### Andrzej PRADEL

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Morphology of the hamster Cricetus cricetus (Linnaeus, 1758) from Poland with some remarks on the evolution of this species

[7 text-figs., pls. II—X]

Morfologia chomika Cricetus cricetus (Linnaeus 1758) z Polski i uwagi o ewolucji tego gatunku

Abstract: Some dimensions of the skull of the modern hamster from Poland are discussed in this paper. It is the nominative subspecies C.c. cricetus (Linnaeus 1758). The morphology of the dentition, especially that of the third molars and also the ranges of variation in the dimensions of isolated teeth and their rows are dealt with. It has been demonstrated on the basis of the results obtained that the ranking of the specimen of the hamster from Vypustek by Woldkich (1880) as a subspecies (Cricetus frumentarius major sensu Woldkich 1880) was not justified and neither was the use of this denomination on specific level for the tooth specimens of a huge hamster from Petersbuch 1 by Fahlbusch, 1976 (Cricetus major sensu Fahlbusch 1976).

#### I. INTRODUCTION

Fossil remains of hamsters of the genus *Cricetus* are very often found in excavations. It has been reported from at least 80 localities in Europe and Asia (about 20 localities in Poland), situated more or less in the area of its present distribution. Comprehensive literature on this subject appeared towards the end of the 19th century (e. g., Liebe, 1879; Woldkich, 1880; Nehring, 1893) and a discussion on the evolution of this genus has been continued up to now.

In fossil materials hamsters are preserved fragmentarily. Most material consists of isolated molars, the complete tooth rows are rare and the undamaged mandibles and skulls are rarities sought for. For this reason the dimensions and morphology of molars form the basis for evolutionary considerations. A comparison of the fossil materials with contemporary ones becomes necessary, but it is not easy for the faunists and taxonomists dealing with contemporary species base their diagnoses on a number of characters which, as a rule, are not preserved in the fossil state. Scanty data obtained from literature and concerning the dentition of the contemporary hamster are incomplete and not always reliable.

In the course of a study of the fossil *Cricetinae* from the territory of Poland it was necessary to acquire contemporary comparative materials. The results of these studies are given in the present paper.

At the present time only one member of the subfamily *Cricetinae*, belonging to the genus *Cricetus*, occurs in the Polish territory. It is a big hamster of the nominative subspecies *Cricetus cricetus cricetus cricetus* (L.). The following dimensions measured in this subspecies are presented in the paper: the lengths of skulls, mandibles and tooth-rows and also the dimensions of isolated molars. Some morphological characters of tooth crowns are described and compared with the data from literature.

I wish to express my thanks to Dr A. RUPRECHT, Curator of the collection of the Mammals Research Institute, Polish Academy of Sciences, at Białowieża for giving access to their materials, of which some have been utilized here.

### II. MATERIAL AND METHOD

The skulls of hamsters discussed in this paper are stored in three collections. Thirty-three skulls come from the collection of Institute of Systematic and Experimental Zoology, PAS in Cracow, 7 skulls from the collection of the Mammals Research Institute, Polish Academy of Sciences, at Białowieża and two from Dr A. Ruprecht's collection (Białowieża). Materials obtained from owls' pellets and kept in the collection of the Mammals Research Institute at Białowieża have also been included. The catalogus numbers of specimens and other data are specified in Table I\*. The situation of places where the specimens were found or caught is presented in Figure 1.

I had 42 more or less complete skulls at my disposal on which I managed to take 34 measurements of skull length, 81 measurements of mandibles, 63 measurements of the upper and 75 of the lower tooth-rows. Moreover,  $86M_1$ ,  $84M_2$ ,  $76M_3$ ,  $97M^1$ ,  $90M^2$ ,  $65M^3$  were measured and so were not fully grown  $M_3$  and  $M^3$ , 8 and 19 in number, respectively.

The condylobasal length of tkulls (Cb) and the length of mandibles (Lmd) were measured with the help of a slide caliper to an accuracy of 0.1 mm. The length of mandibular rami was measured between the posterosuperior median edge of the alveolus of the incisor and the tip of the condylar process. This method of measurements was adopted to obtain results comparable with the magnitudes which can sometimes be measured on fossil material where this point of the alveolus of the lower incisor may be preserved. The length of toothrows at a height of the greatest bulge of the crowns (LM<sup>1-3</sup>, LM <sub>1-3</sub>) and the lengths (LM with an appropriate number) and widths (Wf, Wb) of particular

<sup>\*</sup> In the author's previous paper (PRADEL, 1981b) the data concerning contemporary C. cricetus from Poland were given on the basis of some specimens from the collection of ISEZ, PAS in Cracow; these are the first eight specimens in Table I.

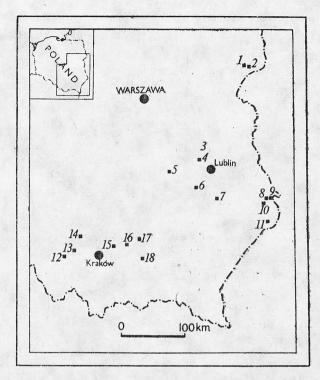


Fig. 1. The situation of localities from the environs of which the specimens discussed in this paper come

1 — Dubicze-Tofilowce	FD 36	52°40.3′N	23°25.3′E
2 — Istok	FD 36	52°40.7′N	23°28.2′E
3 — Michów	EC 90	51°31.5′N	22°19′E
4 — Markuszów	EB 89	51°21.9′N	22°16′E
5 — Ciepielów	EB 47	51°15.5′N	21°35′E
6 — Popkowice	EB 84	51°00′N	22°12.6′E
7 — Guzówka	FB 13	50°50.7′N	22°41′E
8 — Sławęcin	GB 03	50°48.5′N	23°52′E
9 — Hrubieszów	GB 03	50°49′N	23°53′E
10 — Hostynne	FB 92	50°45′N	23°42.4′E
11 — Rzeplin	GA 09	50°28.3′N	23°51′E
12 — Oświęcim	CA 74	50°02.7′N	19°13.5′E
13 — Chrzanów	CA 85	50°08.6′N	19°24.5′E
14 — Kobylica	DA 07	50°20′N	19°35′E
15 — Proszowice	DA 45	50°11.7′N	20°17.7′E
16 — Książnice Wielkie	DA 65	50°10.5′N	20°32′E
17 — Borusowa	DA 86	50°17′N	20°47.7′E
18 — Tarnów	DA 9	50°01.1′N	20°58.7′E

molars were measured using a measuring microscope to an accuracy of 0.01 mm. The anterior width of teeth (Wf) was measured at the protecone-paracone height in the upper dentition and at the protoconid-metaconid height in the lower dentition and the posterior width (Wb) at the hypocone-metacone height in the

case of the upper teeth and at the hypoconid-entoconid height in the case of the lower teeth. As regards the third molars only the anterior width was measured.

#### III. RESULTS

# Morphology

The morphology of the first and second molars in the upper and lower dentition in most of the specimens examined does not differ in anything from the description given for C. cricetus (e. g., Schaub, 1930; Newton, 1909; Miller, 1912; Fahlbusch, 1976), whereas the crowns of M3 in a number of specimens from Borusowa and specimens M/977/59, 54999 and 98265 bear additional ridges. These have also been found in all the incompletely grown third molars (3M<sub>3</sub> and 7 M³) obtained from owls' pellets. In the lower teeth these additional ridges occur as a rule on the internal wall of the entoconid and also in the syncline between the metaconid and the entoconid and between the entoconid and the hypoconid, or in the posterolingual region of these teeth. In the upper teeth they are chiefly situated in the syncline between the metacone and the paracone and on the medial wall of the metacone, or on the posterobuccal side of the teeth. Examples of such morphology can be seen in Plates V and VI, which show the third molars of specimen M/977/59.

In adult specimens the degree of development of these additional ridges is rather differentiated, from teeth in which they are completely lacking to such as found in specimen M/977/59. However, as has been said, they always occur on developing teeth, at the final stage of their growth. Delicate as they were originally, they were soon worn out and cannot be observed in older specimens. However, singular teeth, even very heavily worn, bear their distinct traces in the form of additional enamel loops. Specimen 54999 seems to be interesting; a few additional elements occur in it on both M3 and on right M2, whereas they are completely absent from left M3. These additional ridges hardly ever occur on M2 (the exceptions are really very few). Specimens with developing M2 were missing in the study material, and so it is hard to state definitively that towards the end of their development they go through a stage of numerous additional ridges. I may only suppose that it is so. Thorough knowledge of the ontogeny of the dentition in C. cricetus would be very helpful in considerations on evolution and in palaeozoological studies. Owing to the occurrence of these additional ridges, the surfaces of the crowns of M3 in modern C. c. cricetus resemble the morphology observed sporadically in big Pleistocene hamsters and recognized by Fahlbusch (1976) as one of the set of characteristic features of the big Middle-Pleistocene hamster from Petersbuch 1. Also the other features of this set are encountered, together or separately, in some specimens of molars of contemporary C. c. cricetus (cf. Discussion, p. 47).

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Modern C. c. cricetus from Poland. Dimensions of skulls (Cb) and mandibles (Lmd), lengths of cheek tooth-rows (upper -  $LM^{1-3}$ , lower -  $LM_{1-3}$ ) and lengths (L) and width (Wf,Wb) of successive molars. Within the range of one specimen: upper -right side,lower-left side. The measurements of undergrown teeth are given in brackets (in mm)

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7 8

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Properties   Pro	1	Description	Lmd	L M <sub>1-3</sub>	L	M <sub>1</sub> Wf	Wb	L	M <sub>2</sub> Wf	Wb	M <sub>3</sub>	3 Wf	Ср	L M1-3	L	M <sup>1</sup> Wf	Wb	L	M <sup>2</sup>	L/De	м	3
1.	L	Specimens from the collection	of th	-	-								ology	L				1 4.	Wf	Wb	L	Wf
The companies   The companie	T	1. Oświęcim, 10 Aug. 1936	T	T	3.24	1.80	1.99	2,88	2.25	2.29	(2.86)	(1.93)	72.0		3.37	1.94	2.01	2.86	2.21	2.11	(2.26)	(2.01)
2. Segretary 20 - 19 - 19 - 19 - 19 - 19 - 19 - 19 - 1		2. Chrzanów, 14 Sep. 1952	-		3.16	1.64	1.75	2.60	2.04	2.09	2.65	2.09	2.9	7.74	3.52	1.96	2.10	2.88	2.25	2.10	(2.23)	(1.91)
Section   1979		3. Proszowice,3 Oct. 1969	-	8.36	3.04	1.59	1.81	2.81	2.05	2.16	2.90	2.10			3.15	1.96	2.03	2.63	2.19	2.08		
The content of the		4. Proszowice,3 Oct. 1969		8.08	2.98	1.64	1.78	2.66	2.18	2.24	2.75	2.17	30.2	7.73	3.18	1.96	2.06	2.63	2.29	2.07	2.13	2.06
Stratistics		5. Tarnów, 1975	27.4	7.87	2.82	1.54	1.69	2.60	1.96	2.03	2.79	2.00		7.70	2.98	1.81	1,90	2.46	2.02	1.92	2.43	
The companies		6. Tarnów, 1975	29.8	8.22	3.05	1.70	1.83	2.65	2.09	2.14	2.70	2.04		8.00	3.23	2.02	2.13	2.74	2.28	2.11	2.25	2.01
5. 1		7. Borusowa, 1975	35.9	8.62	3.10	1.69	1.80	2.74	2.15	2.14	2.98	2.24		7.89	3.28	2.05	2.15	2.65	2.31	2.16	2.29	2.03
Section   Sect		8. Książnice W., 1954	-	-	-	-	-	-	-	-	_	-		7.47	2.98	2.13	2.22	2.57	2.35	2.18	2.61	2.30
Marchanist		9. Borusowa, 21-25 Sep. 1981	27.8	8.07	3.03	1.61	1.72	2.61	2.00	1.95	2.87	2.03		7.74	2.95	1.99	1.92	2.58	2.17	1.98	2.49	2.18
State   Stat		10"-	29.5	8.34	3.04	1.74	1.85	2.63	2.11	2.10	3.06	2.01		7.60	3.02	1.77	1.90	2.52	2.05	1.95	2.37	2.03
State   Stat		11"-			3.09	1.71	1.81	2.65	2.09	2.11	2.87	2.13			3.23	2.00	2.13	2.69	2.27	2.13	2.45	2.15
1.		12"-	100 B 100 B 100 B	7.99	3.04	1.71	1.78	2.59	2.06	1.99	2.64	2.02		Magdin Fore	3.12	2.00	2.07	2.59	2.20	2.06	(2.21)	(2.01)
MySTANDAN		13"-	100000000000000000000000000000000000000	1.4413 753	3.12	1.72	1.80	2.56	2,06	2.05	2.91	2.04		8.01	3.17	2.04	2.13	2.70	2.23	2.08	2.35	2.12
No.		14"-	31.2	7.89	3.01	1.71	1.80	2.50	2.04	2.01	2.62	2.04	52.1	7.65	3.10	1.99	2.04	2.41	2.21	2.01	2.33	2.09
Section   Sect		15"-	30.0		3.06	1.75	1.84	2.66	2.08	2.22	2.55	2.00	-	7.76	3.24	1.99	2.05	2.64	2.22	2.05	2.26	2.01
1.		16"-	100000000000000000000000000000000000000	The state of the s	3.04	1.69	1.76	2.43	1.97	2.05	2.70	2.05	49.7	7.65	3.10	1.97	2.04	2.51	2.06	1.93	2.22	1.95
10			24.6	8.18	3.17	1.70	1.87	2.70	2.17	2.22	2.76	2.06	-	8.25	3.26	1.91	2.08	2.90	2.29	2.15	2.43	2.00
March   State   Stat		M/5753/81 18"-	23.9	7.95	3.05	1.73	1.83	2.60	2.06	2.07	2.70	2.01		7.45	3.12	2.02	2.05	2.54	2.16	2.00	(2.10X	(1.95)
Marchester   St.		M/5754/81	32.0	7.85	3.10	1.69	1.90	2.65	2.10	2.15	2.75	2.13		1.01	3.20	2.08	2.12	2.70	2.29	2.13	2.28	2.00
Section   Sect		M/5755/81	23.2	8.10	3.07	1.70	1.80	2.69	2.02	2.05	2.74	1.99	38.5	7.78	3.17	1.95	2.03	2.57	2.17	2.01	(2:30)	2.09
### 1979/1911   2014   0.151   1.50		M/5756/81	23.6	7.96	2.80	1.68	1.73	2.55	1.98	2.04	(2.83X	1.97)	_	7-9/	3.18	1.97	2.03	2.52	2.11	1.97	2 /10	2.00
## 1978/6/18   50.4   61.22   50.7   1.79   1.77   1.78   2.78   2.09   2.09   2.00		M/5757/81	28.4	8.17	3.00	1.61	1.69	2.65	2.01	2.07	2.84	2.06		7.90	3.10	1.92	1.97	2.61	2.08	1.98	2.40	1.99
Mystory   Myst		M/5758/81	24.4	8.22	3.07	1.73	1.77	2.71	2.09	2.03	2.79	2.05		-	-	-	1.90	2.65	2.13	2.00	2.18	2.00
My760/91		M/5759/81	-	8.24	3.11	1.76	1.91	2.70	2.10	2.13	2.91. 2	2.12		8.16	3.17		ESSENCE OF THE PARTY OF THE PAR	2.76	2.30	2.14	2.53	2.10
M.75761/91			26.3	8.31	3.10	1.75	1.88	2.65	2.12	2.16	2.88 2	2.17		8.02	3.15	2.06	2.22	2.63	2.28	2.16	2.47	2.04
My766296			27.5	8.06	3.01	1.74	1.77	2.59	2.06	2.13	2,76 2	2.02		7.70	3.13	1.98	2.08	2,60	2.20	2.08	2.30	1.98
28.   M/9766/81		M/5762/81	23.0	7.89	3.00	1.70	1.76	2.67	2.04	2.07	2.62 1	1.96	138	7.58	3.11	1.92	2.03	2.60	2.19	2.05	(2.23)	1.96)
39. My9764/81		M/5763/81	23.6	7.88	2.95	1.65	1.74	2.55	2.02	2.03	2.70 1	1.96			3.07	1.99	2.06	2.71	2.24	2.07	2.21	2.00
30. My9765/81			33.8	8.03	3.03	1.70	1.83	2.68	2.04	2.12	2.80 2	2.09		7.81	3.12	2.02	2.14	2.50	2.24	2.09		
### 197566/81   23,4 (8,03 k.93 1.62 1.69 2.63 2.03 2.08 2.78 2.09 2.78 2.78 2.09 2.78 2.78 2.78 2.78 2.78 2.78 2.78 2.78			23.0	8.13	3.18	1.68	1.77	2.62	2.08	2.04	2.67 2	2.16	-	7.84	3.18	1.86	1.92	2.73	2.21	1.98	2.35	2.00
32. N/5766/8"   32.1 1   1.02   2.93 1.70 1.76   2.92 2.00 2.00   2.77 2.00   3.5   7.66   3.77 1.90 2.00   2.40 2.10 2.00   2.17 2.00   3.5   7.78   3.5   7.7		M/5766/81	23.4	8.03	2.93	1.62	1.69	2.63	2.02	1.98	2.74 2	2.09	38.0	7.64	3.16	1.83	1.89	2.48	2.14	1.93		
My5768/61		M/5767/81	24.3									2 02	-				2013/04/2012			COLCUPATION !		
My9769/61		M/5768/81	32.5	7.81	2.98	1.68	1.73	2.50	2.01	2.03	2.73 1	1.96		7.81	3.18	1.94	2,02	2.48	2.19	1.99	2.32	2.12
34. Dubicne-Teffitowee 180 Cs. 1966, no 184999 25. 6 7.89 2.95 1.67 1.76 2.53 2.08 2.05 2.08 2.05 2.84 2.09 35. Revoker, 1969, no 186514 25. 2 7.88 2.95 1.78 2.86 1.07 1.73 2.53 2.08 2.05 2.78 2.17 2.07 2.05 2.78 2.17 2.05 2.05 2.78 2.17 2.05 2.05 2.78 2.17 2.05 2.05 2.05 2.78 2.17 2.05 2.05 2.05 2.05 2.05 2.05 2.05 2.05	1	M/5769/81	34.4	8.02	3.03	1.68	1.79	2.58	2.06	2.11	2.73	2.13	55.9		-			2.44	2.11	2.02		- 1
18 Oct. 1966, nois4699 25, 5, 57, 66 2, 96 1, 67 1, 73 2, 51 2, 04 2, 05 2, 78 2, 77 1, 76 3, 10 1, 93 1, 96 2, 245 2, 12 1, 97 2, 19 2, 09 1 36 3 3 48, 1969, nois6614 29, 8, 77, 22, 29 5, 165 1, 17 17 2, 74 2, 02 2, 06 2, 78 2, 17 2, 10 4, 07 5, 07 3, 14 1, 99 2, 01 2, 29 2, 15 2, 20 1, 19 4, 23 1 2, 29 1 2, 10 4, 10 1, 1	_	Specimens from the collection	of the	Mamr	nals F	lesear	ch Ir	stitu	te,	P.A.S	c. at	Biał	owież	а								
9 Aug. 1959, no186614 5. Szewerio, poly 10, no196265 5. Szewerio, poly 10, no196265 5. Szewerio, poly 10, no196266 5. Szewerio, poly 10, no196267 5. Szewer		34. Dubicze-Tefiłowce, 18 Oct. 1966, no:54999	25.6 25.5	7.95 7.86	2.95	1.67	1.76	2.53	2.08	2.06	2.84 2	2.09	42.8	7.48	3.08 3.10	1.90	2.00	2.48	2.06	1.90	2.20 2	2.09
11 May 1951, no:98265 28.5 8.7 93.7 1.67 1.67 2.46 2.06 2.08 2.79 2.07 1.67 2.53 1.23 2.09 2.10 2.58 2.26 2.11 2.18 2.07 27. Markuszów, no:98266 28.5 8.2 3.11 1.76 1.88 2.66 2.27 2.29 2.93 2.48 4.7 2.7 8.8 3.20 2.10 2.58 2.66 2.32 2.17 2.38 2.18 2.37 2.88 4.78 2.89 2.89 2.89 2.89 2.89 2.89 2.89 2.8		35. Istok, 9 Aug. 1969, no:86614	29.8	7.92 7.88	2.95	1.65	1.74	2.48	2.04	2.13	2.71 2	2.08	49.0									
8.6 (a) 8.7 (b) 1.1 (c) 1.6 (a) 2.60 (c) 2.7 (c) 2.9 (c) 2.7 (c) 2.9 (c) 2.19 (c) 7. (a) 3.19		36. Sławęcin, 11 May 1961, no:98265											48.8									
77 no:98267  19. Dubtoze-fortizore, 1 Nov. 1972, no:10799  20. Type 1. Nov. 1972, no:10799  40. Guzówka, 1960, no: 7?  Specimens from Dr A. Ruprecht** collection (Bialowiteka)  41. Kabylinga, 50, no: 77  Specimens from Dr A. Ruprecht** collection (Bialowiteka)  41. Kabylinga, 1963, no: 570  42. Kabylinga, 1963, no: 570  42. Kabylinga, 1963, no: 570  43. Kabylinga, 1963, no: 570  44. Kabylinga, 1963, no: 570  45. Roylinga, 1963, no: 570  46. Kabylinga, 1963, no: 570  47. Mag. 1963, no: 570  48. Roylinga, 1963, no: 570  49. Roylinga, 1963, no: 570  40. Roylinga, 1963, no: 570  40. Roylinga, 1963, no: 570  41. Kabylinga, 1963, no: 570  42. Kabylinga, 1963, no: 570  43. Roylinga, 1963, no: 570  44. Kabylinga, 1963, no: 570  45. Roylinga, 1963, no: 570  46. Roylinga, 1963, no: 570  47. Mag. 1963, no: 570  48. Roylinga, 1963, no: 570  49. Roylinga, 1963, no: 570  40. Roylinga, 19			28.5	8.36	3.09 3.11	1.74	1.92	2.62	2.22	2.31	2.94 2	2.15										
1 Nov. 1972, no:107993 40. Guzówk, 1960, no: 7?  Aug. 1960, no: 7?  Specimens from Dr A. Ruprecht** collection (Balowieża)  41. Kabylica; 42. Kabylica; 42. Kabylica; 43. Ratymne, 44. Sabylica; 44. Ratymne, 45. Get. 1958, no: 570  46. Hrupteszów, no: 571  47. Nov. 1958, no: 1750  48. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  49. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  49. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  49. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  49. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  49. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  40. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  40. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  40. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  40. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  41. Kabylica; 42. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  42. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  43. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  44. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  45. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  45. Balos Specimens from owls* pellets in the collection of the Nammals Research Institute at Bialowieża  46. Brupterschi* pellets Specimens from owls* pellets in													47.6	8.04	3.30 3.44	2.10	2.18	2.66	2.32	2.17		
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$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$				2	2.86	1.74	1.82	2.69	2.12	2.09	2.70 X2 2.66 X2	2.12)	-									
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max   35.9   8.65   3.35   1.87   2.01   2.88   2.27   2.31   3.08   2.24   58.7   8.29   3.52   2.14   2.22   2.90   2.38   2.18   2.61   2.30     SD			81	75	2.78	86 1.54	86	84	84	84	76	76	34	63	2.95	96 1.76	96 1.89	90	90	90	65 2.01	65
V   14.5   2.71   3.29 3.40 3.82   3.12 3.59 3.58   4.07 3.35   14.0   2.67   3.25 4.19 3.98   4.16 3.52 3.87   5.17 4.34   Wmax 84   1.99-2.31		mex *	27.1 35.9	8.09 8.65	3.03 3.35	1.69	2.01	2.88	2.27	2.31	3.08 2	2.24	58.7	8.29	3.16 3.52	1.97	2.05	2.59	2.20	2.04	2.31 2	2.05
1.99-2.31			3.92 14.5	2.71	0.10 3.29	.057 3.40	.069 3.82	.081	3.59	3.58	4.07 3	068	14.0	2.67	.103 3.25	.082 4.19	.082 3.98	.108 4.16	.077 3.52	.079 3.87	.119 . 5.17 L	,089 4.34
2.11									84 1 <b>.</b> 99-	2.31												

#### Measurements

The results of measurements are presented in Table I. Because all the basic values are given, the statistical computations have been reduced to a minimum and placed in the lower part of the table. The values given in brackets are not included in computation; they refer to teeth which were not quite grown. In discussing particular problems, I also present graphic interpretations of the data from Table I.

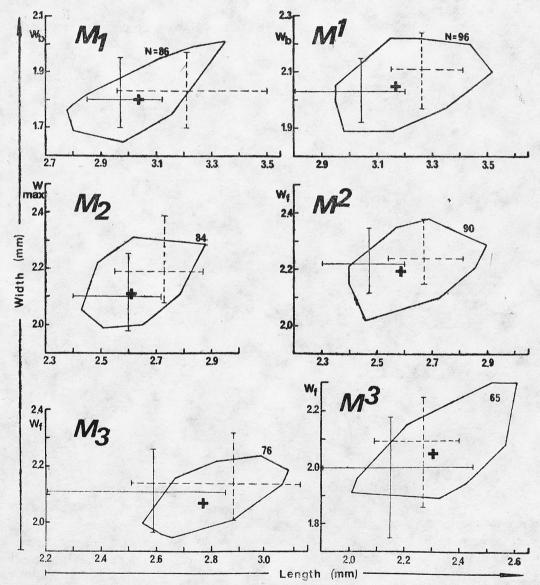


Fig. 2. An L/W graph of molars. Area surrounded by solid line — recent *C. c. cricetus* from Poland. Crosses indicate the intersections of respective means. Ranges of variation: solid line — recent hamster from Rheinhessen (Fahlbusch, 1976), broken line — *C. cricetus* from the Würm of Poland (Pradel, 1981b)

### Dimensions of isolated molars

The dimensions of successive teeth are shown in the form of an L/W graph in Fig. 2 and the frequencies of specimens in particular length groups are illustrated in a histogram in Fig. 3.

For comparison the L/W graph includes also the values for the recent hamster from Hesse in Germany (Raum-Alzey-Mainz — Fahlbusch, 1976) and the fossil hamster population from Poland (Sąspowska Zachodnia Cave, end of the Würm, Pradel, 1981b).

In respect of length the teeth of the recent hamster from Poland are as a rule intermediate between the values with which they are being compared, but they

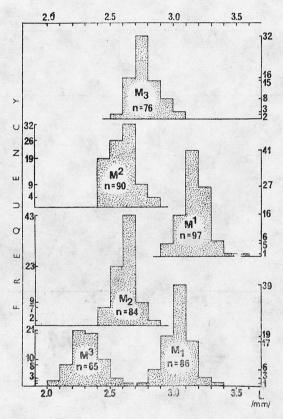


Fig. 3. A histogram illustrating the distribution of lengths of successive molars

are proportionally somewhat narrower. These relations do not occur merely in the case of  $M^3$ , which is characterized by the highest coefficient of variation:  $V_L = 5.17$ ,  $V_{Wf} = 4.34$ , and are probably connected with subspecific differences (cf. Pradel, 1981b, Discussion).

Figure 4 shows the differences found between Wf and Wb in the first two upper and lower molars compared with those observed in the population of C. cricetus from Sąspowska Zachodnia Cave. This comparison does not show

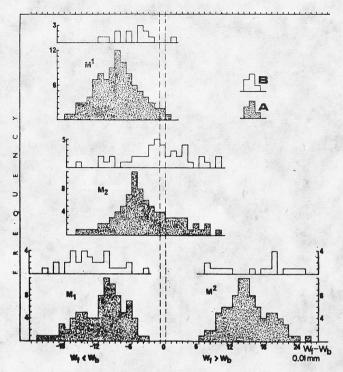


Fig. 4. Histogram of Wf-Wb differences A — recent C. c. cricetus from Poland, B — C. cricetus — Sąspowska Zachodnia Cave, Würm, Poland (Pradel, 1981b)

any major differences between these two populations, at least in respect of ranges of variation. As regards  $M^1$  only, the differences (Wf—Wb) seem to be somewhat greater in the recent hamster, but this may be a chance result, for the number of these teeth in the material from Sąspowska Zachodnia Cave (N=8) is small.

# Lenghts of tooth-rows and relationships within their range

The numbers of tooth-rows in particular length groups are presented in Fig. 5 and their statistical description is given in Table II. Unlike the dimensions of the isolated teeth of relatively great variability (V = 3.12-5.17), the lengths

Table II
Lengths of tooth-rows at the height of the greatest bulge of the crowns (in mm)

	M <sup>1-3</sup>	M <sub>1-3</sub>
N	63	75
Min-max	7.40-8.29	7.80 - 8.65
x	7.791	8.089
SD	0.208	0.219
v	2.673	2.709

of the tooth-rows are less variable:  $VLM^{1-3} = 2.67$ ,  $VLM_{1-3} = 2.71$ . The lower tooth-rows are dinstinctly longer (by about 3.7%) than the upper ones, the minimum noted for the lower row (7.8 mm) being slightly greater than the mean length of the upper rows ( $\bar{x}LM^{1-3} = 7.79$  mm). Similar relationships have been

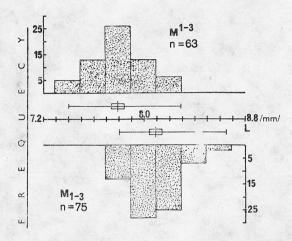


Fig. 5. A histogram illustrating the distribution of the lengths of tooth-rows (lengths at the height of tooth-crowns)

found also in *Cricetulus migratorius* from Syria (PRADEL, 1981a) and in *Cricetus cricetus* from Sąspowska Zachodnia Cave (PRADEL, 1981b). This seems to be a constant relationship within the subfamily *Cricetinae*. The results that can be obtained on the basis of the data comprised in MILLER'S work (1912, p. 604) are at variance with the foregoing opinion. This matter is discussed in PRADEL'S (1981b) paper.

The proportion of the lengths of particular teeth in a row in relation to LM2 has been calculated by both comparison of mean lengths and the method proposed in PRADEL's paper (1981a).

Table III

Lengths of first and third molars in relation to LM2. Calculated from the proportions found in particular rows

	$\mathrm{M}^{\scriptscriptstyle 1}:\mathrm{M}^{\scriptscriptstyle 2}$	$\mathrm{M}^3:\mathrm{M}^2$	$M_1:M_2$	$M_3:M_2$
N	86	65	84	75
min-max	1.124—1.315	0.791—1.025	1.063 - 1.251	0.946 - 1.162
$\bar{\mathbf{x}}$	1.222	0.891	1.163	1.063
SD	0.042	0.057	0.041	0.046
V	3.44	6.35	3.49	4.30

Identical values have been obtained by comparing the mean lengths of successive molars; they are in round figures:

$$\frac{\rm LM^1\!-\!LM^2\!-\!LM^3}{\rm LM_1\!-\!LM_2\!-\!LM_3} = \frac{1.22\!-\!1\!-\!0.86}{1.16\!-\!1\!-\!1.06}$$

The values presented in Table IV are similar. A relatively shorter  $M_3$  occurs only in the population of recent hamster from Rheinhessen. This may be a character of the subspecies  $C.\ c.\ canescens$  Nehring 1899.  $M^3$  of the hamster from

Table IV

A comparison of the relative lengths of successive molars in two modern and two fossil populations of hamsters

	M <sup>1</sup>	M <sub>1</sub> M <sub>2</sub> M <sub>3</sub>
C. cricetus, recent, Poland	1.22—1—0.89	1.16—1—1.06
C. cricetus, final phase of Würm, Sąspowska Cave, Poland, (PRADEL 1981b)	1.21—1—0.84	1.17—1—1.05
C. cricetus, recent, Rheinhessen, (FAHLBUSCH 1976)	1.23—1—0.87	1.14—1—0.99
C. major sensu Fahlbusch 1976 Middle Pleistocene, Petersbuch 1	1.21—1—0.89	1.16—1—1.10

Sąspowska Zachodnia Cave also seems to be relatively shorter, but here this may be due to the small number of specimens (N=14). A statistical comparison of these indices was possible only between the recent hamster from Poland being discussed in this paper, and the population from Sąspowska Zachodnia Cave. Student's test shows no differences between these populations as regards the lengths of  $M^1$ ,  $M_1$  and  $M_3$ . In the case of  $M^3$  the F test did not permit the application of Student's t test. It should be kept in mind at the same time that these are mean values. In particular cases these relations differ from them fairly considerably (Table III).

# Lenghts of skulls and mandibles

Unlike the linear dimensions of isolated molars and their rows, which bear no signs of age variation, the lengths of skulls and mandibles are characterized by very distinct variation of this kind (Fig. 6, Pl. VIII, IX). Four size groups correlated with age and in consequence with the degree of development and wear of the teeth can be distinguished in the material under study.

The first group comprises juvenile specimens (juv.). Most of them come from the material of owls' pellets (5 rami of mandibles), their skulls being destroyed. Only in the case of specimen M/977/59, caught in the field, I managed to measure

Cb. Tooth crowns without traces of wear, M3 still incompletely developed (at various stages of growth) (Pl. II—IV).

Group II consists of nearly adult specimens (subad.). Tooth enamel mostly without signs of wear, sometimes with very slight wear at tops of basic cusps. M3 fully developed.

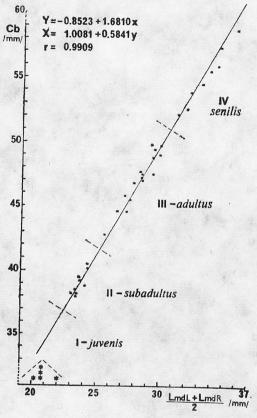


Fig. 6. Lengths of mandibles compared with condylobasal length of skull. In the bottom left-hand corner the point delimited with a broken line show the lengths of the mandibles from owls' pellets (without respective lengths of skulls)

Group III — adults (ad.). Teeth distinctly worn to a various degree. Worn places visible, notably in the middle of the tooth: connective ridges and median walls of cusps. External walls of cusps always well seen.

Group IV — senile specimens (sen.). Crowns heavily worn, external walls of cusps sometimes still visible, but there are also some teeth with quite flat or even concave crowns.

With the foregoing changes are also associated the changes in the degree of ossification of the whole skull. The curvature of the profile of the cranial vault changes from rounded to straightened (Pl. VII).

Table V gives statistical descriptions of each age group. The homogeneity

Table V
Condylobasal length of skulls (Cb) and lengths of mandibles (Lmd) in different age groups of modern C. c. cricetus from Poland (in mm)

		Сь	Lmd
	N	1	7
	min-max	32.9	20.1—22.2
	min-max X	34.9	21.07
juv.	SD		0.750
	V		3.56
1	-   <del></del>		0.00
	N	9	25
	min-max	38.0-40.5	23.0-24.7
subad.	$\bar{\mathbf{x}}$	39.01	23.74
	SD	0.905	0.565
	V	2.32	2.38
r .	N	16	35
	min-max	42.8—49.8	25.5—30.0
ad.	T X	47.11	28.22
	SD	2.032	1.285
	v	4.31	4.55
- 17	N	8	14
	min-max	52.1-58.7	31.2—35.9
sen.	x	55.06	33.37
Soli.	SD	2.278	1.558
	V	4.14	4.67
	N	24	49
ad.	min-max	42.8—58.7	25.5—35.9
+	$\bar{\mathbf{x}}$	49.76	29.69
sen.	SD	4.351	2.712
	v	8.74	9.13
juv.	N	34	81
subad.	min-max	32.9—58.7	20.1—35.9
ad.	x	46.42	27.11
sen.	SD	6.483	3.921
	v	13.97	14.46

of each of them is indicated by their low coefficients of variation (V = 2.32 - 4.67). The joint treatment of adult and senile specimens (excluding juniles and subadults) brings about an increase in the coefficient of variation to 8.74 (Cb) and 9.13 (Lmd). These coefficients still lie within the ranges of the values given for mammals.

The last item of this table refers to all the age groups together. It provides information about their global range of variation and very strong variation associated with age (V = 13.97, 14.46).

This variations must be kept in mind when fossil and recent materials are

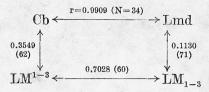
being compared with each other. Most of the fossil materials come from owls pellets. The remains of juveniles prevail in them, because it is young specimens leaving their material burrows that fall an easy prey to even medium-sized owls (e. g., barn owl Tyto alba), it is worth emphasizing here once again that the material obtained from pellets contained exclusively remains of hamsters of group I (juv.). Student's t test used in an analysis of the results of comparison of this fossil material, in which juveniles predominate, with the means computed for only adult specimens (as they are usually given for recent species) indicates the existence of statistically significant differences.

The values of Lmd and, notably, Cb, so far given for C. c. cricetus, should be verified in the light of the data obtained. "Klucz do oznaczania zwierząt ssących Polski" (Key to the Mammals of Poland) by Niezabitowski (1933) informs that the Cb length of the skull of C. c. cricetus comes up to 51 mm. The Cb length of the skull presented after Surdacki for C. c. cricetus in "Kluez do oznaczania kręgowców Polski" (Key to the Vertebrates of Poland), Part V, 1964, ranges from 44.0 to 51.4 mm. It seems that in this case the author gave the old data concerning the German hamster according to MILLER'S work (1912), i. e. the smallest and largest values of Cb from a series of measurements given in the table on p. 604 of that work (MILLER, 1912). And so they cannot describe the size of Cb of hamsters occurring in Poland at the present time. They should be suitably modified and the dimensions given in the present paper should be accepted for the Polish population of C. cricetus. Also the latest revised edition of the last mentioned Key (1981, p. 180) gives narrow-range data — Cb = =46-55 mm. Because of the limited amount of material neither may these data be regarded as final maxima for this subspecies. The range of C. c. cricetus is not restricted to the territory of Poland, it extends far into the Asiatic continent. Kowalski (1967) writes that "in the opinion of Gromov et al. (1963), there is generally a tendency towards the increase of measurements proceeding from the west towards east and from the north southwards". Unluckily, I have not numerical data defining the dimensions of the skull of C. cricetus in the Asiatic part of its range. Nevertheless, it may well be that there may occur populations there comparable in respect of the dimensions of teeth even with big Pleistocene hamsters.

# Analysis of the coefficients of variation (V) and correlation (r)

MAYR (1974) writes that in mammals the coefficients of variation (V) of linear measurements amount usually to 4-10, sometimes to 3-4. The coefficients of variation of L and W in isolated molars comprised in the recapitulation of Table I range from 3.12 to 5.17. So their values are not high. The lengths of the tooth-rows are however characterized by still lower variation, V=2.67, 2.71, and they are the most constant linear parameter in the skull of the hamster. This is due to the fact once the tooth-row has grown, it does not undergo any changes, whereas the rest of the skull goes on growing and achieves variation

expressed by a high value of the coefficient — VCb = 8.74, VLmd = 9.13 — in adult specimens (ad. + sen.). Also the correlations found illustrate these relationships



A relatively strong correlation is marked both between the constantly growing elements (Cb and Lmd) and between the lengths of tooth-rows, whereas it does not occur between the constantly growing elements and the tooth-rows set in them. Neither are significant correlations between Cb and  $\rm LM^{1-3}$  and between Lmd and  $\rm LM_{1-3}$  found when particular age groups are examined separately. In specimens of group IV (sen.), which are the most markedly grown up, both very short and very long tooth-rows are observed and it is just these lengths that mark out the full range of variation of the lengths of tooth-rows.

In most cases the correlation between the length of successive teeth in a row does not exist, either:

FAHLBUSCH (1976) determined big molars of a hamster from Petersbuch 1 as belonging to C. major Woldfich 1880. Thereby he identified the hamster specimen from Vypustek described under this denomination with his material. At the same time that specimen was ranked as a species, the name "major" being originally used by Woldfich as subspecific: Cricetus frumentarius major (C. frumentarius = C. vulgaris = C. cricetus).

In this connection it must be considered

- 1 whether Woldkich was justified to give a new name to the specimen from Vypustek and
- 2 whether the remains of the big Middle-Pleistocene hamster from Petersbuch 1 may be identified with those described by Woldkich.

In my opinion, the answers to both these questions are negative.

On the basis of the values presented in the results of this study we can distinguish a number of mathematically describable relationships in the hamster's dentition. We may assume that in all probability these relationships occur also in other populations of *Cricetus*, which permits a comparison of the data from literature which have hitherto been incomparable in a direct manner.

Woldfich (1880) compared the skull and mandible of a medium-sized specimen of *C. ericetus* from Winterberg with the big skull and mandible of the specimen from Vypustek. He gives drawings of the big skull (lateral and ventral views) but no drawings of that big mandible, so important in this case. Neither

does Woldfich provide any remarks on the morphology of the molar crowns. He considers the differences demonstrated by the comparison to be sufficiently big to permit him to erect a new subspecies for that big specimen. In his considerations no attention is given to either age or individual variation within local populations and to geographical variation within the whole range of C. cricetus. He compared his specimens with those from literature in respect of only one parameter (Cb). Woldfich (1880, pp. 24-25) gives a number of dimensions of the skull and mandible from Vypustek (unfortunately, although the measuring points are described they are hard to interpret quite univocally). Table VI shows a comparison of these dimensions with those measured on big specimens of these dimensions with those measured on big specimens of the recent hamster from Poland and the hamster from Sąspowska Zachodnia Cave. As regards two specimens of recent C. c. cricetus, they are the biggest examined, whereas the specimens from Sąspowska Zachodnia Cave are randomly preserved fragments of skulls, their general view being given in a previous paper by the author (PRADEL, 1981b, Pl. XVI). On the basis of their wear one of these teeth, MF/ /1284/A-1, must be included in age group III (ad.) and the other, MF/1284/A-2, in group IV (sen.). The skulls under comparison are of a similar order of magnitude, but some unproportionalities of dimensions are visible in them. They are caused by two overlapping factors: 1 — changes in the proportions of the cranial elements in ontogeny (age variation) and 2 — individual characters of the skull (individual variation). In this context it is worth while drawing attention to the fact that Woldkich defines the specimen from Vypustek as "not belonging to an old individual". I cannot agree to this statement. The worn middle regions of tooth crowns, the straightened line of the vault of the skull, the sharply marked suture between the occipital squama and the parietal and temporal bones indicate that this specimen stands on the border-line between group III and group IV (ad.-sen.) or represents an early period of senility (cf. Plates VII, VIII, X).

The lengths of tooth-rows given by Wolderch also call for an adequate interpretation. This dimension is given in two ways: once as the dimension of alveoli and another time as the length of tooth crowns. These two dimensions differ rather markedly and are well distinguished from each other by authors. E. g. Newton (1909) gives the lengths for the upper tooth-row from Forest Bed equal to 10.3 mm (alveoli) and 9.3 (crowns). Schaub (1930, p. 16) writes: "Die Länge der Alveolen einer Hamstermandibel ist etwas grösser als die Zahnreihenlänge. Bei den in Frage stehenden Grössenklassen dürfte der Underschied etwa 1/2 mm betragen." Here we are concerned with a tooth-row length range from 6.1 to 9 mm. These relationships are observed in all hamsters regardless of size. Storch (1974) gives the lengths of the upper tooth-rows of Cricetulus migratorius measured across the crowns — 3.95—4.15 mm — and across the alveoli — 4.3—4.45 mm. Wolderch writes about the skull from Vypustek that we are interested in: "Länge der Backenzahnreihe (Alveolen) ...9.5" and about the length of the lower tooth-row: "Länge der Backenzahnreihe an den Alveolen...

A comparison of some dimensions of skulls in fossil and modern hamsters. 1. Specimen from Vypustek, data from Woldkich, 1880, pp. 24—25. 2 and 3. Fragments of skulls from Saspowska Zachodnia Cave. Their general view is presented in Pl. XVI in Pradel's (1981b) paper; 2—MF/1284/74, A—1; 3—MF/1284/74, A—2. 4 and 5. Specimens of modern C. c. cricetus presented in this paper.

in this paper. 4 — M/5533/79, see also Pl. IX, 5 — M/5534/79, see also Pl. X

Notes: 1. The mandibles from Sąspowska Zachodnia Cave have not been compared. Out of the 50 mandibles found there, only 21 were not damaged. They belonged to young specimens and their dimensions do not reach values comparable with those of the specimens included in the table.

2. The lengths of mandibles of modern specimens measured between the foremost edge of the alveolus of the incisor and the end of the condylar process are given in brackets (in mm,

<u> </u>		1	2	3	4	5
	Condylobasal length	56.0	_	_	58.7	57.4
	Distance between the lower anterior edge of the nasal aperture and the external posterior edge of the					
	infraorbital foramen	18.0	18.5	18.0	19.0	18.8
	Length of tooth-row (alveoli)	9.5	9.5	9.5	9.3	8.9
	Length of tooth-row at the level R of crowns	7	8.03	8.00 7.98	7.89 8.03	7.47
Skull	Width at the height of the external edges of the incisor alveoli	8.0	8.4	7.6	8.5	8.3
	Width at the height of the lower edge of the infraorbital foramen	12.0	12.3	12.3	13.2	13.0
Greatest width of the infraorbital foramen  Height of the skull measured at the first molar	foramen	4.0	4.4	5.0	4.4	4.3
		17.0	17.4		18.0	17.8
	Width of wear of both incisors	5.0	4.3	4.2	_	4.4
	Length from the posterior edge of the incisor alveolus to the end of the condylar process	39.0			(38.9) 35.9	(36.6) 34.6
	Distance from the same point to the anterior edge of M <sub>1</sub>	11.0	_	_	11.4	11.3
	Length of tooth-row (alveoli)	10.0	_	_	9.3	9.0
Ian-	Length of tooth-row at the level R				8.62	
lible	of crowns L	_	_	_	8.65	7.8
deepe Heigh	Height of the mandible at the deepest place in front of M <sub>1</sub>	8.0			6.2	6.2
	Height of the mandible from the edge of the alveolus of M <sub>1</sub>	11.5	- 4°	_	10.7	10.2
	Distance between the lower edge of the angular process and the upper					
	edge of the coronoid process	19.0	_		21.4	18.2

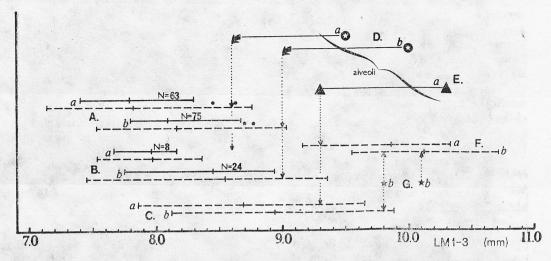


Fig. 7. A comparison of the lengths of tooth-rows (measured at the height of the greatest bulge of the crowns). Solid lines — lengths of tooth-rows actually measured. Broken lines — theoretical lengths of tooth-rows calculated from the lengths of isolated molars (see Discussion). a — upper tooth-rows, b — lower tooth-rows, A — Modern C. c. cricetus from Poland. Points indicate the presumable lengths of the tooth-rows of specimen M/977/59 after the complete growth of its third molars. B — C. c. cricetus, Poland, various phases of Würm. Based on the data from Sąspowska Zachodnia Cave (PRADEL, 1981b) and unpublished data obtained from materials from 9 other localities in Poland. C — C. c. runtonensis from five Polish localities, from the Middle Villafranchian to the final phase of Mindel I. Author's own unpublished data (in prep.). D — C. c. major sensu Woldkich 1880. Specimen from Vypustek. Dimensions given by Wol-DKICH refere to alveoli. Lines indicate the approximate lengths of tooth-rows at the height of crowns. E - C. c. runtonensis Newton 1909. Specimen from Forest Bed, Runton, Norfolk. Lengths given by Newton: upper alveolus — 10.3 mm, tooth-row set in it — 9.3 mm. F — Big form of hamster from Petersbuch 1, Middle Pleistocene (C. major sensu Fahlbusch 1976), on the basis of the data from Fahlbusch's (1976) work. G - Lower tooth-rows of hamster from Vypustek: 9.8 and 10.1 mm, Liebe, 1879. Liebe recognized them as remains of a common hamster and gave then only the specific name Cricetus frumentarius (= C. vulgaris, = C. cricetus)

10". Thus we are concerned here with the larger dimension, across the alveoli. In the material of recent *C. cricetus* under study these differences fluctuate about 1 mm. They are smaller in young individuals and increase with age. The difference is particularly distinct in the lower teeth owing to the growth of the posterior section of the alveolar ridge. On the basis of the foregoing we can estimate that in the specimen from Vypustek the length of the tooth-rows across the crowns was about 8.5—8.7 mm for the upper rows and 8.9—9.1 mm for the lower rows. And so they lie either in the upper region of the range of variation of the contemporary hamster from Poland (upper rows) or within the range of *C. cricetus* from the Würm of Poland (lower rows) (see Fig. 7). However, it is much more that they depart considerably from the theoertical lower boundary of the lengths of tooth rows (across the crowns) calculated for a big hamster from Petersbuch 1.

This proposition needs full explanation. We may state on the basis of the results obtained that the length of a tooth-row is always smaller than the sum of the lengths of the teeth that make up this row. It is so because successive teeth overlap each other. We may assume in the case of both the upper and the lower teeth that the length of a row constitutes 97% of the sum of the lengths of particular teeth:

$$LM1-3 = 0.97 (LM1+LM2+LM3)$$

The ranges of variation (Lmin $-\overline{L}$ -Lmax) of particular teeth being known, the appropriate magnitudes (e. g. LminM<sup>1</sup>+LminM<sup>2</sup>+LminM<sup>3</sup>) were added and the sums of the lengths of successive molars in theoretical rows made up of the smallest, mean and largest teeth were obtained, from which the 97% values were calculated. The values thus obtained give only a tentative, theoretical picture of the lengths of tooth-rows (Fig. 7). The minimum values are slightly underestimated, the maximum ones overestimated and the means stand close to the actual values. This is well illustrated by the data presented in Fig. 7. for the recent C. cricetus from Poland, in which specimen all the teeth examined come from complete tooth-rows and despite this the range of variation of the lengths of actual tooth-rows is smaller than the theoretical range calculated by the method described above. It is so because no single tooth-row was found in which all the teeth were the shortest or the longest. If, for instance, M1 in a row was the longest of all the first molars examined, then both or at least one of the remaining molars were somewhat shorter than the maximum values established for these teeth. Therefore, the greatest and smallest length values of M1, M2 and M3 from various tooth-rows were used to compute the longest and the shortest length of the theoretical tooth-row. The calculation of the mean length of the theoretical tooth-row was based on appropriate mean values, e. g.  $T\overline{L}M_{1-3} = 0.97(\overline{L}M_1 + \overline{L}M_2 + \overline{L}M_3)$ . This drawing of the external values of variation ranges apart does not cause too grievous an error and at the same time leaves a tolerance range, as there is no certainty whether the largest and the smallest tooth-rows possible in a given population really found themselves in the material examined. E. g., it was impossible to determine the length of M1—3 in specimen M/977/56, because the third molars were not fully grown yet. The lengths of the first and second lower and upper molars of this specimen are given in Table I. It can be found on the basis of the relationships in complete tooth-rows that the sum LM1+LM2 forms 73.9% of LM1-3 and LM1+LM2 69.8% of LM<sub>1-3</sub>. Using these proportions we can calculate that this specimen. after its third molars had grown, would have had the following lengths of the tooth-rows: upper right 8.63 mm and left 8.46 mm, lower right 8.77 mm and left 8.70 mm. These lengths are greater than those observed, but they still lie within the range determined theoretically. We may therefore assume that the thus calculated lengths of theoretical tooth-rows, obtained from the data given by Fahlbusch (1976), reflect the actual ranges of variation of LM<sub>1-3</sub> and  $LM^{1-3}$  in the hamster from Petersbuch 1.

Taking into consideration the conclusion from a comparison of the measurements of skulls and mandibles (Table VI) and those from the foregoing reasoning (graphic interpretation in Fig. 7), we must state that the hamster described by Woldfich is a big specimen of the subspecies  $C.\ c.\ cricetus$  and in no case can it be identified with the hamster from Petersbuch 1.

Not only the linear dimensions of isolated teeth and their rows play an important part in the determination of species and subspecies of fossil hamsters. The morphological characters of the dental crowns are also important in this respect. In his description of the hamster from Petersbuch 1 Fahlbusch gives a number of morphological characters of the tooth crowns in which they differ from the teeth of the recent *C. cricetus*. At the same time he writes that these characters occur in a vast majority of specimens but not in all of them.

FAHLBUSCH inferred from a drawing in Woldkich's work that in the specimen from Vypustek, as in the hamster from Petersbuch 1, the cusps of the anterocone of M<sup>1</sup> are displaced outwards towards the cheek. In fact, the drawing in WOLDRICH'S work shows this character but the thing is that this character is also present in recent C. c. cricetus. And not only that character. I can state on the basis of the material examined that all the characters given as typical of the hamster from Petersbuch 1 occur also in the dentition of the contemporary hamster, being however less conspicuous and present in a smaller number of specimens. It is interesting that they are not coupled together and occur independently. And so, for instance, in the left teeth of the M/5747/81 mandible we can distinguish the rounded anteroconid of M<sub>1</sub>, the presence of a "funnel" (Trichter in the German original) in the centre of M2 and additional ridges on M<sub>3</sub>. As regards the right teeth of the same specimen, only the rounded anteroconid of M<sub>1</sub> and additional ridges on M<sub>3</sub> are present, the "funnel" being absent from Mo. The "funnel" may however occur quite independently and so it is observed, e. g., on left M<sub>2</sub> of specimen M/5757/81 but missing on right M<sub>2</sub>. Except for this single "funnel" that specimen has no other characters relating it to the hamster from Petersbuch 1. A ridge crossing the depression between the posterolophid and the posterior wall of the entoconid was found, e. g., in left and right Ma of mandibles No 816 in the material from owls' pellets. Here it appears independently, without any other "additional" characters on the adjacent teeth. On the other hand, in left and right M2 of specimen No 98267 that character is associated with the presence of additional ridges on M<sub>3</sub>. A similar analysis can be carried out for the remaining morphological characters of the lower and upper teeth.

It can be seen from the foregoing that the difference in the morphology of the tooth crowns between these forms is rahter reduced to a difference in the frequency of their occurrence than dependent on the unqualified occurrence of any of the characters mentioned or their whole set.

The scanty material does not permit us to carry out a reliable description of these differences by mathematical methods; nevertheless, all that has been said so far about the dimensions and morphology may be gathered together 

- 1. Big hamster from Petersbuch 1 (Fahlbusch, 1976), Middle Pleistocene,  $T\overline{L}M_{1-3}=10.12$  mm. Anterocone of  $M^1$ , broad and displaced towards the cheek in all these teeth, additional ridges occur on M2 and M3 in large numbers and on a large number of specimens (although not on all of them).
- 2. C. c. runtonensis, Polish localities, Lower Pleistocene,  $\overline{\text{TLM}}_{1-3} = 8.94$ . Anterocone mostly broad and displaced, but not always, for some specimens have the same structure as recent C. c. cricetus, all kinds of intermediate forms being met with. Additional ridges on M2 and M3 occur in smaller numbers and in a smaller number of specimens than they do in the hamster from Petersbuch 1. They occur more frequently on M3.
- 3. C. c. cricetus from the successive phases of the Würm in Poland (Sąspowska Zachodnia Cave Pradel, 1981b, supplemented with unpublished data from other Ojców caves)  $T\overline{L}M_{1-3} = 8.52$  mm. C. c. cricetus, recent, Poland, discussed in present paper,  $T\overline{L}M_{1-3} = 8.12$  mm. The differences in the frequencies of the discussed characters between these populations are so slight that they may be treated together. The anterocone of  $M^1$  in nearly all these teeth is not very broad and not displaced or only slightly displaced. Such picture of  $M^1$  as in the hamster from Petersbuch 1 was observed in one fossil specimen, MF/1663/162, and in a recent specimen, M/5534/79. Additional ridges hardly ever occur on M2 (sometimes very delicate between the posterior cusps) and are relatively frequent on M3, but delicate and less numerous than in the population from Petersbuch 1. However, they occur always and in all specimens during the growth of the tooth, right before its full development.

The comparison above shows that the occurrence of the characters under discussion increases in proportion to the size of the dentition, irrespective of the time represented by the material. And so we must take it that the appearance of these characters depends on the same gene complex that is responsible for the increase in the length of the tooth-row or on another one but linked to it.

# The origin of the recent C. cricetus

The successive stages of the evolution of the recent *Cricetidae* have already been considered (e. g. Fahlbusch, 1967, 1969, 1976; Frendenthal, 1967). Here, I should like to present my opinions on the final stages of this evolution.

Remains of hamsters numbered in the genus Cricetus are encountered in localities as old as the Villafranchian. That transition period may be variously

included, either in the Pliocene or in the Pleistocene. The view that the Villafranchian is an initial phase of the Pleistocene and that it is sharply demarcated from the Pliocene seems better grounded. I think that the description of Cricetus vulgaris runtonensis (vulgaris = frumentarius = cricetus) from Forest Bed by NEWTON (1909) as an unquestionable member of the Pliocene fauna is a stratigraphic mistake. We are here probably concerned with a younger material deposited in a Pliocene bed. A similar phenomenon was observed in several Polish localities, e. g. numerous admixtures of the Pleistocene fauna, even from the Günz-Mindel interglacial, at Rebielice Królewskie I, referred on the whole to the Upper Pliocene (Kowalski, 1977). The teeth of Allocricetus bursae and Cricetus c. runtonensis found here (FAHLBUSCH, 1969). should be regarded just as such an admixture. Having taken the foregoing into consideration, we may state that the genus Cricetus, in a form much resembling the modern species, appears at Polish localities as late as the Villafranchian. Only transition forms, provisionally designated Cricetus sp. 1, sp. 2, and sp. 3 (FAHLBUSCH, 1969), occurred in the Pliocene.

And so the hamster, whose precursor was one of the above-mentioned Pliocene forms, probably Cricetus sp. 1, appeared in Europe in the period of a fauna exchange on the Pliocene-Villafranchian boundary. That new species was characterized by very great individual variation. The picture, obtained by us, showing the occurrence of the groups of bigger and smaller hamsters, with various frequencies of certain morphological characters of the dentition, suggests the existence of different species. This is so, because particular excavations represent local populations distant one from another in time and space. The biology of the hamster, its partiality for inhabiting open areas and its great requirements concerning soil favour the formation of these populations. For this reason the range of occurrence of the hamster is not continuous now and certainly it was not continuous in the past either. It is made up of isolated populations. This picture is static. In course of fairly long time the environment underwent changes, the ranges merged and the genes were exchanged. In this sense panmixia remained characteristic of the hamster's population.

In studying various materials of *Cricetus* sp., I found that in all their forms, both fossil and recent, a certain characteristic distribution of points appears in the L/W graph of their molars. It presents itself so that most of the points are situated close to a centre, but at the same time there happen less numerous points displaced (even rather considerably) upwards of that region. We do not seem to be concerned here with specimens belonging to two subspecies. This is rather a phenomenon of the incessantly repeating births of specimens decidedly bigger than the average and these individuals constantly occur in small numbers and illustrate a great genetic diversity persisting in populations. This may be connected with the occurrence of defined recessive alleles in a homozygous arrangement or with the existence of genes of deficient penetration and expression. To be sure, a whole complex of different genes and their alleles which determine the changes in the size of body and dentition is here involved.

In accordance with the Hardy-Weinberg ratio the frequency of genes in a panmictic population remains constant and this is why the occurrence of those "over-sized" specimens in the population kept on more or less constant level. The fact that it did not come to the isolation and fixation of that big form of hamsters as long as the hamster population remained approximate to a penmictic one indicates that the set of genes occurring in them was rather indifferent in respect of adaptation, since otherwise it would have undergone a rapid elimination or fixation owing to selection pressure. It must have happened in a manner different from the disjunctive selection that this set of genes was in the position to become the only one present in the population and thereby to give rise to a homogeneous form of big hamsters (such as at Petersbuch 1).

This may have been realized in two way: 1. the occurrence of Sewall WRIGHT's effect, i. e. genetic drift and 2. the occurrence of the ancestor's effect. Both cases are based on the restriction of the number of specimens and their isolation from the main range of the species. Each period of cooling created conditions that enhanced the chances of the occurrence of one of the processes mentioned. It was most probable in the period of the greatest Pleistocene glaciation (Mindel II). The northern boundary of the distribution was then formed by small refuges of small numbers of specimens. And it was just there and at that time that it may have come to the isolation and fixation of the big form of hamsters which formed the population from Petersbuch 1 referred to the Middle Pleistocene. It may well be also that the relationships lying at the basis of BERGMAN's rule participated in that process. What became of that big form of hamsters, after the natural boundaries, dividing it from the original population, had disappeared and their ranges had merged, remains an open question. Several possibilities must be taken into account: 1. the population of those big hamsters differed genetically to such a degree that crossing did not occur and it became extinct owing to changes in the climate and to competition from smaller hamsters; 2. crossing took place, to be sure, but a) the embryos died out, b) the offspring were born infertile or c) although the specimens born were fertile, their vitality was reduced, which eventually led to the extinction of the less abundant population of big hamsters, and 3. the changes of the genotype were so small that as a result of crossing the big hamsters "dissolved" again in the original population. I consider the third of the possibilities listed above to be most probable, although it is impossible to prove the rightness of this opinion at present.

# Evolutionary conclusion

All the big Pleistocene forms of hamsters, regardless of the fact whether they are ranked as species or subspecies, make up a common line leading to the recent hamster *Cricetus cricetus* (differentiated into three subspecies). They probably descend from the Pliocene form provisionally referred to as *Cricetus* sp. 1 (Fahlbusch, 1969). The big form of the hamster from Petersbuch 1 constitutes only a slight deviation from that line and it may well be that it

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was re-united with it, unless the process of its speciation had been completed. The differences observed in the size and morphology of the dentition are due to the great genetic variation persisting in different populations. It may be assumed, using MAC ARTHUR and WILSON'S nomenclature, that these hamsters evolve according to the "r" type.

#### Taxonomic-nomenclatural conclusion

Irrespective of the fact whether Voldetich (1880) justly designated the hamster from Vypustek "major" or not, that name should not have been applied for the giant Middle-Pleistocene hamster from Petersbuch 1, because it had already been used in combinations with the generic name *Cricetus*.

The hamster population from Petersbuch 1 fully deserves to have its distinctness emphasized by a new name, at least, at the rank of subspecies, but it cannot and should not be identified with the hamster from Vypustek in any case.

Translated into English by Jerzy Zawadzki

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STRESZCZENIE

Praca przedstawia zmienność metryczną i morfologiczną uzębienia dużego chomika współcześnie występującego w stanie dzikim na terenie Polski. Jest to podgatunek nominatywny  $C.\ e.\ ericetus$  (L. 1758).

W pracy przedstawiono też stwierdzone zakresy zmienności condylobazalnej długości czaszki (Cb) i długości gałęzi żuchw (Lmd) w poszczególnych klasach wiekowych.

W oparciu o uzyskane wyniki pomiarów Cb zaproponowano zmianę dotychczas podawanych w kluczach wartości tego wymiaru z 44—51.4 mm na 32.9— —58.7 mm.

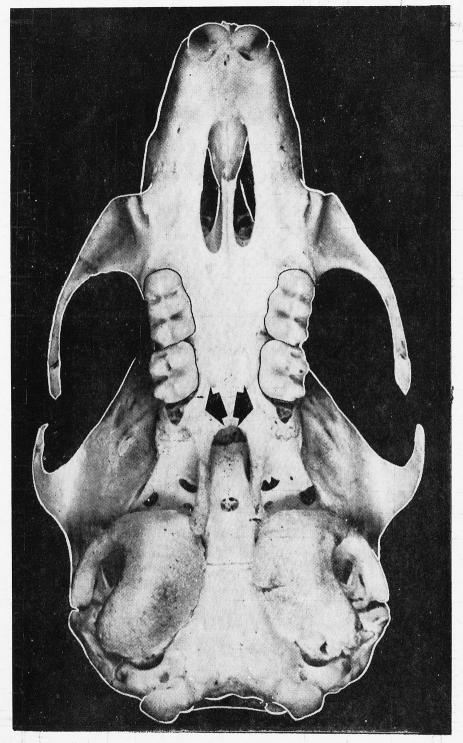
Z przeprowadzonych porównań wymiarów i morfologii trzonowców chomika współczesnego z danymi literaturowymi, omawiającymi formy kopalne, autor wnioskuje, że chomiki plejstoceńskie wywodzą się z formy *Cricetus* sp. 1 sensu FAHLBUSCH 1969 i stanowią, bez względu na to czy obecnie przypisujemy im

rangę gatunku czy też podgatunku, jeden wspólny pień prowadzący do obecnego (zróżnicowanego na trzy podgatunki) chomika *C. cricetus*.

Stwierdzono, że, zgodnie z nomenklaturą Mac Arthura i Wilsona (1967), chomiki ewoluują według typu "r".

Autor wyciąga też wniosek systematyczno-nomenklaturowy stwierdzając, że kopalna forma olbrzymiego chomika z Petersbuch 1 (*Cricetus major* sensu FAHLBUSCH 1976) w pełni zasługuje na uznanie jej odrębności, przez nadanie jej nowej nazwy na szczeblu co najmniej podgatunkowym, ale do określania jej nie może być stosowana nazwa "major". Nazwa ta była już użyta przez Voldkicha (1880) dla okazu chomika z Vypustek, a który to okaz — jak autor wykazuje — ma niewiele wspólnego z olbrzymią formą chomika środkowoplejstoceńskiego z Petersbuch 1.

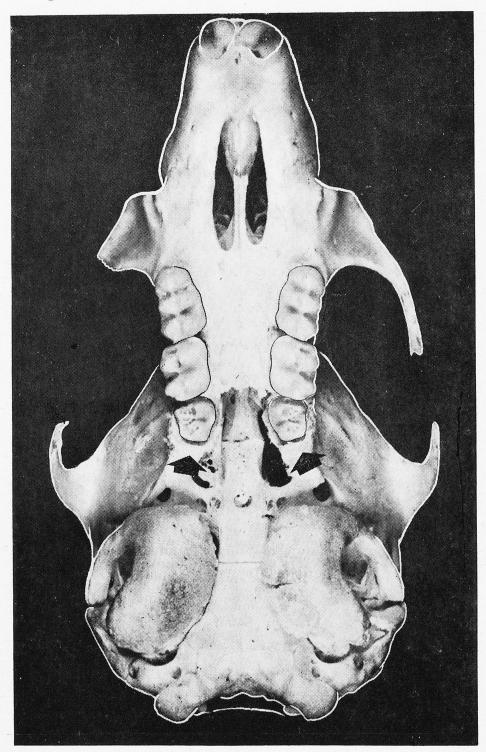
Redaktor pracy: dr A. Nadachowski



A. Pradel

Plate III

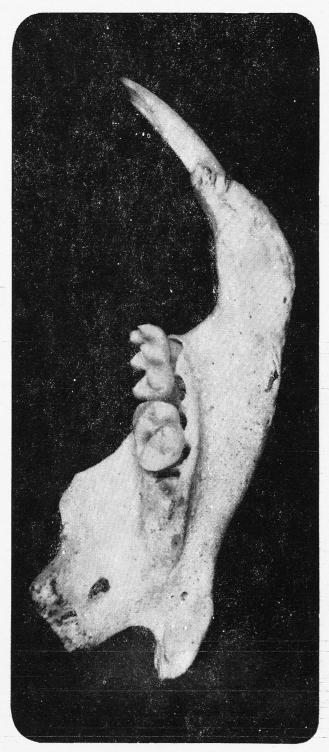
Specimen M/977/59 with M<sup>3</sup> exposed



A. Pradel

## Plate IV

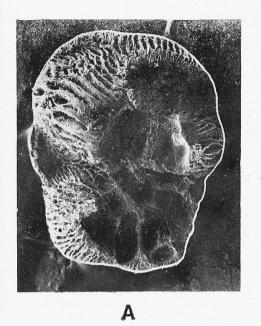
Left mandible of M/977/59 before the exposure of  $M_3$ 

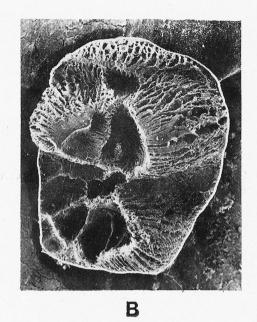


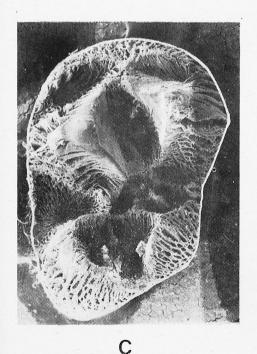
A. Pradel

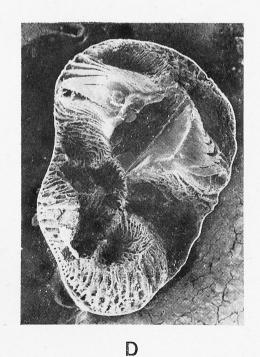
## Plate V

Third molars of specimen M/977/59, (Phot. SEM). A — left M³, B — right M³, C — left M₃, D — right M₃





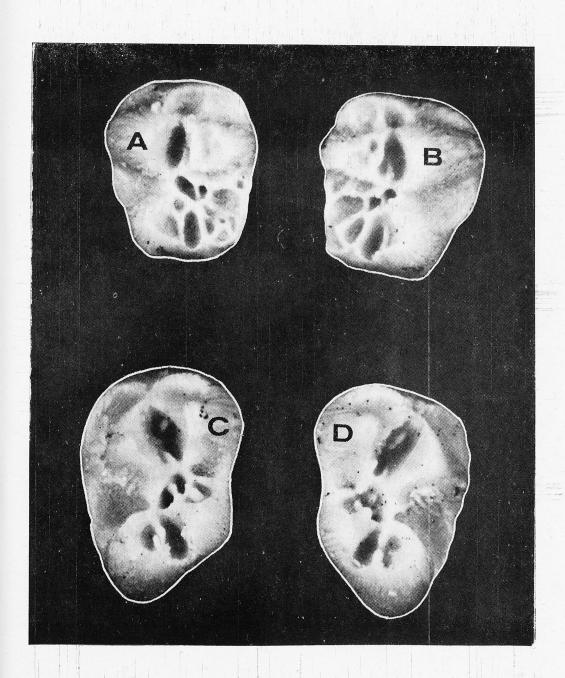




A. Pradel

### Plate VI

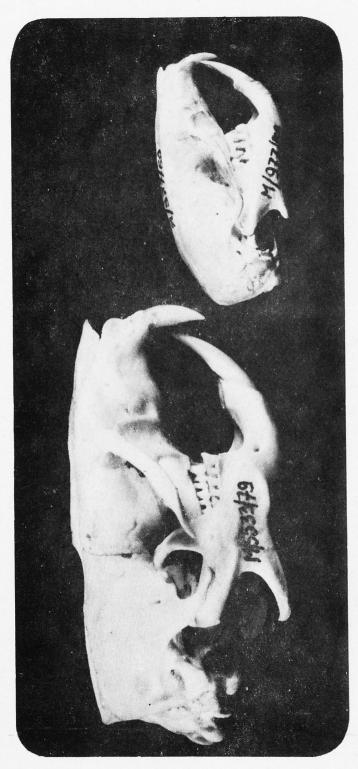
Third molars of specimen M/577/59, macroscopic photographs. A — left M³, B — right M³, C — left M₃, D — right M₃



A. Pradel

## Plate VII

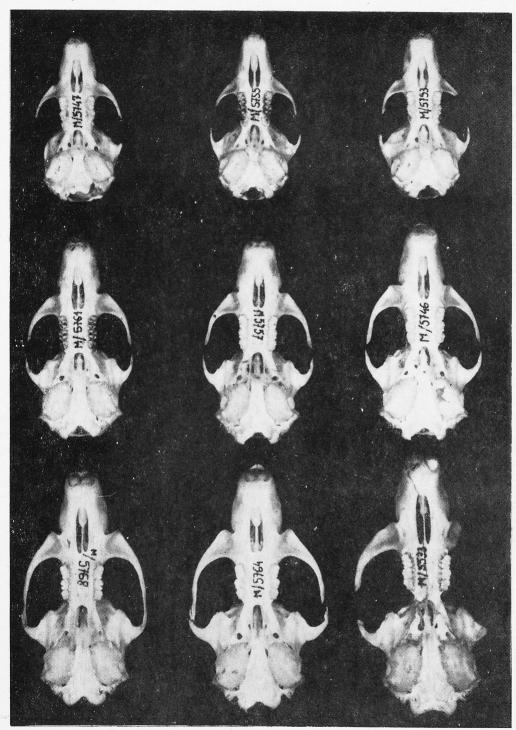
Age variation of skulls of modern  $C.\ c.\ cricetus.$  Senile specimen (sen.) — M/5533/79; juvenile specimen (juv.) — M/977/59



A. Pradel

### Plate VIII

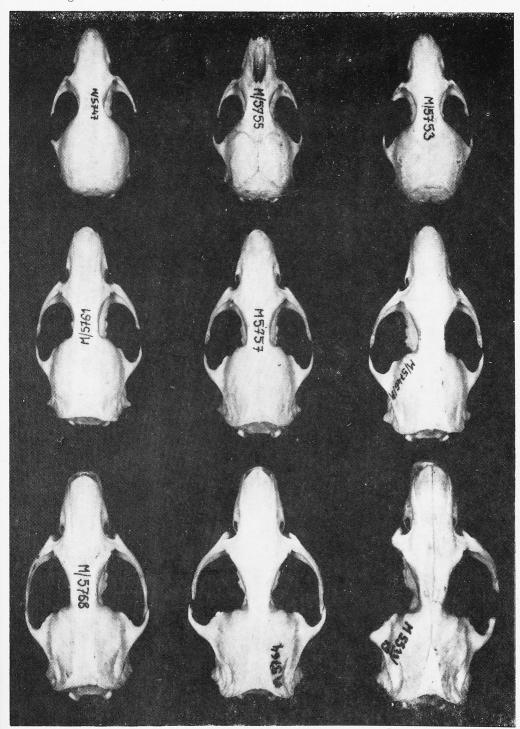
Age variation of skulls of C. c. cricetus. In rows: Subadult specimens (subad.): M/5747/81, M/5755/81, M/5753/81 Adult specimens (ad.): M/5761/81, M/5757/81, M/5746/81 Senile specimens (sen.): M/5768/81, M/5764/81, M/5533/79



A. Pradel

# Plate IX

The same skulls as in Pl. VIII seen from above



A. Pradel

#### Plate X

Skulls of modern C. c. cricetus compared with the drawing of C. c. major sensu Woldkich 1880.

A — C.~c.~cricetus, Książnice Wielkie, M/5534/79 Cb = 57.4 mm LM<sup>1-3</sup>: right 7.47, left 7.77 mm

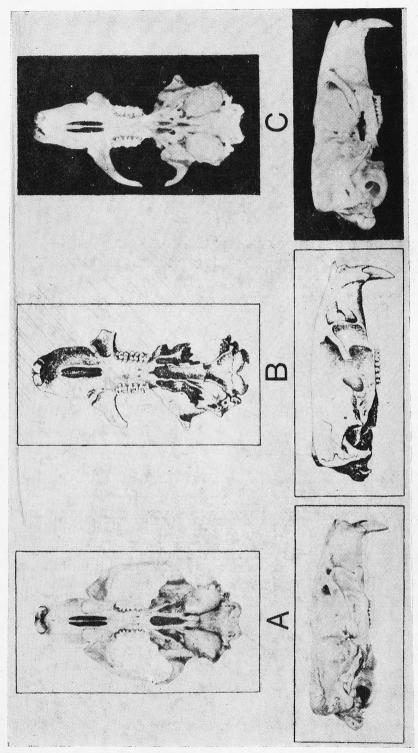
 $LM_{1-3}$ : lacking, left 7.80 mm

B — C. cricetus major sensu Woldkich 1880. Specimen from Vypustek, Reproduction made from a xerocopy of Woldkich's paper, Pl. II, Figs. 22 and 23. Woldkich's data: Cb = 56 mm, length of upper alveoli — 9.5 mm, length of lower alveoli — 10 mm.

C — C. c. cricetus, Borusowa, M/5533/79

 $\label{eq:Cb} \mbox{Cb} \, = \, 58.7 \mbox{ mm} \mbox{ LM$^{1-3}$: right } \, 7.89 \mbox{ mm}, \, \mbox{left } \, 8.03 \mbox{ mm} \\ \mbox{ LM$_{1-3}$: right } \, 8.62 \mbox{ mm}, \, \mbox{left } \, 8.65 \mbox{ mm}$ 

(Note. Not to scale.)



A. Pradel