeneous material from Sąspowska Cave has been given a separate paper (PRADEL 1981b) and here is used as comparative material for the teeth obtained from other localities.

The results of measurements of detached molars from different localities are given against the extrema and means for the specimens from Sąspowska Cave in Table XVI and in the L/W diagram in Text-fig. 10. They indicate the homogeneity of the material. This is also confirmed by the coefficients of variation (2.62—4.48) obtained in the cumulative statistical analysis of the dimensions of teeth from all the localities, presented in Table XVII. Ranges of variation for the lengths and widths of molars of other big-hamster populations — the modern *C. c. cricetus* from Poland, huge *C. major* sensu FAHLBUSCH 1976 from Petersbuch 1 (FAHLBUSCH 1976) — have been plotted on the L/W diagram in Text-fig. 10. As regards this last form, it is probably the subspecies *C. c. canascens* NEHRING, 1899, which is, admittedly, somewhat smaller than the nominative subspecies (MILLER 1912, NIEZABITOWSKI-LUBICZ 1933). The dimensions of molars in the hamsters from the localities named in Table XVI generally lie within the range of variation of the lengths and widths observed in the present-day hamster from Poland or only little differ from them. One tooth from the Bramka Rock-shelter, left M_3 (NF/1202/74_2), differs considerably from the remaining teeth, its length being 3.25 mm and anterior width 2.49 mm (Text-fig. 10; Pl. XI, fig. 10), while both in dimensions and in morphology it corresponds exactly to the teeth of *C. major* from Petersbuch 1. Five teeth have been found at Bramka: M_3 being just discussed and M_1 in layer 4 and M_1, M_2 and M_3 in layer 5a. Layer 5a comes from a slightly younger and warmer period than does layer 4, but the size difference between these specimens does not seem to have been caused by climatic changes, since in respect of its dimensions M_1 which occurred in the same layer as M_3 (Text-fig. 10) lies below the mean lengths and widths of both the modern hamsters and the other specimens from the localities under study. The inclusion of all the lengths of M_3 — which are besides known to be characterized by the greatest variability — in statistical calculations is reflected in the coefficient of variation $V = 4.48$ ($N = 50$; Table XVII), which departs to a very small degree from its value obtained for a uniform population of the modern *C. cricetus* from Germany,

Table XVI

Cricetus cricetus. Dimensions of molars obtained from various localities, compared with the means calculated from the material from Sąspowska Cave, in mm

	M^1			M^2			M^3		M_1			M_2			M_3	
	L	Wb	Wf	L	Wb	Wf	L	Wf	L	Wb	Wf	L	Wb	Wf	L	Wf
Nietoperzowa Cave									3.22	1.82	1.63					
Koziarnia Cave				2.63	2.06	2.23										
Mamutowa Cave	3.41	2.13	2.16	2.78	2.11	2.31			3.13	1.86	1.75	2.72	2.25	2.27		
	3.19	1.98	1.87	2.72	2.01	2.22			3.19	1.86	1.80	2.44	1.99	1.93		
				2.52	1.94	2.11										
Żytnia Skała Rock-shelter	3.37	2.10	1.98	2.59	1.99	2.17			3.37	1.81	1.71	2.91	2.15	2.15	2.79	2.07
	3.26	2.10	2.06	2.57	1.98	2.20			3.11	1.97	1.79	2.71	2.12	2.18	2.77	2.05
	?	?	?						?	?	1.77	2.80	2.27	2.18	3.08	2.19
									3.16	1.78	1.68	2.61	2.14	2.11		
Rock-shelter above Niedostępna Cave	3.40	2.30	2.22	2.71	2.14	2.31			3.32	1.89	1.73	2.83	2.24	2.25	2.85	2.28
	3.22	2.04	?	2.61	2.09	2.19			?	?	?	2.30	1.94	2.03		
									3.13	1.80	1.68					
									3.29	1.82	1.72					
Rock-shelter Bramka									?	?	1.81	2.69	2.06	2.11	3.25	2.49
									3.09	1.79	1.63				3.00	2.10
Witkowice									2.87	1.71	1.62	2.47	2.07	2.00	2.73	2.02
Zalas	3.28	2.04	2.09	2.73	2.16	2.32	2.33	2.01	3.10	1.80	1.68	2.75	2.10	2.13	2.83	2.14
	?	?	2.07									2.66	2.11	2.11	2.82	2.12
									3.19	1.82	1.71	2.59	2.15	2.20	2.81	2.18
Sąspowska Cave min	3.15	1.97	1.91	2.54	1.98	2.15	2.09	1.86	2.96	1.70	1.61	2.55	1.99	2.05	2.51	2.01
$\bar{x}$	3.26	2.11	2.06	2.07	2.08	2.24	2.27	2.09	3.21	1.83	1.71	2.73	2.17	2.17	2.88	2.14
max	3.41	2.24	2.14	2.81	2.26	2.38	2.40	2.25	3.50	1.97	1.80	2.87	2.39	2.25	3.12	2.32

Table XVII

Cricetus cricetus. Statistical analysis of the dimensions of molars, including all the specimens from the localities listed in Table XVI

	M^1			M^2			M^3	
	L	Wb	Wf	L	Wb	Wf	L	Wf
N	20	20	20	26	26	26	17	17
min — max	3.15—3.41	1.97—2.30	1.87—2.22	2.52—2.81	1.94—2.26	2.11—2.38	2.09—2.40	1.86—2.25
$\bar{x}$	3.277	2.105	2.060	2.664	2.068	2.239	2.275	2.083
SD	0.086	0.078	0.084	0.079	0.069	0.066	0.083	0.087
V	2.62	3.70	4.07	2.97	3.36	2.95	3.64	4.19

	M_1			M_2			M_3	
	L	Wb	Wf	L	Wb	Wf	L	Wf
N	45	45	47	57	57	57	50	50
min — max	2.87—3.50	1.70—1.97	1.61—1.81	2.30—2.91	1.94—2.39	1.93—2.27	2.51—3.25	2.01—2.49
$\bar{x}$	3.196	1.827	1.707	2.712	2.162	2.157	2.879	2.145
SD	0.104	0.059	0.053	0.111	0.086	0.063	0.129	0.087
V	3.27	3.24	3.11	4.09	3.97	2.91	4.48	4.03

Wmax
57
1.99—2.39
2.181
0.071
3.27

where V = 4.35 for M_3 and 4.76 for M^3 (FAHLBUSCH 1976, p. 75, Table 1), and the present-day *C. cricetus* from Poland, in which V = 4.07 for LM_3 (N = 76) and 5.17 for LM^3 (N = 65) (PRADEL 1985).

All the eight upper tooth-rows found (Table XVIII), 7.67 — 7.95 — 8.16 mm in length, come from Sąspowska Cave and their mean length is somewhat

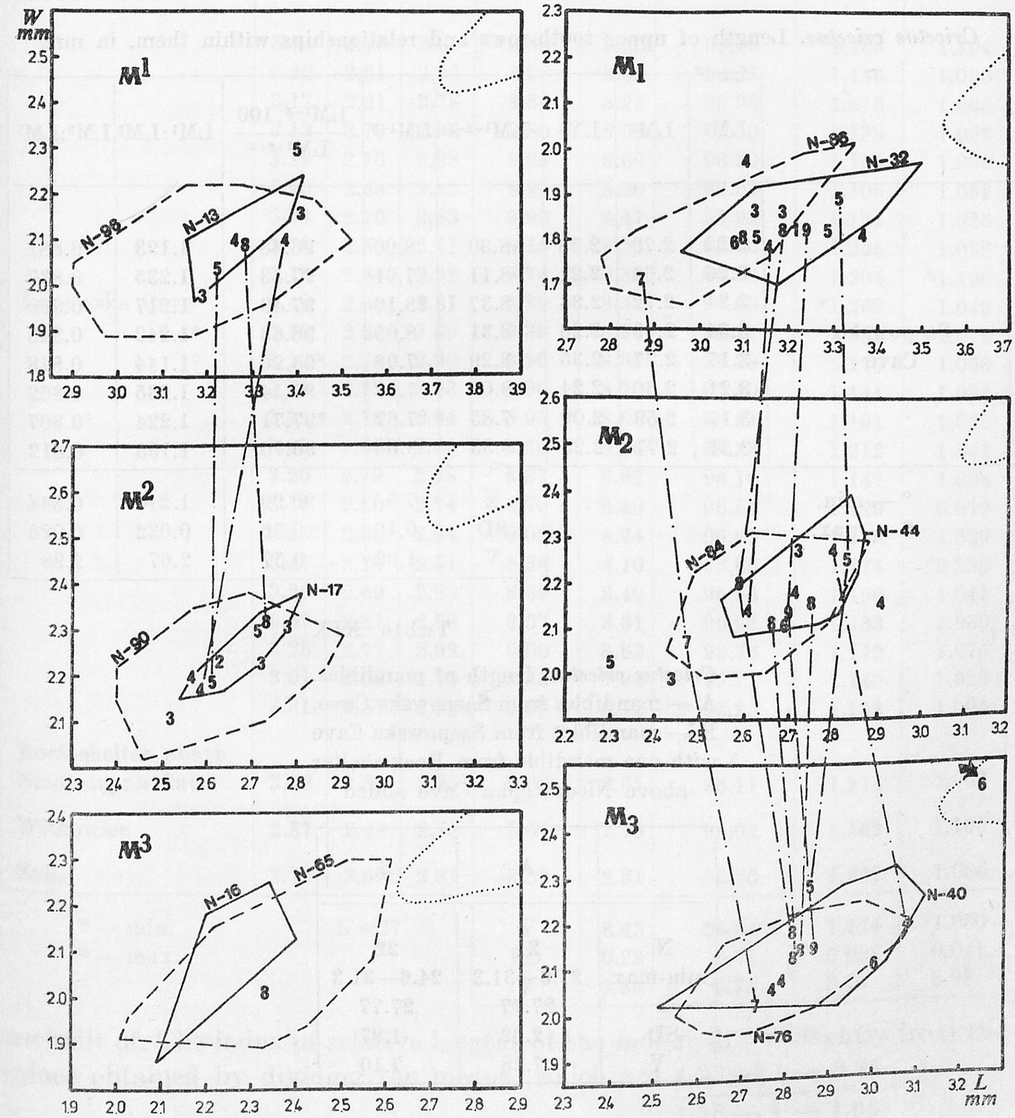

Fig. 10. *Cricetus cricetus*. L/W diagram of molars. 1 — Nietoperzowa Cave; 2 — Koziarnia Cave; 3 — Mamutowa Cave; 4 — Żytnia Skała Rock-shelter; 5 — Rock-shelter above Niedostępna Cave; 6 — Bramka Rock-shelter; 7 — Witkowice; 8 — Zalas; 9 — Kadzielnia; solid line — *C. cricetus*, last glaciation, Sąspowska Cave (PRADEL 1981b); dashed line — *C. c. cricetus*, recent, Poland (PRADEL 1985); dotted line — approximate lower boundary of variation of the lengths and widths in *Cricetus major* s. FAHLBUSCH (after FAHLBUSCH 1976, Fig. 1, Tab. 1)

greater than that of the tooth-rows of the modern hamster from Poland, in which LM^{1-3} = 7.40 — 7.791 — 8.29 mm (N = 63). The lower teeth rows preserved whole occurred in large numbers (N = 27) in Sąspowska Cave and

Table XVIII

Cricetus cricetus. Length of upper tooth-rows and relationships within them, in mm

	LM^1	LM^2	LM^3	LM^{1-2-3}	LM^{1-3}	$\frac{LM^{1-3} . 100}{LM^{1+2+3}}$	$LM^1:LM^2$	$LM^3:LM^2$
Sąspowska Cave	3.22	2.70	2.38	8.30	8.00	96.38	1.193	*0.881
	3.26	2.64	2.21	8.11	7.91	97.53	1.235	0.837
	3.31	2.72	2.34	8.37	*8.16	97.49	1.217	0.860
	3.34	2.69	2.28	8.31	8.03	96.63	*1.242	0.848
	3.17	2.77	2.35	8.29	7.98	°96.26	°1.144	0.848
	3.21	2.6C	2.24	8.05	7.82	97.14	1.235	0.862
	3.17	2.59	2.09	7.85	°7.67	*97.71	1.224	°0.807
	3.31	2.77	2.25	8.33	8.06	96.76	1.195	0.812
° — min.				$\overline{x}$	7.95	96.99	1.210	0.844
* — max.				SD	0.15	0.56	0.032	0.025
				V	1.92	0.57	2.67	2.98

Table XIX

Cricetus cricetus, length of mandibles.
A — mandibles from Sąspowska Cave,
B — mandibles from Sąspowska Cave with one mandible from Rock-shelter above Niedostępna Cave added

	A	B
N	21	22
min-max	27.6—31.3	24.6—31.3
$\overline{x}$	27.77	27.77
SD	2.02	1.97
V	7.28	7.10

were also found in the materials, one specimen in each, from Witkowice, Zalas, Rock-shelter above Niedostępna Cave and Kadzielnia. Their lengths lie within a range of 7.75 — 8.45 — 8.94 mm and like the upper tooth-rows are somewhat longer than in the present-day *C. cricetus* from Poland, in which LM_{1-3} = 7.80 — 8.09 — 8.65 mm. Tables XVIII and XX, which present the tooth-rows, provide also the data characterizing the relationships between the teeth these rows

Table XX

Cricetus cricetus. Length of lower tooth-rows and relationships within them, in mm

	LM_1	LM_2	LM_3	LM_{1+2+3}	LM_{1-3}	$\frac{LM_{1-3} . 100}{LM_{1+2+3}}$	$LM_1:LM_2$	$LM_3:LM_2$
	3.14	2.70	2.98	8.82	8.66	98.19	1.163	1.104
	3.22	2.81	2.95	8.98	8.82	*98.22	1.146	1.050
	3.17	2.61	2.78	8.56	8.25	96.38	1.215	1.065
	3.13	2.75	2.92	8.80	8.58	97.50	1.138	1.062
	3.19	2.76	2.98	8.93	8.60	96.30	1.156	1.080
	2.96	2.68	2.82	8.46	8.20	96.93	°1.105	1.052
	3.24	2.76	2.83	8.83	8.47	95.92	1.174	1.025
	3.16	2.58	2.81	8.55	8.29	96.96	1.225	1.089
	3.18	2.64	2.92	8.74	8.38	95.88	1.204	*1.106
Sąspowska Cave	3.40	2.68	2.81	8.89	8.59	96.63	*1.269	1.049
	3.50	2.84	3.05	9.39	*8.94	°95.21	1.232	1.074
	3.22	2.74	2.90	8.86	8.53	96.28	1.175	1.058
	3.16	2.77	3.03	8.96	8.70	97.10	1.141	1.094
	3.31	2.78	2.84	8.93	8.63	96.64	1.191	1.022
	3.09	2.55	2.66	8.30	8.00	96.38	1.212	1.043
	3.20	2.79	2.98	8.97	8.62	96.10	1.147	1.068
	3.16	2.80	2.74	8.70	8.40	96.55	1.129	0.979
	3.25	2.83	2.94	9.02	8.74	96.89	1.148	1.039
	3.17	2.70	2.51	8.38	8.10	96.66	1.174	°0.930
	3.20	2.69	2.80	8.69	8.40	96.66	1.190	1.041
	3.07	2,81	2.79	8.57	8.31	96.96	1.133	1.030
	3.25	2.77	2.98	9.00	8.62	95.78	1.173	1.076
	3.01	2.64	2.70	8.35	7.95	95.21	1.140	1.023
	3.31	2.87	2.88	9.06	8.72	96.25	1.153	1.004
Rock-shelter above Niedostępna Cave	3.32	2.83	2.85	9.00	8.65	96.11	1.173	1.007
Witkowice	2.87	2.47	2.73	8.07	°7.75	96.03	1.162	1.105
Zalas	3.19	2.59	2.81	8.59	8.31	96.70	1.232	1.085
° — min.		N=27		$\bar{x}$	8.45	96.54	1.174	1.050
* — max.				SD	0.28	0.71	0.038	0.041
				V	3.35	0.74	3.26	3.88

are built of. The index of relative lengths of the molars differs slightly from the values obtained by dividing the means, which are $\frac{1.23 - 1 - 0.85}{1.18 - 1 - 1.06}$.

I managed to measure the length of the mandibles on 22 specimens (Table XIX). The coefficient of variation V is relatively high here: 7.28 and 7.10, but it reflects changes in the mandible length in the course of individual growth. In the present-day *C. cricetus* from Poland the mandible length is 20.1 — 27.11 — 35.9 mm (N = 81, V = 14.5) and it includes specimens of all the age groups (from juv. to sen.).

A decided majority of teeth have a typical structure of the modern *C. cricetus*, but some specimens bear elements which occur in the dentition of *C. runtonensis*. Several teeth of this sort are shown in Pl. XI, figs. 5—11. Some additional elements (grooves and ridges), frequently present in *C. runtonensis*, appear sporadically on the upper and lower third molars of *C. cricetus* from the last glaciation, both on relatively small teeth (Pl. XI, fig. 7) and on big ones (Pl. XI, fig. 10). The meroloph(id), varying in development, also occurs (Pl. XI, fig. 9), whereas the anterocone of M^1 is sometimes broad and displaced beyong the buccal margin of the tooth crown at the heigth of the paracone. And so the teeth of *C. cricetus* from the Weichselian of Poland are intermediate in respect of morphological characters and size between older *C. runtonensis* and the modern *C. cricetus* from Poland. The morphological differences between these forms are limited to different frequences of particular morphotypes in different populations. As stated in a previous paper (PRADEL 1985), the use of the name *major* for the giant hamster from Petersbuch 1 is not justified.

V. BIOMETRICAL RELATIONSHIPS IN THE DENTITION OF THE *CRICETINAE*

Text-fig. 1a, b, c gives cumulative L/W graphs of molars belonging to both modern and fossil populations of the *Cricetinae*. At the same time, the line of regression and correlation coefficient are calculated on the basis of the means of L and W_{max} for 10 species (see the explanation of Text-fig. 4). The results obtained are as follows:

M^1 $W = 0.0157 + 0.6427\ L$ $r = 0.9987$
M^2 $W = 0.0595 + 0.8215\ L$ $r = 0.9960$
M^3 $W = 0.1220 + 0.8156\ L$ $r = 0.9899$
M_1 $W = 0.0880 + 0.5578\ L$ $r = 0.9981$
M_2 $W = 0.0101 + 0.8105\ L$ $r = 0.9997$
M_3 $W = 0.0917 + 0.7223\ L$ $r = 0.9937$

So great values of the correlation coefficient indicate a very strong relationships between the length and the width of molars inside the *Cricetinae*, irrespective of the period from which the material is derived but only in dependence upon the absolute size of specimens which make up the given species. This relationship refers merely to the subfamily *Cricetinae* as a whole, because, which is interesting, the regression lines for each of the species included in these calculations have quite different courses and the correlation coefficient between L and W is considerably lower. The values of the correlation coefficienter between L and W are juxtaposed below by way of example for A — *Cricetulus migratorius*, Recent, Syria (PRADEL 1981a) and B — *Cricetus cricetus*, Weichselian, Sąspowska Cave (data obtained on the basis of the material discussed in my previous paper; PRADEL 1981b).

	A	B
M^1	$r = 0.6911$ ($N = 97$)	$r = 0.7172$ ($N = 13$)
M^2	$r = 0.4331$ ($N = 87$)	$r = 0.8455$ ($N = 17$)
M^3	$r = 0.5501$ ($N = 66$)	$r = 0.6403$ ($N = 16$)
M_1	$r = 0.5157$ ($N = 150$)	$r = 0.5461$ ($N = 32$)
M_2	$r = 0.2927$ ($N = 136$)	$r = 0.5490$ ($N = 47$)
M_3	$r = 0.4833$ ($N = 110$)	$r = 0.5642$ ($N = 40$)

These two species were chosen for comparison for three reasons: 1 — their specimens occurred in large numbers, 2 — out of the hamsters under study they represent almost extremal differences in size, and 3 — one of them is a living species and the other comes from fossil materials and yet they both show a decrease in the value of r as compared with that obtained for the *Cricetinae* as a whole.

It may be inferred from the foregoing considerations that the drop in the value of the correlation coefficient r between the length and the width of molars at specific level, which coefficient is so high at the level of subfamily, is caused by the modifying influence of environment at the time of individual development. This is not a new statement but it seems interesting that the genetically controlled correlation of L and W is not limited to a species but concerns the whole subfamily and that it is exceptionally stable, it has persisted since the beginning of the Pliocene.

In discussing *Kowalskia* I quoted FAHLBUSCH'S opinion, according to which, the species of this genus are perhaps more closely related to the modern hamsters than to the Miocene ones. The present study proves that the correlations observed in the dentition of *Kowalskia* are quite consistent with the relations observed in the *Cricetinae*. This would support the opinion held by FAHLBUSCH.

The changes in the length of the successive teeth of a row also show a definite directionality and as a result infuence the value of the index illustrating the relative lengths of the first and third molars compared with the length of M2 (PRADEL 1981a). The values of this index are given for 10 species of hamsters in Text-fig. 11. The mean lengths of the 2nd molar of a given species (population) are marked along the x axis by means of arrows (higher arrow: M^2, lower: M_1) designated with successive letters. The relative lengths of M^1 and M^3 obtained by dividing the mean length of the given tooth by the appropriate mean lengths of M^2 are marked along the y axis. The points obtained have a linear arrangement. The regression equation is given in the explanation for the figure. These correlations are relatively strong (r = —0.9375, —0.7973, +0.9081). Only in one case the correlation is very weak, namely, that between the relative length of M^3 and the length of M^2. This is so, because the increments in the lengths of M^2 and M^3 are almost identical and in consequence the ratio $LM^2 : LM^2$ oscillates about a constant value. The straight lines in Text-fig. 11 show well that the changes in the size of the 1st and 3rd molars relative to M2 are subject to definite trends irrespective, as I have already emphasized, of their geological age but in dependence upon the absolute size of the given species, expressed here by the length of the second molar. As the length of M^2 increases, the relative length of M^1 decreases distinctly and the relative length of M^3 undergoes a very slight change (from 0.84 to 0.90). The value 0.98, departing from the remaining ones, refers to the relative length of M^3 in *Kowalskia magna*, in which case N was very low. As regards the lower teeth, a rise in the length of M_2 is accompanied by a decrease in the relative length of M_1 and a distinct increase in the relative length of M_3. It even becomes evident that in small species M_2 is longer than M_3, whereas in larger ones M_3 is the longer of them.

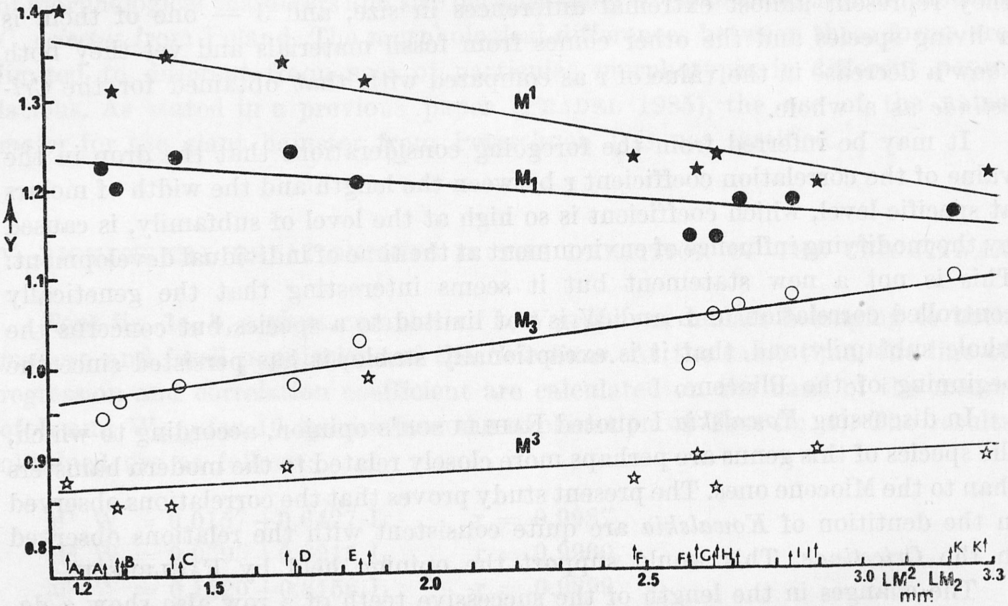

Fig. 11. Changes in the proportion index for the teeth in a row (LM1-LM2-LM3) relative to the length of M2. Axis x — mean length of 2nd molar (LM^2, LM_2, in mm). Axis y — relative length of M^1, M^3, M_1, M_3. M^1 (black stars); $y = 1.465—0.087x$, $r = —0.937$; M^3 (white stars); $y = 0.865+0.010x$, $r = 0.175$; M_1 (black circle); $y = 1.280—0.040x$, $r = —0.797$; M_3 (white circle); $y = 0.881+0.064x$, $e = 0.908$. A — *C. migratorius*, recent, Syria (Pradel 1981a); B — *K. polonica*; C — *A. bursae*; D — *A. ehiki*; E — *K. magna*; F — *C. cricetus*, recent, Germany (Fahlbusch 1976); G — *C. c. cricetus*, recent, Poland (Pradel 1988); H — *C. cricetus*, last glaciation, Poland; I — *C. runtonensis*; K — *C. major* s. Fahlbusch 1976, Petersbuch 1

Text-fig. 11 does not illustrate very clearly the changes occurring between the lengths of successive molars in a row. The choice of the length of M2 as the basis for comparisons causes that the changes to which also this dimension is subject do not become revealed. Text-fig. 12a, b is designed to better show the changes in the relations between the successive molars of a row, as their absolute dimensions increase. It shows the changes in the percentage contributions that the mean lengths of the successive molars make to their sum (LM1 + LM2 + LM3 = 100%) in a given species. This text-figure well il-

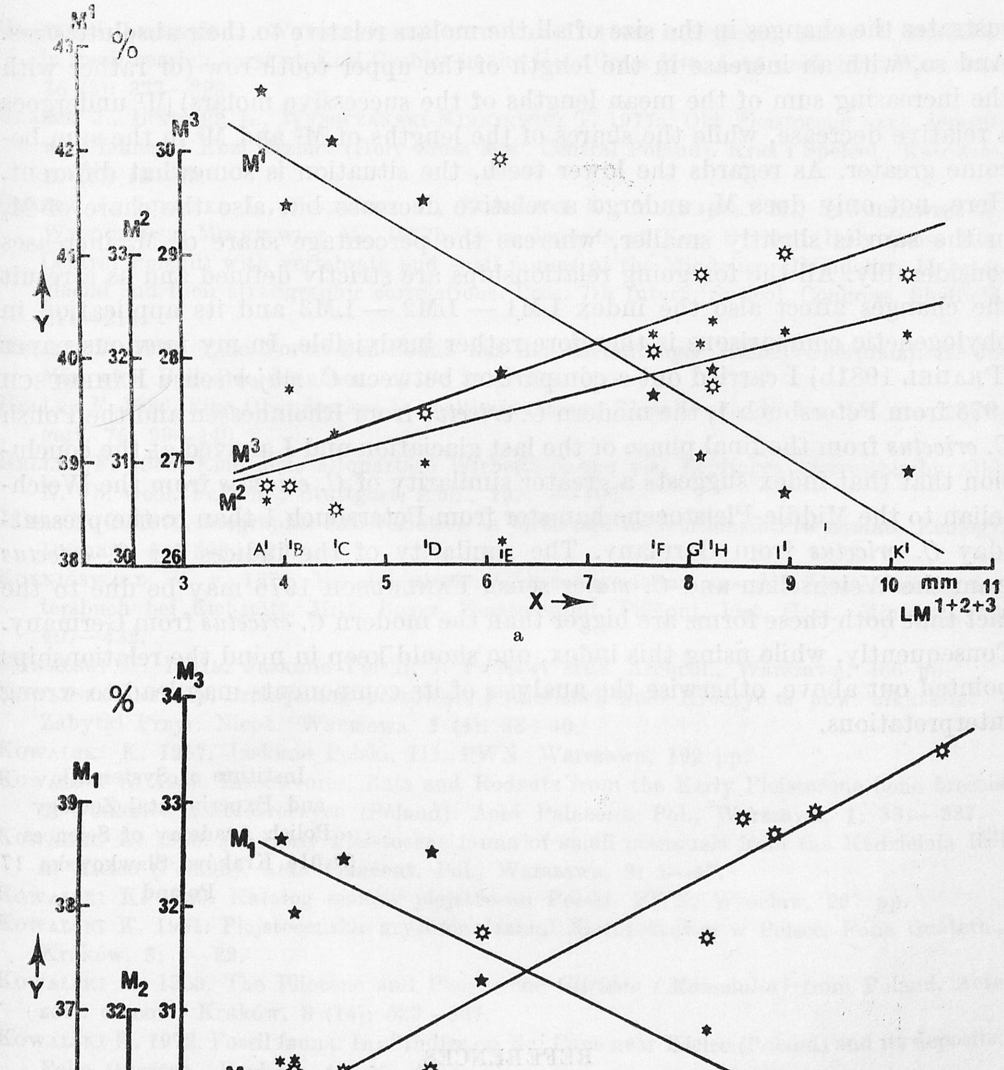

Fig. 12. Changes in the percentage share of successive molars in the sum of their lengths. Axi x — sum of mean lengths of successive molars for given species (in mm). Fig. 12a: $x = LM^1 + LM^2 + LM^3$. Fig. 12b: $x = LM_1 + LM_2 + LM_3$. Axis y — percentage share of the length of successive molars in their sum. Fig. 12a: M^1 (big stars), $y = 44.37 - 0.59a$, $r = -0.929$; M^2 (little stars), $y = 29.96 + 0.24x$, $r = 0.710$; M^3 (radiate circles), $y = 25.67 + 0.35x$, $r = 0.685$; Fig. 12b: M_1 (big stars), $y = 40.37 - 0.46x$, $r = -0.938$; M_2 (little stars), $y = 31.67 - 0.08x$, $r = -0.446$; M_3 (radiate circles), $y = 27.97 + 0.54x$, $r = 0.959$. A-K — as in the explanation for Fig. 11

lustrates the changes in the size of all the molars relative to their absolute sizes. And so, with an increase in the length of the upper tooth-row (or rather with the increasing sum of the mean lengths of the successive molars) M^1 undergoes a relative decrease, while the shares of the lengths of M^2 and M^3 in the sum become greater. As regards the lower teeth, the situation is somewhat different. Here, not only does M_1 undergo a relative decrease but also the share of M_2 in the sum is slightly smaller, whereas the percentage share of M_3 increases considerably. All the foregoing relationships are strictly defined and as a result the changes affect also the index LM1 — LM2 — LM3 and its application in phylogenetic comparisons is therefore rather inadvisible. In my previous paper (PRADEL 1981b) I carried out a comparison between *C. major* sensu FAHLBUSCH 1976 from Petersbuch 1, the modern *C. cricetus* from Rheinhessen and the Polish *C. cricetus* from the final phase of the last glaciation and I arrived at the conclusion that that index suggests a greater similarity of *C. cricetus* from the Weichselian to the Middle-Pleistocene hamster from Petersbuch 1 than to the present-day *C. cricetus* from Germany. The similarity of the indices for *C. cricetus* from the Weichselian and *C. major* sensu FAHLBUSCH 1976 may be due to the fact that both these forms are bigger than the modern *C. cricetus* from Germany. Consequently, while using this index, one should keep in mind the relationships pointed out above, otherwise the analysis of its components may lead to wrong interpretations.

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REFERENCES

BOCHEŃSKI Z. 1977. Ptaki młodszego czwartorzędu Polski. PWN, Warszawa, Kraków, 212 pp.

BOCHEŃSKI Z., NADACHOWSKI A., STWORZEWICZ E., SZYNDLAR Z. 1985. Fauna kopalna. In: Badania osadów schronisk podskalnych w Zalasie k. Krakowa. Folia Quatern., Kraków, **56**: 15—37.

CHMIELEWSKI W., KOWALSKI K., MADEYSKA-NIKLEWSKA T., SYCH L. 1967. Wyniki badań osadów jaskini Koziarni w Sąspowie, pow. Olkusz. Folia Quatern., Kraków, **26**: 1—69.

ELLERMANN J. R., MORRISON-SCOTT T. C. S. 1951. Checklist of Palaearctic and Indian Mammals 1978 to 1946. Brit. Mus. (Nat. Hist.), London, 810 pp.

FAHLBUSCH V. 1969. Pliozäne und Pleistozäne *Cricetinae (Rodentia, Mammalia)* aus Polen. Acta zool. cracov., Kraków, **14** (8): 99—137.

FAHLBUSCH V. 1976. *Cricetus major* WOLDŘICH *(Mammalia, Rodentia)* aus der mittelpleistozänen Spaltenfüllung Petersbuch 1. Mitt. Bayer. Staatssamml. Paläont. hist. Geol., München, **16**: 71—81.

Głazek J. Lindner L., Wysoczański-Minkiewicz T. 1976. Interglacial Mindel I /Mindel II in fossil-bearing karst at Kozi Grzbiet in the Holy Cross Mts. Acta Geol. Pol., Warszawa, **26** (3): 377—393.

Głazek J., Lindner L., Wysoczański-Minkiewicz T. 1977a. Old Pleistocene cave deposits with fauna at Kozi Grzbiet (Holy Cross Mts., Central Poland). Kras i Speleol., Katowice, **10** (1): 13—29.

Głazek J., Lindner L., Tuchołka P., Kowalski K., Młynarski M., Stworzewicz E., Wysoczański-Minkiewicz M., 1977b. Cave deposits at Kozi Grzbiet (Holy Cross Mts., Central Poland) with vertebrate and snail faunas of the Mindelian I/Mindelian II Interglacial and their stratigraphic correlations. Proc. 7th Intern. Speleol. Congress, Sheffield, 211—214.

Heller F. 1930. Eine Forest-Bed-Fauna aus der Sackdillinger Höhle (Oberpfalz). N. Jb. Min. etc., Beil.-Bd., München, **63** B: 247—298.

Heller F. 1936. Eine Oberpliozäne Wirbeltierfauna aus Rheinhessen. N. Jb. Min. etc., Stuttgart, **76**: 99—140.

Heller F. 1958. Eine neue altquartäre Wirbeltierfauna von Erpfingen (Schwäbische Alb). N. Jb. Geol. Paläont., Stuttgart, Abh., **107**: 1—102.

James F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology, Durham, **51**: 365—390.

Koenigswald W. v. 1970. Mittelpleistozäne Kleinsäugerfauna aus der Spaltenfüllung Petersbuch bei Eichstätt. Mitt. Bayer. Staatssamml. Paläont. hist. Geol., München, **10**: 407—432.

Kowalski K. 1951a. Jaskinie Polski. I. Państw. Muz. Archeol., Warszawa, 466 pp.

Kowalski K. 1951b. Brekcja nietoperzowa w Podlesicach koło Kroczyc w pow. olkuskim. Zabytki Przyr. Nieoż. Warszawa **1** (4): 38—40.

Kowalski K. 1957. Jaskinie Polski. III. PWN Warszawa, 192 pp.

Kowalski K. 1956. Insectivores, Bats and Rodents from the Early Pleistocene bone breccia of Podlesice near Kroczyce (Poland). Acta Palaeont. Pol., Warszawa, **1**: 331—387.

Kowalski K. 1958. An Early Pleistocene fauna of small mammals from the Kadzielnia Hill in Kielce (Poland). Acta Palaeont. Pol., Warszawa, **3**: 1—47.

Kowalski K. 1959. Katalog ssaków plejstocenu Polski. PWN, Wrocław, 267 pp.

Kowalski K. 1961. Plejstoceńskie gryzonie Jaskini Nietoperzowej w Polsce. Folia Quatern., Kraków, **5**: 1—22.

Kowalski K. 1963. The Pliocene and Pleistocene *Gliridae (Mammalia)* from Poland. Acta zool. cracov., Kraków, **8** (14): 533—567.

Kowalski K. 1972. Fossil fauna. In: Studies on Raj Cave near Kielce (Poland) and its deposits. Folia Quatern., Kraków **41**: 45—59.

Kowalski K. 1975. Earliest appearance of Lemmings in the Quaternary of Poland. Actas I Coloquio Intern. Biostr. Contin. Neogeno Sup. y Cuatern. Inf.. Madrid, 99—104.

Kowalski K. 1977. Fossil Lemmings *(Mammalia, Rodentia)* from the Pliocene and Early Pleistocene of Poland. Acta zool. cracov., Kraków, **22** (7): 297—317.

Kowalski K., Kozłowski J. K., Krysowska-Iwaszkiewicz M., Pawlikowa B., Wiktor A. 1967. Badania osadów schronisk podskalnych w Żytniej Skale (Bębło, pow. Kraków). Folia Quatern., Kraków, **25**: 1—48.

Kretzoi M. 1941. Die unterpleistozäne Säugetierfauna von Betfia bei Nagyvarad. Földt. Közl., Budapest, **71**: 308—335.

Kubasiewicz M. 1957. Szczątki niedźwiedzia jaskiniowego z Jaskini Nietoperzowej. Przegląd Zool., Wrocław, **3** (3): 171—176.

Kurtén B. 1960. Chronology and faunal evolution of the earlier European glaciations. Comment. Biol. Sc. Fenn., Helsingfors, **21**: 1—62.

Kurtén B. 1968. Pleistocene mammals of Europe. Weidenfeld and Nicolson, London, VIII+317 pp.

LIEBE K. Th. 1879. Die fossile Fauna der Höhle Vypustek in Mähren nebst Bemerkungen betreffs einiger Knochenreste aus der Kreuzberghöhle in Krain. Sitz.-Ber. Akad. Wiss., Wien, **79**: 472—490.

MADEYSKA T. 1972. Litostratygraficzne serie osadów archeologicznych stanowisk jaskiniowych Wyżyny Krakowskiej. Speleologia, Warszawa, **7**: 7—24.

MILLER G. S. 1912. Catalogue of the Mammals of Western Europe. Brit. Mus. (Nat. Hist.), London, XV+1019 pp.

MŁYNARSKI M. 1977. New notes on the Amphibian and Reptilian fauna of the Polish Pliocene and Pleistocene. Acta zool. cracov., Kraków, **22** (2): 13—36.

MOSSOCZY Z. 1959. Odkrycie miejsc występowania kości kręgowców kopalnych w okolicach Kłobucka. Przegl. Geol., Warszawa, **7** (3): 132—134.

NADACHOWSKI A. 1976. Fauna kopalna w osadach Jaskini Mamutowej w Wierzchowiu koło Krakowa. Folia Quatern., Kraków, **48**: 1—36.

NADACHOWSKI A. 1982. Late Quaternary Rodents of Poland with special reference to morphotype dentition analysis of voles. PWN, Warszawa, Kraków, 108 pp.

NEHRING A. 1893. Über pleistozäne Hamster-Reste aus Mittel- und Westeuropa. Jahrb. k. k. geol. Reichsanst., Wien, **43** (2).

NEWTON E. T. 1909. Hamster remains from the Norfolk Forest Bed. Geol. Mag., London, **6**: 110—117.

NIEZABITOWSKI-LUBICZ E. 1932. Pardwy *Lagopus lagopus* L. i *Lagopus mutus* MONTIN oraz towarzysząca im fauna w czwartorzędzie Polski. Roczn. Pol. Tow. Geol., Kraków, **7** (2): 179—192.

NIEZABITOWSKI-LUBICZ E. 1933. Klucz do oznaczania zwierząt ssących Polski. 2nd ed. Koło Przyr. Uczniów UJ, Kraków, 124 pp.

PRADEL A. 1981a. Biometrical remarks on the rodent *Cricetulus migratorius* (PALLAS, 1773) *(Rodentia, Mammalia)* from Krak des Chevaliers (Syria). Acta zool. cracov., Kraków, **25** (11): 271—292.

PRADEL A. 1981b. *Cricetus cricetus* (LINNAEUS, 1758) *(Rodentia, Mammalia)* from the Pleistocene-Holocene deposits of Sąspowska Cave (Ojców, Poland). Acta zool. cracov., Kraków, **25** (12): 293—306.

PRADEL A. 1985. Morphology of the hamster *Cricetus cricetus* (LINNAEUS, 1758) from Poland with some remarks on the evolution of this species. Acta zool. cracov., Kraków, **29** (3): 29—52.

ROMER F. 1883. Die Knochenhöhlen von Ojców in Polen. Palaeontogr., Cassel, **29**: 1—41.

RZEBIK-KOWALSKA B. 1976. The Neogene and Pleistocene Insectivores *(Mammalia)* of Poland. III. *Soricidae*: *Beremendia* and *Blarinoides*. Acta zool. cracov., Kraków, **21** (12): 359—386.

SCHAUB S. 1930. Quartäre und jungtertiäre Hamster. Abh. Schweiz. Pal. Ges., Basel, **49**: 1—49.

STORCH G. 1977. Neue Zwerghamster aus dem Holozän von Aserbeidschan, Iran *(Rodentia: Cricetinae)*. Senckenberg. Biol., Frankfurt a. M., **55**: 21—28.

STORCH G. 1975. Eine mittelpleistozäne Nager-Fauna von der Insel Chios, Agäis *(Mammalia, Rodentia)*. Senckenberg. Biol., Frankfurt a. M., **56**: 163—189.

SZYNDLAR Z. 1984. Fossil snakes from Poland. Acta zool. cracov., Kraków, **28** (1): 1—156.

VOGEL R. 1940. Die alluvialen Säugetiere Württembergs. Jh. Ver. Vaterl. Naturkde. Württ., **96**: 89—112.

VORONTSOV N. N. 1982. Nizhschie khomiakoobraznye *(Cricetinae)* mirovoy fauny. I. Morfologija i ekologija. In: Fauna SSSR, Leningrad, **3**: 1—449.

WERTH E. 1936. Der gegenwärtige Stand der Hamsterfrage in Deutschland. Arb. Biol. Reichsanst. Land- u. Forstwirt., Berlin, **21**: 201—253.

WOLDŘICH J. 1980. Über die diluviale Fauna von Zuzlawitz. Sitz.-Ber. Math. Naturw. Kl. Kais. Akad. Wiss., Wien, **82**: 1—60.

ZOTZ L. 1939. Die Altsteinzeit in Niederschlesien. Kabitsch, Leipzig, 146 pp.

STRESZCZENIE

Praca zawiera opis 1630 zębów trzonowych chomików znalezionych w 20 stanowiskach fauny kopalnej w Polsce, datowanych na czas od początku pliocenu po koniec plejstocenu, z niewielką domieszką okazów z holocenu. Jedynie 16 zębów nie można było definitywnie określić do gatunku. Cechy ich wskazują, że mogą należeć do czterech dotychczas nie opisanych gatunków, lecz zbyt skąpy materiał nie pozwala na ich opisanie. Równolegle z nimi w stanowiskach plioceńskich występują: *Kowalskia polonica* i *K. magna*. W okresie Villanianu i Biharianu (przełom pliocenu i plejstocenu) występują: *Allocricetus bursae*, *A. ehiki* i *Cricetus runtonensis*, w górnym plejstocenie natomiast stwierdzono obecność *Cricetulus migratorium* i *Cricetus cricetus*. W końcowej części pracy omówiono zależności biometryczne w uzębieniu *Cricetinae*.

Redaktor pracy: prof. dr Kazimierz Kowalski

Plate VIII

Specimens of indeterminate species

1. *Cricetus* sp. 3 (Fahlbusch 1969) left M^2. MF/827/1, Rębielice Królewskie 1, L = 1.99, Wb = 1.63, Wf = 1.7
2. *Cricetus* sp. 3 (Fahlbusch 1969), left M^3, MF/827/2, Rębielice Królewskie 1, L = 2.1. Wf = 1.82
3. *Cricetus*? sp., right M_1, MF/1713, Rębielice Królewskie 1, L = 2.74, Wb = 1.63, Wf = 1.53
4. *Cricetus*? sp., left M_1, MF/1712/C-1, Podlesice, L = 2.54, Wb = 1.56, WF = 1.36
5. *Cricetus*? sp., right M_1, MF/1712/C-5, Podlesice, L = 2.6, Wb = 1.48, Wf = 1.38
6. *Cricetus*? sp., right M_1, MF/1712/C-4, Podlesice, L = 2.36, Wb = 1.56, Wf = 1.43
7. *Cricetus*? sp., right M^1, MF/1715/1, Rębielice Królewskie 2, L = 2.66, Wb = 1.77, Wf = 1.68
8. *Cricetus*? sp., right M^2, MF/1715/2, Rębielice Królewskie 2, L = 2.21, Wb = 1.69, Wf = 1.76
9. *Copemys (Democricetodon)*? sp. (Fahlbusch 1969), left M_2, MF/834, Węże 1, L = 2.4, Wb = 1.95, Wf = 1.87
10. *Cricetus* sp. 1 (Fahlbusch 1969), right M_1, MF/824/1, Podlesice, L = 3.08, Wb = 1.83
11. *Cricetus* sp. 1 (Fahlbusch 1969), left M^2, MF/824/3, Podlesice, Wf = 2.13
12. *Cricetus* sp. 1 (Fahlbusch 1969), left M_3, MF/824/2, Podlesice, L = 2.6, Wb = 1.72, Wf = 1.95
13. *Cricetus*? sp., right M^1, MF/1685/1, Podlesice, L = 3.16, Wb = 1.96, Wf = 1.91
14. *Cricetus*? sp., left M_1, MF/1685/2, Podlesice, L = 3.16, Wb = 1.9, Wf = 1.67
15. *Cricetus*? sp., left M_1, MF/1685/3, Podlesice, L = 3.06, Wb = 2.02, Wf = 1.74

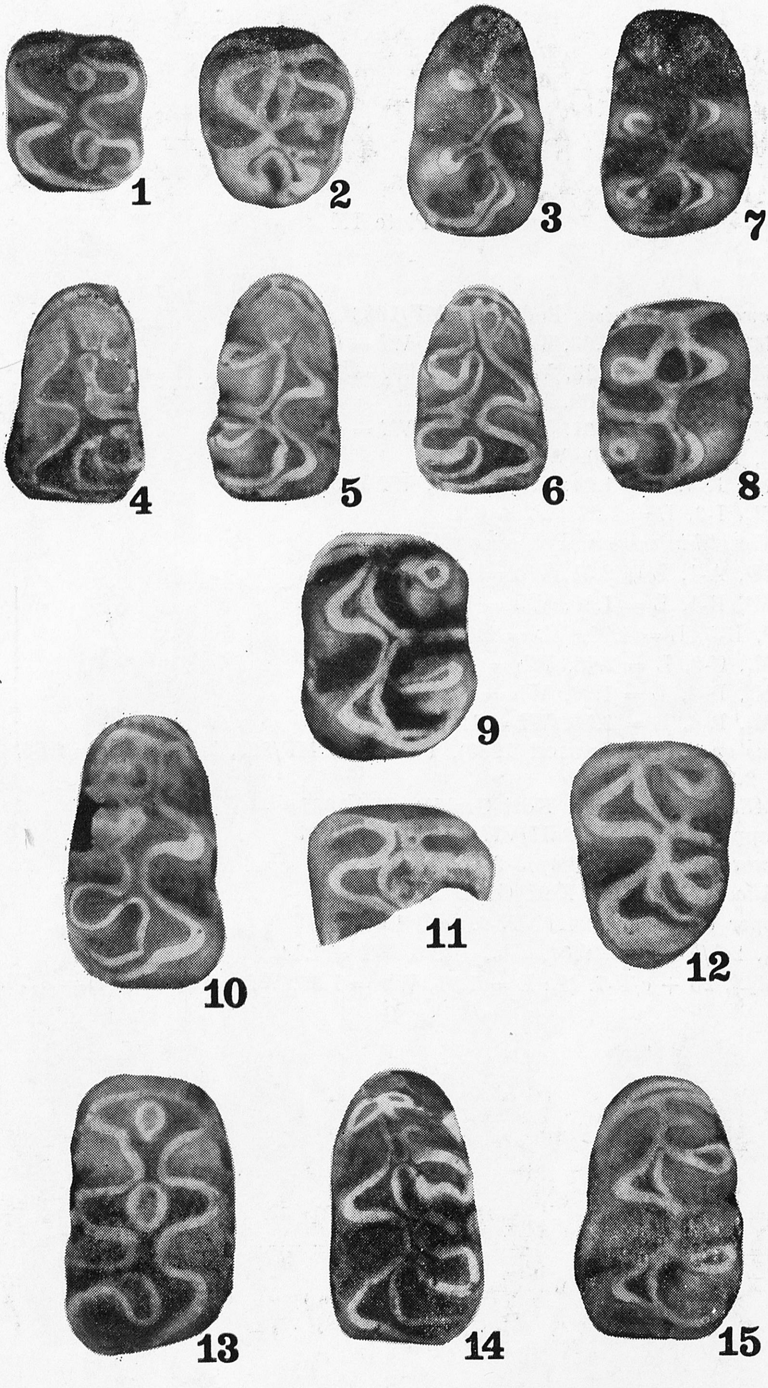

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Plate IX

1—7 — *Kowalskia polonica*, Podlesice, MF/1683
1. Right M^1, B-2, L = 1.69, Wb = 1.00, Wf = 0.98
2. Right M^2, C-6, L = 1.38, Wb = 1.02, Wf = 1.07
3. Right M^3, E-1, L = 1.08, Wf = 1.03
4. Right M_1, F-3, L = 1.61, Wb = 0.93, Wf = 0.85
5. Left M_1, F-1, L = 1.60, Wf = 0.87
6. Right M_2, H-4, L = 1.24, Wb = 1.02, Wf = 0.98
7. Right M_3, I-3, L = 1.27, Wf = 0.91

8—13 — *Kowalskia magna*, Podlesice, MF/1684
8. Right M^1, A-1, L = 2.51, Wb = 1.54, Wf = 1.53
9. Right M^2, B-1, L = 1.80, Wb = 1.50, Wf = 1.55
10. Left M^3, B-5, L = 1.70, Wf = 1.61
11. Right M_1, C-2, L = 2.26, Wb = 1.29, Wf = 1.19
12. Right M_2, D-4, L = 1.96, Wb = 1.60, Wf = 1.57
13. Right M_3, E-4, L = 1.96, Wf = 1.41

14 — *Cricetus* sp. 2 (FAHLBUSCH 1969), Podlesice, MF/825, left M_3, L = 2.68, Wb = 1.95, Wf = 2.30

15—16. — *Allocricetus bursae*, Kozi Grzbiet, MF/1681
15. Right upper tooth-row, 2aII/VII-3, LM^{1-3} = 4.51
16. Left lower tooth-row, dump/J-2, LM_{1-3} = 4.42

17—19 — *Allocricetus ehiki*, Kozi Grzbiet, MF/1682
17. Left upper tooth-row, 2aII/VII-9, LM^{1-3} = 5.06
18. Left M_1, 2cI/F-8, L = 2.04, Wb = 1.26, Wf = 1.14
19. Right M_{2-3}, 2b + c/F-7. M_2: L = 1.71, Wb = 1.35, Wf = 1.37; M_3: L = 1.76, Wf = 1.35

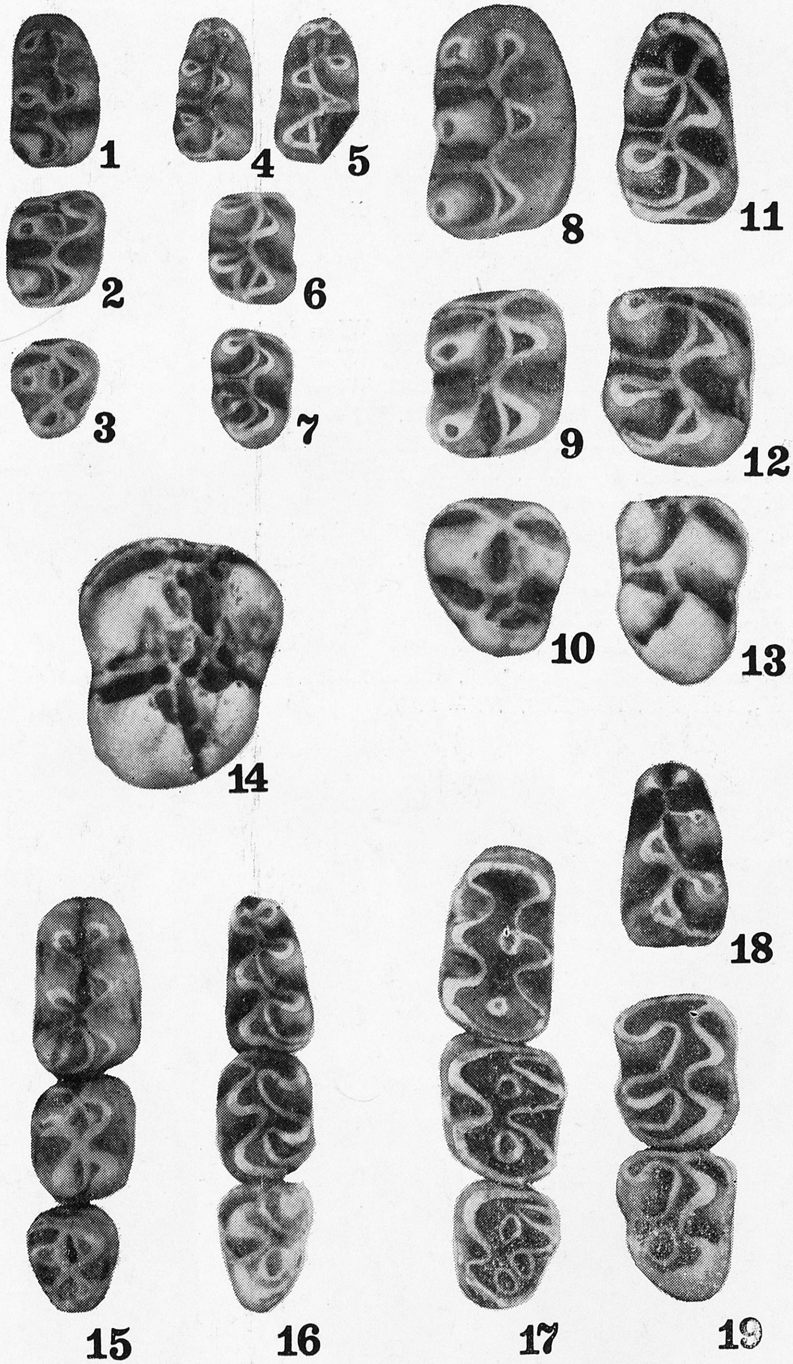

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Plate X

Cricetus runtonensis, Kozi Grzbiet, MF/1675

1. Right M^1, 2cII/A-2, L = 3.75, Wb = 2.46, Wf = 2.32
2. Right M^1, 2cII/A-1, L = 3.25, Wb = 1.92, Wf = 1.95
3. Right M^2, 2cII/B-1, L = 2.89, Wb = 2.33, Wf = 2.51
4. Left M^2, 2cII/B-7, L = 3.13, Wb = 2.33, Wf = 2.56
5. Right M^3, 2cII/C-1, L = 2.66, Wf = 2.22
6. Left M^3, dump/M-6, L = 2.96, Wb = ±2.20
4. Left M^3, 2cII/C-7, L = 2.51 Wf = 2.19
8. Left M_1. dump/N-1, L = 3.19, Wb = 1.85, Wf = 1.65
9. Left M_2, 2cII/E-1, L = 2.82, Wb = 2.14, Wf = 2.11
10. Right M_3, 2aII/VI-3, L = 2.87, Wf = 2.19
11. Right M_{1-3}, 2cII/I-5—7. LM_{1-3} = 8.98
12. Left M_1, 2cII/D-3, L = 3.68, Wb = 2.06
13. Left M_2, 2a + b + c/P-1, L = 3.09, Wb = 2.55, Wf = 2.41
14. Right M_3, 2cII/F-8, L = 3.09, Wf = 2.39

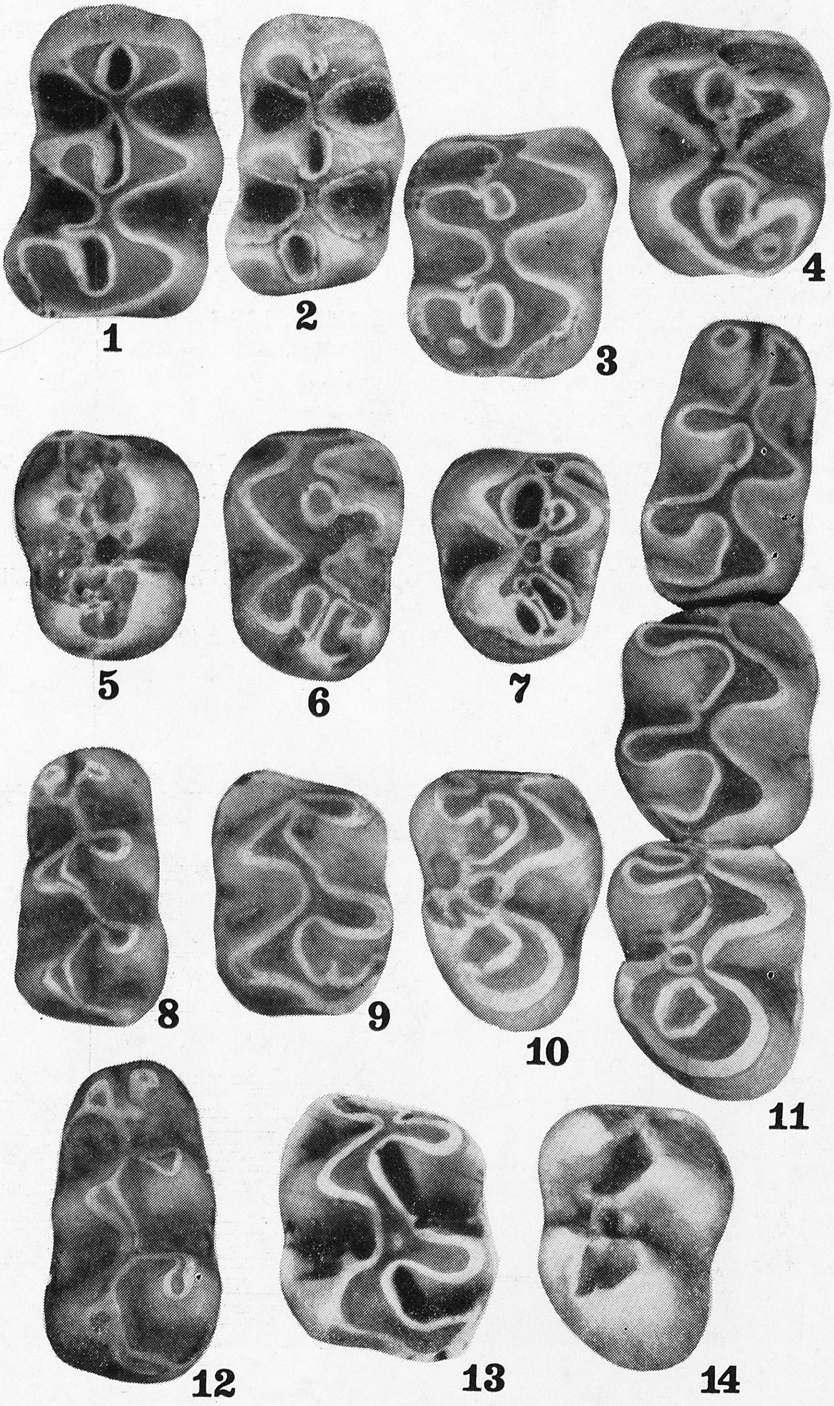
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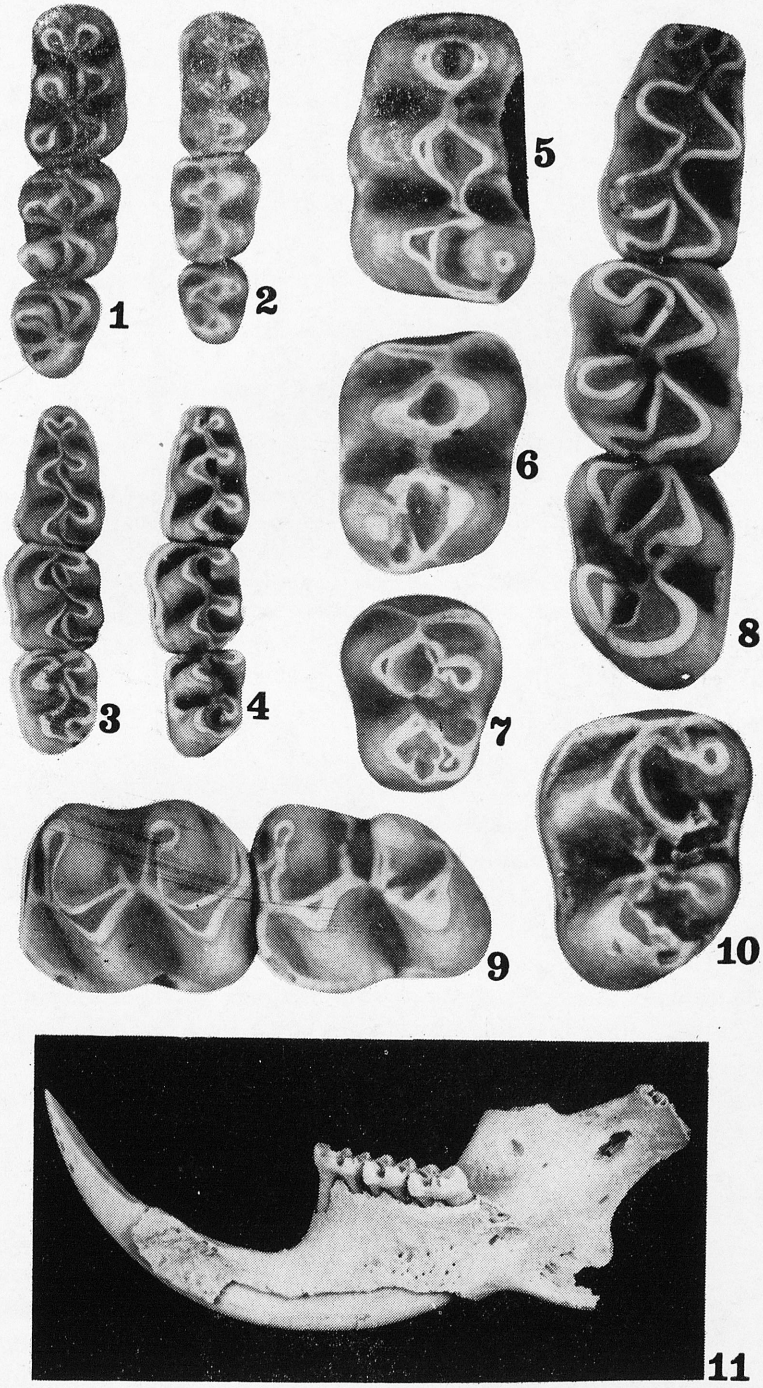
Plate XI

1—4 — *Cricetulus migratorius*

1. Right upper tooth-row, Mamutowa Cave, MF/1125/1, $LM^{1-3} = 4.33$
2. Right upper tooth-row, Mamutowa Cave, MF/1125/2, $LM^{1-3} = 3.95$
3. Left lower tooth-row, Zalas, MF/1664, $LM_{1-3} = 4.06$
4. Left lower tooth-row, Raj Cave, MF/1067, $LM_{1-3} = 3.94$

5—11 — *Cricetus cricetus*

5. Left M^1, Rock-shelter above Niedostępna Cave, MF/1161, L = 3.40, Wb = 2.30
6. Right M^2, Mamutowa Cave, MF/1124, L = 2.78, Wb = 2.11, Wf = 2.31
7. Left M^3, Zalas, MF/1663, L = 2.33, Wf = 2.01
8. and 11. Right mandible and its teeth, Witkowice, MF/816, $LM_{1-3} = 7.75$
9. Left M_{2-3}, Zalas, MF/1663. M_2: L = 2.75, Wb = 2.10, Wf = 2.13; M_3: L = 2.83, Wb = 1.83, Wf = 2.14.
10. Left M_3, Bramka Rock-shelter, MF/1202, L = 3.25, Wf = 2.49



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