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Biometrical Remarks on the Hamster Cricetulus migratorius (PALLAS 1773) (Rodentia, Mammalia) from Krak des Chevaliers (Syria)

[Pls. XII—XV, 5 text-figures]

Uwagi biometryczne o chomiku Cricetulus migratorius (PALLAS 1773) (Rodentia, Mammalia) z Krak des Chevaliers (Syria)

Abstract. A morphological analysis of the dentition of the hamster from Syria is given. Various measurements and anatomical details are compared and discussed with other data concerning this species. Problems of individual variability are considered from taxonomical point of view.

I. INTRODUCTION

In the systematic group designated as the tribe Cricetini (true hamsters). made up of 6 genera, the genus Cricetulus MILNE-EDWARDS 1867 includes the greatest number of species (Anderson and Jons, 1976). The area of distribution of this genus extends wide from south-eastern Europe through Asia Minor as far as southern Siberia. Its species inhabit dry open areas, cultivated fields and the edges of deserts (WALKER, 1964). The group Cricetulus is marked by great variation in morphology and body size. Cricetulus triton de Winton 1899 is the largest and Cricetulus migratorius PALLAS 1773 one of the smaller forms (Ellerman and Morrison-Scott, 1951). The range of this last species covers a large area, from which, after the synonymizing of at least 23 names, 13 subspecies have been described (ELLERMAN and Morrison-Scott, 1951). According to these authors, the approximate distribution of this species is, as follows: Greece, southern USSR from Ukraine as far north as Zhitomir, Kiev, Chernigov, Kaluga, Riazan, Gorki, Kazan and Ufa, Caucassus, Russian Turkestan, south-western Siberia, Afghanistan, Iran, Asia Minor, Syria, Palestine, Baluchistan, Kashmir and Chinese Turkestan. Such a wide distribution of the species, with the simultaneous existence of a large number of more or less well-documented subspecies, permits the supposition that here we are concerned with at most several subspecies of great morphological variation brought about by environmental conditions. Circetulus migratorius is the only member of the genus Cricetulus in the territory of Syria.

The finding of pellets with bones of *Cricetulus migratorius*, which most probably come nearest *Cricetulus migratorius cinerascens* Wagner 1848, in Syria made it possible to obtain a number of biometrical data, both characterizing individual variation and particularly useful in palaeozoological comparisons. For this reason the review of such data is particularly expedient and it is the objective of the present paper.

II. MATERIAL

I had at my disposal numerous remains of small hamsters obtained from owls' pellets found in the ruins of the eastle Krak des Chevaliers in Syria (the original Arabic name was Kalaat el Hosn). The situation of the locality is shown in Fig. 1. The nesting of owls did not occur before the settlement existing on the premises of the eastle till about 1926 had been abandoned. Thus, the pellets collected had been accumulating there for about 50 years. Thanks to the warm and dry climate of Syria, free from the destructive action of water and frost, the material was in a very good state of preservation.

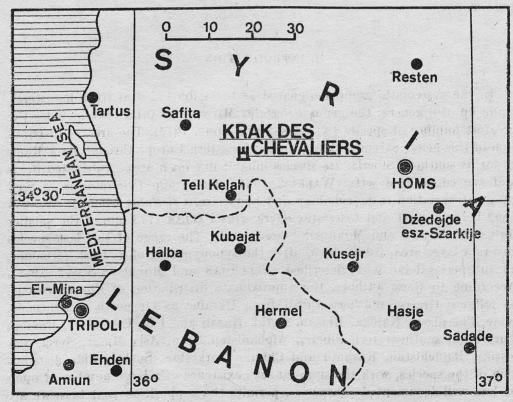


Fig. 1. The situation of the castle ruins at Krak des Chevaliers in Syria

The pellets were found and determined by Prof. Dr. K. Kowalski of the Polish Academy of Sciences in Cracow in 1977, to whom I wish to thank heartily for giving me access to them and thus making this study possible. I also owe thanks to Dr. I. Sych for his critical remarks during my work.

The material is stored in the collection of the Pol. Acad. of Scs. in Cracow under No. M/5532/79 and is divided, for technical reasons, into three groups:

I - right mandibles and teeth,

II - left mandibles and teeth,

III - right and left maxillae.

Within each of these groups each specimen is marked, e. g. A-13, B-5, etc. In further parts of this paper the designations will be given in an abbreviated form, e. g. I/A-12, III/C-19. Such a symbol, denoting, e. g., a mandible, may include three teeth, but as they are teeth of one row (i. e. M₁, M₂ and M₃), there is no room for mistakes.

The material consists of 10 large fragments of skulls with complete upper dentition and single maxillae and mandibles also, for the most part, with complete rows of molars.

The detailed data are as follows:

Maxillae	with full M1-M3 row	Mandibles with full M ₁ —M ₃ row
right	27	right 51
left	31	left 49
total	58	total 100

The remaing maxillae (39 specimens) and mandibles (50) had incomplete dentition. There were besides 10 detached upper teeth and 22 lower teeth. There were altogether 653 teeth, their composition being as follows:

Upper teeth

	Right	Left	Total
M¹	45	54	99
M²	40	48	88
M ⁸	29	37	66
			253

Lower teeth

	Right	Left	Total
M ₁	74	78	152
M ₂	65	73	138
M ₃	54	56	110
			400

The differences between the total number of specimens given above and their number used in statistical calculations resulted from the fact that some specimens were damaged.

The material contained 150 (72 left and 78 right) mandibles. A hundred of them had full rows of molars in their alveoli (group B), in the remaining ones (50) these rows of teeth were incomplete or missing (group A). At the time of measurement it was noted that

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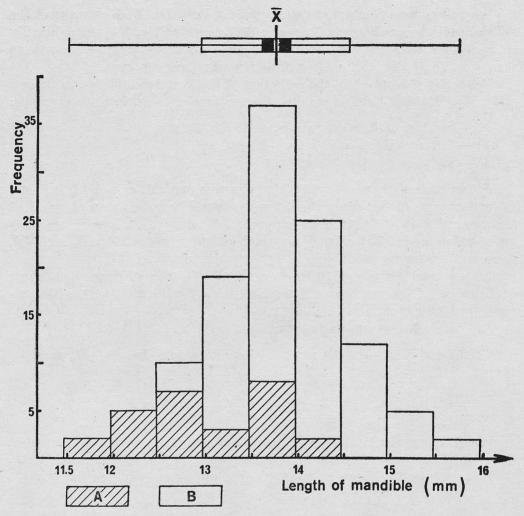


Fig. 2. Lengths of mandibles of *Cricetulus migratiorius* from Syria. A — group of mandibles with incomplete dentition; B — mandibles with complete tooth-row. More details are given at the end of the sections "Material" and "Results"

- 1. the mandibles with complete dentition (B) were, as a rule, larger than those of group A (Fig. 2) and
- 2. the mandibles suitable for measuring (undamaged alveolus of incisor and whole condylar process) were more numerous in the group of mandibles with the whole set of molars than in that with an incomplete row. Out of the 100 mandibles with the complete M₁—M₃ row, 90 were fit to be measured, whereas out of the 50 remaining mandibles only 27 were not damaged.

This may be explained by the fact that the smaller mandibles, frequently devoid of teeth, came from very young animals. A thin young bone is more readily crushed and the teeth with their roots not very well developed come

out also more readily. This is, in addition, corroborated by the appearance of the cups on single teeth preserved in these smaller mandibles; they are not worn at all.

III. METHOD

Measurements were taken using a measuring microscope with a cross-stage to an accuracy of 0.01 mm. The following dimensions were measured:

- length of tooth crown, L

- anterior width of crown at the protocone-paracone height in the upper teeth and, correspondingly, at the protoconid-paraconid height in the lower teeth,

- posterior width at the hypocone-metacone height in the upper teeth Wh and at the hypoconid-metaconid height in the lower teeth,

LM1-3 — length of upper row of molars,

 LM_{1-3} — length of lower row of molars,

- condylar length of mandible, measured between the posterior edge of the incisor alveolus and the end of the condylar process.

The measurements obtained were used to trace L/W graphs and worked out by the basic statistical methods. The following symbols are applied in the description of the tables summarizing the results of measurements and calculations:

N - sample size,

min-max - observation range,

X - arithmetic mean,

Sx - standard error of mean,

SD - standard deviation,

- standard error of SD, SSD

- coefficient of variation, V

Sv - standard error of V.

The length of mandibles was measured from the supero-postero-medial margin of the incisor alveolus to the end of the condylar process, using a calliper, to an accuracy of 0.05 mm.

The results obtained from calculations and given in this paper are exact to the fourth significant figure so that they can be used in calculations for

their comparison with the data for other populations.

The additionally introduced symbols, LM1+2+3 and LM1+2+3, denote the

sums of lengths of particular upper and lower teeth, respectively.

At first, the material used in analyses was divided into right and left teeth, but eventually this division was given up, because they showed no differences either in morphology or in measurements.

Morphology of dentition

M¹. The outline of these teeth shows visible depressions at the height of the reëntrants. They are distinct on the lingual side, being deformed by a deflected enamel fold on the labial margin of the tooth.

The anterocone is big, broad and divided into two summits, which are equal to primary cusps in size. Its anterior side, slightly flattened and mildly sloping to the front, is smooth in most cases but sometimes covered with fine grooves (Pl. XII, A, B).

All the cusps are slightly inclined backwards.

The anterior mure (Reig 1977), formed by the union of the ridges descending backwards from the tops of the anterocone and two anterior ridges of the proto-and paracones, is well developed in the form of the letter X. In some cases this pattern is disturbed by the reduction of the ridge coming down from the lingual top of the anterocone or the anterior ridge of the paracone (e. g. III/B-8, 9, 10, II/C-1, III/D-4) (PL. XII, B) the reduction of the latter occurring more often.

The median mure, formed by the fusion of the posterior ridges of the protoand paracones with anterior ridges of the hypo- and metacones, is also X-shaped. Here, too, the pattern may undergo a deformation, but in this case owing to the reduction of the anterior ridge of the metacone.

The posteroloph, formed by the extension of the posterior ridge of the hypocone, is poorly developed and more often than not comes on to the posterior wall of the metacone.

The teeth are four-rooted. The anterior root is robust, oval in cross-section and situated under the anterocone. It is markedly bent forward. The other three roots, smaller and round in cross-section, are placed under the proto-, hypo- and metacones.

M². Its cusps are well developed and slightly inclined to the rear. The median mure is well developed and, as in M¹, its pattern may undergo deformations owing to the reduction of the anterior ridge of the metacone.

The anterior cingulum is well developed, especially on the labial side of the tooth. It frequently passes on to the lingual side, where however it is less conspicuous. When it is missing here, the front of the tooth is formed by the anterior wall of the protocone. The posterior cingulum is present but poorly seen.

It is a four-rooted tooth, the roots being round in section.

M³. The morphology of these teeth is very variable. Out of the 4 primary cusp, the protocone is dominant, the other three undergo a reduction to a greater or smaller degree (Pl. XII). The metacone often disappears completely. The anterior cingulum is well developed on the labial side (anteriorly to the paracone); it sometimes passes on to the anterolingual side, forming a distinct furrow on the anterior wall of the protocone. However, in most cases the anterior side of the tooth is formed by the smooth wall of the protocone. The

region of the hypo- and metacones, including the posteroloph, is developed very variously and may have some additional elements.

M³ is a two- or three-rooted tooth. If there are three roots, the anterior two, slender and round in section, are placed under the proto- and paracones, and the third one, posterior, is robust and oval in section. The anterior roots may be found, and so may the anterior roots of M², in which this is a rarer phenomenon, resulting in its three-rootedness, a robust anterior root and two posterior ones. The four-rooted M² and three-rooted M³ in the same row are the commonest occurrence, but other combinations can also be seen: four-rooted M² and two-rooted M³ and two-rooted M³. The combination of three-rooted M² and three-rooted M³ was not observed. If M² has three roots, M³ of the same row is always two-rooted. The occurrence of two-rootedness in M³ seems to be the prerequisite of the fusion of the anterior roots of M² (Pl. XIII).

M₁. The anteroconid is divided in two by a depression, varying in depth but always very well seen. Its two summits lie as a rule at the same height in relation to the long axis of the tooth, at various distances from each other; they may be very near each other (e. g. I/B-6, I/B-23) or relatively wide apart (e. g. I/A-17) (Pl. XIV). The lingual (internal) cusp of the enteroconid is sometimes pushed forward in relation to the other one (e. g. II/A-15). For the most part, two ridges descend from these summits to join the anterior ridges of the proto- and metaconids and form the centrally situated anterior murid. The ridge coming down from the lingual (internal) top of the anteroconid undergoes a reduction varying in degree (Fig. 3). In several cases this ridge is lacking



Fig. 3. Schematic representations of the anterior region of right M_1 , showing the range of possible morphological changes here encountered. The drawings represent no particular specimens. The appearance of additional furrows on the front wall of the tooth is not dependent on the degree of reduction of the ridge coming off from the lingual cusp of the anteroconid (anterolingual conulid of Reig, 1977)

utterly (e. g. I/A-3, II/A-6) and then the contour of this region resembles that of the posteromedial region of the metaconid: the deep arcuate furrow that divides the cusps of the anteroconid passes fluently into the anterior lingual reëntrant (Pl. XIV, B). The anterior wall of the anteroconid is mostly smooth, but often some additional irregularities, varying in degree, appear on it (Pl. XIV A). This unevenness seems to be formed by a kind of ridges corresponding to the ridges of the other primary cusps. There may be a distinct arched hillock connecting the two tops of the anteroconid anteriorly, but most frequently there is a single small ridge directed downwards and towards the middle

of the tooth axis, on the front side of the lingual (internal) top of the anteroconid (e. g. II/B-5, 16, 17, II/C-3, 4, 9, 16, 17 etc.).

The other cusps are inclined forward. The meta- and entoconids have no posterior ridges. There is a depression in the outline of these teeth at the height of the reëntrants and in some teeth it is masked by an enamel fold which arises on the margin of the crown and closes the reëntrant.

On several teeth there is a small ridge, as if the posterior arm of the entoconid, which crosses the posterior lingual reentrant and reaches the posterior eingulum (e. g. II/C-15, II/B-49).

The median murid is formed by the fusion of the posterior ridge of the protoconid and the anterior ridges of the ento- and hypoconids. The posterior ridge of the hypoconid passes into the well developed posterolophid, which frequently comes on to the posteroexternal wall of the entoconid. M_1 has two roots, an anterior, round in section, and a posterior, oval; both are directed vertically downwards.

M₂. All the four primary cusps are well developed, slightly inclined forward. The distinctly marked anterior cingulum goes off from the union of the anterior ridges of the proto- and metaconids. The anterior lingual reëntrant, which runs in a half-circle between the protoconid and metaconid, is sometimes parted by a small ridge (e. g. II/C-12, II/A-2) that starts at the posterior wall of the metaconid and reaches the median murid, made up of the posterior ridge of the protoconid and the anterior ridges of the hypo- and entoconids. The posterior ridge of the hypoconid passes into the well-developed posterolophid, which sometimes comes on to the posterior wall of the entoconid (e. g. II/B-17, II /B-3).

As in M_1 , there are depressions in the outline of the tooth at the height of the reëntrants, and here, too, they are masked by a ridge formed on the margin of the crown.

M₂ has two roots. The anterior root, round in section, runs vertically downwards and the posterior one, oval and sturdier, is arcuately bent towards the external side of the mandible.

M₃. The morphology of this tooth is very variable. Three cusps, the proto-, meta- and hypoconids, are always well developed, whereas the entoconid undergoes a reduction to a various degree. Sometimes it is hardly discernible (e. g. II/B-13).

The anterior eingulum is distinct on the front wall of the tooth. The anterior wall of the metaconid may be smooth, falling steeply downwards, or with a distinct additional ridge, which is the extension of the anterior eingulum towards the lingual side of the tooth.

The greatest variation characterizes the manner in which the posterior ridge of the protoconid joins the anterior ridges of the hypo- and entoconids. There may be a union here, like that in the corresponding regions of M_1 and M_2 , or no union at all. The posterior ridge of the protoconid very often extends for the whole length of the lingual reëntrant as far as the lingual margin of

the tooth, forming the distinct mesolophid. Additional ridges may also appear. It may be stated that among the 110 teeth examined there were not two teeth with an identical pattern.

M₃ is two-rooted. The anterior root is fine and strongly flattened, the po-

sterior one oval and bent backwards.

Linear dimensions

The results of measurements taken directly on particular molars are shown in an L/W graph, Fig. 4 and those concerning whole tooth-rows are given in Fig. 5.

The results of basic statistical calculations are summarized in Table I A, B and C. Parts A and B concern single teeth, while the calculations in which

whole tooth-rows are dealt with are presented in part C.

The mean values of the lengths of the upper and lower tooth-rows given in part B differ hardly by 0.122 mm, nevertheless, subjected to Student's t test, they appear to be significant even at the level of p = 0.0995. The upper tooth-row is decidedly shorter than the lower one. This is also visible in Fig. 4.

The use of the "greatest width" of tooth is generally no problem. It is its posterior width (Wb) in M1 and the anterior width (Wt) in M2 and M3. As regards M2, Wb is the greatest width in 11.7 per cent of the specimens, Wb equals Wr also in 11.7 per cent, while in the remaining specimens (76.6 per cent) Wr is the greater. In the L/W graph the points for M2 represent W1. The differences between W_f and the actual greatest width of tooth — which is sometimes W_b are small. This is illustrated by a comparison of the data from the section presenting W₁ for M₂ in Table IA with the data in Table IB, which gives the value of Wmax for this tooth. In order to calculate the value of Wmax, out of the pair Wr and Wb the greater value was always used for particular teeth. As can be seen, the observation range underwent a small rise and extension and the mean value of the width increased only by 0.002 mm.

Similar relationships were also checked for the other molars. The results of this analysis are given in Table II. In addition to the demonstration that the differences between Wb and Wf in particular kinds of teeth are incidental and resemble a normal distribution, this comparison may be of purely practical importance. For in comparisons of different populations, the shifting of the remainder W_f — W_b in relation to $W_f = W_b$ may suggest the existence of differences between these populations. As regards fossil materials, the application of such a test for populations derived from different periods can

demonstrate certain evolutionary tendencies.

Correlations between particular tooth dimensions were also examined. It was known that such correlations exist. The problem was discussed at length, among other authors, by Kurtén (1953), Sych (1966) and Gould and Gar-WOOD (1969). Here, I was concerned only with the height level of correlations of particular pairs of dimensions. The results are as follows:

Correlation between:

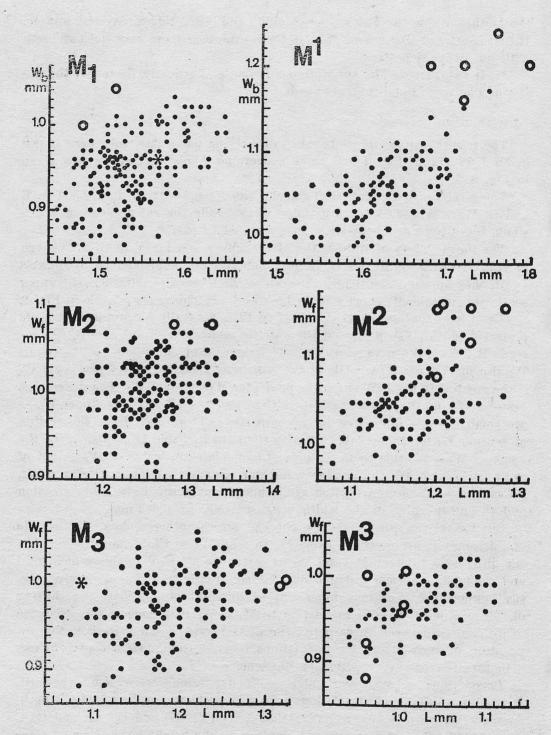


Fig. 4. Length-width graph of molars of *Cricetulus migratorius*. • — population from Krak des Chevaliers (present species), o — data given by Storch (1974) for the specimens from Bastam (subfossil), * — the specimen described by Storch (1974) as *Cricetine* n. gen., n. sp.

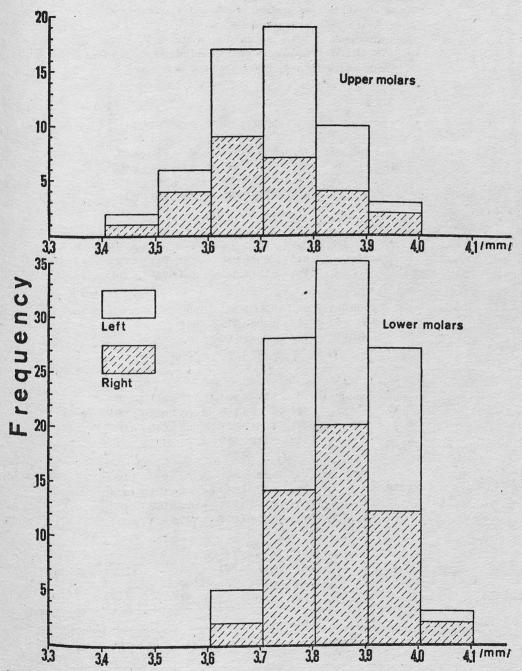


Fig. 5. Lengths of tooth-rows in the population of the small hamster Cricetulus migratorius from Krak des Chevaliers

Fundamental statistical magnitudes describing the linear parameters of molars of *Cricetulus migratorius* from Krak des Chevaliers. A — length and width of successive molars; B — the greatest width of M₂, the pair W_f and W_b was always used in calculations; C — length of tooth-row. All measurements in mm

1		1		
	A	L	$\mathbf{W_f}$	Wb
	N	150	152	152
	min-max	1.45 —1.65	o.73 —o.93	0.85 —1.03
M ₁	$\bar{x} \pm S_{\bar{x}}$	1.537 ± 0.004	0.843 ± 0.003	0.945 ± 0.003
	SD +SSD	0.046 ± 0.003	0.039 ± 0.002	0.042 ± 0.002
	$V \pm S_V$	3.015 ± 0.174	4.575 ± 0.262	4.405 ± 0.253
	N	138	136	138
	min-max	1.17 —1.35	o.91 —1.08	o.88 —1.12
M _a	x +S;	1.254 ± 0.003	1.006 ± 0.003	0.981 ± 0.004
	SD +SSD	0.040 ± 0.002	0.036 ± 0.002	0.043 ± 0.003
	V ±Sv	3.173 ± 0.191	3.545 ± 0.215	4.335 ± 0.261
	N	- 110	110	
	min-max	1.06 —1.30	0.88 -1.06	
M _a		1.186 ± 0.005		
		0.054 ± 0.004		
	$V \pm S_V$	4.594 ± 0.309	4.088 ± 0.276	
	N	97	96	97
	min-max	1.49 —1.78	o.90 —1.11	o.98 —1.20
M¹				1.056 ± 0.004
				0.040 ± 0.003
	V ±Sv	3.376 ± 0.242	4.099 ± 0.296	3.761 ± 0.270
-	N	87	87	88
	min-max	1.03 —1.28	0.99 —1.15	o.90 —1.05
M ²	$\bar{x} \pm S_{\bar{x}}$		1.049 ± 0.003	0.971 ± 0.004
	SD ±SSD	0.044 ± 0.003	0.032 ± 0.002	0.037 ± 0.003
	V ±Sv	3.742 ± 0.284	3.074 ± 0.233	3.824 ± 0.288
	N	66	66	
	min-max	0.94 —1.11	0.88 —1.02	
M ⁸	$\frac{1}{x} \pm S_{x}$	1.021 ± 0.006	0.963 ± 0.004	
	SD ±SSD	0.046 ± 0.004		
	V +Sv	4.527 ± 0.394	3.263 + 0.284	

	В	W _{max} (W _f or W _b)
M ₂	$ \begin{array}{c c} N \\ \min\text{-max} \\ \overline{x} & \pm S\overline{x} \\ SD \pm S_{SD} \\ V & \pm S_{V} \end{array} $	$\begin{array}{c} 138 \\ \text{o.92} \ -1.12 \\ 1.008 \pm \text{o.003} \\ \text{o.036} \pm \text{o.002} \\ 3.602 \pm \text{o.217} \end{array}$

1	C	L _{M1-3}	L _M 1-3
	N	98	57
		3.61 —4.01	
10.00	$\bar{x} \pm S_{\bar{x}}$	3.846 ± 0.010	3.724 ± 0.015
	SD±S _{SD}	0.097 ± 0.007	o.115±0.011
	$v \pm s_v$	2.526 ± 0.180	3.077 ± 0.288

Differences between the widths Wf and Wb in particular molars of Cricetulus migratorius from Syria

		XX	XXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXX XXX XXXX	x			
FREQUENCY	XX XXXXX XXXXXXXX XXXXXXXXXXXXXXXXXXXX	XXX	X	XX XX XXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	M	4 M
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$W_t - W_b$ (mm)	0.14 0.13 0.12 0.11 0.09 W _t > W _b 0.08 0.07 0.06 0.05 0.05 0.05 0.03	$W_f = W_b$ 0.00	—0.01 —0.02	0.03	—0.06 —0.07 —0.07	$W_f < W_b$ —0.09 —0.10	-0.11 -0.12	-0.15 -0.15	-0.16	—0.17 —c.18

	L -Wr	r = 0.38	1		L -Wr	r = 0.63
M¹	L -Wb			$\mathbf{M_1}$	$L - W_b$	r = 0.52
	W_f — W_b	r = 0.80			W_f — W_b	r = 0.72
	L -Wr	r = 0.43			L -Wr	r = 0.29
M^2	L -W _b	r = 0.49		M_2	$L - W_b$	r = 0.34
	W_f — W_b	r = 0.61		1 1	W_f — W_b	r = 0.68
$\overline{\mathbf{M}^3}$	L -Wf	r = 0.55		M_3	L —Wr	r = 0.48

After the rather differentiated values of the coefficient of variation between particular dimensions of teeth, suggesting the independence of the factors determining the length and width of individual teeth, had been found, an attempt was made to check the hypothesis that the length of the toothrows is dependent upon the genes responsible for the skull length. This hypothesis was checked by computing the correlation between LM₁₋₃ and the length of the mandibles in which these rows are set. A total of 90 mandibles were examined, in which both their length and the length of the rows of the molars set in them could be measured. A low correlation, if not more, was expected. The result was however different. The values obtained are given below:

With the lengths of mandibles, in cm, given along the abscissa and LM_{1-3} , also in cm, along the ordinate, the regression curves

r = 0.0956

$$Y = 3.6499 + 0.0142 X$$

X = 11.4938+0.6439 Y
The mandibles of juveniles, in which the complete lack of such correlations could be expected, were not included in these calculations (they were mandibles with incomplete tooth-rows or broken ones. — See above).

In order to calculate the mean length of the mandibles, measurements were taken on 117 specimens. The results are represented on Fig. 2 and given below:

Lengths of mandibles (in mm)

Group	A .	В	A+B
N	27	90	117
min-max	11.50—14.00	12.50—15.75	11.50—15.75
X	12.94	13.99	13.74
SD	0.76	0.65	0.80
V	5.85	4.64	5.85

A slight rise in the number of mandibles of class A (cf. the section on material and Fig. 2) in the 13.5—13.99 mm length group and their occurrence in the 14.0—14.49 mm lengthgroup are due to the fact that the mandibles of old specimens also lose their teeth, though somewhat more rarely.

The highest values of correlation were found between the anterior and posterior widths of crown in each of the teeth. The lowest values of correlation occur between the length of the tooth and its anterior width. It may therefore be stated that the length: width ratio is less constant in these teeth than the ratio of the two widths. The unexpected lack of correlation between the length of tooth-row and that of mandible might be explained by the fact that the length of tooth-row is influenced, in addition to genotype, also by external factors (temperature, amount of food, etc.), but only for a short time. Once the teeth have developed, they cannot grow any more. On the other hand, the mandibles keep their capacity to grow in a later period. The improvement in living conditions of an individual on those in the first period, in which the length of its tooth-row was determined, may effect a greater growth of the mandible or, vice versa, a sudden deterioration of the initially favourable conditions causes that it is somewhat smaller. It is impossible directly to compare the sizes of changes that the mandibles and tooth-rows undergo. A comparison of the observation ranges in relation to x may indicate the size of variation. Thus, the length of the rows of molars was, min. = 3.61, max. = 4.01. with $\bar{x} = 3.8457$. The range of changes was 0.4 mm, which makes 10.40 per cent of the mean value, whereas the range of changes noted in the lengths of the mandibles was 1) 15.75-11.5 = 4.25 mm or as much as 30.92 per cent of the mean (n = 117), which is $\bar{x} = 13.7440$ mm, from all the mandibles, i. e. those with a complete and incomplete row of molars and 2) for the mandibles with full tooth-rows (n = 90), where the minimum is 12.5 mm and the maximum 15.75 mm with $\bar{x} = 13.9855$ mm, the percentage is 23.24.

This indicates that the variation in the lengths of mandibles is 2—3 times as large as that in the lengths of tooth-rows.

The degree of correlation of the dimensions, i. e. both those of particular teeth and the length of tooth-rows, with the length of mandible is, in general, rather low. In keeping with the studies made by Gould and Garwood (1969) the degree of morphological integration of the rows of molars might be regarded as not very high. This would evidence that the phenomenon of stabilizing selection may be excluded here in favour of a fairly great tolerance persisting in the population as regards morphology.

One of the parameters that describe the relationships between the successive teeth of a row is the index which defines the mutual proportions of the lengths of these teeth, calculated in relation to one of them (in the *Cricetidae* we assume the length of the second molar as unity). For instance, FAHLBUSCH (1976) used this index and treated it as one of the criteria that permitted the determination of the teeth of Pleistocene hamsters found at Petersbuch as *Cricetus major* Woldfich.

This index of proportion of particular teeth in a row (in relation to LM2 = 1)

can be calculated direct from the mean lengths of successive molars, which in our case were as follows (exact figures):

$LM^1 \bar{x} = 1.6228$	(N = 97)	$LM_1 \ \overline{x} = 1.5368$	(N=150)
$LM^2 \bar{x} = 1.1679$	(N=87)	$LM_2 \ \bar{x} = 1.2536$	(N = 138)
$LM^3 \bar{x} = 1.0214$	(N = 66)	$LM_3 \overline{x} = 1.1860$	(N = 110)

Dividing M1 and M3 by M2, we obtain the following values of the index (round figures):

 $LM^{1}:LM^{2}:LM^{3}$ $LM_{1}:LM_{2}:LM_{3}$ 1.39:1:0.87 1.23:1:0.95

These values suggest a very strong relationship, but, as we know, they were calculated on the basis of means. The index obtained by this method provides no information about the size of changes that the values contained in it may undergo, neither does it make it possible to check whether the index calculated in a similar way for another population, e. g. for the upper teeth — 1.34:1:0.95—reflects significant differences or lies within the limits of variation.

If these indices are to be comparable and are to indicate the existing relationships fully, they must be calculated in a different way.

In the Syrian material under study there were 57 upper and 98 lower complete tooth-rows. The ratios in question were calculated for each of these tooth-rows separately and it was only then that their mean values were calculated on the basis of the data obtained. This procedure permitted the more precise determination of the magnitudes contained in this index and the size of changes that they may undergo. At the same time it was possible to calculate the fundamental statistical magnitudes (e. g. SD), which permit their mathematical comparison with other similarly calculated indices. The index thus obtained for the upper teeth is

		LM^1	:	LM^2	:	LM^3
in round	figures	1.39	:	1	:	0.87
N		57				57
Min-max	1.2683	3 ± 1.4771			0.7	966 ± 0.9464
$\bar{x}\pm S_{X}$	1.3899	± 0.0057			0.8	711 ± 0.0045
$\mathrm{SD}\pm\mathrm{S}_{\mathtt{SD}}$	0.0429	0.0040			0.0	336 ± 0.0031
$v_{\pm s_v}$	3.08	5 ± 0.289			3.	863 ± 0.362

Correspondingly for the lower teeth

		LM_1	:	LM_2	:	LM_3	
in round	figures	1.22	:	. 1	:	0.95	

N	98	98
Min-max	1.1527 ± 1.3008	0.8615 ± 1.0484
$\bar{x} \pm S_{x}$	1.2248±0.0034	0.9482 ± 0.0039
$SD \pm S_{SD}$	0.0339 ± 0.0024	0.0394 ± 0.0028
$v_{\pm s_v}$	2.771 ± 0.198	4.155 ± 0.296

These data are presented according to the scheme that can be encountered in various publications. For my part, I think that it suffices to give the number of specimens (N), the mean (\bar{x}) , the standard deviation (SD) and the coefficient of variation (V), whereas the presentation of standard errors is less important. If \bar{x} , SD and N are given, everybody who needs the values of standard errors can calculate them on condition that the magnitudes mentioned are given to a greater accuracy than 0.01, which is important inasmuch as we shall be able to use them in further calculation, e. g. Student's t test, with more confidence.

The data concerning Cricetulus migratorius described by Storch (1974) are plotted in the length-width diagram (Fig. 3, large open circlets). These specimens come from Bastam (85 km south of Maku in north-western Azerbaydzan, Iran), most probably from 2200—700 B. C. Their distribution shows that either this is a very different population (e. g. the situation of the points for M¹ in the upper range of the population from Krak des Chevaliers and M³ in its lower range. The same is true of M₁, 2, 3. Such a distribution would be acceptable, if they were detached teeth, but the data refer to the teeth from 5 complete and 1 incomplete maxillae and 2 complete mandibles) or that the data are not exact. As I shall point out further, here we are concerned with this latter alternative.

A comparison of the dimensions of the Middle Pleistocene remains of *C. mi-gratorius* from Khios I. in the Aegean Sea described by Storch (1975) shows that all their dimensions are greater than those of the modern specimens from Syria (Table III). This is probably the effect of great morphological variation in the populations of the genus *Cricetus*, which variation has already been discussed in the introduction and in the text of this paper.

Another parameter describing a row of molars may be the percentage index which shows the relationship between the sum of the lengths of particular teeth in the row (LM1+2+3) and the length of the tooth-row (LM1-3). As far as hamsters are concerned, the sum of the lengths of particular teeth is always greater than the length of the tooth-row made up of these teeth. This is due to the overlap of successive teeth.

In the material from Krak des Chevaliers the length of the upper toothrow forms 97.4 per cent of the sum of the lengths of particular teeth. It is the mean from the results of calculations concerning 57 rows. In particular cases this value ranges from 96.0 to 98.5 per cent with V=0.68. As regards the lower teeth, this length makes 96.8 per cent for n=98, the range of variation being 94.5 to 98.3 per cent and V=0.96. The difference may seem small. How-

A comparison of the length and width of particular molars and the length of tooth-rows in two populations of *Cricetulus migratorius*. A — data concerning the present-day population from Syria; B — Middle Pleistocene population from Khios I. (after Storch, 1975). Data in mm

	L (N)	Wmax (N)		L (N)	Wmax (N)
M¹ A	1.49—1.78 (97)	0.98—1.20 (97)	M ₁ A B M ₂ A B M ₃ A B	1.45—1.65 (150)	o.85—1.03 (152)
B	1.70—1.90 (20)	1.10—1.20 (20)		1.60—1.80 (20)	1.00—1.10 (20)
M² A	1.03—1.28 (87)	0.99—1.15 (87)		1.17—1.35 (138)	o.92—1.12 (138)
B	1.20—1.40 (20)	1.10—1.20 (20)		1.20—1.40 (20)	1.10—1.20 (20)
M³ A	0.94—1.11 (66)	0.88—1.02 (66)		1.06—1.30 (110)	o.88—1.06 (110)
B	1.00—1.20 (20)	0.90—1.10 (20)		1.30—1.40 (20)	1.00—1.10 (20)

T 36	A 3.61—4.01	(98)
LM1-8	A 3.61—4.01 B 4.30—4.50	(6)

ever, checked with Student's t test, it turns out very significant, even at the confidence level p=0.9995. The overlap is decidedly greater in the lower tooth-row.

This index may be helpful, though not decisive, in making decisions as to the description of a new species or subspecies, but, like the previous one, it should be used only for fairly abundant material. Moreover, it can also be applied for a quick check of the results of own measurements and those given in publications.

As has already been mentioned, a somewhat strange distribution of the points concerning the specimens of *C. migratorius* described by Storch (1974) in relation to the data obtained with the hamsters from Syria was observed in the L/W diagram. Thus the data given by Storch had to be checked and the index just mentioned was used for this purpose. An abridged version of Table 1 from the paper cited (p. 25) is given below:

C. migratorius

Author's calculations

SMF	OZr. Kro.	(Alv)	M¹L	M ² L	M ₃ L	LM ¹⁺²⁺⁸	Percent. index
73/1	4.0	(4.30)	1.76	1.24	1.00	4.00	100
73/2	4.0	(4.35)	1.72	1.20	0.96	3.88	103.09
73/3	4.15	(4.45)	1.72	1.28	1.00	4.00	103.75
73/4	3.95	(4.35)	1.68	1.20	0.96	3.84	102.86
73/5	_	(4.20)		1.20	0.96		_
73/6	4.10	(4.40)	1.80	1.24	1.00	4.04	101.49

^{*} The value of LM^{1+2+3} was calculated using the lengths of particular teeth given by Storch, $LM^{1+2+3} = M^1L + M^2L + M^3L$.

The denotation of the abbreviations used here is given in a paper by Kock, MALEC and STORCH (1972, p. 205):

OZr. (UZr.) = Länge der oberen (unteren) Zahnreihe; Kro. = Kronenmass; Alv. = Alveolenmass; SMF = Sammlungen... Forschungs-Institut Senckenberg, Frankfurt a. M.

The designation OZr.Kro corresponds to the symbol LM¹-³ used in this paper and standing for the length of the crowns of the upper tooth-row. Even if we take into account that the dimensions OZr.Kro were probably given to an accuracy of 0.05 mm and all the lengths of particular teeth to an accuracy of 0.02 mm, as suggested by the exclusive presence of even final digits, it remains an unchanged fact that the data given by that author are not reliable. In nearly all cases the length of the tooth-row is greater than the sum of the lengths of particular teeth of which the row is composed. As has already been said, this disagrees with the relationships observed in the teeth of *C. mi-gratorius*.

In the same paper Storch (1974, p. 26 ff., Fig. on p. 22) describes a mandible to which he proposes to assign the rank of new species or even genus (*Cricetine*, n. gen., n. sp.). He based his diagnosis on the following characters observed in this mandible:

1 — the strongly built angular process, with a crest giving attachment to the medial pterygoid muscle on its internal side;

2 — in side view the anteroconid only slightly protrudes beyond the margin of the root;

3 - narrow but deep-split anteroconid; and

4 — strongly reduced M₃.

In the light of individual variation observed in the population from Krak des Chevaliers, all these characters do not suffice even to erect a new subspecies.

Ad 1 — The angular process is developed to a very various degree, from narrow to broad and spatular. The outline of the angular process of the mandible under discussion (cf. Storch 1974; Fig. 5) lies well within the range of variation of the material from Syria.

ad 2 — The degree to which the anteroconid protrudes beyond the margin of the root is also fairly considerably differentiated, from very low to high. The description "bei seitlicher Betrachtung überragt der Anteroconid die Vorderkante der oralen Wurzel nur geringfügig" corresponds well to many a mandible in my material.

ad 3 — The description of the morpology of teeth includes a detailed description of M_1 . As has been said in it, the anterior region of this tooth is characterized by very great variation. The distance between the summits of the anteroconid, additional furrows on its anterior wall and the depth of its cleft are very variable characters. M_1 represented in Storch's paper cf. 1974; Fig. 8) corresponds perfectly to an average tooth of C. migratorius.

ad 4 — Neither does M₃ shown in the same drawing go beyond the va-

riation range defined in the description of this tooth in *C. migratorius* from Syria. An additional furrow on the front wall of the metaconid and the reduced entoconid are normal occurrences in M₃ of *C. migratorius*. Also the linear measurements lie within the range of variation observed in *C. migratorius* (cf. Fig. 4, in which the measurements LM₁ and LM₃ of the mandible discussed are marked with asterisks).

However, even in this case there is good reason to regard the measurements given by Storch as unreliable. In Table 1 he gives the following measurements of M_3 for *Cricetine*: L=1.08 mm and W=1.00 mm, whereas in drawing 8 on p. 23 the dimensions of this tooth are: L=33 mm and W=25 mm. The L:W ratio for the measurements from Table 1 is 1.08 and in the drawing L:W=1.32. Even if corrections have been made for the fact the tabulated data are given to an accuracy of 0.02 and the changes made are most favourable to the author, i. e. the whole interval (0.02 mm) and not its half, as should be done, has been added to L and substracted from W, the ratio obtained will be 1.1: 0.98 or 1.12 and thus it will deviate too far from the ratio resulting from the drawing.

The only character of the mandible discussed which actually differs from the description of an average mandible of *Cricetulus migratorius* is the presence of a crest on the angular process. Photographs of two left mandibles from Krak des Chevaliers are given in Pl. XVI. In one of them the angular process is narrow and in the other broad and, besides, folded all over. The crest giving attachment to the medial pterygoid muscle is also well developed here, which unfortunately is not shown well enough in the photograph.

Only one of the 150 mandibles of the material from Krak des Chevaliers has such an uneven angular process. In all the other mandibles the angular process is smooth. The teeth set in this mandible (M 5532/99-II/A5) differ in no detail from the description for *Cricetulus migratorius*. The cusps of the anteroconid are wide apart, divided by a depression of medium depth and pushed slightly forward in relation to the anterior edge of the root. M_2 is typical, M_3 has its anteroconid moderately reduced. The posterior ridge of the protoconid of M_3 divides the internal reëntrant into two and eventually ramifies into two smaller ridges by the lingual margin of the tooth.

The measurements do not deviate much from the average ones, either. $LM_{1-3} = 3.77$ mm and then it lies within the interval $LM_{1-3} - SD$.

 $LM_{1+2+3} = 3.88$, or the length of the tooth-row forms 97.2 per cent of the sum of the lengths of the teeth it consists of. Thus, it also comes near the mean which is 96.8 per cent.

Even the ratio of the teeth against M2 little deviate from the average and it is

 M_1 : M_2 : $M_3 = 1.25 : 1 : 0.93$

Consequently, except for the configuration of the surface of the angular process and the foramina for blood-vessels all over the surface, this mandible does not differ from an average mandible of *Cricetulus migratorius*.

Both the mandible from Krak des Chevaliers (M 5532/79-II/A5) and that described by Storch (1974) as Cricetine n. gen., n. sp. must be referred to Cricetulus migratorius. The origin of the changes observed should be explained though. If on the mandible from Bastam only the single crest described had developed and there were no other changes (Fig. 5 in Storch's paper, 1974, does not show this), it may be assumed that 1) it was formed owing to damage to the musculature of the right mandible, as a result of which the left half of the skull had to take over all the work and, in consequence, the region of their attachment was strengthened; 2) it is one of the anomalies often occurring in nature and 3) it is the effect of a pathologic process.

On the other hand, the changes observed in the mandible (M 5532/79-II A5) from Krak des Chevaliers should be treated as resulting from a pathologic

process.

The following conclusions may be made on the basis of the present results: While studying contemporary populations, it is necessary to take measurements other than those conventionally applied by investigators in standardized systematical descriptions. This results from need to acquire data indispensable in their comparison with the data obtainable from palaeozoological materials. It is this very manner of treatment of biometrical data in the present paper, showing a wide range of variation that persist in contemporary populations, that permitted the verification of certain tendencies of investigators to ascribe too great taxonomic importance to slight characters, which leads to a superfluous increase in the number of species described.

Translated into English by Jerzy Zawadzki

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STRESZCZENIE

Praca zawiera szczegółową analizę biometryczno-morfologiczną uzębienia chomika Cricetulus migratorius (PALLAS 1773), opracowaną na materiale pochodzącym ze zrzutek sów na terenie ruin zamku Krak des Chevaliers w Syrii. Autor porównuje zebrane wyniki z danymi dotyczącymi morfologii tego gatunku z materiałów z terenów Iranu i z wyspy Khios I na Morzu Egejskim. Rozważa szczegółowo zagadnienia szczególnie wielkiej zmienności indywidualnej chomików i dyskutuje je szeroko z danymi Storcha. Dochodzi do wniosków, że do badania współczesnych i kopalnych populacji tej grupy ssaków konieczne jest wprowadzenie nowych metod mierzenia materiału oraz że w grupie Cricetinae zbyt wiele taksonomicznej ważności przypisuje się drobnym cechom morfologicznym uzębienia i czaszki, zaniedbując fakt bardzo szerokiej zmienności indywidualnej w obrębie jednej i tej samej populacji, co powoduje opisywanie nowych taksonów w sposób niedostatecznie udokumentowany.

Redaktor pracy: dr hab. L. Sych

Plate XII

Present-day Cricetulus migratorius from Syria. Left upper tooth-rows (Phot. SEM, proportions grievously deformed). A—M 5532/g9—III/D—1. Additional furrows visible on the anterior wall of the anterocone of M¹. B—M 5532/79—III/D—20. Additional elements on the anterior wall of the anterocone. Paracone of M¹ without anterior ridge. Additional elements visible on the edge of the external reëntrants

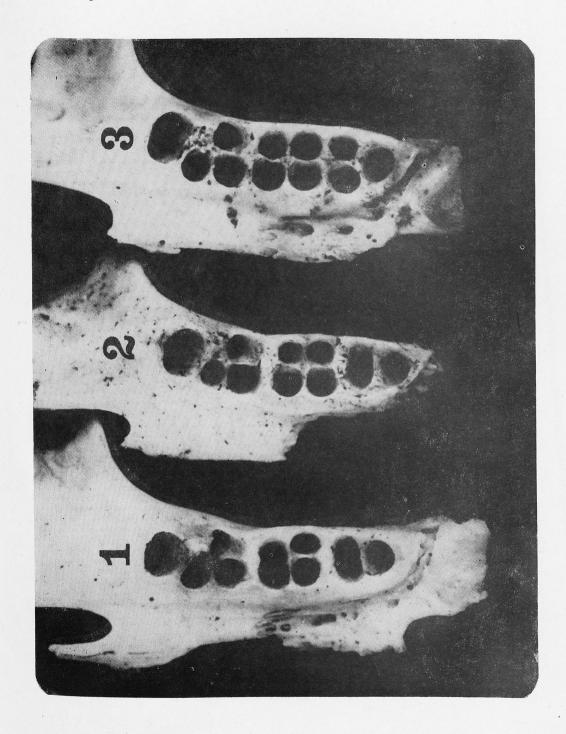


A. Pradel Biometrical...

Plate XIII

Alveoli of the left upper rows of molars of Cricetulus migratorius from Krak des Chevaliers:

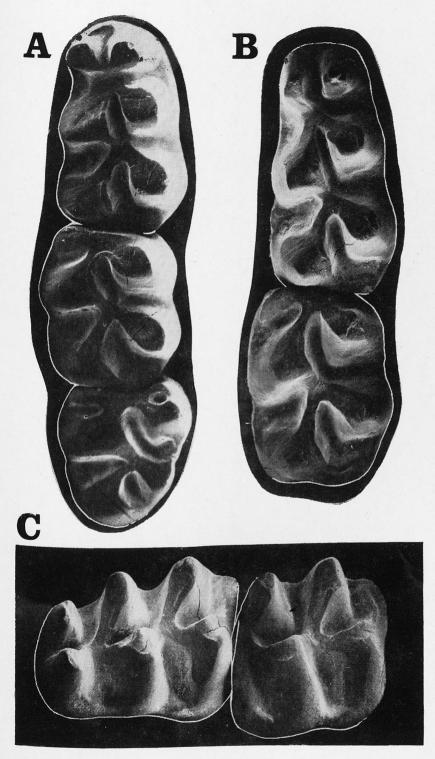
1. M 5532/79—III/D—19, 2. M 5532/79—III/D—12 and 3. M 5532/79—III/D—17. More detailed explanations are given in the morphological description of M³



A. Pradel, Biometrical...

Plate XIV

Contemporary Cricetulus migratorius from Krak des Chevaliers (phot. SEM, proportions grievously deformed). A—M 5532/79—II) A—16. Left lower tooth-row. Additional ridge in the front of M_1 . Two summits of the anteroconid divided by a shallow depression. B, C—M 5532/79—II/A—6. Two views of left lower molars. Anteroconid cleft deep, its lingual cusp anterolingual conulid) void of a ridge



A. Pradel, Biometrical...

Plate XV

Left mandibles of Cricetulus migratorius from Syria. 1 — M 5532/79—II/A—18; 2 — M 532/79—II/A—5



A. Pradel, Biometrical.