Cricetus polgardiensis sp. nov. and *Cricetus kormosi* Schaub, 1930 from the Late Miocene Polgárdi localities (Hungary)

M. Freudenthal & L. Kordos

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The various fossiliferous localities at Polgárdi are described. One of them has yielded a very rich material of a new species of hamsters, *Cricetus polgardiensis*. The phylogenetical relationships of the Polgárdi hamsters are discussed.

M. Freudenthal, Rijksmuseum van Geologie en Mineralogie, P.O. Box 9517, 2300 RA Leiden, The Netherlands; L. Kordos, Hungarian Geological Institute, Népstadion U 14, H 1143 Budapest, Hungary.

Introduction

The Upper Carboniferous crystalline limestone in the vicinity of the village of Polgárdi (Somlyó Hill, 226 m alt.) has been quarried since Roman times. In the contained karst fissures various Upper Miocene vertebrate localities have been found:
Polgárdi 1 – In 1909, when the lower quarry was opened, L. Lóczy sr found fossil mammal bones. These remains were found in the sediment originating from a karstic cave filling (Kormos, 1911; Kretzoi, 1982).

Polgárdi 2 – This locality is generally cited as 'Polgárdi' in the literature. It was a filled-in cave, opened up in the NW part of the quarry in 1910. That same year Kormos carried out two excavation campaigns. This was the first time washing and sieving techniques were used in Hungary in order to obtain fossil vertebrate remains. In the cave, from the sinkhole upwards, he could distinguish five fossiliferous beds (Kormos, 1911, fig. 13):
The lowermost bed (1) was rich in Testudinata.
The second bed (2) contained several *Ictitherium* mandibles.
The next bed (3) was rich in *Hipparion* bones.
Then comes a bed (4) rich in *Gazella* and *Capreolus* remains.
Finally in the uppermost bed (5) bones of small mammals are predominant.

Unfortunately, Kormos did not separate the fossils from these different beds. As far as we can judge now, they all represent the same biostratigraphic unit, i.e. MN unit 13. The first description of the fauna of this locality is by Kormos, 1911. Further contributions are by Kormos, 1913, 1914, 1926; Bolkay, 1913; Fejérváry-Lángh, 1923; Kretzoi, 1942, 1952.

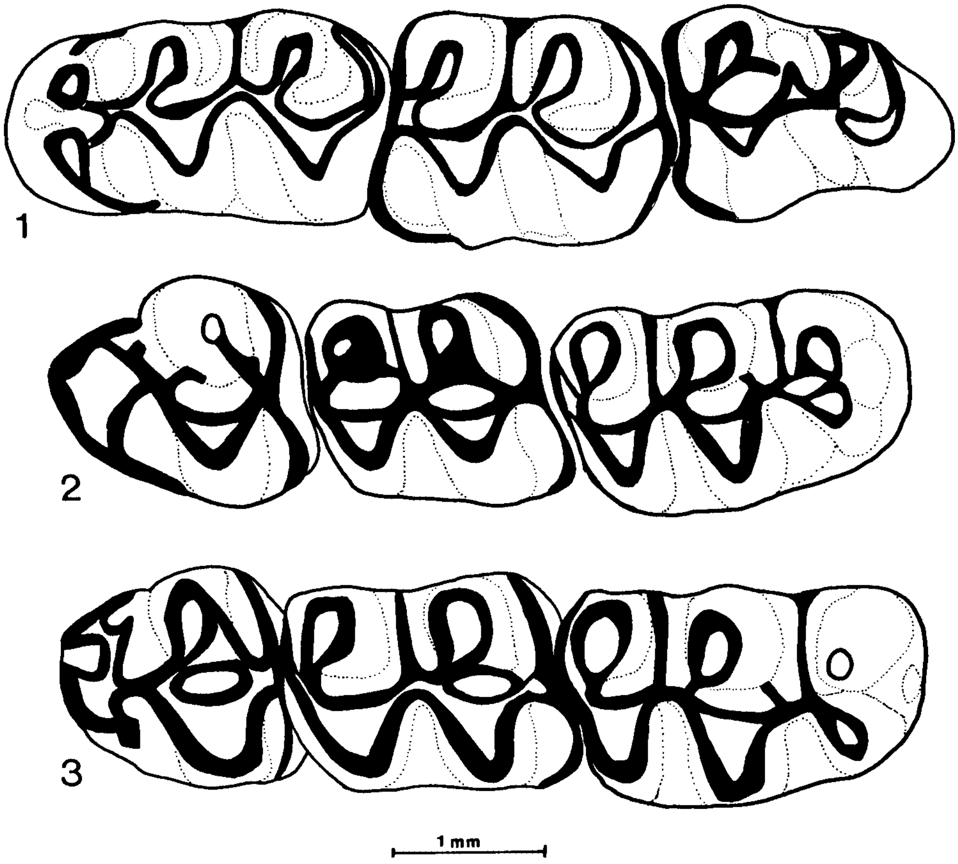

Fig. 1. *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.
1: Holotype, M_1-M_3 sin., V. 14033/Vt.126.
2: Paratype, M^1-M^3 dext., V. 14034.
3: Paratype, M^1-M^3 dext., V. 14035.

Polgárdi 3 – This locality was discovered by the geologist S. Mihály in 1971. It is a strongly cemented bone breccia from a small karst hole in the then working quarry on the SW side of Kószárhegy Hill (226 m) under the top (Mihály, 1975). After a large amount of bone breccia had been collected for the Hungarian Geological Institute, the locality disappeared through quarrying activities in 1971. The matrix is harder than the bone material, and so far only about 50 % of the samples have been processed. The *Cricetus* material from this locality will be discussed in this paper. Mihály, 1975 denotes this locality as No. II, but as from now we will call it Polgárdi 3.

Polgárdi 4 – In 1984, due to quarrying, two richly fossiliferous fissures were found in the southern wall of the quarry, from the base of the quarry up to about five metres above the base. The upper part of the fissures was very narrow and corroded. The discoverers, university students I. Dunkl, S. Józsa, and K. Schlemmer, reported these finds to the Hungarian Geological Institute. The second author, with the help of the discoverers, removed all the sediment (0.6 m^3) from these fissures during the years

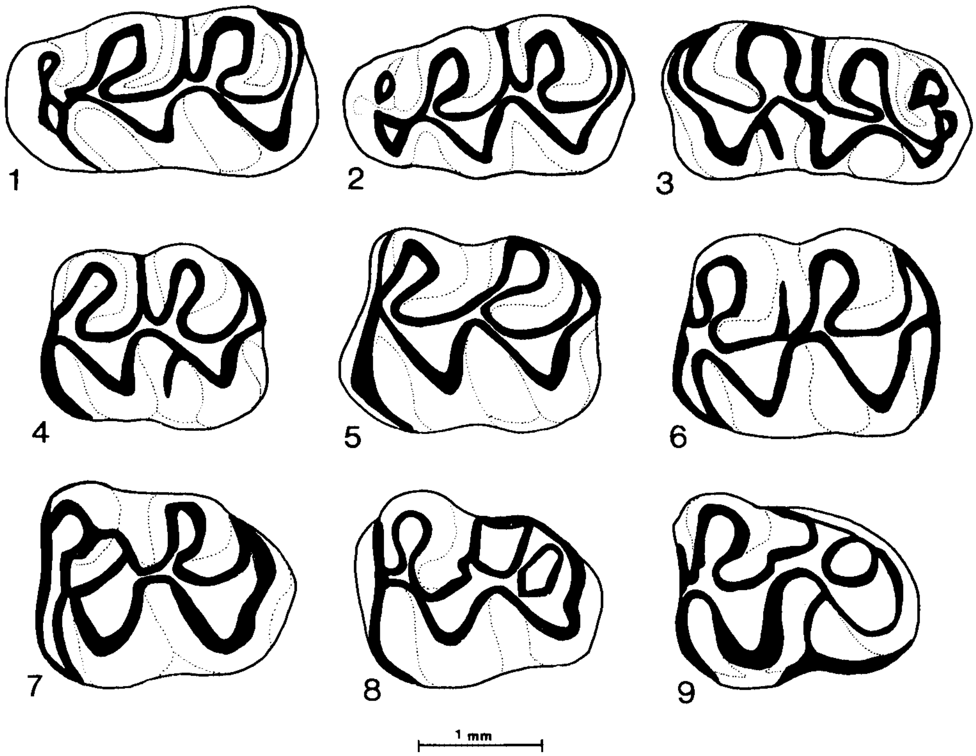

Fig. 2. *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.
1: M_1 sin., V. 14036/8.
2: M_1 sin., V. 14036/17.
3: M_1 dext., V. 14036/66.
4: M_2 sin., V. 14036/6.
5: M_2 sin., V. 14036/16.
6: M_2 sin., V. 14036/19.
7: M_3 sin., V. 14036/20.
8: M_3 sin., V. 14036/27.
9: M_3 sin., V. 14036/29.

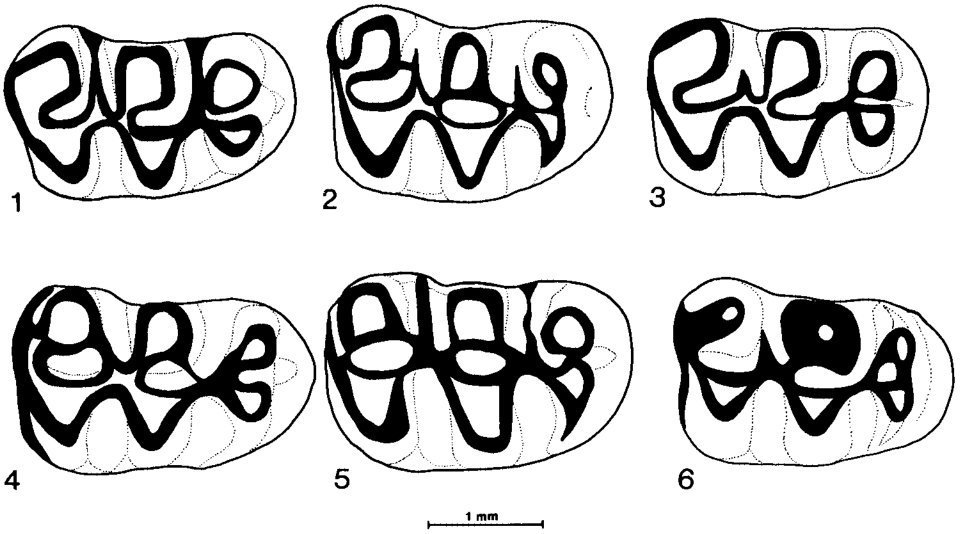

Fig. 3. M^1 of *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.
1: M^1 dext., V. 14037/246.
2: M^1 dext., V. 14037/244 (in maxilla).
3: M^1 dext., V. 14037/52.
4: M^1 dext., V. 14037/28.
5: M^1 dext., V. 14037/172.
6: M^1 dext., V. 14037/194.

1984-1985. This locality, richer in micromammals than any of the previous ones, was given the name Polgárdi 4. In this paper the eastern fissure is called 'Lower', the western one is denominated 'Upper'. Probably these two belong to the same fissure system, and they appear to be of the same age.

Systematic descriptions

CRICETIDAE ROCHEBRUNE, 1883
CRICETINAE ROCHEBRUNE, 1883
Cricetus Leske, 1779

Cricetus polgardiensis sp. nov.
Figs. 1-7.

Holotype — Mandibula sin. with M_1-M_3, coll. Hungarian Geological Institute, no. V. 14033 (Vt. 126), Fig. 1, 1; Fig. 5.
Type-locality — Polgárdi 4, 'Upper', Hungary.
Age — MN unit 13, older than Polgárdi 2, but in the same unit; Pontian in the Eastern Paratethys; Upper Turolian in the Western-European mammal stratigraphy.
Derivatio nominis — After the name of the locality.

Diagnosis — Medium-sized species, smaller than *C. kormosi* Schaub, 1930. M^1 always with subdivided anterocone, anteroconid of M_1 subdivided in 92 %. Mesoloph(id)

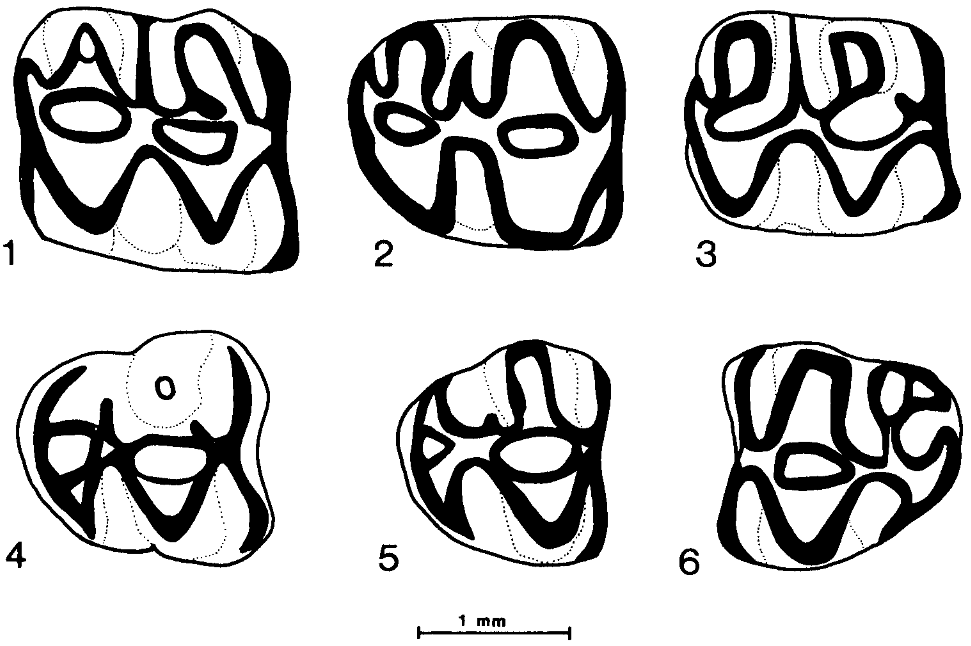

Fig. 4. *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.
1: M^2 dext., V. 14037/244 (in maxilla).
2: M^2 dext., V. 14037/11.
3: M^2 dext., V. 14037/19.
4: M^3 dext., V. 14037/54.
5: M^3 dext., V. 14037/244 (in maxilla).
6: M^3 sin., V. 14037/251.

generally long (M^1: 65 %, M^2: 64 %, M_1: 69 %, M_2: 59 %). The ectomesolophid is present in almost 25 % of the M_1 and M_2. M^1 frequently has a labial spur on the anterolophule, which may be long (56 %), of medium length (24 %), or short (7 %).

Material
Polgárdi 4 'Upper':
252 maxillae with 79 M^1-M^3
189 M^1, 190 M^2, 99 M^3
347 mandibles with 101 M_1-M_3
180 M_1, 260 M_2, 192 M_3
Polgárdi 4 'Lower':
174 maxilla fragments with 24 M^1-M^3
115 M^1, 88 M^2, 39 M^3
195 mandibles with 4 M_1-M_3
106 M_1, 68 M_2, 21 M_3
Polgárdi 3:
5 M^1, 3 M^2, 2 M^3
7 mandibles, 13 M_1, 11 M_2, 2 M_3

Measurements — See Tables 1-5, Figs. 11-15.

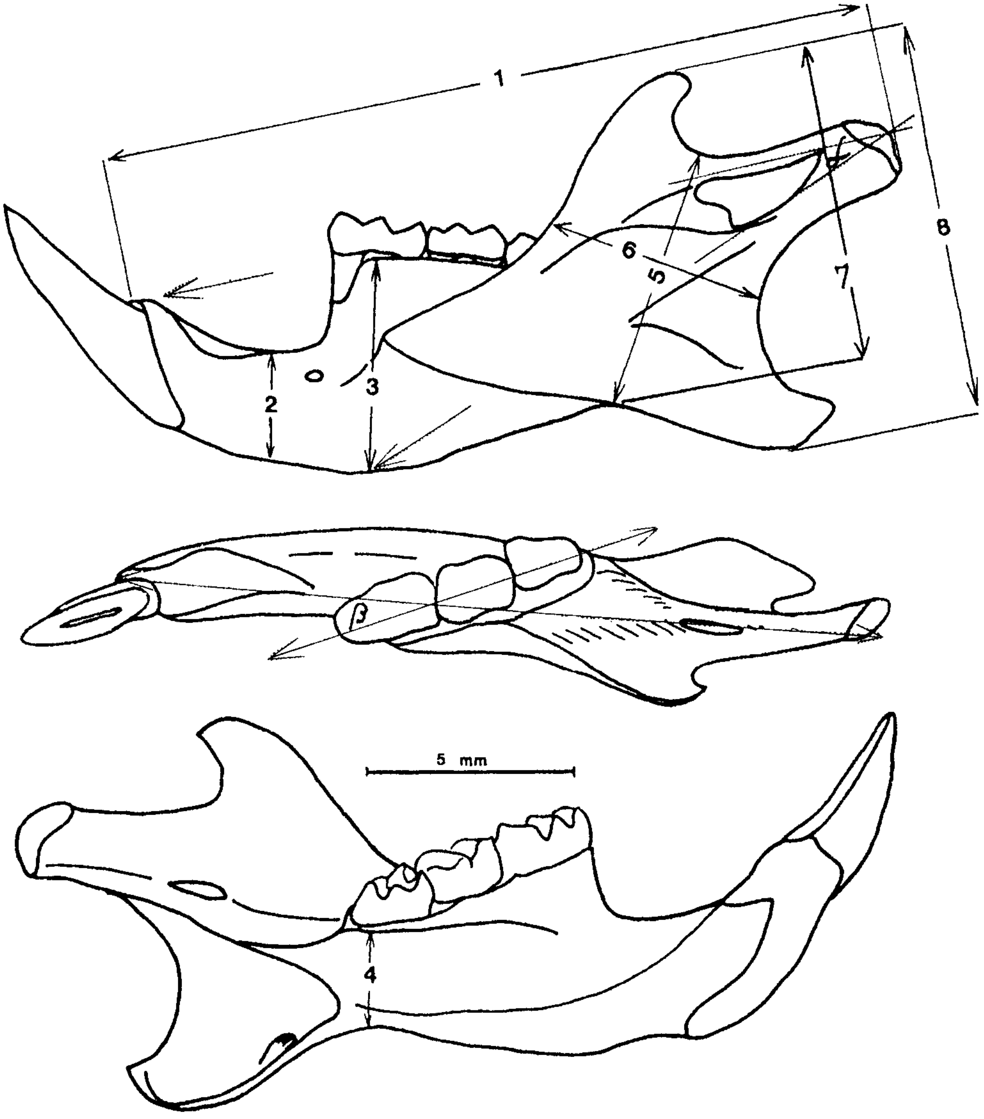

Fig. 5. Holotype mandible of *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper', V. 14033 (Vt.126), with indication of the measured parameters.

Description

M^1 – The outline of the tooth is rectangular. The anterocone is the narrowest part of the tooth; it is always subdivided, either strongly (72 %), or weakly (28 %). The anterolophule is connected to the top of the lingual anterocone cusp. A labial spur on the anterolophule is absent in 13 % of the teeth, it is long in 56 %, of medium length in 24 %, and short in 7 %. The posterior protolophule is always present; in 72 % of the specimens there also is an anterior protolophule, closing a funnel between protocone and paracone. The mesoloph is absent in only 4 % of the cases; in the other ones it is either long (56 %), of medium length (24 %), or short (7 %). In about half the number of

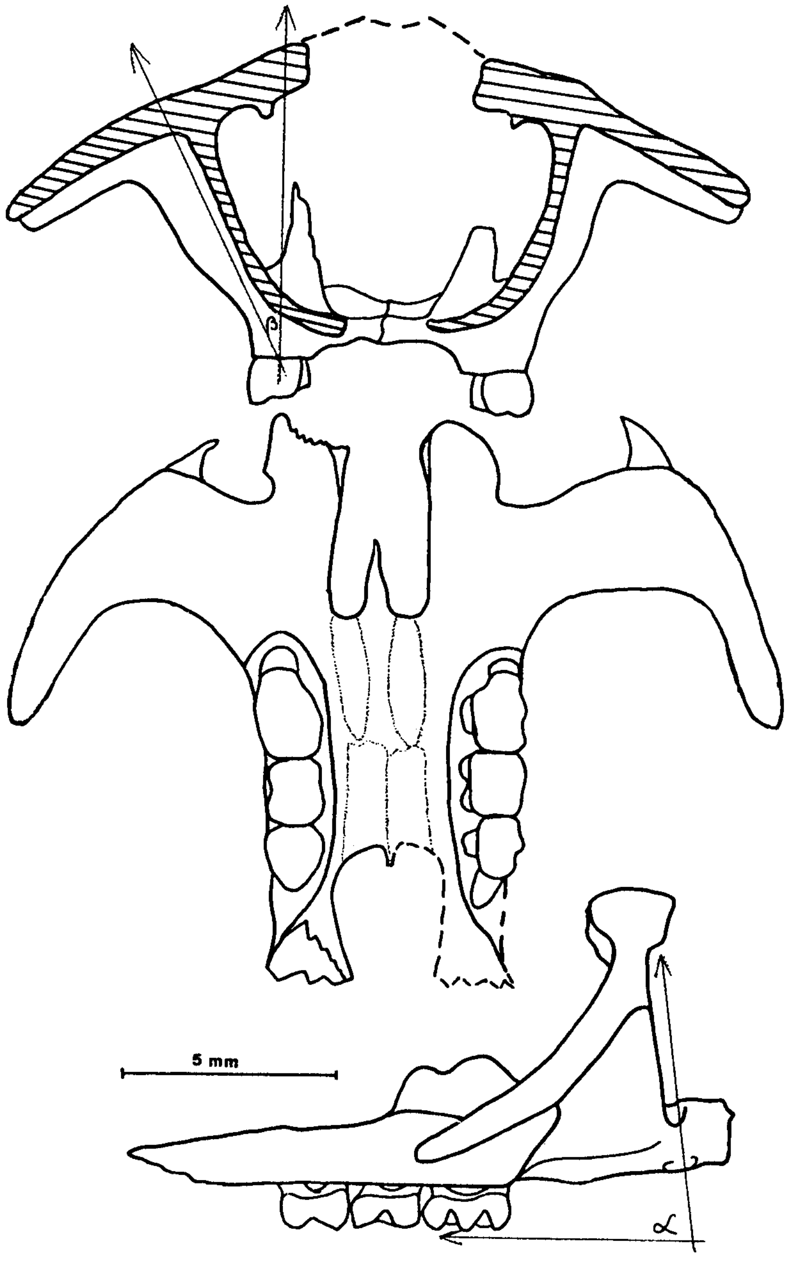

Fig. 6. *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'. Reconstruction of cranium and maxilla, with indication of the measured parameters.

specimens the valley between hypocone and metacone is separated from the sinus by an anterior metalophule.

M^2 — This element is subrectangular, slightly wider anteriorly. The protolophule is double in 99 % of the cases, the metalophule in 76 %, resulting in funnels between

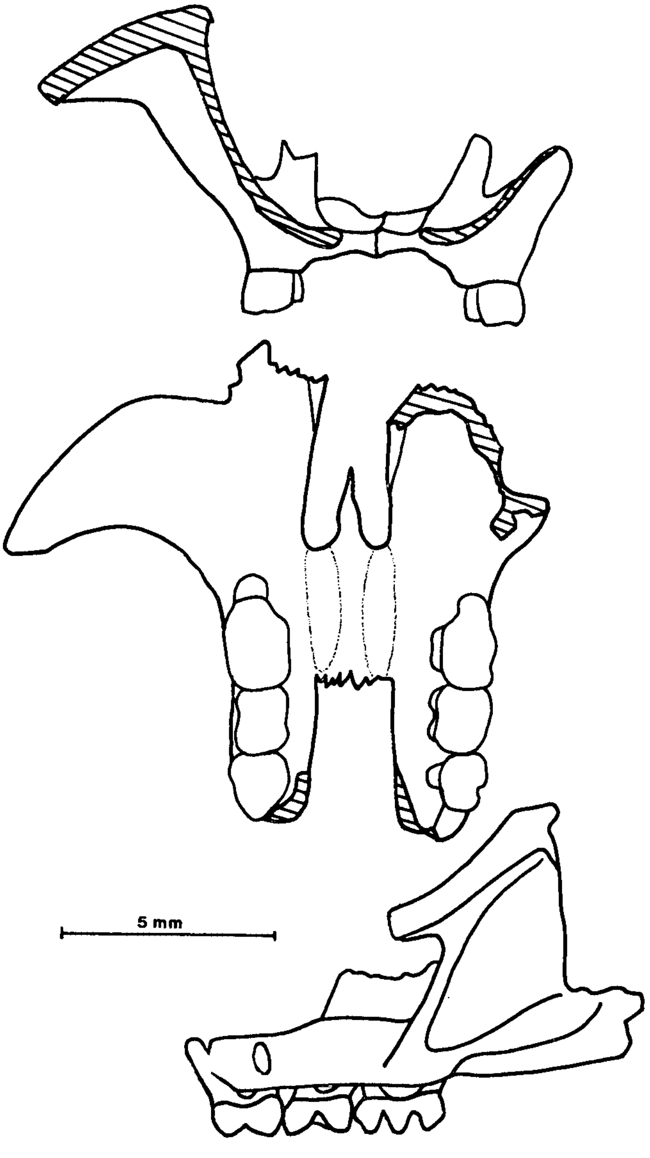

Fig. 7. The best preserved maxilla of *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper', V. 14034.

protocone- paracone and hypocone-metacone respectively. The mesoloph is always present, long (64 %), of medium length (28 %), or short (7 %).

M^3 – The funnel between protocone and paracone is closed in most cases. The mesoloph is absent in 7 %, and of medium length in 41 % of the specimens. In the remainder short and long mesolophs are about equally frequent. The posterior wall of the tooth is generally a smooth connection between hypocone and metacone, but in 29 % of the specimens the posterior metalophule is interrupted, resulting in an indentation of the posterior wall of the molar.

M_1 – Slightly narrower anteriorly than posteriorly. Broad teeth with thick enamel, and slender teeth with thin enamel are about equally frequent, but these two types do not present differences in dental pattern. The anteroconid is well set off from the rest of the tooth; it is undivided in 3 % of the specimens only. It is well subdivided in 51 %, slightly subdivided in 41 %, and in 5 % of the specimens it is divided into 3 cusps. The anterolophulid is simple and connected to the labial anteroconid cusp (50 %), or bifurcated and connected to both anteroconid cusps (50 %). There is no posterior metalophulid. The mesolophid is almost always present, absent only in 5 % of the specimens. In 70 % it reaches the border of the molar. The ectomesolophid occurs frequently (23 %).

M_2 – The labial anterolophid is stronger than the lingual one; protosinusid and anterosinusid remain open. The mesolophid is absent (7 %), short (17 %), of medium length (17 %), or long (59 %). The ectomesolophid is present in 24 % of the specimens. In complete tooth rows its presence usually coincides with the presence of an ectomesolophid in M_1. In 99 % of the specimens the posterolophid closes a funnel between hypoconid and entoconid.

M_3 – The posterior metalophulid may be absent (50 %), or it closes a funnel between protoconid and metaconid (50 %). The mesolophid is absent (16 %), short (37 %), of medium length (25 %), or long (22 %). The ectomesolophid is present in 4 % of the teeth only. In complete tooth rows it does not occur in specimens that do not present the same phenomenon in M_1 and M_2.

Cricetus kormosi Schaub, 1930
Figs. 8-10.

Synonymy and literature citations.
Cricetus sp. - Kormos, 1911, Polgárdi.
Cricetus kormosi sp. nov. - Schaub, 1930, Polgárdi.
Cricetus kormosi - Kretzoi, 1952, Polgárdi.
Cricetus kormosi - Mein & Michaux, 1970, Polgárdi.
'*Cricetus*' cf. *kormosi* - Aguirre et al., 1973, Venta del Moro.
'*Cricetus*' *kormosi* - Mein et al., 1973, La Alberca.
Cricetus cf. *kormosi* - de Bruijn et al., 1975, Crevillente 6.
Cricetus cf. *kormosi* - van de Weerd, 1976, Valdecebro 3, Masada del Valle 7.
Cricetus cf. *kormosi* - Montenat, 1977, Librilla, La Alberca.
'*Cricetus*' cf. *kormosi* - Boné et al., 1978, Arenas del Rey.
Cricetus cf. *kormosi* - Aguilar et al., 1982, La Tour (La Bégude).
Cricetus kormosi - Agustí et al., 1985, Molina de Segura 9.

Type-locality – Polgárdi 2.
Type-material – Schaub, 1930 figured 1 mandible (figs. 25-26), 2 M_1-M_3 (pl. II, figs. 5, 7), and 2 maxillae (pl. II, figs. 6, 8, 9, 10). He did, however, not designate a holotype. We therefore propose a lectotype.
Lectotype – Mandibula with M_1-M_3 dext., MAFI Ob. 4185, Fig. 8, 1 (also figured by Schaub, 1930, figs. 25-26).

Emended diagnosis – Medium-sized species, slightly larger than *Cricetus polgardiensis* sp. nov. In M^1 the anterocone is deeply split, the anteroconid of M_1 is slightly bifid. The labial spur on the anterolophule of M^1 is absent in 90 % of the cases. The mesoloph(id) is usually absent in M^1, and absent, or medium-sized in M_1. The ectomesolophid occasionally occurs in M_1 and M_2.

Measurements – See Table 6, Figs. 11-15.

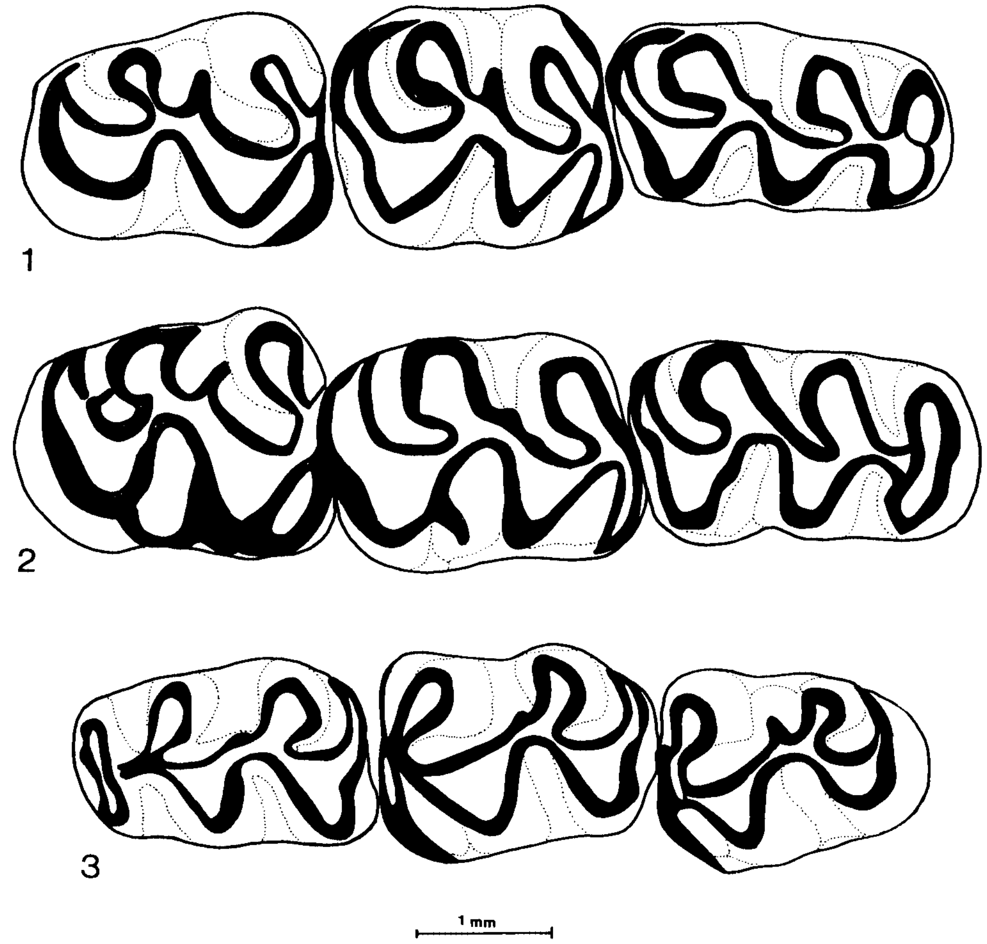

Fig. 8. *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
1: M_1-M_3 dext. (Schaub, 1930, figs. 25, 26).
2: M_1-M_3 dext.
3: M_1-M_3 sin. (Schaub, 1930, pl. 2, fig. 5).

Material from Polgárdi 2 – According to Kormos '30 pieces of mandible fragments and other bones'. Of these 30 pieces the following are present in the Palaeovertebrate Collection of the Hungarian Geological Institute:
Ob. 4185: 1 maxilla with M^1-M^3, 2 maxillae with M^1-M^2, 3 M_1, 1 M_3.
V. 14059: 3 maxilla fragments with M^1-M^2.
V. 14060: 3 mandible fragments with M_1-M_3.
In the Natural History Museum, Basel: 9 M^1, 5 M^2, 1 M^3, 12 M_1, 5 M_2, 5 M_3 (de Bruijn et al., 1975).

Description

M^1 – (Figs. 9-10) Strongly built tooth with thick enamel. The anterocone is always strongly bifid. The anterocone and the protocone are connected by a lingually placed anterolophule. In the type-material the labial spur on the anterolophule is

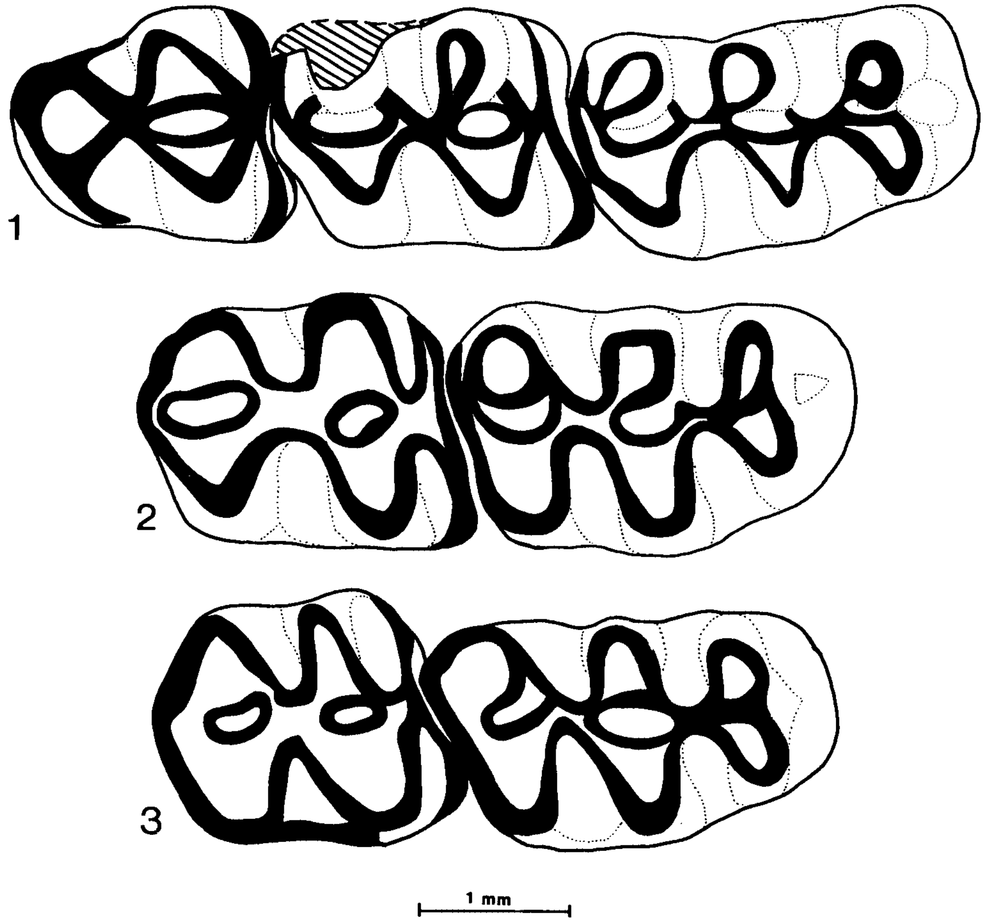

Fig. 9. *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
1: M^1-M^3 dext., Ob.4185.
2: M^1-M^2 dext., Ob.4185/2.
3: M^1-M^2 dext., Ob.4185/3.

absent. In 1 of the 8 HGI specimens it is of medium length. The protolophule is double, enclosing a funnel between protocone and metacone. In Schaub's specimens (op. cit., pl. 2, figs. 6, 8) the mesoloph is rudimentary, in 1 of the 8 HGI specimens it is long.

M^2 – (Figs. 9-10) Protolophule and metalophule are double, enclosing funnels between the lingual and labial cusps. The mesoloph is variable: it is absent in Schaub's material and in 3 other specimens, it is short in 2 and long in 1 case.

M^3 – (Fig. 9) There is no mesoloph. The double protolophule encloses a funnel. A second funnel is present between the metalophule and the posteroloph. The posterior wall of the molar is smooth, the posteroloph is not indented.

M_1 – (Fig. 8) The anteroconid is a transverse crest, hardly or not at all subdivided. The anterolophulid is a simple crest, from the protoconid towards the anteroconid. There is no posterior metalophulid. In Schaub's specimens there is no meso-

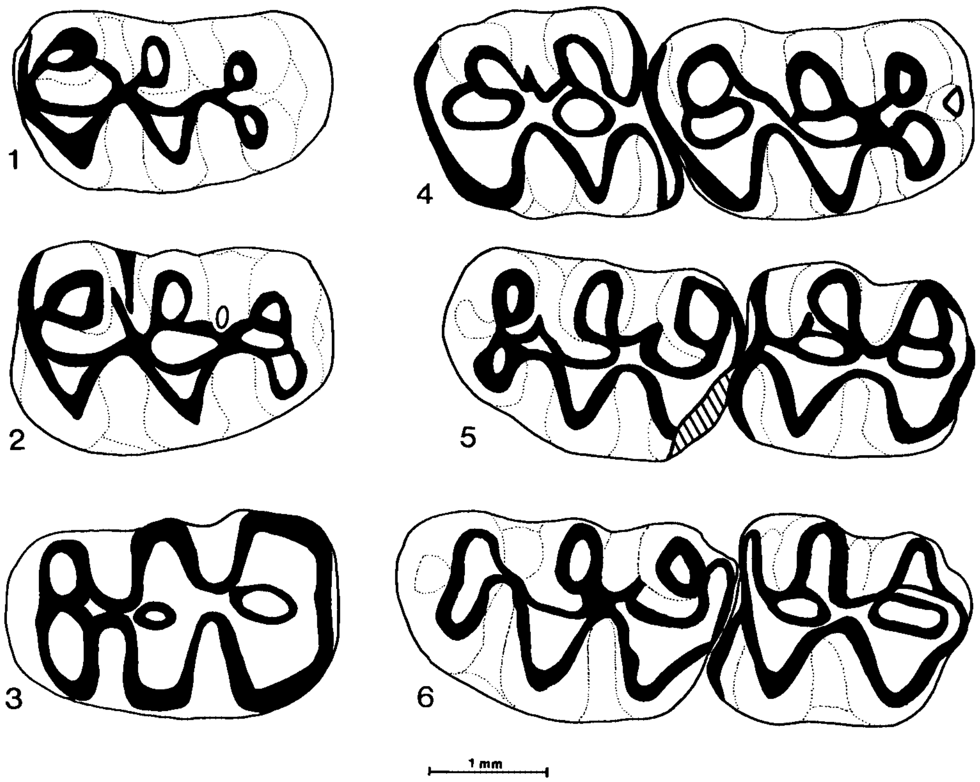

Fig. 10. *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
1-3: M^1, Ob. 4185/4-6; 4-5: M^1-M^2; 6: M^1-M^2 sin. (Schaub, 1930, pl. 2, fig. 7).

lophid. Among the other material only 1 specimen has a very small mesolophid. Occasionally there is an ectomesolophid.

M$_2$ — (Fig. 8) The outline of this element is rectangular. It is about as large as M$_3$. Metalophulid and hypolophulid are anterior, so the valleys between the labial and lingual cusps are open posteriorly. The mesolophid is absent or very short. An ectomesolophid occurs in about 50 % of the cases.

M$_3$ — (Fig. 8) The labial anterolophid is strongly developed. The mesolophid is always present, of medium length. There is no ectomesolophid.

Taxonomic and phylogenetic relationships

DISCUSSION OF THE GENERA *NEOCRICETODON*, *CRICETULODON* AND *KOWALSKIA*

Cricetulodon Hartenberger, 1966 is based on *C. sabadelliensis* Hartenberger, 1966 from Can Llobateres (Spain). A definition of this species, based on the description by Agustí (1981) is as follows:

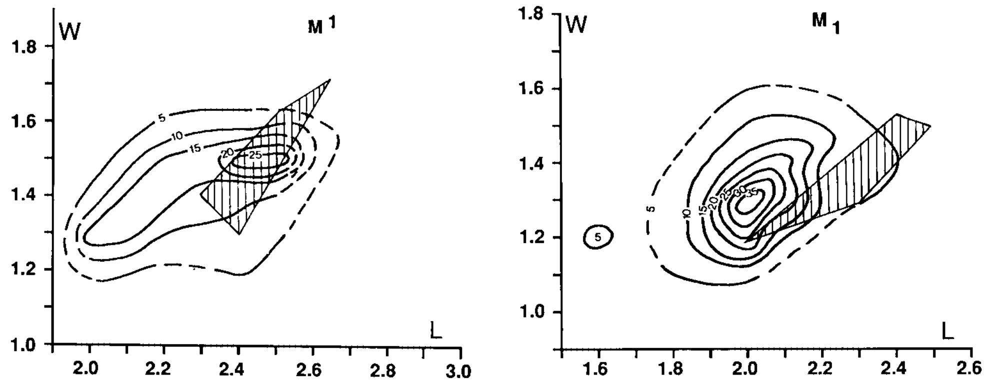

Fig. 11. Length/width diagrams of first molars, scale in mm.
Hatched area: *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
Frequency contour lines: *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.

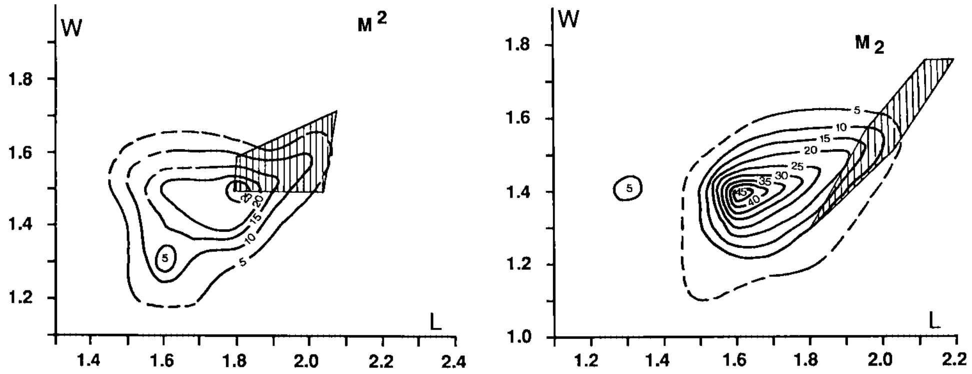

Fig. 12. Length/width diagrams of second molars, scale in mm.
Hatched area: *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
Frequency contour lines: *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.

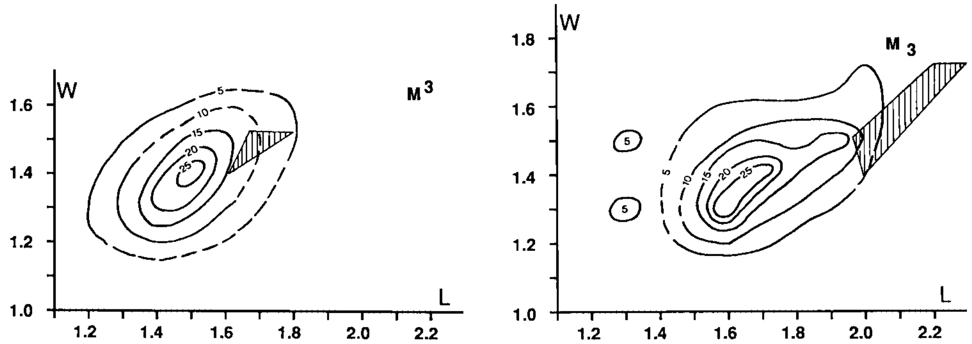

Fig. 13. Length/width diagrams of third molars, scale in mm.
Hatched area: *Cricetus kormosi* Schaub, 1930 from Polgárdi 2.
Frequency contour lines: *Cricetus polgardiensis* sp. nov. from Polgárdi 4 'Upper'.

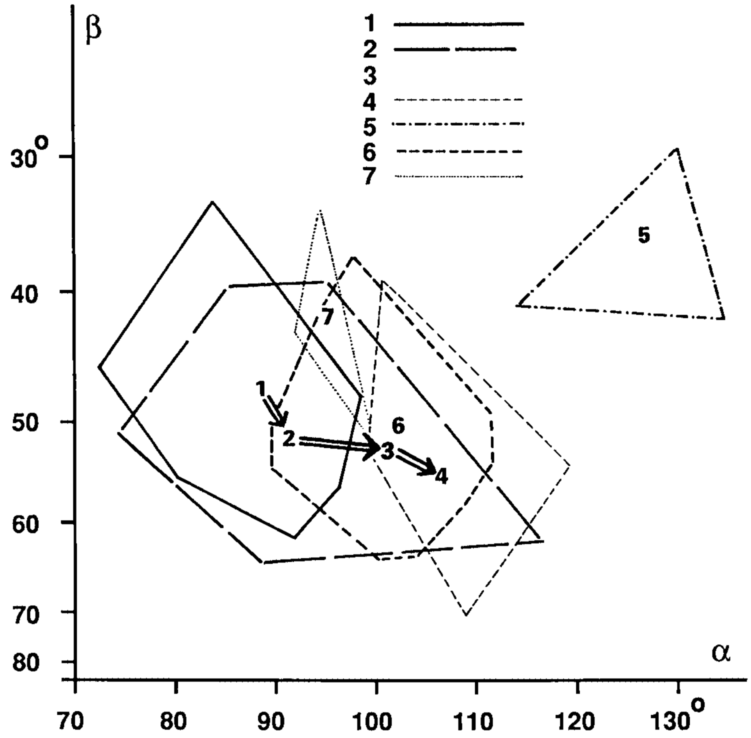

Fig. 14. Cranial morphology of various Cricetidae. The vertical axis is the transverse inclination of the maxilla with respect to the os zygomaticus (α in Fig. 6); the horizontal axis is the longitudinal declination of the os zygomaticus with respect to the maxilla (β in Fig. 6).
1: *Cricetus polgardiensis* from Polgárdi 4 'Upper'.
2: *C. polgardiensis* from Polgárdi 4 'Lower'.
3: *C. praeglacialis* from Villány 8.
4: *C. cricetus nanus* from Betfia.
5: *C. cricetus* from Jankovich Cave.
6: *C. cricetus* (Recent) from Balmazujváros.
7: *Cricetulus* sp. (Recent) from the USSR.
The numbers are placed at the mid-points of the respective populations.

M^1 — The anterocone is subdivided into 2 cusps that are connected by a high crest. In some specimens the 2 cusps are separated by a deep valley. The anterolophule is connected to the lingual cusp. There maybe a lingual spur on the anterolophule, either short (24 %), or of medium length (5 %). The protolophule is double (34 %), or posterior (66 %). The mesoloph is long (1 %), of medium length (20 %), short to very short (57 %), or absent. The posteroloph may be fused to the posterior wall of the metacone, but in most cases there are a distinct metalophule and posterosinus.

M^2 — The protolophule is double (87 %), posterior with a low trace of the anterior connection (6 %), or posterior only. The mesoloph is long (4 %), of medium length (8 %), short to very short (52 %), or absent. If present it is directed towards the anterior wall of the metacone. The metalophule is posterior, only in 1 case there is an anterior connection as well. There is a small posterosinus. Seven out of 110 specimens have 4 roots.

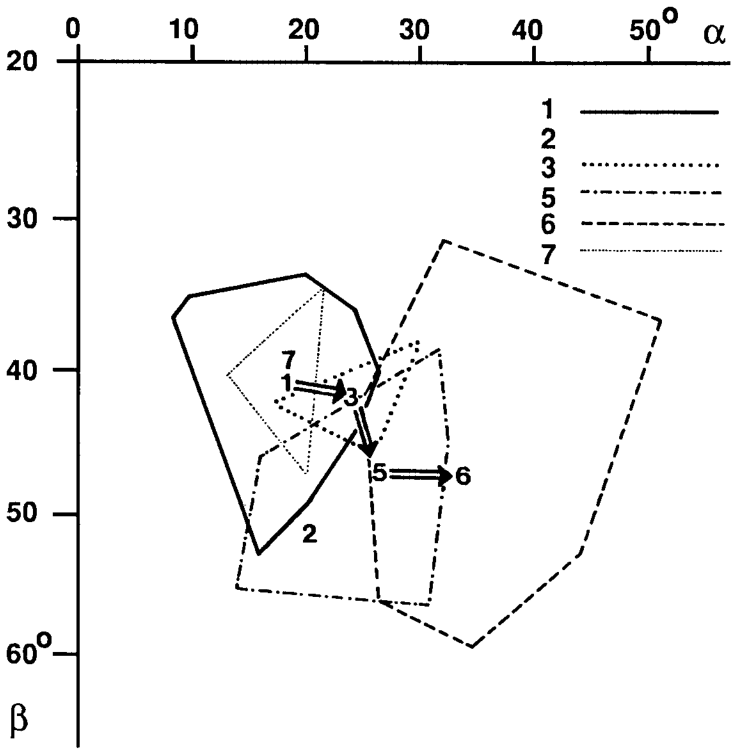

Fig. 15. Mandible morphology of various Cricetidae. The vertical axis is the angle between the tooth row and the corpus mandibulae (β in Fig. 5), the horizontal axis is the vertical angle of the mandible (α in Fig. 5). Symbols as in Fig. 14.

M^3 – The protolophule is double (95 %), or posterior only (5 %). The mesoloph is of medium length or long (20 %), short (18 %), or absent. In 80 % the metalophule is double.

M_1 – The anteroconid is subdivided into 2 cusps, or - in 15 % - even 3 cusps. In 17 % it is undivided. The anterolophulid is low, directed towards the lingual cusp (81 %), the central cusp (3 %), double and connected to both cusps (3 %), or absent (12 %). The mesolophid is short (32 %), or absent (68 %).

M_2 – The mesolophid is generally absent, sometimes very short (10 %).

M_3 – The mesolophid is generally absent, but varies between long and absent.

Kowalskia is based on *K. polonica* Fahlbusch, 1969 from Podlesice (Poland). It was defined as follows:

M^1 – The anterocone consists of 2 cusps, separated only by a groove in the posterior wall. The anterior wall is smooth or hardly grooved. Only rarely the 2 cusps are separated deeply. The lingual cusp is connected to the protocone by the anterolophule, that bears a long labial spur. The protolophule is posterior (2), or double (8). The mesoloph is of medium length (1), or long (9). The posteroloph is fused with the posterior wall of the metacone. One specimen has 3 roots, the other ones have 4 roots.

M^2 – The protolophule is double, in 1 specimen the anterior connection is interrupted. The mesoloph is long. The metalophule is anterior (5), or double (2). There are 4 roots.

M^3 – The protolophule is double, the mesoloph is distinct.

M_1 – The anteroconid is a transverse wall, either undivided, or slightly subdivided into 2 or 3 cusps. It is connected to the protoconid by a low crest (10), or by 2 crests (2). The mesolophid is always long and reaches the border of the tooth. One specimen has an ectomesolophid.

M_2 – The mesolophid is long (4), or of medium length (4).

M_3 – The mesolophid is long.

Fahlbusch places *Rotundomys hartenbergeri* Freudenthal, 1967, in *Kowalskia.* He states that *Rotundomys montisrotundi* Mein, 1966 is quite close to *Kowalskia*, but differs from the latter by its hypsodonty, and several other morphological features. He seems to place *sabadelliensis* in the genus *Rotundomys*, without saying why he does not recognize the genus *Cricetulodon.* This is a pity because it is fundamental for the validity of the genus *Kowalskia.*

Freudenthal, 1967 supposed an evolutionary lineage *hartenbergeri-sabadelliensis-montisrotundi*, a supposition that has not met with any serious objections. The problem is, however, how many genera are involved in this lineage. There are four possibilities:

1. *hartenbergeri, sabadelliensis*, and *montisrotundi* belong to one single genus.
2. *Cricetulodon sabadelliensis* belongs to the genus *Rotundomys.*
3. *Cricetulodon sabadelliensis* belongs to the same genus as to which *hartenbergeri* belongs.
4. *hartenbergeri, sabadelliensis*, and *montisrotundi* belong to three different genera.

It is not convenient to place the high-crowned *montisrotundi* and the brachyodont *hartenbergeri* in the same genus, so possibility 1 may be discarded. *Sabadelliensis* is morphologically much closer to *hartenbergeri* than to *montisrotundi*, so possibility 2 is discarded as well.

In our opinion the differences between *hartenbergeri* and *sabadelliensis* are not sufficiently large to distinguish them generically. This discards possibility 4, and leads to the conclusion that *hartenbergeri* and *sabadelliensis* belong to the genus *Cricetulodon.*

The relation between *Cricetulodon* and *Kowalskia* Fahlbusch, 1969 has to be decided on the basis of a comparison of the two type-species:

	C. sabadelliensis	*K. polonica*
lower molars: mesolophid	absent or short	long
upper molars: mesoloph	absent or short, rarely medium or long	long, (medium)
posterosinus	distinct	absent
M^1: lingual spur on the anterolophule	absent-medium	long
anterior protolophule	in 35 %	in 80 %
roots	3	4
M^2: anterior protolophule	in 83 %	in 100 %
anterior metalophule	rare	frequent
roots	3, rarely 4	4

This table shows that the differences between these two species are only gradual, and do not warrant a generic separation. All features found in one species, do also occur in the other one, though frequencies differ. When *C. hartenbergeri*, *K. magna* and *K. fahlbuschi* Bachmeyer & Wilson, 1970 are taken into account, the supposed differences between *Cricetulodon* and *Kowalskia* become even more blurred.

In *C. hartenbergeri* long mesoloph(id)s are fairly frequent, and the anterior protolophule in M^1 is rarely absent, like in *K. polonica.*

In *K. magna* only 1 of the 4 M^1 has four distinct roots, in the other ones the lingual root is undivided, or slightly divided.

In *K. fahlbuschi* only 30 % percent of the M^1 have four roots, and the posterosinus is distinct.

De Bruijn, 1976 states that '...paleontological classification is unduly influenced by supposed phylogenetical reconstructions. In order to avoid confusion, I once again stress that we should base our system on morphology, not on theory. The dental pattern of *hartenbergeri* is very close to that of *C. sabadelliensis*, the type-species of *Cricetulodon*, and differs considerably from that of *R. montisrotundi* Mein and *Kowalskia polonica* Fahlbusch, so there need not be any difference of opinion...', and then gives a compact definition of the three genera. We are not in a position to exclude the possibility that the material discussed above represents two genera, but de Bruijn's compact definitions are clearly untenable. On the basis of morphology only, *Cricetulodon* and *Kowalskia* evidently are synonyms. The only proof for the existence of two different genera might be found in a better knowledge of the evolution of this complex group, and its phylogenetic relationships, precisely the method rejected by de Bruijn.

So, for the time being, *Kowalskia* is considered to be a junior synonym of *Cricetulodon.*

Neocricetodon was first mentioned by Kretzoi (in Kadic & Kretzoi, 1930), but since it was not described, it remained a nomen nudum. Kretzoi described it in 1954, and the holotype and some additional material from Csákvár are present in the collection of the Hungarian Geological Institute. There can be no doubt, that this material is generically identical with *Kowalskia* and *Cricetulodon.* Since *Neocricetodon* is an available name in the sense of the rules for zoological nomenclature, both *Kowalskia* and *Cricetulodon* are to be considered junior synonyms, and the correct name to be used is *Neocricetodon.*

DISCUSSION OF *C. KORMOSI* AND *C. POLGARDIENSIS*

The *Cricetus* species from Polgárdi strongly differ from each other in size. Also with other Late Neogene populations there are considerable size differences. The data on the lengths and widths of the teeth are presented in Figs. 11-13; Figs. 14-15 give the measurements of the maxillae and mandibles.

The teeth of *C. kormosi* are larger than those of *C. polgardiensis.* This is not only true for the Budapest material, but also for the specimens deposited in the Natural History Museum of Basel (de Bruijn et al., 1975). *C.* cf. *kormosi* from Crevillente 6 is slightly larger than *C. polgardiensis* and smaller than *C. kormosi* (de Bruijn et al., 1975).

Karstocricetus Kordos, 1987 is smaller than *C. kormosi*, and covers about the size range of *C. polgardiensis.* All other Late Neogene European Cricetidae differ from the Polgárdi species, both in size, and in tooth morphology.

One characteristic feature of *C. kormosi* is the elongated M_3. Length ratios M_3/M_1 and M_3/M_2 for some populations are given in Table 1.

Table 1

	M_3/M_1	M_3/M_2
C. kormosi - Polgárdi 2	91	105
C. cf. *kormosi* - Crevillente 6	89	104
C. polgardiensis - Polgárdi 4 'Lower'	87	102
C. polgardiensis - Polgárdi 4 'Upper'	84	100
Karstocricetus - Tardosbánya	82	100

The M_3, in comparison with M_1 and M_2, is smallest in *Karstocricetus*, and largest in *C. kormosi.* The same trend is visible in the values for the crown surface. In more or less comparable and contemporaneous forms like *Neocricetodon* the M_3 is relatively smaller.

Freudenthal, 1985 suggested that *C. kormosi* might be not too far from *Cricetulodon* and *Hattomys.* The excellent conservation of the material from Polgárdi allowed us to study some of the features of maxillae and mandibles; these were compared with the values found in some fossil and recent *Cricetus* and *Cricetulus*, in order to see whether there are important differences. Unfortunately, similarly well-preserved material of *Cricetulodon* is not available.

In the maxilla we measured the longitudinal and lateral inclination of the os zygomaticus with respect to the tooth row. The way of measuring is defined in Fig. 6, the measuring data are given in Table 5 and Fig. 14. Medium values (degrees) are given in Table 2.

Table 2

	α	β
C. kormosi - Polgárdi 2	89	47
C. polgardiensis - Polgárdi 4 'Upper'	88	47
C. polgardiensis - Polgárdi 4 'Lower'	91	51
C. praeglacialis - Villány 8/12	101	52
C. cricetus nanus - Betfia	107	54
C. cricetus - Jankovich Cave	127	36
C. cricetus - Balmazujváros	101	51
Cricetulus sp. - USSR	95	42

By these results, especially the α values, the Polgárdi species appear to be closest to Recent *Cricetulus.* Furthermore there seems to be an increase of the α values from the Late Miocene cricetids towards the Lower and Middle Pleistocene *C. praeglacialis* and *C. cricetus nanus.* The postglacial material of *C. cricetus* from Jankovich Cave (Hungary) differs considerably from all other populations.

Similar results (Table 3) are obtained from the study of the orientation of the corpus mandibulae with respect to the tooth row (definition in Fig. 5; measuring data in Table 5 and Fig. 15):

Table 3

	α	β
C. kormosi - Polgárdi 2	–	–
C. polgardiensis - Polgárdi 4 'Lower'	20	50
C. praeglacialis - Villány 8/12	24	41
C. cricetus - Jankovich Cave	25	46
C. cricetus - Balmazujváros	33	47
Cricetulus sp. - USSR	20	46

In order to get an idea of the relative variability of the tooth morphology the following method is used. In Figs. 16-21 the various morphotypes of important parts of the teeth are figured, and each one is defined by a letter or a cypher. E. g. in M^1 there occur 2 types of anterocone (type A and D never occur), 4 types of labial spur on the anterolophule, 4 types of mesoloph, and 2 types of anterior metalophule, resulting in a total of 64 possible combinations. Of these 64 possibilities only 4 occur in *Karstocricetus* (see Tables 7 and 8), resulting in a variability value of 4/64, or 6 %. In the M^1 from Polgárdi 4 'Upper' 30 combinations occur, giving a value of 30/64 or 47 %. Higher values indicate a larger morphological variation; the frequency of each of the different morphotypes is in this case not taken into account. The mean of the six values (Table 4) found in each population gives an idea of its general variability (all values are percentages):

Table 4

	Karstocricetus Tardosbánya	*C. polgardiensis* Polgárdi 4 'Upper'	*C. polgardiensis* Polgárdi 4 'Lower'
M^1	6	47	30
M^2	12	25	25
M^3	25	54	33
M_1	19	42	33
M_2	21	25	33
M_3	10	35	21
mean	15.5	31.3	25.3

In all populations the variability is greater in M^3, and smaller in M^2 and M_3. The two *polgardiensis* populations agree quite well, whereas *Karstocricetus* differs significantly from them, not only because of the extremely low value for M^1, but all values are lower. The material of *C. kormosi* is not sufficiently rich for this kind of analysis.

DISCUSSION OF THE MORPHOTYPES IN VARIOUS POPULATIONS

M^1 (Fig. 16) – The C1A1 type (anterocone strongly bifid, long labial spur, long mesoloph, anterior metalophule not closed) dominates in *Karstocricetus* (75 %), and occurs frequently in *C. polgardiensis* from Polgárdi 4 (20-28 %); in *C. kormosi* (Polgárdi 2) C4D2 is the dominant type (labial spur and mesoloph absent).

M^2 (Fig. 17) – 2A2 (long mesoloph, closed funnels) dominates in *Karstocricetus* and *C. polgardiensis* with values around 50 %. The mesoloph in *Karstocricetus* is always long, in *polgardiensis* long mesolophs dominate (64-73 %), mesolophs of medium length are frequent (27-29 %); in *C. kormosi* 5 out of 6 specimens have a short or absent mesoloph.

M^3 (Fig. 18) – In *Karstocricetus* and *C.polgardiensis* the mesoloph is long or medium (about 70 %), short or absent (about 30 %); in *C. kormosi* (1 specimen only) there is no mesoloph.

M_1 (Fig. 19) – The combinations A1A2 and B1A2 (undivided or slightly bifid anteroconid, simple anterolophulid, long mesolophid) are characteristic for *Karstocricetus*, a well-divided anteroconid occurs in 32 %. In *C. polgardiensis* C1A2 and C2A2 are characteristic; simple anteroconids occur rarely, mesolophids are on the average shorter; the subdivision of the anteroconid is more pronounced in Polgárdi 'Lower' than in Polgárdi 'Upper'. *C. kormosi* is characterized by a slightly divided anteroconid, and short or absent mesolophid (B2C1 and C1D2).

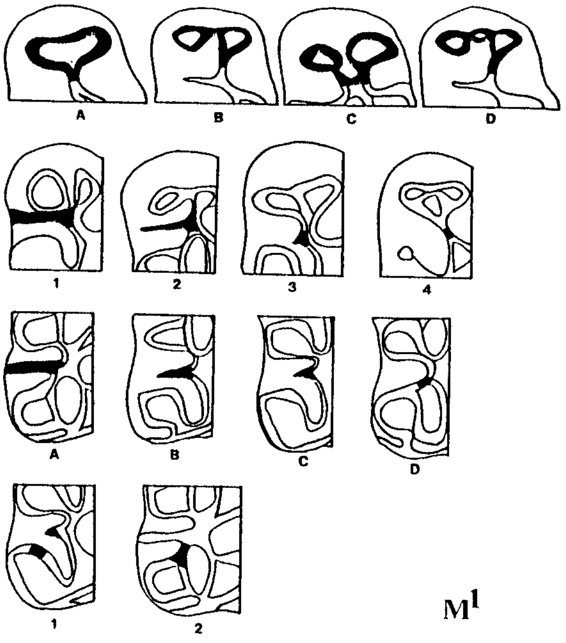

Fig. 16. Morphotypes of M^1.

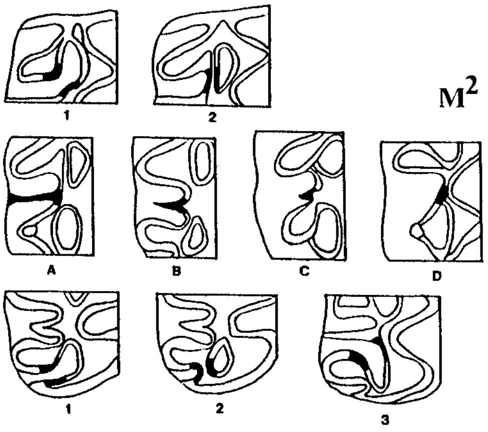

Fig. 17. Morphotypes of M^2.

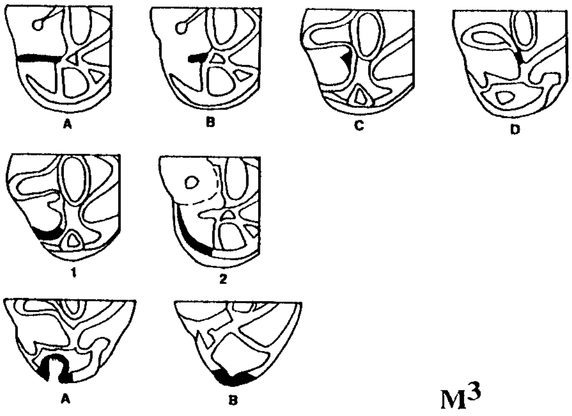

Fig. 18. Morphotypes of M^3.

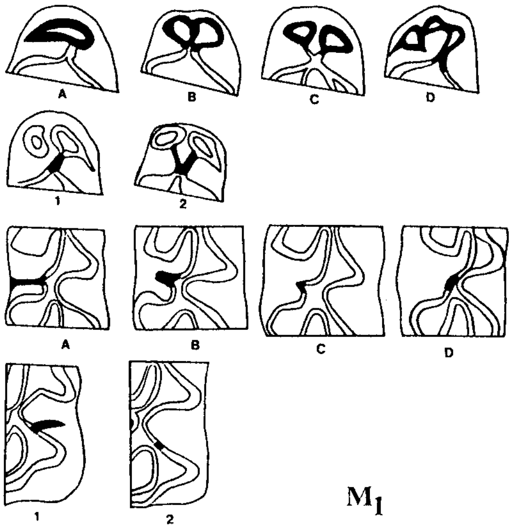

Fig. 19. Morphotypes of M_1.

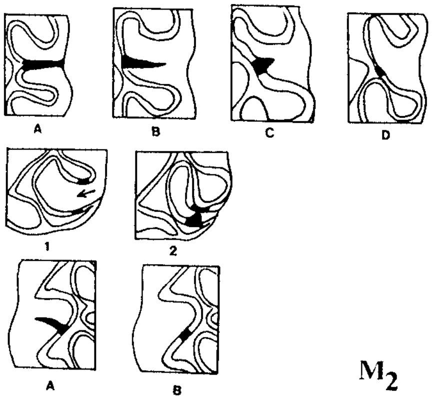

Fig. 20. Morphotypes of M_2.

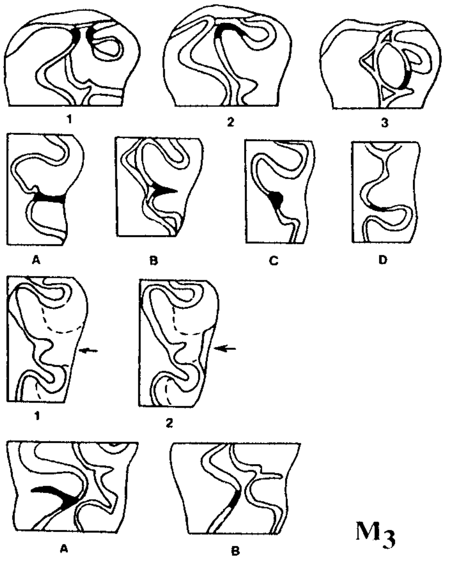

Fig. 21. Morphotypes of M_3.

M_2 (Fig. 20) – The A1B type (long mesolophid, posterosinusid open, no ectomesolophid) decreases from 72 % in *Karstocricetus* to 35-49 % in *C. polgardiensis*. It is absent in *C. kormosi*, where the mesolophid is short or of medium length (C1A and D1B)

M_3 (Fig. 21) – The 2A2B and 2B2B types (no posterior metalophulid, well-developed mesolophid, mesosinusid closed, no ectomesolophid) dominate in *Karstocricetus* (64 %). The similar types with open sinusid constitute almost all the other specimens (31 %). As far as the open or closed mesosinusid is concerned the two Polgárdi populations differ strongly from each other. In *C. kormosi* the types 2B1B, 2B2B and 3B2B (with or without posterior metalophulid, mesolophid well-developed) occur.

Conclusions

On the assumption of the chronological sequence Tardosbánya–Polgárdi 4–Polgárdi 2 we see the following developments through time:

more subdivided anteroconids, and more undivided anterocones,

labial spurs on the anterolophules and mesolophs become shorter and tend to disappear,

in M^2-M^3 the protolophule is almost always double, the metalophule at first is variable, and tends to become double.

By the general appearance of the dental morphology *Karstocricetus skofleki* Kordos, 1987, *Cricetus polgardiensis* sp. nov., and *Cricetus kormosi* Schaub, 1930 appear to be closely related among each other, and less related to *Neocricetodon*. However, *C. polgardiensis* cannot be derived from *Karstocricetus*. *C. polgardiensis* may well be the direct ancestor of *C. kormosi*. Successors of *C. kormosi* are not known, because in the period following Polgárdi (MN units 14-16) no *Cricetus* is known in Hungary. Pleistocene and Recent *Cricetus* in Hungary seem to originate from a new immigration wave.

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Table 5. Mandible measurements of cricetid taxa. Parameters 1-8 in mm, α and β in degrees. The meaning of the parameters is explained in Fig. 5.

1	2	3	4	5	6	7	8	α	β
Cricetus polgardiensis sp. nov. from Polgárdi 4 'Upper'									
20.3	3.0	4.8	3.8	7.4	5.5	7.8	10.2	21	39
21.0	3.6	5.5	3.8	7.2	5.2	8.0	10.4	20	46
18.6	3.1	4.2	3.1	6.3	5.2	8.0	9.0	17	44
18.0	3.3	4.6	3.6	6.8	4.9	7.5	8.3	10	35
18.4	4.0	5.1	3.5	7.4	5.6	8.4	10.0	14	44
19.0	4.0	5.8	4.2	7.4	6.0	8.2	9.0	24	43
19.0	3.3	4.8	3.3	7.0	5.2	7.9	9.0	20	39
20.3	3.8	5.3	3.6	7.1	6.0	7.6	9.8	24	37
17.7	3.3	4.3	3.0	6.0	5.3	7.3	8.5	22	43
17.7	2.9	4.6	3.1	6.2	5.1	6.6	8.2	20	37
18.4	3.2	5.4	8.5	7.5	5.7	7.9	9.4	19	38
21.2	3.6	6.1	3.4	7.4	5.6	8.7	10.0	20	48
17.5	2.7	4.7	3.4	6.8	4.7	8.1	9.4	14	38
18.0	3.6	5.3	4.1	7.2	6.0	9.2	10.7	16	44
19.3	3.9	5.8	3.9	7.3	6.0	8.0	9.3	13	44
20.8	3.6	5.2	3.6	7.2	5.8	7.5	9.8	16	39
18.2	3.4	5.0	3.4	7.0	4.8	8.1	9.5	14	39
16.4	2.6	3.3	2.3	5.6	4.8	6.4	8.0	9	36
18.0	3.8	4.4	2.8	6.0	4.9	6.4	7.8	19	37
20.8	3.5	5.8	3.9	7.4	6.0	7.2	10.0	19	40
18.6	3.5	5.4	4.7	7.1	5.8	8.0	9.9	21	45
20.6	3.5	5.2	3.6	6.9	5.8	7.0	8.7	13	43
24.0	4.1	6.8	3.8	7.8	6.6	9.5	10.6	16	52
21.4	3.7	5.8	3.9	7.4	5.9	7.0	10.2	27	41
17.9	3.4	5.9	3.6	7.3	5.2	8.7	10.4	21	36
19.0	3.3	5.0	3.5	7.0	5.2	7.6	9.0	20	34
Cricetus praeglacialis from Villány 8/12									
26.5	4.6	7.0	4.2	8.6	7.1	11.7	13.2.	24	41
31.0	5.4	8.6	5.4	10.6	8.8	15.0	18.9	25	44
30.0	5.2	8.6	5.2	10.9	8.0	13.6	15.6	27	40
23.0	3.9	6.3	4.0	7.6	7.0	10.0	12.3	26	41
23.4	4.4	6.9	4.3	8.2	6.5	11.8	12.4	25	44
24.4	4.3	6.7	4.8	8.3	6.7	10.9	13.4	18	42
25.6	4.3	7.0	4.5	8.4	7.4	12.8	14.3	18	43
27.2	4.7	7.4	4.8	9.8	7.9	12.9	14.4	29	39
Cricetus cricetus from Jankovich Cave									
29.0	4.6	8.6	4.5	9.2	7.9	13.8	15.2	24	50
28.0	4.5	8.1	4.2	9.0	7.8	12.9	14.4	31	44
27.4	4.3	8.0	4.5	8.6	8.6	11.9	15.3	30	46
26.0	4.1	7.2	4.4	9.2	7.2	11.6	13.2	16	46
22.6	3.9	6.3	4.4	7.4	6.8	9.8	11.5	25	48
24.6	3.7	6.5	4.3	7.8	7.0	10.9	12.0	30	40
28.6	5.0	7.3	5.0	9.4	8.8	12.1	14.4	30	44
26.3	4.0	7.2	3.7	8.1	7.4	12.0	13.0	30	54
26.8	4.8	9.4	5.4	9.0	8.8	14.0	15.6	15	50
22.0	3.6	6.7	4.0	8.8	7.4	10.6	12.2	14	52
27.0	4.4	9.0	5.0	9.3	7.8	13.4	14.3	29	48
26.0	4.5	7.8	4.2	8.0	7.6	11.4	14.2	32	39
27.9	4.3	8.2	4.4	8.6	8.2	11.6	14.5	26	45
26.0	3.6	7.5	4.2	8.0	7.4	10.8	13.0	29	48

1	2	3	4	5	6	7	8	α	β
Cricetus (Phodopus) songarus from USSR, Recent									
15.0	2.2	3.3	2.2	4.3	3.8	6.4	6.8	21	35
16.2	2.4	4.3	2.4	4.6	4.6	6.7	7.2	14	42
Cricetulus sp. from USSR, Recent									
22.0	3.8	6.3	4.0	6.2	6.4	10.3	11.0	20	46
Cricetus cricetus from Balmazujváros, Recent									
26.0	4.4	7.0	4.8	8.6	7.2	12.5	14.4	28	44
26.6	3.9	7.3	4.5	8.4	7.0	12.0	13.2	33	40
25.4	4.0	7.0	4.5	8.4	7.2	12.0	13.5	32	32
24.2	4.0	6.7	4.1	8.4	6.8	12.0	12.9	30	35
27.8	4.6	8.0	5.0	8.6	8.9	13.0	15.0	28	40
29.4	4.5	8.0	4.7	9.9	7.9	13.4	14.5	35	38
25.0	4.0	7.2	4.8	8.0	7.1	11.4	13.2	30	46
29.0	5.3	9.0	5.4	10.0	9.1	15.0	16.4	29	45
27.1	4.4	7.2	4.0	8.3	7.6	11.2	13.4	36	52
24.8	4.3	7.4	5.0	9.3	7.2	13.9	14.0	26	46
28.0	4.4	7.7	4.5	9.0	8.0	13.0	14.2	35	48
28.5	4.5	8.1	4.8	9.8	7.8	13.0	14.8	35	49
27.9	4.8	7.8	4.6	9.4	7.7	12.9	14.4	43	46
32.2	5.5	8.9	5.3	10.4	8.8	15.0	16.6	35	49
26.8	4.0	7.2	4.1	8.5	6.5	12.0	13.2	43	52
26.7	4.3	7.8	4.6	9.0	8.8	13.0	14.7	29	49
26.2	4.4	7.8	4.8	9.0	7.5	12.7	14.0	30	48
25.4	4.8	7.9	5.0	10.0	8.0	13.4	14.8	25	44
28.4	5.0	8.2	5.3	9.4	8.2	13.7	14.8	35	45
24.4	4.3	7.3	4.0	8.0	7.4	12.1	13.0	28	44
27.8	4.4	7.9	4.9	9.0	7.6	13.2	14.6	39	43
28.4	4.2	7.4	4.7	9.0	8.4	13.0	15.5	28	40
24.0	4.2	7.8	4.5	8.5	7.6	12.2	13.6	30	52
27.9	4.4	7.6	4.8	8.7	7.6	12.4	14.2	25	42
28.9	4.6	7.6	4.7	9.0	8.2	12.7	14.8	34	46
27.4	4.3	7.5	4.6	9.0	8.1	12.9	14.3	32	43
28.8	4.5	8.0	4.8	9.8	7.9	13.4	15.3	33	38
30.0	4.6	8.0	4.4	9.3	8.0	13.6	15.6	40	41
27.4	4.3	7.4	4.5	8.6	7.6	12.0	14.0	33	50
26.4	4.7	7.8	4.6	9.2	7.4	13.0	14.5	40	48
27.8	4.5	7.7	4.6	8.8	7.5	12.6	14.2	41	47
28.9	4.6	7.9	4.8	9.3	7.6	13.4	14.6	37	54
27.4	4.2	7.3	5.O	8.9	7.0	12.8	13.8	31	54
27.6	4.3	7.8	4.2	8.8	8.0	12.9	14.3	33	46
30.6	5.2	8.6	5.0	9.3	9.5	14.0	16.2	28	54
28.0	4.3	7.4	4.8	9.0	7.8	12.6	14.4	43	52
27.4	4.5	7.4	4.8	9.0	7.4	12.8	14.0	37	51
31.8	4.8	8.4	5.2	10.1	8.9	15.3	17.0	38	45
29.6	5.1	8.8	5.2	9.3	8.1	13.6	15.5	45	56
30.0	4.8	7.8	5.0	10.0	8.2	13.8	15.8	38	47
27.0	4.3	7.4	4.6	8.4	8.4	12.0	13.0	32	53
29.0	4.4	7.8	4.8	9.0	8.2	13.8	15.7	34	58
30.3	5.0	8.3	5.2	10.5	8.7	15.0	16.2	34	41
30.0	4.6	7.9	4.8	9.5	8.6	13.4	15.0	30	45
30.0	4.9	8.2	4.8	9.3	8.2	13.5	15.0	26	55
30.4	4.7	8.1	5.0	9.4	8.1	14.0	15.8	31	44
29.6	5.0	8.3	5.3	9.7	8.0	13.8	15.3	38	55
31.6	5.1	8.9	5.2	9.8	9.0	14.8	16.8	36	54
28.4	4.7	8.2	4.6	8.8	8.1	13.8	14.6	28	52
28.4	4.4	7.8	4.7	8.9	8.2	13.6	15.4	35	53

Table 5a. Maxilla measurements of cricetid taxa; α and β in degrees. The meaning of the parameters is explained in Fig. 6.

Cricetus polgardiensis sp.nov. from Polgárdi 4 'Upper'
α/β: 50/92, 83/34, 92/61, 96/56, 89/40, 88/42, 80/55, 91/45, 98/48, 90/42, 84/46, 72/46, 90/55, 90/46, 90/46.

Cricetus polgardiensis sp. nov. from Polgárdi 4 'Lower'
α/β: 79/50, 82/56, 94/56, 95/38, 88/52, 108/54, 98/41, 84/50, 85/50, 96/47, 73/51, 93/56, 88/58, 100/54, 116/61, 100/54, 91/49, 92/54, 85/40, 104/53, 86/48, 95/49, 89/57, 98/61, 85/52, 93/47, 96/53, 89/49, 88/46, 89/45, 77/49, 86/52, 89/64

Cricetus praeglacialis from Villány 8/12
α/β: 100/52, 101/52, 101/52

Cricetus cricetus nanus from Betfia
α/β: 110/65, 109/69, 109/63, 101/40, 99/51, 118/54, 107/50

Cricetulus (Phodopus) songarus from USSR, Recent
α/β: 93/43, 94/34, 98/50

Cricetus cricetus from Jankovich Cave
α/β: 130/30, 133/42, 131/32, 115/41

Cricetus cricetus from Balmazujváros, Recent
α/β: 98/38, 104/58, 106/44, 98/41, 107/52, 108/59, 98/51, 102/44, 94/42, 101/51, 100/50, 106/49, 108/55, 111/54, 93/47, 104/54, 104/55, 90/50, 92/56, 97/48, 106/50, 105/50, 104/50, 94/47, 98/55, 101/55, 109/52, 106/51, 111/50, 105/56, 90/55, 104/50, 110/ 54, 97/48, 98/46, 95/48, 109/49, 104/57, 104/50, 102/50, 99/63, 115/58, 103/62, 98/59, 91/54, 103/44, 102/56, 103/53, 103/45, 99/48

Table 6. Measurements of *Cricetus kormosi* Schaub from Polgárdi 2 (length x width in mm).

M^1	M^2	M^3
2.5 xx 1.6		
2.5 xx 1.5		
2.4 xx 1.5		
2.4 xx 1.3	1.8 xx 1.5	
2.5 xx 1.6	2.0 xx 1.6	
2.5 xx 1.5	2.0 xx 1.5	1.6 xx 1.4
2.5 xx 1.5	2. xx 1.5	
2.3 xx 1.4	1.9 xx 1.5	
2.5 xx 1.6	2.0 xx 1.6	
M_1	M_2	M_3
2.0 xx 1.2	1.8 xx 1.3	2.0 xx 1.4
2.3 xx 1.3	2.0 xx 1.6	2.0 xx 1.5
2.5 xx 1.5	2.0 xx 1.5	2.0 xx 1.5
		2.0 xx 1.5

Table 7. Frequency of morphotypes in *Karstocricetus* from Tardosbánya, *C. polgardiensis* from Polgárdi 4 'Lower', *C. polgardiensis* from Polgárdi 4 'Upper', *C. kormosi* from Polgárdi 2. The meaning of the symbols is explained in Figs. 16-21.

Type	Tardosbánya		Polgárdi 4 'Lower'		Polgárdi 4 'Upper'		Polgárdi 2
	n	%	n	%	n	%	n
M^1							
C1A1	30	75	29	28	20	20	–
C1A2	3	7.5	28	27	18	18	–
B2B2	–	–	1	1	5	5	–
C2B2	–	–	1	1	4	4	–
B1A2	–	–	2	2	4	4	–
C1B1	–	–	7	7	4	4	–
C2A1	–	–	–	–	4	4	–
C4A2	2	5	4	4	4	4	–
B1A1	–	–	3	3	4	4	–
B2A2	–	–	–	–	3	3	–
C4D2	–	–	2	2	3	3	8
B1B2	–	–	–	–	3	3	–
C4A1	5	12.5	5	5	2	2	–
C2C1	–	–	–	–	2	2	–
C3A1	–	–	–	–	2	2	–
C1B2	–	–	4	4	2	2	–
B1B1	–	–	1	1	2	2	–
C3C2	–	–	1	1	2	2	–
B2A1	–	–	–	–	1	1	–
C1B1	–	–	–	–	1	1	–
B2B1	–	–	–	–	1	1	–
B4A2	–	–	2	2	1	1	–
B3C2	–	–	–	–	1	1	–
C2C2	–	–	–	–	1	1	–
C3C1	–	–	–	–	1	1	–
B3A1	–	–	–	–	1	1	–
C4C2	–	–	–	–	1	1	–
C4B1	–	–	5	5	1	1	–
B1D2	–	–	–	–	1	1	–
B4D2	–	–	–	–	1	1	–
C2B1	–	–	2	2	–	–	–
C4B2	–	–	2	2	–	–	–
C2A2	–	–	2	2	–	–	1
B2C2	–	–	1	1	–	–	–
M^2							
2A2	23	56	48	54	49	49	1
2B2	–	–	15	17	18	18	–
2A3	11	27	15	17	13	13	–
2B3	–	–	5	6	11	11	–
2C2	–	–	–	–	8	8	2
1A1	–	–	–	–	1	1	–
2A1	7	17	4	5	–	–	–
2B1	–	–	1	1	–	–	–
2D2	–	–	–	–	–	–	3

Type	Tardosbánya		Polgárdi 4		'Lower'Polgárdi 4		'Upper'Polgárdi 2
	n	%	n	%	n	%	n
M^3							
B1B	6	43	2	13	10	14.7	–
C1B	–	–	1	6	10	14.7	–
A1B	3	21	4	30	8	11.7	–
B2B	–	–	2	13	8	11.7	–
B1A	–	–	1	6	5	7.3	–
A2A	–	–	–	–	5	7.3	–
B2A	–	–	2	13	5	7.3	–
A2B	1	7	–	–	5	7.3	–
C1A	–	–	1	6	4	5.8	–
D2B	2	14	2	13	4	5.8	1
C2B	–	–	–	–	2	2.9	–
A1A	–	–	–	–	1	1.4	–
D1B	–	–	–	–	1	1.4	–
C2A	1	7	–	–	–	–	–
M_1							
C2A2	4	7	19	19.5	14	15	–
B1A2	7	14	4	4.1	10	11	–
C1A2	10	20	22	22.6	9	10	–
B2A2	5	10	4	4.1	6	7	–
B1A1	1	2	1	1	5	6	–
B2A1	–	–	1	1	5	6	–
C2A1	1	2	13	13.4	4	5	–
C1B2	–	–	3	3.1	4	5	–
B2B2	–	–	–	–	3	3	–
C2B2	–	–	2	2.1	3	3	–
C1C2	–	–	2	2.1	3	3	–
B2C2	–	–	–	–	3	3	–
C1A1	2	4	10	10.3	3	3	–
C2C2	–	–	1	1	2	2.2	–
D2A2	–	–	–	–	2	2.2	–
C2B1	–	–	–	–	2	2.2	–
B1D2	–	–	–	–	2	2.2	–
C1D2	–	–	–	–	1	1.1	1
C1C1	–	–	1	1	1	1.1	–
D1A2	–	–	3	3.1	1	1.1	–
CD2	–	–	–	–	1	1.1	–
D1A1	–	–	–	–	1	1.1	–
A1A1	1	2	1	1	1	1.1	–
B1B2	–	–	1	1	1	1.1	–
A1A2	14	27	3	3.1	1	1.1	–
A1D2	–	–	–	–	1	1.1	–
B1C2	–	–	1	1	1	1.1	–
A2A2	5	10	–	–	–	–	–
C3A2	1	2	–	–	–	–	–
A2A1	1	2	–	–	–	–	–
A1C2	–	–	2	2.1	–	–	–
D2A1	–	–	3	3.1	–	–	–
B1D1	–	–	–	–	–	–	1
B2C1	–	–	–	–	–	–	1

Type	Tardosbánya		Polgárdi 4	’Lower’Polgárdi 4		’Upper’Polgárdi 2	
	n	%	n	%	n	%	n
M_2							
A1B	31	72	30	49	35	35	–
A1A	2	5	12	20	24	24	–
B1B	8	19	7	10	16	16	–
C1B	–	–	6	9	16	16	–
D1B	–	–	6	9	7	7	1
B2B	–	–	–	–	1	1	–
B1A	1	2	2	2	–	–	–
A2B	1	2	–	–	–	–	–
C1A	–	–	–	–	–	–	2
M_3							
2C2B	–	–	–	–	16	16	–
2D2B	–	–	–	–	13	13	1
3A2B	8	43	–	–	11	11	–
3B2B	4	21	–	–	9	9	2
3C1B	–	–	2	10	9	9	–
3B1B	2	10	1	5	8	8	–
3C2B	–	–	–	–	7	7	–
2A2B	–	–	1	5	6	6	–
2B2B	–	–	–	–	5	5	–
2D1B	–	–	2	10	4	4	–
2B1B	–	–	1	5	3	3	1
3A1B	4	21	3	15	2	2	–
2A1B	–	–	1	5	2	2	–
3C1A	–	–	–	–	2	2	–
3D2A	–	–	–	–	1	1	–
2A2A	–	–	–	–	1	1	–
3D2B	–	–	–	–	1	1	–
3B2A	1	5	–	–	–	–	–
3B1B	–	–	3	15	–	–	–
2C1B	–	–	4	25	–	–	–
2A2B	–	–	1	5	–	–	–
3D1B	–	–	1	5	–	–	–

Table 8. Frequency of morphotypes in *Karstocricetus* from Tardosbánya, *C. polgardiensis* from Polgárdi 4 ’Lower’, *C. polgardiensis* from Polgárdi 4 ’Upper’, *C. kormosi* from Polgárdi 2. The meaning of the symbols is explained in Fig. 16-21.

Type	Tardosbánya	Polgárdi 4	’Lower’Polgárdi 4	’Upper’Polgárdi 2
	%	%	%	n
M^1				
B	–	10	28	–
C	100	90	72	9
1	85	75	56	–
2	–	6	24	1
3	–	1	7	–
4	15	18	13	7
A	100	73	65	1
B	–	23	24	–
C	–	2	7	–
D	–	2	4	7
1	94	50	48	–
2	6	50	52	8

Type	Tardosbánya	Polgárdi 4	'Lower'Polgárdi 4	'Upper'Polgárdi 2
	%	%	%	n
M^2				
1	–	–	1	–
2	100	100	99	7
A	100	76	64	1
B	–	24	29	–
C	–	–	7	2
D	–	–	–	3
1	17	5.5	–	–
2	56	67.5	76	6
3	27	26	24	–
M^3				
A	28	26	26	–
B	42	52	41	–
C	7	11	25	–
D	23	11	8	1
1	71	60	57	–
2	29	40	43	1
A	14	26	29	–
B	86	74	74	1
M_1				
A	40	5	3	–
B	28	12	42	2
C	32	79	50	1
D	–	4	5	–
1	66	52	51	2
2	34	48	49	1
A	100	88	69	–
B	–	7	13	–
C	–	5	13	1
D	–	–	5	2
1	75	32	23	2
2	25	68	77	1
M_2				
A	79	69	59	–
B	21	17	17	–
C	–	7	17	2
D	–	7	7	1
1	100	100	99	1
2	–	–	1	–
A	7	31	24	2
B	93	69	76	1
M_3				
2	–	52	51	2
3	100	48	49	2
A	63	31	22	–
B	37	26	25	4
C	–	37	37	–
D	–	6	16	–
1	31	89	30	1
2	69	11	70	3
A	5	–	4	–
B	95	100	96	4