

The Cricetidae (Mammalia, Rodentia) from the Late Miocene of Crevillente (prov. Alicante, Spain)

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The Cricetidae from various new localities in the area of Crevillente are described, and compared with the material published by de Bruijn et al. (1975). Among the material there are two new species: *Neocricetodon plinii* and *N. lucentensis*.

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Introduction

De Bruijn et al. (1975) described the micromammal fauna from six Late Miocene localities in the area of Crevillente (Alicante, Spain), and their correlation with marine biostratigraphy. Since 1986 we have carried out several collecting campaigns in the same area. In this paper the Cricetidae from a number of newly discovered localities are described (for a map of the area see Freudenthal et al., 1991, fig. 1), and compared with the original material of de Bruijn et al. (1975).

The material from the new localities is kept in the collections of the National Museum of Natural History, Leiden, The Netherlands. The measurements are given in units of 0.1 mm. The graphs were drawn on the Apple Laser Writer attached to the mainframe computer of Leiden University, by means of programs written by the

first author. The micrographs were made on the Zeiss 950 scanning microscope of the University of Granada. The terminology used in the description of the specimens is the one proposed by Mein & Freudenthal (1971). The measuring equipment and the orientation of the specimens are as defined by Freudenthal (1966).

Acknowledgements – We are grateful to Messrs P. Montoya and J. Coloma who helped us during our field work. We thank Dr H. de Bruijn for letting us study the material from Crevillente and Teruel in the collections of Utrecht University. Dr L. Kordos (Budapest) provided us with material of *Cricetus polgardiensis* from Polgárdi 5, for which we are very grateful. This study was financially supported by the Netherlands Organization for the Advancement of Pure Research (Z.W.O., now N.W.O.).

Taxonomic descriptions

Family CRICETIDAE Murray, 1866

Subfamily CRICETODONTINAE Schaub, 1925

Genus *Hispanomys* Mein & Freudenthal, 1971

'Hispanomys freudenthali van de Weerd, 1976'

Type-locality – Masada del Valle 2.

Discussion – Though no material of this species has been found in the Crevillente area, we will pay some attention to it because it plays a crucial role in a discussion on the phylogeny of *Hispanomys* and *Ruscinomys*.

The choice of the M¹ MDV2-1241 as the holotype is quite an unfortunate one. It is by far the largest specimen (40.2 × 26.6) in the sample, and probably does not belong to the same species as the other specimens. Neither by size nor by morphology it can be distinguished from *Pseudoruscinomys schaubi* (Villalta & Crusafont, 1956), so *H. freudenthali* is a junior synonym of *P. schaubi*. The length and width of this specimen are somewhat larger than the mean values given by Adrover (1986, p. 68) for the population of Los Mansuetos.

The M₂, MDV2-1212: dimensions 34.7 × 24.1, described by van de Weerd as *Hispanomys* sp. A (op. cit., p. 112), may well go with this M¹, and be attributed to *P. schaubi* as well. Its length is identical to the maximum given by Adrover (1986, p. 68) for the population of Los Mansuetos, its width surpasses the maximum for Los Mansuetos. It is a hardly worn specimen with a height of at least 25.0, no trace of an anterolophid, mesolophid connected to the metaconid at mid-height, protoconid and hypoconid very elongated, anteroconid pointing far forward. The specimen MDV2-1217, dimensions 27.4 × 18.4, is morphologically very similar to the specimen mentioned before, but it is much smaller. It differs from the remainder of the M₂ by the pointed shape of the anteroconid, the absence of a labial anterolophid, and the well-developed mesolophid, that is firmly connected to the posterior wall of the metaconid. By size and morphology it fits perfectly well in *Hispanomys adro-*

veri Agustí, 1986. Some of the M_3 from Masada del Valle 2 may be attributed to that species too.

The specimen MDV2-1255 is one of the smallest M^1 from Masada del Valle 2. It is the only specimen with a lingual posteroloph. It may be attributed to *H. peralensis* van de Weerd, 1976.

After eliminating these four specimens, the remainder of the material from Masada del Valle 2 may be characterized as a form, larger than *H. peralensis* and with a basically identical morphology. The labial anterolophid in M_1 is nearly always present, in M_2 always (discarding the very worn specimens). The most important difference between this form and *H. peralensis* is probably, that it never has a lingual posteroloph in M^1 and M^2 , whereas in *H. peralensis* this feature is (nearly always) present. Its measurements are:

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	7	28.2	29.76	31.7	1.182	8	17.1	18.91	20.0	1.064
M_2	6	26.2	28.27	30.0	1.516	6	18.8	20.62	21.6	1.028
M_3	10	21.8	23.75	26.0	1.282	10	16.1	17.71	20.2	1.186
M^1	7	33.6	36.93	39.7	2.151	10	21.5	22.87	24.4	0.937
M^2	9	25.5	26.58	28.1	0.926	8	18.0	19.75	21.3	1.072
M^3	24	16.0	19.14	20.7	1.258	24	14.8	16.93	19.6	1.328

So, there may be four different species of Cricetodontini in Masada del Valle 2: *P. schaubi*, *H. adroveri*, *H. peralensis*, and an unnamed form comprising the majority of the material. A possible explanation is, that the material is not homogeneous; there are remarkable differences in the colour of the sediment adhering to the specimens. Adrover (1986) describes rich collections of *H. freudenthali* from Los Aguanaces and Vivero del Pino, that may serve as a basis for the description of a new species.

Hispanomys peralensis van de Weerd, 1976

Pl. 1, figs. 1-7; Fig. 1.

1975 *Cricetodon* (*Hispanomys*) sp. A – de Bruijn, Mein et al., p. 297.

1976 *Hispanomys freudenthali* from Tortajada A – van de Weerd, p. 109, pl. 12, figs. 1-8.

Localities – Peralejos B, C (type), D, 4; Masia del Barbo 2A, 2B; Tortajada A (van de Weerd, 1976). Crevillente 1, 3 (de Bruijn et al., 1975). Crevillente 2 and 4B (this publication).

Locality Crevillente 2

Material – RGM 402 273 - 402 301, 404 851 - 404 868.

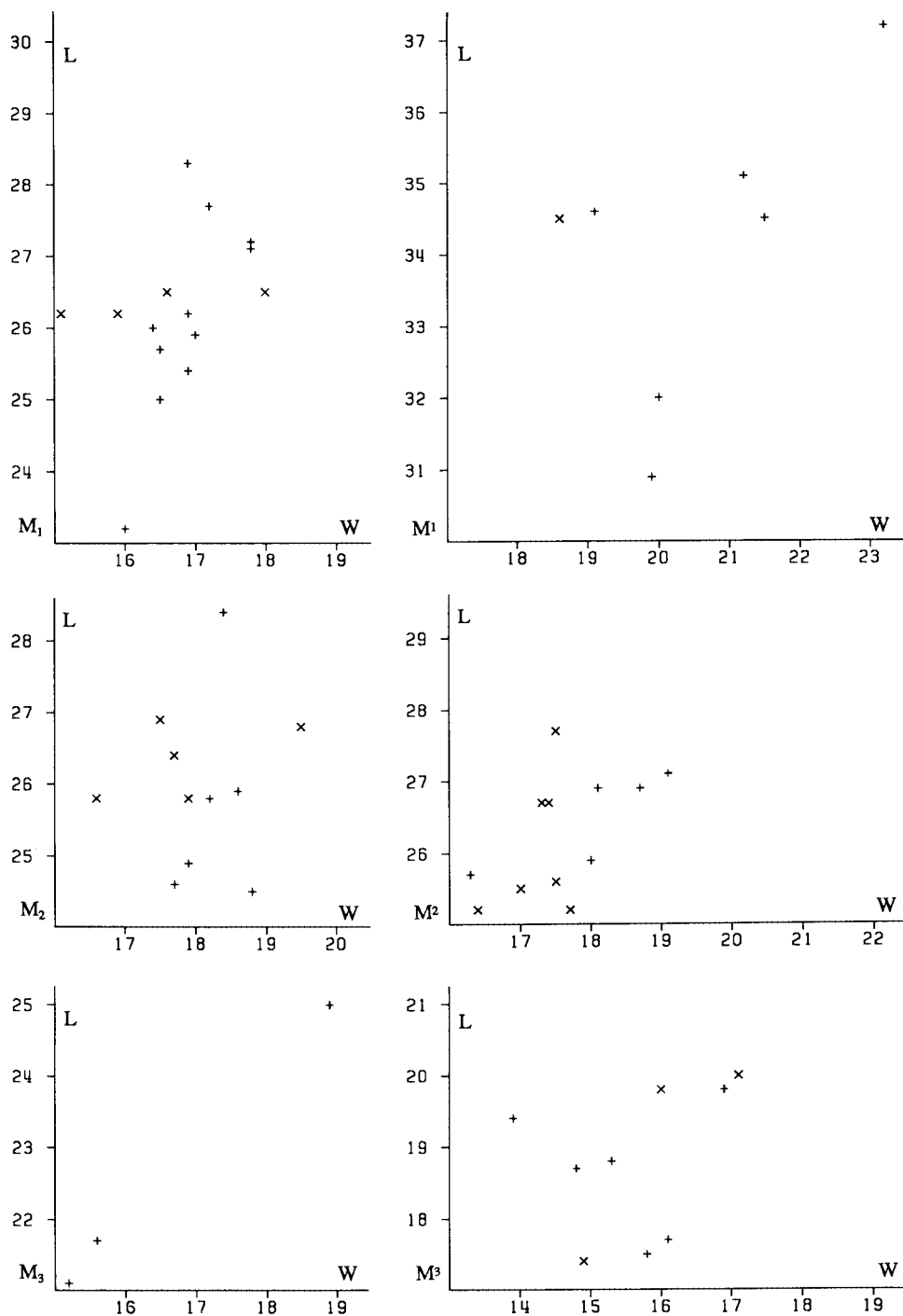


Fig. 1. Length/width diagrams of *Hispanomys peralensis* van de Weerd, 1976 from Crevillente 2 (+) and Crevillente 4B (x).

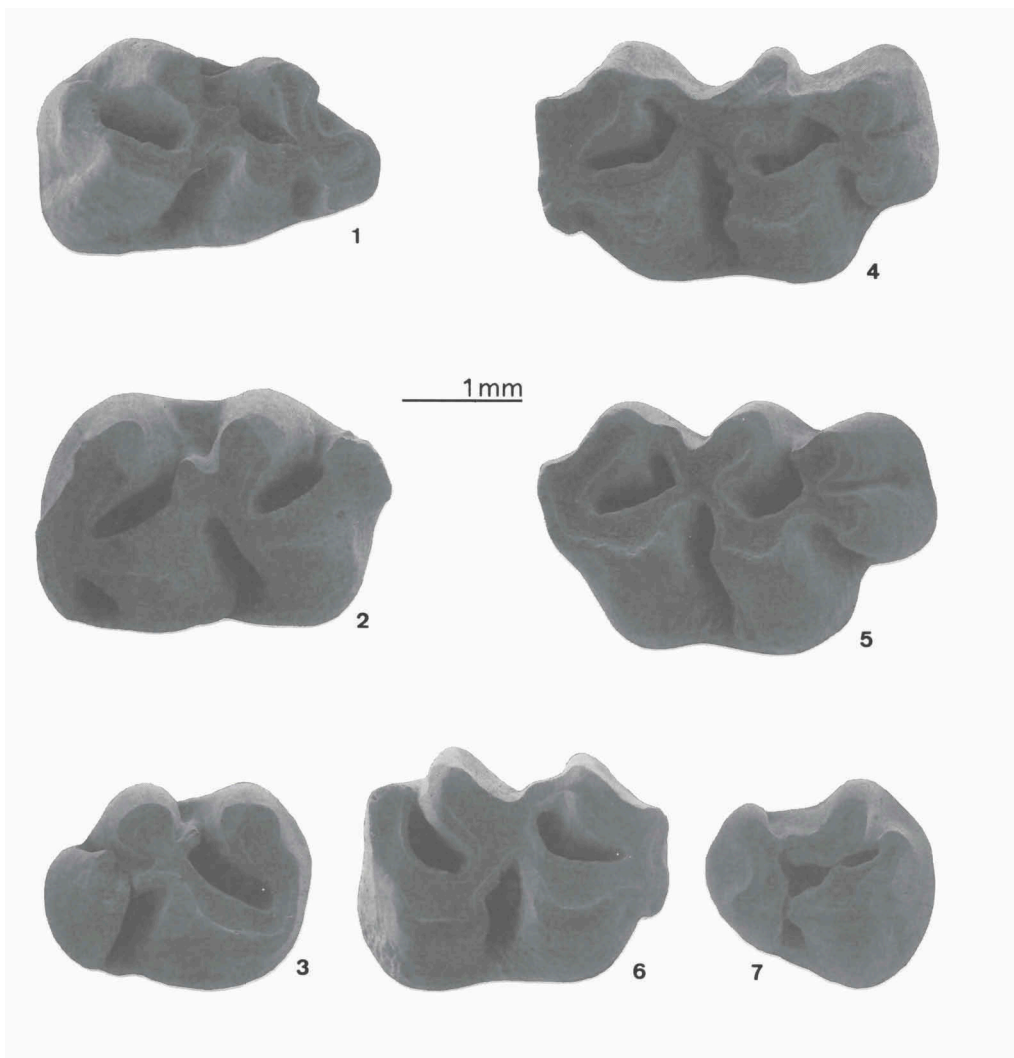


Plate 1

Hispanomys peralensis van de Weerd, 1976

From Crevillente 2.

Fig. 1. M_1 dext., RGM 402 278.

Fig. 2. M_2 sin., RGM 404 856.

Fig. 3. M_3 dext., RGM 402 286.

Fig. 4. M^1 dext., RGM 402 292.

Fig. 5. M^1 dext., RGM 404 864.

Fig. 6. M^2 sin., RGM 404 865.

Fig. 7. M^3 dext., RGM 404 868.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	10	25.0	26.45	28.3	1.070	10	16.4	16.99	17.8	0.495
M ₂	6	24.5	25.68	28.4	1.458	7	17.7	18.31	18.8	0.402
M ₃	4	21.1	22.63	25.0	1.715	5	15.0	16.30	18.9	1.612
M ¹	6	30.9	34.05	37.2	2.265	8	18.0	20.25	23.2	1.650
M ²	5	25.7	26.50	27.1	0.648	7	16.3	18.36	19.5	1.049
M ³	6	17.5	18.65	19.8	0.909	6	13.9	15.47	16.9	1.048

Description

M₁ – The labial anterolophid is weak (3) or strong (7). The protosinusid is well developed. The mesolophid is connected to the posterior wall of the metaconid (5), short (2), or absent (4). The sinusid is closed by a crest (6) or a cusp (4). The posterosinusid is open (8) or closed (2).

M₂ – The labial anterolophid is strong (5) or weak (1). The mesolophid is connected to the metaconid (5) or free (1). The posterosinusid is open (4) or closed at a low level (1).

M₃ – The labial anterolophid is strong (4), weak (1), or absent (1). The mesolophid is free (4), connected to the posterior wall of the metaconid (1), or there is a spur on the anterior wall of the entoconid (1). The posterosinusid is open.

There are small specimens, almost without posterolophid, and large specimens with a long posterolophid. They might be attributed to two different species, but the other elements of the dentition do not support such a separation.

M¹ – The anterocone is subdivided by a groove that reaches halfway down its height. In unworn specimens the anterior ectoloph is slightly lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is nearly always present. There is a certain degree of enamel differentiation: the enamel may be very thin or even absent on the posterior wall of the protocone and the internal part of the sinus.

There are strong size differences, in part caused by the degree of wear of the specimens, in part by the inclination of the anterocone; RGM 404 861 is very much worn and would give a higher length value if it were a fresh specimen; in RGM 404 864 the base of the anterocone may be missing, which would result in too small a value for the length. The true length minimum is certainly not under 32.0.

M² – In unworn specimens the anterior ectoloph is slightly lower than the anteroloph. The protocone has a posterior hook. The lingual posteroloph is present.

M³ – The lingual anteroloph is present (1) or absent (4). The anterior ectoloph is not very low. The protocone-hypocone connection is complete (3) or interrupted (4).

Hypsodonty is difficult to assess without a sufficient number of unworn teeth. We can only estimate that the height of unworn M¹ must be 16.2 or more, and that of M³ over 13.2.

Locality Crevillente 4B

Material – RGM 404 758 - 404 786.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	4	26.2	26.35	26.5	0.174	4	15.1	16.40	18.0	1.230
M ₂	5	25.8	26.34	26.9	0.527	5	16.6	17.84	19.5	1.053
M ¹	2	34.5	35.30	36.1	1.131	1	–	18.60	–	–
M ²	7	25.2	26.09	27.7	0.958	8	16.4	17.16	17.7	0.484
M ³	3	17.4	19.07	20.0	1.447	3	14.9	16.00	17.1	1.100

Description

M₁ – The labial anterolophid is strong (6). The protosinusid is well developed. The mesolophid is connected to the posterior wall of the metaconid (1) or short (5). The sinusid is closed by a crest (3) or a cusp (2). The posterosinusid is open (5).

The strongest anterolophids coincide with the sinusid cusps (2 specimens).

M₂ – The labial anterolophid is strong (6). The mesolophid is connected to the metaconid at a very low level (5). The posterosinusid is open (6).

M¹ – In unworn specimens the anterior ectoloph is lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is present and well developed.

M² – In unworn specimens the anterior ectoloph is lower than the anteroloph. The protocone has a posterior hook. The lingual posteroloph is present and well developed.

M³ – The lingual anteroloph is absent (3). The anterior ectoloph is low. The protocone-hypocone connection is complete (3).

The height of unworn M¹ is estimated at more than 16.0, and that of M³ at more than 14.6.

Discussion – Van de Weerd described *H. peralensis* from Peralejos C. His richest locality is Masia del Barbo 2B. He also described *H. freudenthali* from Masada del Valle 2 and Tortajada A.

Our measurements for Crevillente 2 and 4B seem to give higher values than the ones published by van de Weerd for Masia del Barbo 2B. We remeasured the Masia del Barbo material, and found values that are basically the same as for Crevillente 2 and 4B.

We also compared our material with *H. freudenthali* from Masada del Valle 2 and Tortajada A (van de Weerd, 1976). The measurements for Tortajada A and various populations of *H. peralensis* largely overlap, and morphologically the speci-

mens from Tortajada A do not differ substantially from those of *H. peralensis*. We therefore attribute the Tortajada material to *H. peralensis*. There is, however, one detail in the Tortajada material that we have not found in any other population: Among 5 M_1 , only one specimen has a metalophulid directed to the anteroconid, in one specimen it is transverse, and the other three have a double metalophulid with an anterior branch connected to the anteroconid and a posterior branch connected to the middle of the protoconid.

As argued above, the type-specimen of *H. freudenthali* from Masada del Valle 2 should be attributed to *Pseudoruscinomys schaubi*. The bulk of the material from Masada del Valle 2 is larger than the specimens from Tortajada A to such a degree, that there is no size overlap in the measurements of M_1 . There is size overlap in M^1 , but this is mainly due to one very small specimen (MDV2-1255), that might be a *H. peralensis* (see paragraph on '*H. freudenthali*').

The specimens from Tortajada A seem to be somewhat more hypsodont than those from Masia del Barbo 2B. In Masia del Barbo the lingual posteroloph is present in both M^1 and M^2 , in Tortajada A it is present in M^1 and absent in M^2 . In Masada del Valle 2 it is absent in both M^1 and M^2 .

In *H. peralensis* from Crevillente and from Tortajada A the mesolophid seems to be better developed than in the population from Masia del Barbo 2B.

Differences between *H. peralensis* from the Teruel localities and the Crevillente material are: a somewhat larger degree of hypsodonty, the number of roots in M^1 ; and slightly smaller dimensions in some of the Teruel populations. However, we were not able to reproduce the high values for hypsodonty published by van de Weerd; we found lower values, but one has to keep in mind, that no reliable measuring method has been defined.

Differences between the form from Masada del Valle 2 and the specimens from Crevillente 2 and 4B are: the specimens from Masada del Valle 2 are larger; the fifth root in M^1 is more developed in Masada del Valle 2; the lingual posteroloph of M^1 ; and M^2 is absent in Masada del Valle 2. By these features the Crevillente material appears to be less evolved than the Masada del Valle population, and quite comparable with the Tortajada specimens. However, by these same standards the material from Crevillente 2 would be more evolved than the specimens from the stratigraphically higher locality Crevillente 4B. Also, the anterior ectolophs in Crevillente 4B are lower than in Crevillente 2.

A possible explanation might be, that the Crevillente 2 population is a mixture of two species:

- 1: M_1 with strong labial anterolophid; metalophulid directed far forward towards the anteroconid; mesolophid rather well-developed; sinusid closed by a cusp-like structure.
- 2: M_1 without labial anterolophid; metalophulid directed more transversely, towards anterolophulid or protoconid, or double; mesolophid absent or very weak; sinusid closed by a smooth crest.

In Crevillente 4B only type 1 is present, in Crevillente 2 both types are found. In Crevillente 4B all M^1 have a lingual posteroloph, in some specimens from Crevillente 2 this feature is absent; these specimens might go with the M_1 of type 2. Un-

fortunately the Crevillente material is not sufficiently rich to solve the question, whether there are one or two species. Enlarging the collections is possible, but quite a laborious task. In Crevillente 2 one *Hispanomys* molar was found per 100 kg sediment, in Crevillente 4B only one molar per 180 kg.

Freudenthal (1966) suggested that there might be two species within the material from Masia del Barbo 2B. Van de Weerd (1976) allocated the entire collection to one species, but could not explain the bimodal distribution of the M^3 (op. cit., fig. 21). We still think there are two species, the more so since the predecessors of the previously mentioned types of M_1 may be distinguished in Masia del Barbo 2B.

One of these species would be *H. peralensis*, the other one might be the ancestor of the form from Masada del Valle 2, in which case *H. peralensis* would not be its ancestor as supposed by van de Weerd (1976).

Hispanomys adroveri Agustí, 1986
Pl. 2, figs. 1-8; Fig. 2.

Localities – Casa del Acero (Murcia, Spain; type), Crevillente 5, 15.

Locality Crevillente 15

Material – RGM 402 216 - 402 272, 404 787 - 404 850.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	9	28.7	30.43	31.8	0.960	9	18.6	19.44	20.7	0.789
M_2	20	25.7	28.10	30.8	1.329	24	17.9	19.47	21.0	0.798
M_3	20	23.7	24.81	26.7	0.907	20	15.7	17.21	18.8	0.875
M^1	9	35.0	36.74	38.4	1.291	12	21.5	22.44	23.3	0.605
M^2	20	25.4	27.52	31.4	1.498	20	18.3	19.77	21.6	0.763
M^3	29	16.8	18.71	20.2	0.858	29	14.3	16.21	18.2	0.967

Description

M_1 – The labial anterolophid is weak (5) or absent (4). The protosinusid is present. The metalophulid is directed towards the anteroconid (6) or towards the anterolophulid (2). The mesolophid is connected to the posterior wall of the metaconid (6) or short (2). The sinusid is closed by a crest (9). The posterosinusid is closed (5) or open (4). There is a certain degree of enamel differentiation: the enamel may be very thin on the lingual walls of protoconid and hypoconid, but it is never absent.

M_2 – The labial anterolophid is absent (18). The mesolophid is connected to the metaconid (22), generally at a high level. The posterosinusid is open (20) or closed at a low level (2).

RGM 402 230 is a much smaller specimen than the rest of the material; this is due to the shape of the anteroconid, which is pointed and elongated forward in most specimens, and less pronounced in this one. It might belong to another species.

M₃ – The labial anterolophid is absent (20). The mesolophid is connected to the metaconid at a high level (12) or lower (5). The posterosinusid is open (20).

M¹ – In unworn specimens the anterior ectoloph is slightly lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is absent. There are 4 roots plus a very small one.

RGM 402 245 has a longitudinal crest in the anterosinus between lingual anterocone and paracone.

M² – In unworn specimens the anterior ectoloph is lower than the anteroloph. The protocone has a posterior hook. The lingual posteroloph is absent.

M³ – The lingual anteroloph is absent. The anterior ectoloph is as high as the anteroloph. The protocone-hypocone connection is always interrupted.

The height of unworn M¹ is estimated at more than 20.0, and that of M³ at more than 17.2.

Discussion – The material from Crevillente 15 is morphologically identical to the type-material from Casa del Acero. The dimensions of the type-material seem to be somewhat larger than those of our specimens.

Four genera should be regarded in a discussion on this species: *Ruscinomys* Depéret, 1890; *Pseudoruscinomys* Mein & Freudenthal, 1971; *Pararusruscinomys* Agustí, 1981; *Hispanomys* Mein & Freudenthal, 1971.

The genus *Pseudoruscinomys* was created by Mein & Freudenthal (1971) for *Ruscinomys schaubi* Villalta & Crusafont, 1956. Van de Weerd (1976) synonymized *Pseudoruscinomys* and *Ruscinomys*, without giving an argument for this decision, and most authors followed his interpretation. We think there are sufficient morphological differences to maintain the genus *Pseudoruscinomys*:

In *Pseudoruscinomys schaubi* the mesolophids of the lower molars are smaller than in *Ruscinomys europaeus* from Layna. Adrover (1986, p. 62, 63 and 79, 80) demonstrated that in *P. schaubi* the mesolophid is better developed in Aljezar B than in Los Mansuetos. Since Aljezar B is older than Los Mansuetos (Adrover, 1986, p. 79), the mesolophid is a disappearing feature in this species, in contradiction with the increasing importance of the mesolophid in the supposed lineage *P. schaubi* – *R. europaeus*.

Plate 2

Hispanomys adroveri Agustí, 1986
From Crevillente 15.

- Fig. 1. M₁ dext., RGM 404 791.
- Fig. 2. M₂ sin., RGM 404 793.
- Fig. 3. M₂ sin., RGM 404 794.
- Fig. 4. M₃ sin., RGM 402 236.
- Fig. 5. M¹ sin., RGM 402 247.

Fig. 6. M¹ sin., RGM 402 245.

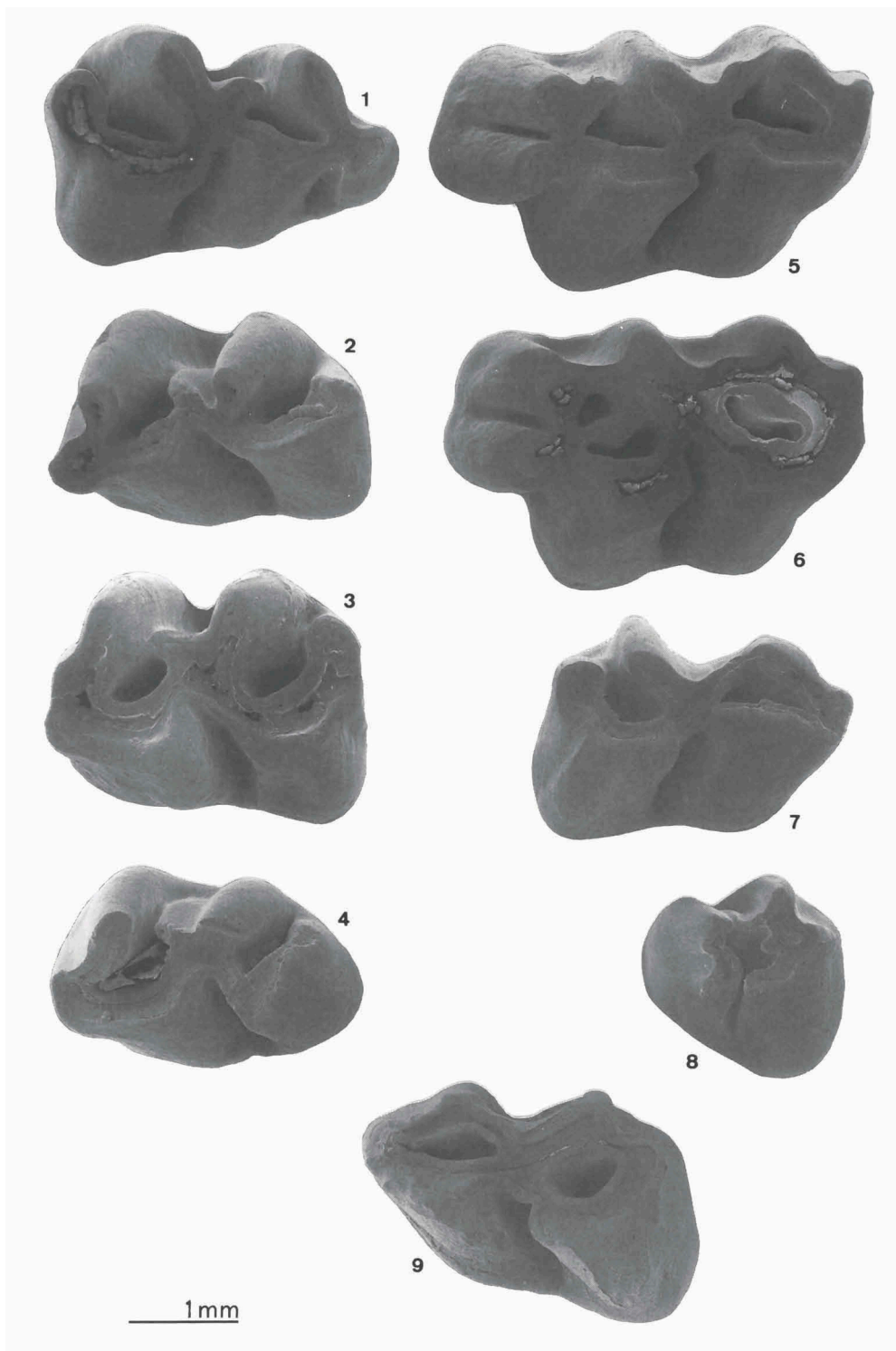
Fig. 7. M² sin., RGM 402 254.

Fig. 8. M³ dext., RGM 402 268.

Hispanomys sp.

From Crevillente 15.

Fig. 9. M² sin., RGM 404 827.



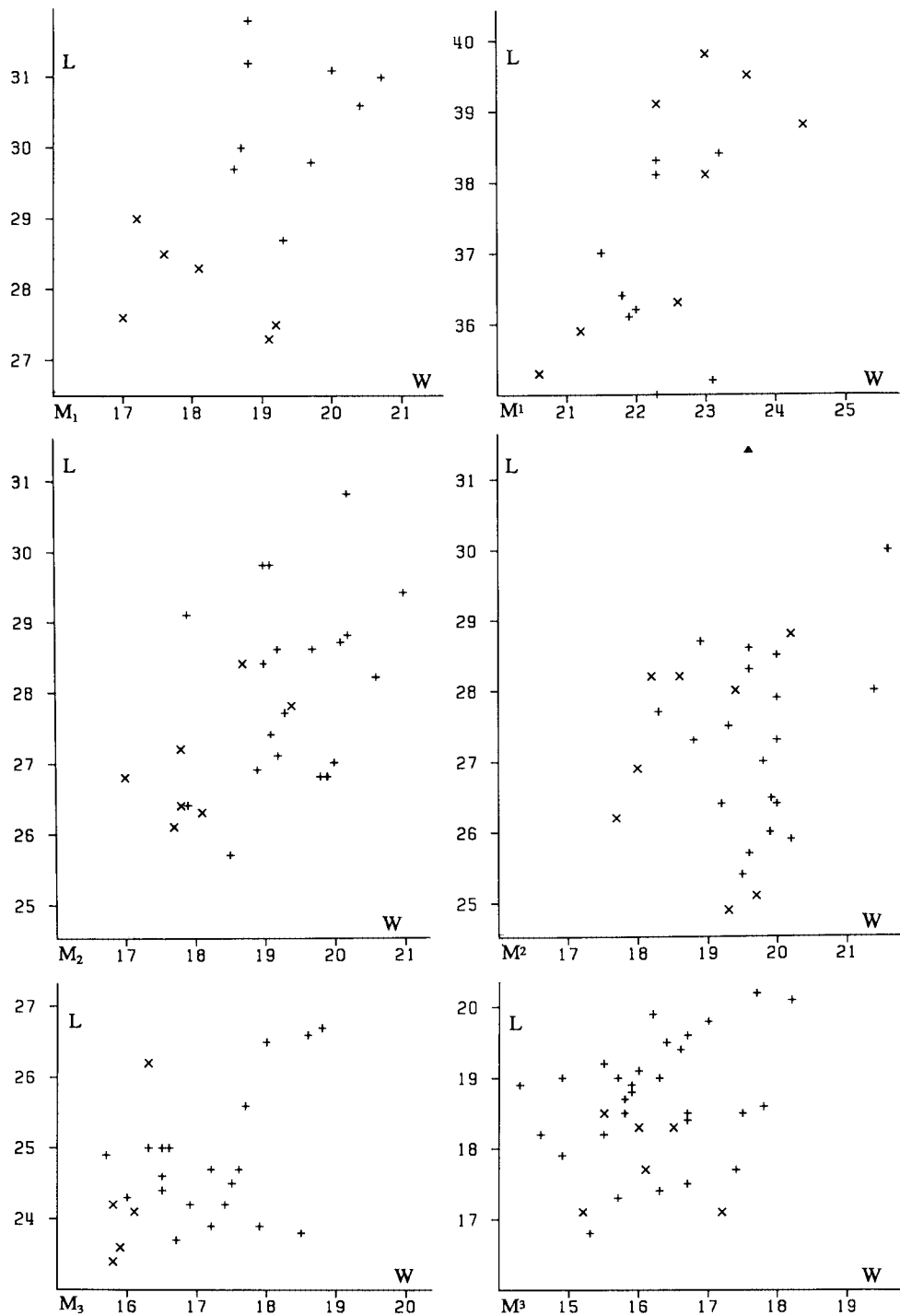


Fig. 2. Length/width diagrams of *Hispanomys adroveri* Agustí, 1986 from Crevillente 15 (+), and *Hispanomys* aff. *adroveri* Agustí, 1986 from Crevillente 17 (x).

In *Pseudoruscinomys schaubi* the metalophulid of the M_1 is directed more obliquely forward than it is in *R. europaeus*. We consider the transverse metalophulid to be a primitive feature.

These characteristics eliminate *P. schaubi* from the evolutionary lineage of *R. europaeus* and demonstrate once more its generic independency. One should keep in mind the possibility hinted at by Adrover (1986), that *P. schaubi* comprises two different species.

The genus *Pararuscinomys* was created by Agustí (1981). Mein & Freudenthal (1971) thought the species *lavocati* Freudenthal, 1966 might be the ancestor of *Pseudoruscinomys schaubi*. Agustí (1981) discards this possibility. However, the description of *P. lavocati* by Agustí adds no argument in pro or in contra of the supposed lineage *lavocati* – *schaubi*. This problem remains unsolved.

Hispanomys adroveri is found in the locality of Crevillente 15, which is undoubtedly younger than Crevillente 2 and 4B. By its larger size, missing labial anterolophids, and missing lingual posterolophs it might be a descendant of *H. peralensis* from the latter localities. In that case the mesolophid in this lineage would be a growing, and not a disappearing feature. We think, however, that the metrical and morphological differences between *H. peralensis* and *H. adroveri* are so abrupt, that a phyletic relationship is improbable.

Van de Weerd (1976) construed the evolutionary lineage *H. freudenthali* – *P. schaubi*. This would mean an even more abrupt change, and we don't support this view, the more so, since *H. freudenthali* sensu van de Weerd and *P. schaubi* concur in the locality Masada del Valle 2 (see also the paragraph on '*H. freudenthali*'). The form from Masada del Valle 2 cannot be the ancestor of *P. schaubi*.

One might consider the possibility that the form from Masada del Valle 2 be the ancestor of *H. adroveri*. Such a lineage would be characterized by the loss of the anterolophids in the lower molars and an increase of the mesolophid. However, in our opinion it is quite possible, that both these forms are present in Masada del Valle 2 (see paragraph on '*H. freudenthali*').

An evolution from *H. adroveri* towards *P. schaubi* would be acceptable, but then we are confronted with the problem that they are contemporaneous or almost contemporaneous species (and possibly concurrent in Masada del Valle 2).

Our conclusion is, that *H. peralensis*, *H. adroveri* and *P. schaubi* represent three different evolutionary lineages. A fourth lineage may be represented by the majority of the material from Masada del Valle 2. A revision of this material seems appropriate, and it should be compared in detail with the rich material described by Adrover (1986) as *H. freudenthali* from Los Aguanaces and Vivero de Pinos.

It should be noted, that *Pseudoruscinomys schaubi* is only known from the Teruel area, and *Hispanomys adroveri* only from Murcia and Alicante. There are reasons to assume that these two areas had quite different climatic and ecological conditions that may have influenced the evolution of the species in question.

Hispanomys aff. *adroveri* Agustí, 1986

1975 *Cricetodon* (*Hispanomys* sp. B – de Bruijn, Mein et al., p. 297.

Localities – Crevillente 5, 8, 14, 17.

Locality Crevillente 17

Material – RGM 404 705 - 404 738, 404 748 - 404 757.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	6	27.3	28.03	29.0	0.668	6	17.0	18.03	19.2	0.944
M ₂	7	26.1	27.00	28.4	0.851	7	17.0	18.07	19.4	0.774
M ₃	5	23.4	24.30	26.2	1.114	7	15.8	16.07	16.5	0.263
M ¹	8	35.3	37.85	39.8	1.763	9	20.5	22.36	24.4	1.345
M ²	8	24.9	27.04	28.8	1.501	8	17.7	18.89	20.2	0.892
M ³	6	17.1	17.83	18.5	0.628	6	15.2	16.08	17.2	0.714

Description

M₁ – The labial anterolophid is weak (5) or absent (1). The protosinusid is present. The metalophulid is directed towards the anteroconid or towards the anterolophulid. The mesolophid is connected to the posterior wall of the metaconid at a low level (4). The sinusid is closed by a crest (5). The posterosinusid is closed (4) or open (2).

M₂ – The labial anterolophid is absent (5). The mesolophid is connected to the metaconid at a high level (5). The posterosinusid is open (3) or closed at a low level (2).

M₃ – The labial anterolophid is absent (4). The mesolophid is connected to the metaconid at a high level (5) or at a low level (1). The posterosinusid is open (7).

M¹ – In unworn specimens the anterior ectoloph is lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is absent. There are 4 roots plus a small fifth root under the paracone.

M² – In unworn specimens the anterior ectoloph is lower than the anteroloph. The protocone has a posterior hook. The lingual posteroloph is absent.

M³ – The lingual anteroloph is absent. The anterior ectoloph is as high as the anteroloph. The protocone-hypocone connection is interrupted (5) or complete (1).

The height of unworn M¹ is estimated at more than 21.0, and that of M³ at more than 16.5.

Discussion – Morphologically this population is identical to the one from Crevillente 15. The molars are, however, consistently smaller, except for M¹. This element is not only on the average larger, but the 3 largest M¹ are even larger than any specimen from Crevillente 15. This may be due to differences in wear, but also to the fact that the anterocone in Crevillente 15 has a curved anterior wall: oblique in the upper part, more vertical at its base. In Crevillente 17 (and in Crevillente 8) the entire anterior wall is oblique.

Crevillente 17 is undoubtedly younger than Crevillente 15. This means that this lineage is characterized by size decrease.

Locality Crevillente 8

Material – RGM 403 175 - 403 180.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₃	1	–	24.60	–	–	1	–	16.80	–	–
M ¹	1	–	37.40	–	–	1	–	22.90	–	–
M ²	1	–	27.80	–	–	1	–	19.00	–	–
M ³	2	17.8	18.50	19.2	0.990	2	15.4	16.70	18.0	1.838

Description

M₃ – The mesolophid is connected to the metaconid at a high level. The posterosinusid is open.

M¹ – The anterior ectoloph is lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is absent.

M² – The lingual posteroloph is absent.

M³ – The lingual anteroloph is absent. The anterior ectoloph is as high as the anteroloph. The protocone-hypocone connection is interrupted (3).

The height of unworn M¹ is estimated at more than 21.0, and that of M³ at more than 16.0.

Locality Crevillente 14

Material – RGM 402 302 - 402 323, 402 899.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	27.9	29.45	31.0	2.192	1	–	17.90	–	–
M ₂	0	–	–	–	–	1	–	15.50	–	–
M ₃	4	24.0	25.43	28.0	1.767	4	16.3	16.97	17.3	0.472
M ¹	2	35.7	36.80	37.9	1.556	2	20.0	21.15	22.3	1.626
M ²	5	25.5	27.34	29.4	1.496	5	17.6	18.48	19.4	0.672
M ³	3	18.9	19.73	20.2	0.723	3	15.4	16.10	16.9	0.755

Description

M₁ – The labial anterolophid is strong (2). The protosinusid is present. The mesolophid is connected to the posterior wall of the metaconid at a high level (2). The sinusid is closed by a crest (2). The posterosinusid is closed (2).

M₂ – The mesolophid is connected to the metaconid at a high level. The posterosinusid is open.

M₃ – The labial anterolophid is absent (4). The mesolophid is connected to the metaconid at a high level (3) or lower (1). The posterosinusid is open (4).

M¹ – In unworn specimens the anterior ectoloph is lower than the anterocone. The protocone has a posterior hook. The lingual posteroloph is absent. There are 4 roots plus a small fifth root under the paracone.

M² – In unworn specimens the anterior ectoloph is lower than the anteroloph. The protocone has a posterior hook. The lingual posteroloph is absent.

M³ – The lingual anteroloph is absent. The anterior ectoloph is high. The protocone-hypocone connection is interrupted (3) or complete (2).

The height of unworn M³ is estimated at more than 16.4.

Discussion – Morphologically, and in size, this population is identical to the one from Crevillente 17. Only one M₃, RGM 402 308, 28.0 × 17.3, is considerably larger than any other *Hispanomys* M₃ found in the area. This specimen may represent another species. In size it agrees with *Hispanomys* sp. described below.

Hispanomys sp.

Pl. 2, fig. 9.

Locality – Crevillente 15.

Material – M², RGM 404 827, 31.4 × 19.6.

This specimen is considerably larger than the specimens of *H. adroveri*. It shows a remnant of the lingual posteroloph, which is not present in the other specimens. It probably belongs to another species. Its size coincides with that of the largest

specimens of *P. schaubi*, but the strong inclination of the anterior and posterior wall, and of the sinus are not characteristic of that species.

Subfamily CRICETINAE Murray, 1866

Genus *Neocricetodon* Kretzoi, 1930

Type-species – *Neocricetodon schaubi* Kretzoi, 1930 (see also Kretzoi, 1951, p. 407; 1954, p. 62).

Species included – *N. lavocati* (Hugueney & Mein, 1965), *N. polonicus* (Fahlbusch, 1969), *N. magnus* (Fahlbusch, 1969), *N. intermedius* (Fejfar, 1970), *N. fahlbuschi* (Bachmayer & Wilson, 1970), *N. cf. fahlbuschi* in Daxner-Höck, 1972, *N. occidentalis* Aguilar, 1982, *N. transdanubicus* Kretzoi, 1985, *N. meini* (Agustí, 1986), *N. nestori* (Engesser, 1989), *N. plinii* sp. nov., and *N. lucentensis* sp. nov.

N.B. In the descriptions the metalophule is called posterior (or double), only if there is a posterosinus labially of the crest; the always existing connection of the metacone with the labial end of the posteroloph is not a metalophule.

Neocricetodon occidentalis (Aguilar, 1982)

Pl. 3, figs. 1-13; Fig. 3.

1970 *Kowalski fahlbuschi* Buchmayer & Wilson – de Bruijn, Mein et al., p. 17.

1982 *Neocricetodon occidentalis* sp. nov. – Aguilar, 1982, p. 10.

Locality Crevillente 2

Material – RGM 385 689 - 385 874, 402 012 - 402 026, 402 688 - 402 692.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	21	18.5	19.83	21.0	0.747	22	11.4	12.26	12.8	0.451
M ₂	39	14.2	16.76	17.7	0.676	40	12.1	13.25	14.5	0.511
M ₃	24	14.0	16.00	17.2	0.867	24	11.6	12.85	14.1	0.623
M ¹	20	20.5	21.44	22.3	0.561	21	12.7	13.62	14.9	0.596
M ²	38	15.2	16.55	17.9	0.682	38	13.3	13.97	14.7	0.364
M ³	30	12.7	13.78	15.7	0.694	31	11.3	12.49	13.5	0.597

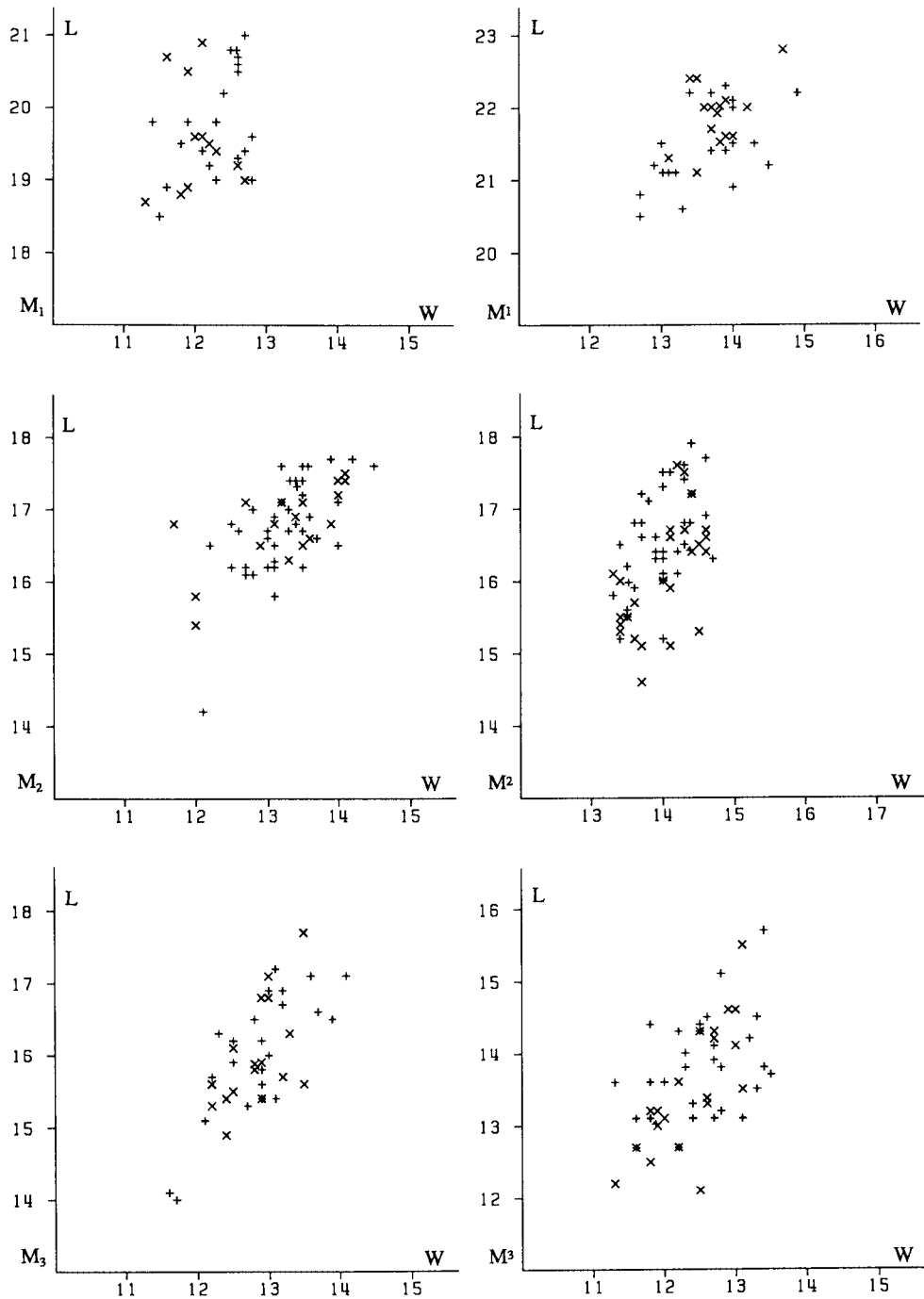


Fig. 3. Length/width diagrams of *Neocricetodon occidentalis* Aquilar, 1982 from Crevillente 2 (+) and Crevillente 4B (x).

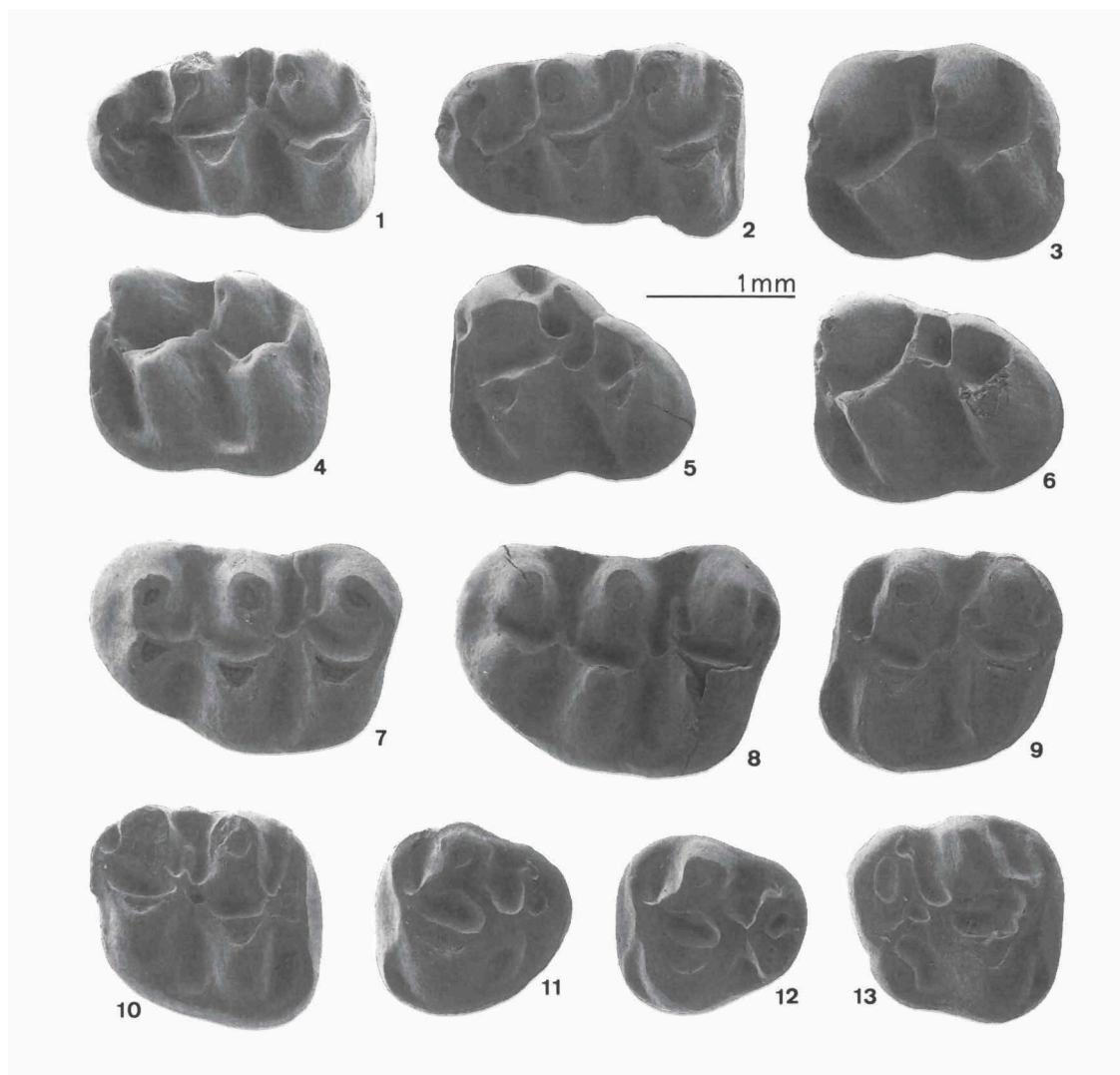


Plate 3

Neocricetodon occidentalis Aquilar, 1982

From Crevillente 2.

Fig. 1. M₁ sin., RGM 385 697.

Fig. 2. M₁ sin., RGM 385 691.

Fig. 3. M₂ sin., RGM 385 717.

Fig. 4. M₂ sin., RGM 385 721.

Fig. 5. M₃ sin., RGM 385 756.

Fig. 6. M₃ sin., RGM 385 762.

Fig. 7. M₁ sin., RGM 385 782.

Fig. 8. M₁ sin., RGM 385 787.

Fig. 9. M₂ sin., RGM 385 819.

Fig. 10. M₂ dext., RGM 385 836.

Fig. 11. M₃ sin., RGM 385 848.

Fig. 12. M₃ sin., RGM 385 853.

Fig. 13. M₃ sin., RGM 385 862.

Description

M_1 – The anteroconid is simple (2) or superficially split (22). The anterolophulid is incomplete (3), simple and connected to the labial part of the anteroconid (10), or forked, sending a branch to each one of the anteroconid cusps (13). The mesosinusid is open (1), closed by a low cingulum ridge (8), or there is a mesostylid in the entrance of the valley (16). The mesolophid is absent (2), short (5), of medium length (1), long (1), or it reaches the molar border (16). The ectomesolophid is absent (20), weak (5), or well developed (1).

M_2 – The anterosinusid is absent (4), very small (29), or small (2). The labial anterolophulid reaches the base of the protoconid. The mesosinusid is open (7), closed by a low cingulum ridge (24), or there is a mesostylid in the entrance of the valley (8). The mesolophid is absent (6), short (4), of medium length (1), long (10), or it reaches the molar border (20). The ectomesolophid is absent (32), weak (7), or well developed (2). The posterior wall of the hypoconid is smooth (2), somewhat irregular (30), or there is some kind of labial posterolophid (5).

M_3 – The anterosinusid is absent (1), very small (21), or small (2). The labial anterolophulid reaches the base of the protoconid. The mesosinusid is closed by a continuous cingulum ridge (22), or by a more or less interrupted cingulum (6). The mesolophid is of medium length (7), long (8), or it reaches the molar border (14). In 10 specimens there is a weak longitudinal connection between the mesolophid and the middle of the posterior wall of the metaconid, and in 2 specimens this connection is strong. The ectomesolophid is always absent.

In one specimen, RGM 385 756, there is a valley and a cingulum ridge, that separate the metaconid from the lingual border.

M^1 – The anterocone is superficially split (14) or deeply split (10). The anterolophule is a single crest connected to the lingual anterocone cusp (5), forked and connected to both the anterocone cusps (6), or forked with a free labial branch (13). The anterosinus is open (2), closed by a cingulum ridge (11), or there is an anterostyl (11). The protolophule is double (14), posterior with a trace of an anterior connection (3), or posterior only (10). The protocone is not separated from the lingual border. The mesosinus is open (2), closed by a low cingulum ridge (14), or there is a mesostyl in the entrance of the valley (6). The mesoloph is absent (3), of medium length (15), long (6), or it reaches the molar border (2). The metalophule is anterior (5), double (9), posterior plus a trace of an anterior connection (1), posterior (5), or the metacone is only connected to the labial end of the posteroloph (2). There are 4 specimens with 3 roots, and 5 specimens with 4 roots.

N.B. In various cases it is a matter of taste, whether the anterior connection is interpreted as a mesoloph, or an anterior metalophule. In fact the 3 specimens without mesoloph, do have a mesoloph of medium length, turned into an anterior metalophule.

M^2 – The protolophule is anterior (2), anterior plus a trace of a posterior connection (2), or double (39). The protocone is not separated from the lingual border (41); only in one case the lingual anteroloph continues around the base of the protocone into the sinus. The mesosinus is open (2), closed by a low cingulum ridge (26), or there is a mesostyl in the entrance of the valley (9). The mesoloph is short

(1), of medium length (21), long (19), or it reaches the molar border (3). The metalophule is anterior (4), anterior plus a trace of a posterior connection (1), double (24), posterior plus a trace of an anterior connection (3), posterior (7), or the metacone is only connected to the labial end of the posteroloph (2). The posterolingual corner of the molar is strongly reduced.

In one specimen, RGM 385 836, there is a small funnel in the centre of the molar, encircled by entoloph, mesoloph, posterior protolophule, and a longitudinal crest from posterior protolophule to mesoloph. This situation reminds one of certain M^3 of *Democricetodon*, described by Freudenthal & Daams (1988, fig. 2B).

M^3 – The protolophule is double (31). The protocone is not separated from the lingual border. The mesosinus is open (4) or closed by a low cingulum ridge (26). The mesoloph is absent (11), short (4), of medium length (9), or long (6). The metalophule is weak (2) or well developed (28). The mesoloph generally presents itself as a forward or labial spur on the metalophule. This spur is bent strongly forward, connected to the paracone, in 5 specimens, and in 4 other specimens there is a backward spur on the paracone.

RGM 385 849, 385 862 and 402 026 have a central funnel, as described by Freudenthal & Daams (1988, fig. 2B) for an M^3 of *Democricetodon*. Two specimens, RGM 385 864 and 385 869, show a situation as figured by Freudenthal & Daams (1988, fig. 1B), with a crest between the centre of the protocone and the paracone. In RGM 385 865 there is longitudinal crest between the two protolophules, splitting up the valley between protocone and paracone.

Locality Crevillente 4B

Material – RGM 385 875 - 385 999, 402 000 - 402 006.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	13	18.7	19.52	20.9	0.743	14	11.3	12.04	12.7	0.374
M_2	17	15.4	16.78	17.5	0.563	18	11.7	13.25	14.1	0.740
M_3	18	14.9	15.94	17.7	0.731	17	12.2	12.82	13.5	0.412
M^1	16	21.1	21.87	22.8	0.463	16	13.1	13.81	14.7	0.383
M^2	26	14.6	16.05	17.6	0.780	25	13.3	13.99	14.6	0.449
M^3	20	12.1	13.50	15.5	0.893	20	11.3	12.37	13.1	0.539

Description

M_1 – The anteroconid is simple (2), superficially split (9), or deeply split (2). The anterolophulid is simple and connected to the labial part of the anteroconid (12), or forked, sending a branch to each one of the anteroconid cusps (3). The mesosinusid is open (1), closed by a low cingulum ridge (2), or there is a mesostylid in the entrance of the valley (12). The mesolophid is absent (4) or it reaches the

molar border (11). The ectomesolophid is absent (13) or weak (2).

N.B. The mesolophid is either absent or very long; no intermediate cases are found. We think this is related to the fact that the mesolophid is very thin and low; instead of disappearing by shortening, it disappears by losing height.

M₂ – The anterosinusid is absent (2), very small (15), or small (1). The labial anterolophulid reaches the base of the protoconid. The mesosinusid is open (1), closed by a low cingulum ridge (11), or there is a mesostylid in the entrance of the valley (7). The mesolophid is absent (2), short (4), of medium length (3), long (3), or it reaches the molar border (11). The ectomesolophid is absent (16) or weak (4). The posterior wall of the hypoconid is smooth (4), somewhat irregular (11), or there is some kind of labial posterolophid (3).

M₃ – The anterosinusid is very small (10) or small (7). The labial anterolophulid reaches the base of the protoconid. The mesosinusid is closed by a continuous cingulum ridge (16) or by a more or less interrupted cingulum (2). The mesolophid is of medium length (4), long (5), or it reaches the molar border (10). In 3 specimens there is a weak longitudinal connection between the mesolophid and the middle of the posterior wall of the metaconid, and in 6 specimens this connection is strong. The ectomesolophid is always absent.

M¹ – The anterocone is superficially split (5) or deeply split (12). The anterolophule is a single crest connected to the lingual anterocone cusp (2), forked and connected to both the anterocone cusps (4), or forked with a free labial branch (10). In 2 specimens both branches of the anterolophule are connected to the anterocone, and there is an extra labial spur on the anterolophule. The anterosinus is open (3), closed by a cingulum ridge (9), or there is an anterostyl (5). The protolophule is double (7), posterior with a trace of an anterior connection (2), or posterior only (10). The protocone is not separated from the lingual border. The mesosinus is open (3), closed by a low cingulum ridge (11), or there is a mesostyl in the entrance of the valley (3). The mesoloph is of medium length (18) or long (1). The metalophule is anterior (2), anterior plus a trace of a posterior connection (1), double (12), posterior (2), or the metacone is only connected to the labial end of the posteroloph (2). Among 10 specimens we found 6 specimens with 3 roots, and 4 specimens with 4 roots.

M² – The protolophule is anterior (2), anterior plus a trace of a posterior connection (4), or double (22). The protocone is not separated from the lingual border (27); only in one case the lingual anteroloph continues around the base of the protocone into the sinus. The mesosinus is open (6), closed by a low cingulum ridge (16), or there is a mesostyl in the entrance of the valley (5). The mesoloph is of medium length (18), long (9), or it reaches the molar border (1). The metalophule is anterior (2), double (16), posterior plus a trace of an anterior connection (4), posterior (4), or the metacone is only connected to the labial end of the posteroloph (1). The posterolingual corner of the molar is strongly reduced.

M³ – The protolophule is anterior plus a trace of a posterior connection (1) or double (20). The protocone is not separated from the lingual border. The mesosinus is open (1) or closed by a low cingulum ridge (17). The mesoloph is absent (6), short (1), of medium length (5), long (5), or it reaches the border of the molar (1).

The metalophule is weak (3), or well developed (16). In 4 specimens the mesoloph is directed longitudinally forward, connected to the paracone. In 2 specimens there is a central funnel between posterior protolophule, entoloph, and metalophule.

Discussion – The *Neocricetodon* from Crevillente 2 was described by de Bruijn et al. (1975) as *Kowalskia fahlbuschi*. Aguilar (1982) named it *Cricetodon occidentalis*, on the basis of de Bruijn's description and figures. The populations most similar to it are *N. fahlbuschi* (Bachmayer & Wilson, 1970) from Kohfidisch and *N. cf. fahlbuschi* from Eichkogel. *Neocricetodon cf. fahlbuschi* from Eichkogel, described by Daxner-Höck (1972) as *Kowalskia cf. fahlbuschi*, is documented by a very rich material. Since the description of the type-material of *fahlbuschi* from Kohfidisch by Bachmayer & Wilson (1970) is somewhat insufficient, most subsequent authors have taken the Eichkogel material as a basis for comparison. We will do the same.

Our material from Crevillente 2 and Crevillente 4B is on the average larger than the Eichkogel specimens. In Crevillente mesolophids and mesolophs are on the average shorter and lower. The entoconid of M_3 is better developed. In M^1 the labial spur on the anterolophule is less-developed. The anterior metalophule of M^1 is more frequent, the posterior metalophule more longitudinal, the posterosinus smaller or even absent; the lingual root is subdivided in about half the number of specimens.

By these differences it may be concluded, that the populations from Eichkogel and Crevillente represent different species.

Daxner-Höck (1972, p. 139) states, that the teeth of *Neocricetodon fahlbuschi* from Kohfidisch are longer and above all broader than the ones from Eichkogel. De Bruijn et al. (1975) think the measurements published by Bachmayer & Wilson (1970) are too high. They attribute the Crevillente material to *N. fahlbuschi* and state the material from Crevillente and Kohfidisch may be identical.

According to Bachmayer & Wilson (1970) the mesoloph of M^1 remains free from the metacone, and there is no anterior metalophule. In Crevillente the anterior metalophule is present in the majority of the specimens, either as a separate crest, or as the lingual part of the mesoloph. The lower incisor in Crevillente bears no furrows in the enamel band. The mesolophids in Crevillente are probably less-developed, and external cingula in the lower molars are hardly developed. If the measurements given by Bachmayer & Wilson are correct, the M_3 and M^3 are considerably larger in Kohfidisch than in Crevillente.

It remains to be decided whether *Neocricetodon fahlbuschi* is a junior synonym of *N. schaubi*.

Neocricetodon plinii sp. nov.

Pl. 4, figs. 1-12; Fig. 4.

Holotype – M_1 sin., RGM 402 101, dimensions 22.0×14.0 .

Type-locality – Crevillente 15.

Type-level – Turolian, *Parapodemus gaudryi barbarae* Zone (van de Weerd, 1976).

Other localities – Crevillente 4 ?, 14.

Derivatio nominis – This species is dedicated to our colleague Plinio Montoya, who discovered the type-locality, and assisted us in all possible ways during our field work in the Crevillente area.

Diagnosis – Large *Neocricetodon* species, without mesolophids in M_1 and M_2 , and with relatively well-developed mesolophids in M_3 . Hypoconid of M_1 protruding labially. Anterior metalophule in M^1 always present; postero-lingual corner of M^2 strongly reduced.

Differential diagnosis – See Discussion.

Material – RGM 402 096 - 402 215.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	14	21.1	22.32	23.2	0.626	15	13.6	14.19	15.0	0.437
M_2	17	17.6	19.21	20.0	0.534	16	14.5	15.44	16.6	0.566
M_3	19	16.3	18.75	19.9	0.979	21	13.6	15.00	16.4	0.684
M^1	12	24.1	25.54	26.6	0.632	13	15.2	16.26	17.4	0.561
M^2	16	17.6	18.72	19.9	0.634	14	15.4	15.99	16.9	0.410
M^3	17	14.7	16.40	17.8	0.857	19	13.5	14.44	16.0	0.723

Description

M_1 – The anteroconid is superficially split (22). The anterolophulid is simple and connected to the labial part of the anteroconid (7), or forked, sending a branch to each one of the anteroconid cusps (10). The mesosinusid is open (1) or closed by a low cingulum ridge (14). The mesolophid is absent. The ectomesolophid is absent (12) or weakly developed (3). The labial border is not straight, due to the fact that the hypoconid protrudes in a labial bulge.

In RGM 402 098 the lingual branch of the anterolophulid is so well developed, that there is a funnel in the anteroconid.

M_2 – The anterosinusid is absent (6) or very small (11). The labial anterolophulid reaches the base of the protoconid (16), or continues around the protoconid (2), separating the protoconid from the molar border. The mesosinusid is closed by a low cingulum ridge. The mesolophid is absent. The ectomesolophid is absent (6), weak (10), or well developed (1). The posterior wall of the hypoconid is smooth (3) or somewhat irregular (13).

M_3 – The anterosinusid is absent (10), very small (7), or small (1). The labial anterolophulid reaches the base of the protoconid (14), or continues around the protoconid (5), separating the protoconid from the molar border. The mesosinusid is closed by a continuous cingulum ridge. The mesolophid is absent (3), short (11), or of medium length (8). In 4 specimens there is a weak longitudinal connection between the mesolophid and the middle of the posterior wall of the metaconid, and in 10 specimens this connection is strong. The ectomesolophid is absent (14), weak (5), or well developed (4).

M^1 – The anterocone is superficially split (4) or deeply split (11). The anterolophule is a single crest connected to the lingual anterocone cusp (2), forked and

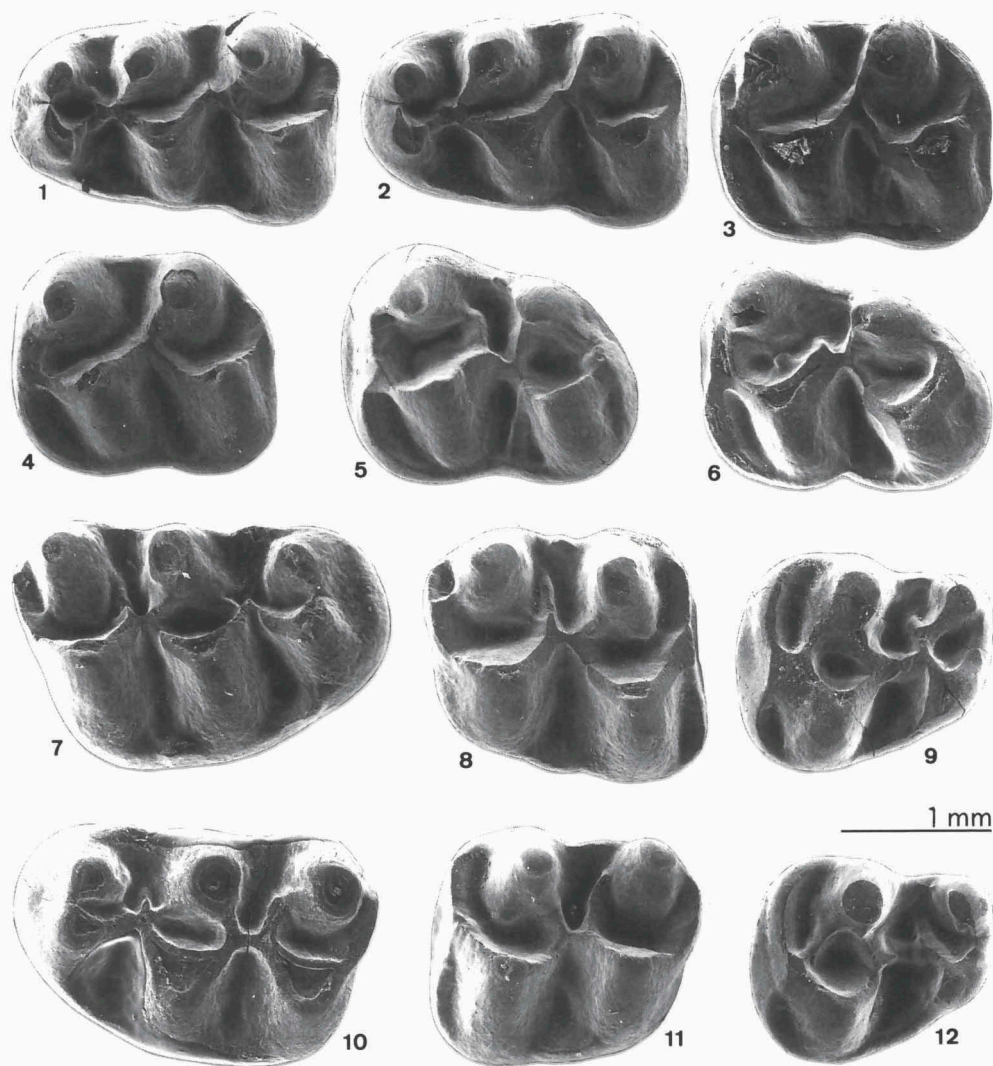


Plate 4

Neocricetodon plinii sp. nov.

From Crevillente 15.

Fig. 1. M₁ sin., RGM 402 101, holotype.

Fig. 2. M₁ sin., RGM 402 102.

Fig. 3. M₂ sin., RGM 402 119.

Fig. 4. M₂ sin., RGM 402 120.

Fig. 5. M₃ sin., RGM 402 133.

Fig. 6. M₃ sin., RGM 402 136.

Fig. 7. M₁ dext., RGM 402 171.

Fig. 8. M₂ dext., RGM 402 187.

Fig. 9. M₃ sin., RGM 402 195.

Fig. 10. M₁ sin., RGM 402 160.

Fig. 11. M₂ sin., RGM 402 175.

Fig. 12. M₃ sin., RGM 402 196.

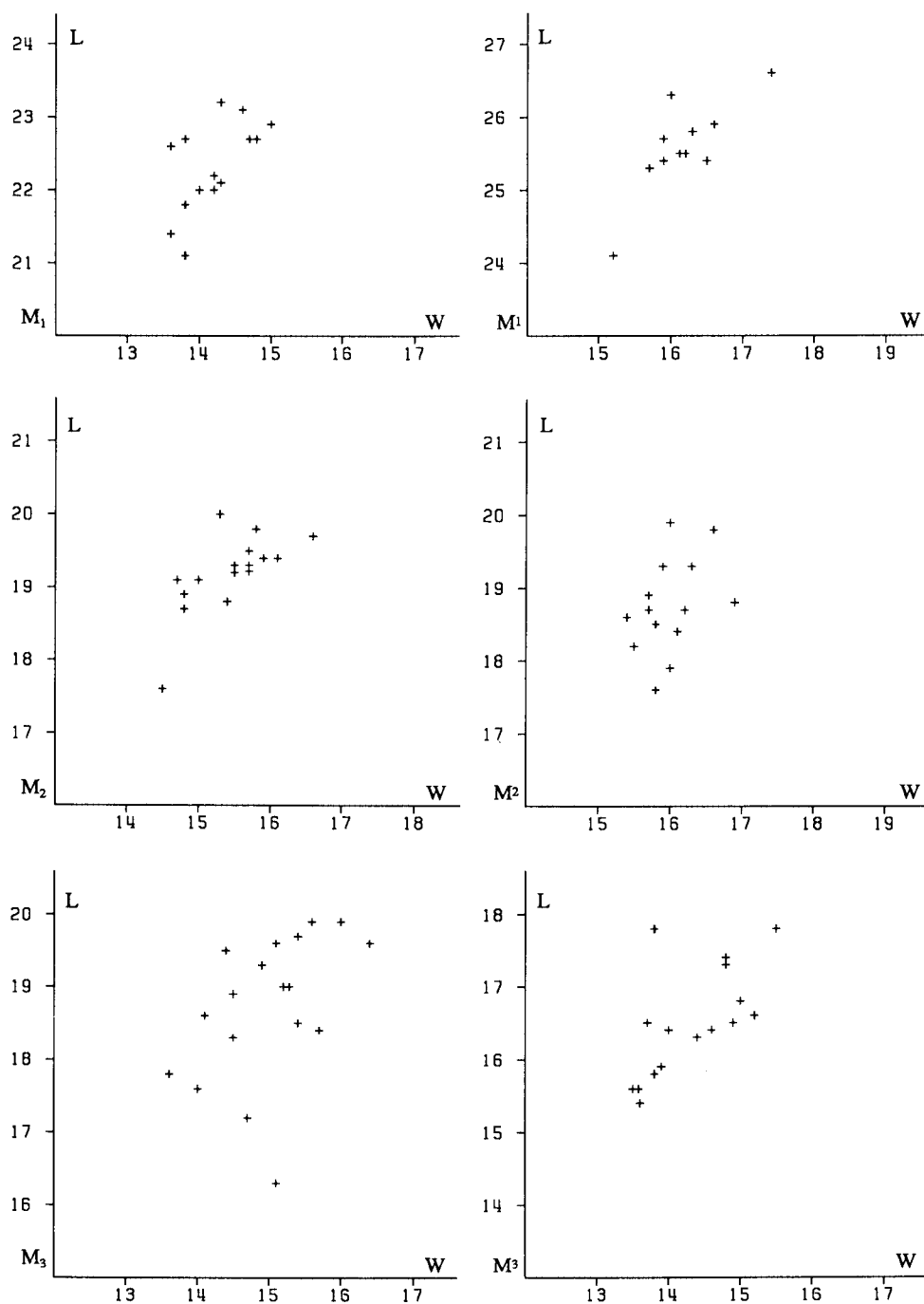


Fig. 4. Length/width diagrams of *Neocricetodon plinii* sp. nov. from Crevillente 15.

connected to both the anterocone cusps (8), or forked with a free labial branch (6). The anterosinus is closed by a cingulum ridge. The protolophule is double (10), posterior with a trace of an anterior connection (2), or posterior only (6). The protocone is not separated from the lingual border. The mesosinus is open (1) or closed by a low cingulum ridge (12). The mesoloph is absent (5), of medium length (9), or long (2). The metalophule is anterior (9), anterior plus a trace of a posterior connection (1), or double (3). There are 21 specimens with 4 roots and not a single one with 3 roots. The 5 specimens without mesoloph do have a mesoloph of medium length, turned into an anterior metalophule.

M² – The protolophule is double (11), posterior plus a trace of an anterior connection (5), or posterior (2). The protocone is not separated from the lingual border. The mesosinus is open (1) or closed by a low cingulum ridge (15). The mesoloph is absent (5), of medium length (11), or long (2). The metalophule is anterior (9), double (8), or posterior plus a trace of an anterior connection (1). The postero-lingual corner of the molar is strongly reduced. The 5 specimens without mesoloph do have a mesoloph of medium length, turned into an anterior metalophule.

M³ – The protolophule is double (21) or posterior plus a trace of an anterior connection (1). The protocone is separated from the lingual border in 4 specimens. The mesosinus is closed by a low cingulum ridge. The mesoloph is absent (6), short (5), of medium length (6), or long (3). When present, it begins halfway the metalophule, and not at the entoloph. The metalophule is absent (3) or well developed (14).

RGM 402 211 has a large central funnel between posterior protolophule, entoloph, metalophule, and a crest that would be an axioloph in the sense of Freudenthal & Daams (1988, p. 137). In RGM 402 208 and 402 210 there is a longitudinal crest between the two protolophules, splitting up the valley between protocone and paracone.

Locality Crevillente 14

Material – RGM 402 054 - 404 056, 402 058 - 402 095, 402 900 - 402 933.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	6	18.3	19.67	21.3	1.201	6	11.5	12.13	13.0	0.585
M ₂	7	15.6	16.96	19.3	1.190	8	12.1	13.44	16.5	1.364
M ₃	6	15.9	16.68	17.6	0.649	8	12.9	13.54	14.9	0.668
M ¹	5	21.1	22.62	23.3	0.876	6	13.8	14.15	14.5	0.259
M ²	11	16.3	16.90	17.8	0.443	11	13.3	14.04	15.2	0.609
M ³	10	12.3	14.23	15.2	0.855	11	12.3	12.93	13.5	0.436

Description

M₁ – The anteroconid is superficially split (7). The anterolophulid is simple

and connected to the labial part of the anteroconid (6), or forked, sending a branch to each one of the anteroconid cusps (2). The mesosinusid is open. The mesolophid is absent (8) or long (1). The ectomesolophid is absent (12).

M_2 – The anterosinusid is absent (9). The labial anterolophulid reaches the base of the protoconid (8). The mesosinusid is open (5) or closed by a low cingulum ridge. The mesolophid is absent (7) or short (3). The ectomesolophid is absent (9) or weak (1). The posterior wall of the hypoconid is smooth (6).

M_3 – The anterosinusid is absent (5), very small (1), or small (1). The labial anterolophulid reaches the base of the protoconid. The mesosinusid is closed by a continuous cingulum ridge (5) or such a ridge is interrupted (2). The mesolophid is short (2), of medium length (1), long (1), or it reaches the molar border (1). In 2 specimens there is a weak longitudinal connection between the mesolophid and the middle of the posterior wall of the metaconid, and in 2 specimens this connection is strong. The ectomesolophid is absent (5).

M^1 – The anterocone is deeply split (8), and in one case the anterocone cusps and the forked anterolophule encircle a well-defined funnel. The anterolophule is a single crest connected to the lingual anterocone cusp (1), forked and connected to both the anterocone cusps (6), or forked with a free labial branch (2). The anterosinus is closed by a cingulum ridge (3) or there is an anterostyl (5). The protolophule is double (5) or posterior (6). The protocone is not separated from the lingual border. The mesosinus is open (2) or there is a mesostyl (3). The mesoloph is of medium length (2), long (3), or it reaches the labial border (2). The metalophule is anterior (1) or the metacone is only connected to the labial end of the posteroloph (4). Four specimens have 3 roots, and in 3 specimens there are 4 roots.

M^2 – The protolophule is double (17). The protocone is not separated from the lingual border. The mesosinus is open (2), closed by a low cingulum ridge (10), or there is a mesostyl (2). The mesoloph is absent (3), of medium length (8), or long (4). The metalophule is anterior (3), double (11), or the metacone is connected to the labial end of the posteroloph only (1). The posterolingual corner of the molar is strongly reduced (6) or the shape of the molar is subrectangular (8). The 3 specimens without mesoloph do have a mesoloph of medium length, turned into an anterior metalophule.

M^3 – The protolophule is anterior (2) or double (14). The protocone is not separated from the lingual border. The mesosinus is closed by a low cingulum ridge. The mesoloph is absent (12), short (1), or of medium length (2). The metalophule is weak (2) or well developed (12).

Discussion – The material from Crevillente 14 is attributed to *N. plinii*, though there are a few differences: Occasionally there is a mesolophid in M_1 and M_2 , which is always absent in Crevillente 15. About half the number of M^1 have only 3 roots, whereas in Crevillente 15 this never occurs. The mesoloph of M^3 is less frequently present in Crevillente 14.

The size of the teeth of *Neocricetodon plinii* is identical to that of *N. magnus* (Fahlbusch, 1969). Contrary to the situation in Crevillente 15, the mesolophids and mesostylids in *N. magnus* are well developed, the posterior metalophules are

(almost) absent, and there are M^1 with only 3 roots.

It also agrees in size with *Cricetus polgardiensis* Freudenthal & Kordos, 1989 from Polgárdi 4. It is easily distinguished by the total absence of mesolophids in M_1 and M_2 in Crevillente 15, whereas these generally reach the molar border in Polgárdi 4. Also the mesolophs are longer and more independent in *C. polgardiensis*. It may be of fundamental importance, that in Crevillente 15 the mesolophid is absent in M_1 and M_2 , and more or less well developed in M_3 . In *C. polgardiensis* the degree of development of the mesolophid diminishes from M_1 to M_3 . In a collection of 10 M^1 of *C. polgardiensis* from Polgárdi 5, provided to us by Dr Kordos (Budapest), we found not a single specimen with 4 roots, and a subdivision of the lingual root is often not even indicated.

Another species of roughly the same size is *Cricetus kormosi* Schaub, 1930 from Polgárdi 2. In comparison with *N. plinii* *C. kormosi* shows the following differences: The anteroconid of M_1 is less subdivided, the anterolophulid is a simple crest, and the valley between protoconid and metaconid is shallower; M_3 is on the average longer than M_2 . The anterocone of M^1 seems to be more subdivided, the labial branch of the anterolophule is equal to the lingual branch, and in solid contact with the anterocone, and the labial spur of the anterolophule is usually absent; there is generally no separate mesoloph, but this crest is fully incorporated in the massive anterior metalophule.

The M^3 from Aljezar B described by Adrover (1986) may belong to *N. plinii*.

Neocricetodon lucentensis sp. nov.

Pl. 5, figs. 1-12; Fig. 5.

1975 *Kowalskia* sp. – de Bruijn et al., p. 302, pl. 3, figs. 2, 13-15; pl. 4, figs. 1-2, 13-15.

Holotype – M_1 dext., RGM 404 677, dimensions 21.4×13.1 .

Type-locality – Crevillente 17.

Type-level – Turolian, *Parapodemus gaudryi barbarae* Zone (van de Weerd, 1976).

Other localities – Crevillente 5, Crevillente 8.

Derivatio nominis – This species is named after Lucentum, the Roman name of Alicante.

Diagnosis – Medium-sized *Neocricetodon* with small M_3 and M^3 , simple anteroconid in M_1 . The protocone and protoconid, and sometimes the hypoconid, may be separated from the molar border by a variably developed cingulum ridge.

Differential diagnosis – *Neocricetodon lucentensis* differs from most *Neocricetodon* species by its very small M_3 and M^3 . Only *N. lavocati* (Hugueney & Mein, 1965), *N. meini* (Agustí, 1986), and *N. nestori* (Engesser, 1989) are comparable in this respect, but they are considerably smaller.

Neocricetodon meini and *N. nestori* have a more subdivided anteroconid in M_1 . *N. nestori* has better developed mesoloph(id)s and mesostyl(id)s.

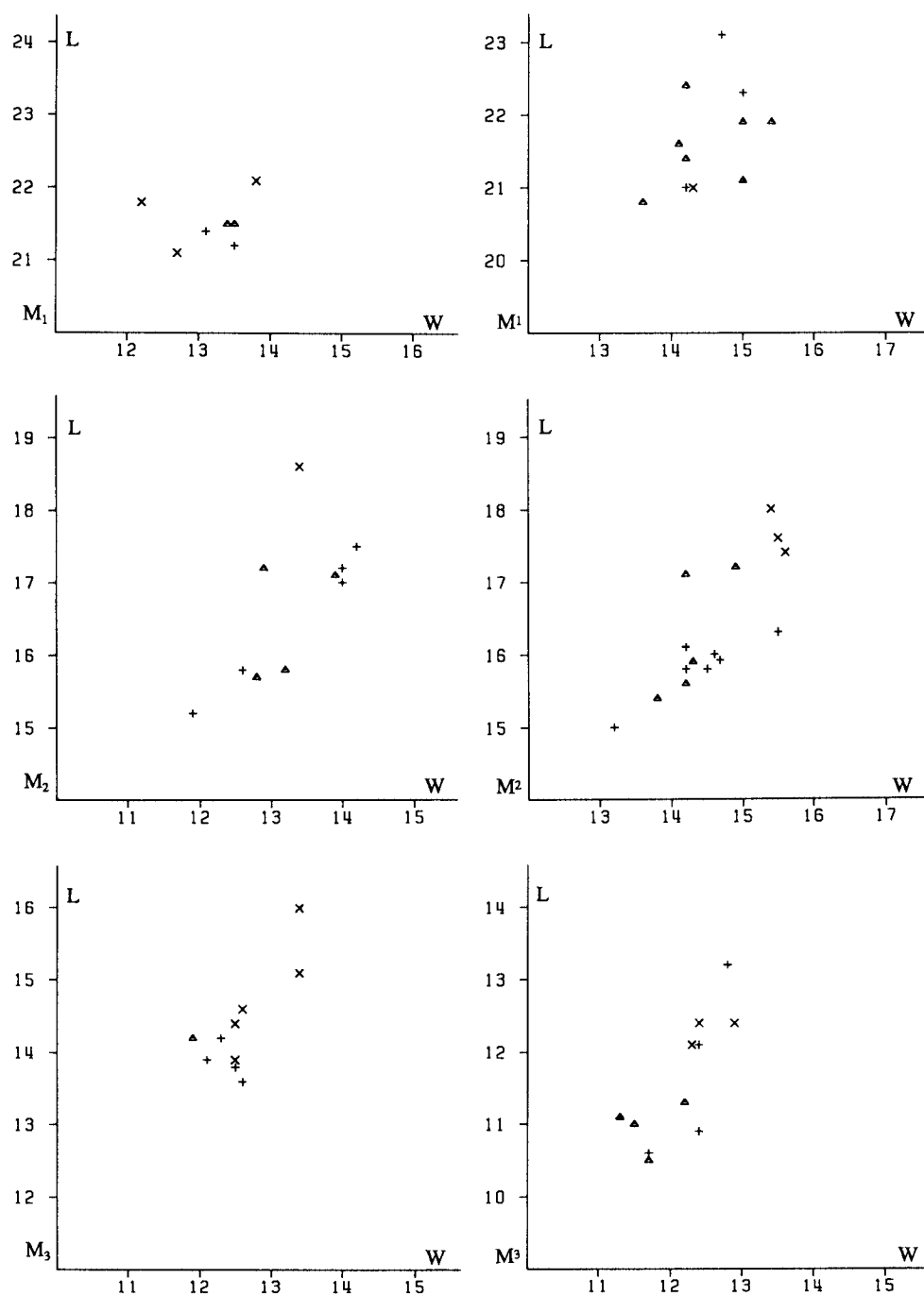


Fig. 5. Length/width diagrams of *Neocricetodon lucentensis* sp. nov. from Crevillente 17 (+), Crevillente 5 (x) and Crevillente 8 (Δ).

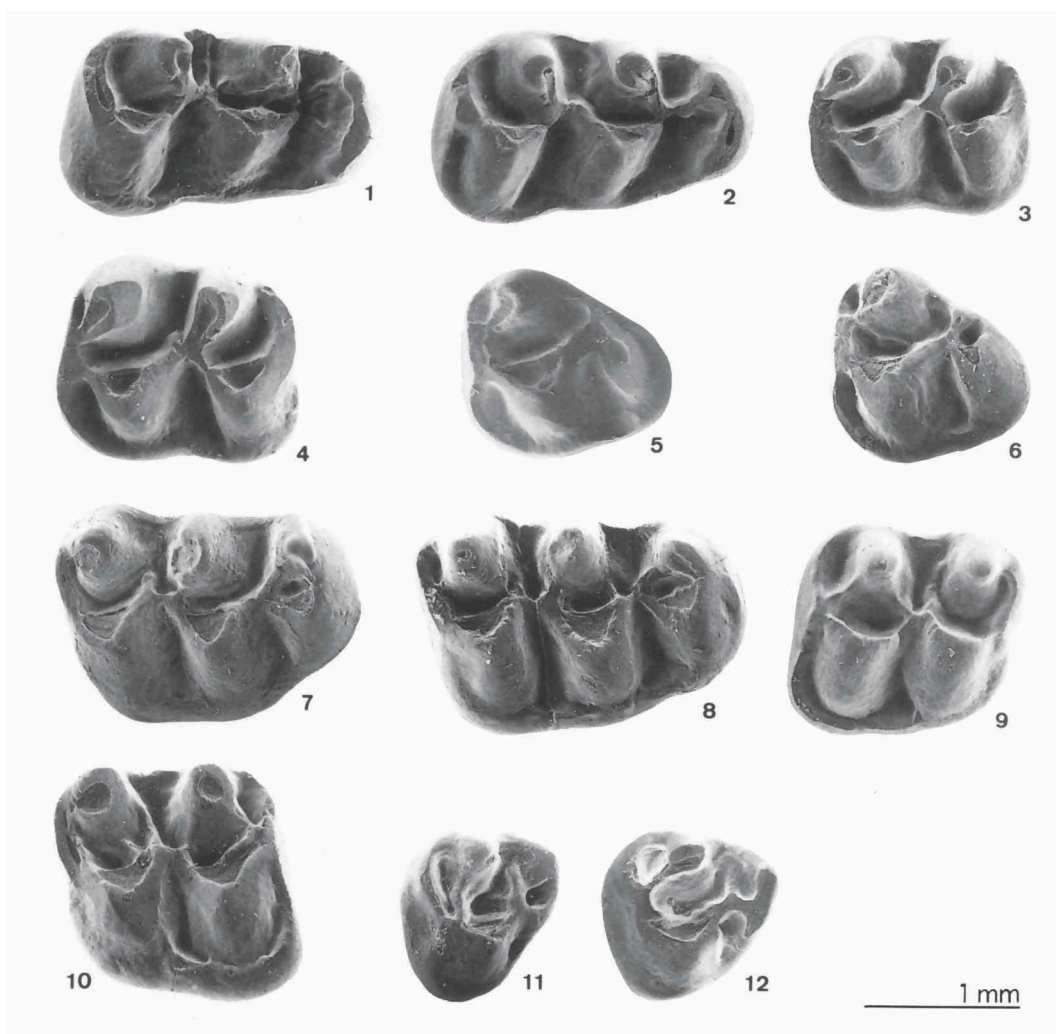


Plate 5

Neocricetodon lucentensis sp. nov.
From Crevillente 17.

- Fig. 1. M₁ dext., RGM 404 677, holotype.
Fig. 2. M₁ dext., RGM 404 740.
Fig. 3. M₂ sin., RGM 404 742.
Fig. 4. M₂ sin., RGM 404 743.
Fig. 5. M₃ sin., RGM 404 683.

- Fig. 6. M₃ sin., RGM 404 684.
Fig. 7. M¹ dext., RGM 404 675.
Fig. 8. M¹ dext., RGM 404 686.
Fig. 9. M₂ sin., RGM 404 692.
Fig. 10. M₂ dext., RGM 404 700.
Fig. 11. M₃ sin., RGM 404 701.
Fig. 12. M₃ sin., RGM 404 702.

Erratum

Corrected version of Plate 5.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	21.2	21.30	21.4	0.142	4	12.9	13.13	13.5	0.263
M ₂	5	15.2	16.54	17.5	0.989	6	11.9	13.38	14.2	0.926
M ₃	5	12.4	13.58	14.2	0.694	4	12.1	12.38	12.6	0.222
M ¹	3	21.0	22.13	23.1	1.060	6	14.2	14.90	15.4	0.410
M ²	8	15.0	15.80	16.3	0.418	10	13.2	14.42	15.5	0.573
M ³	4	10.6	11.70	13.2	1.192	4	11.7	12.33	12.8	0.457

Description

M₁ – The anteroconid is simple (3). The anterolophulid is incomplete (1) or simple (2). The mesosinusid is closed by a low cingulum ridge (2). The mesolophid is absent (1) or it reaches the molar border (1). The ectomesolophid is absent (4). The anterocone of M¹ presents a funnel, delimited posteriorly by the forked anterolophule.

M₂ – The anterosinusid is absent (1), very small (4), or small (1). The labial anterolophulid reaches the base of the protoconid (3) or it continues around the protoconid (3), separating this cusp from the border of the molar. The mesosinusid is open (1) or closed by a low cingulum ridge (4). The mesolophid is absent (3) or short (2); in 1 specimen it forms a posterior metalophulid. The ectomesolophid is absent. The posterior wall of the hypoconid is smooth (1) or somewhat irregular (4).

M₃ – The anterosinusid is very small. The labial anterolophulid separates the protoconid from the molar border. The mesosinusid is closed by a continuous cingulum ridge (3). The mesolophid is absent. There is a very weak longitudinal connection between the ectolophid and the middle of the posterior wall of the metaconid. The ectomesolophid is always absent.

M¹ – The two anterocone cusps and the two branches of the anterolophule encircle a well-developed funnel. The anterosinus is open (1) or closed by a cingulum ridge (1). The protolophule is double (2), posterior with a trace of an anterior connection (2), or posterior only (1). The protocone is not separated from the lingual border (1) or separated from it by the lingual anteroloph (6). The mesosinus is open (5) or closed by a low cingulum ridge (1). The mesoloph is absent (2), short (2), of medium length (1), or long (1). The metalophule is anterior (1), anterior plus a trace of an posterior connection (1), double (1), or the metacone is only connected to the labial end of the posteroloph (2). There are 4 roots. The 2 specimens without mesoloph do have a short mesoloph, turned into an anterior metalophule.

M² – The protolophule is double. The protocone is not separated from the lingual border (1) or the lingual anteroloph continues around the base of the protocone into the sinus (9). The mesosinus is open (6) or closed by a low cingulum ridge (2). The mesoloph is absent (3) or of medium length (6). The metalophule is anterior (1), double (3), posterior (1), or the metacone is only connected to the labial end of the posteroloph (1). The posterolingual corner of the molar is not strongly reduced; the molar has a subrectangular outline.

M³ – The protolophule is anterior (2) or double (2). The protocone is separated from the lingual border. There is a cingulum at the anterolingual corner of the molar, but there is no lingual anteroloph descending along the anterior wall of the tooth. The mesosinus is open (2) or closed by a low cingulum ridge (2). The mesoloph is absent (2), short (1), or of medium length (1). The metalophule is absent (2), weak (1), or well developed (1).

Locality Crevillente 8

Material – RGM 402 039 - 402 053, 403 162 - 403 174.

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	21.5	21.50	21.5	0.000	2	13.4	13.45	13.5	0.071
M ₂	4	15.7	16.45	17.2	0.810	4	12.8	13.20	13.9	0.497
M ₃	1	–	14.20	–	–	1	–	11.90	–	–
M ¹	7	20.8	21.59	22.4	0.540	8	13.6	14.41	15.4	0.642
M ²	5	15.4	16.24	17.2	0.850	6	13.8	14.37	14.9	0.413
M ³	4	10.5	10.98	11.3	0.340	4	11.3	11.68	12.2	0.386

Description

M₁ – A subdivision of the anteroconid is only indicated. The anterolophulid is forked (1) or simple (1). The mesosinusid is open (1) or closed by a low cingulum ridge (2). The mesolophid is absent (1) or it reaches the molar border (2). The ectomesolophid is absent (3). In one specimen the hypoconid is separated from the labial border by a cingulum ridge, and in another specimen such a ridge is indicated.

M₂ – The anterosinusid is very small. The labial anterolophulid reaches the base of the protoconid (2), or it continues around the protoconid (3), separating this cusp from the border of the molar. The mesosinusid is open (1) or closed by a low cingulum ridge (4). The mesolophid is absent (3) or long (2). The ectomesolophid is absent. The posterior wall of the hypoconid is smooth (2) or somewhat irregular (2).

M₃ – The anterosinusid is very small. The labial anterolophulid separates the protoconid from the molar border. The mesosinusid is closed by a continuous cingulum ridge. The mesolophid and the ectomesolophid are absent.

M¹ – The two anterocone cusps and the two branches of the anterolophule encircle a well-developed funnel. The anterosinus is open (1) or closed by a cingulum ridge (7). The protolophule is double (2). The protocone is not separated from the lingual border (2) or separated from it by a very weak cingulum (5). The mesosinus is open (2) or closed by a low cingulum ridge (7). The mesoloph is absent (2), of medium length (4), long (1), or it reaches the border of the molar (1). The metalophule is anterior (1), double (3), or posterior (4). There are 4 roots. The 2 specimens without mesoloph do have a short mesoloph, turned into an anterior metalophule.

M² – The protolophule is anterior plus a trace of a posterior connection (2) or double (4). In 4 specimens there is a longitudinal crest on the labial wall of the paracone. The protocone is not separated from the lingual border (2), or the lingual anteroloph continues around the base of the protocone into the sinus (4). The mesosinus is open (2) or closed by a low cingulum ridge (4). The mesoloph is absent (1), of medium length (2), or long (3). The metalophule is double (5) or the metacone is only connected to the labial end of the posteroloph (1). The postero-lingual corner of the molar is not strongly reduced; the molar has a subrectangular outline.

M³ – The protolophule is double (2) or posterior with a trace of an anterior connection. The protocone is not separated from the lingual border. There is a cingulum at the anterolingual corner of the molar, but there is no lingual anteroloph descending along the anterior wall of the tooth. The mesosinus is open (1) or closed by a low cingulum ridge (3). The mesoloph is absent (4). The metalophule is absent (3) or weak (1).

Discussion – *Neocricetodon lucentensis*, *N. lavocati*, *N. meini*, and *N. nestori* resemble each other more closely than any other *Neocricetodon* species. They seem to form a homogeneous group, that may even be different from *Neocricetodon* at the generic level. In this group *N. meini* and *N. nestori* are almost identical in size, and differ only in the degree of development of mesoloph(id)s and mesostyl(id)s. *N. lucentensis* is considerably larger, and *N. lavocati* is much smaller.

Hugueney & Mein (1965, pl. 2, figs. 51-52) figure two M² that show a peculiar crest between the two protolophules. It is remarkable that this same feature is found in 4 M² and 2 M³ from Crevillente 8, and – though less conspicuous – in 3 M² from Crevillente 17. We don't think this feature is diagnostic for this group, since we also found it in 2 M³ of *N. plinii* from Crevillente 15, in 1 specimen of *N. occidentalis* from Crevillente 2, and in 1 specimen of *Cricetus* cf. *kormosi* from Crevillente 6 (de Bruijn et al., 1975, pl. 4, fig. 6).

Cricetus cf. *kormosi* Schaub, 1930

Type-locality – Polgárdi 2, Hungary.

Locality Crevillente 6

This material was described by de Bruijn et al. (1975). We have not been able to collect more material at this locality since it has vanished under the dam of Crevillente. We found a few other localities in the same level as Crevillente 6, but these were so poor that exploitation was impracticable.

We remeasured the material from Crevillente 6, which gave basically the same results as the ones obtained by de Bruijn et al. (1975):

Measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	8	20.9	21.70	22.4	0.535	8	12.3	13.40	14.1	0.556
M ₂	4	18.1	18.70	19.3	0.516	4	13.6	13.98	14.2	0.263
M ₃	14	18.0	19.43	21.0	0.841	14	13.4	14.49	15.6	0.687
M ¹	6	24.5	25.45	26.0	0.575	6	14.4	15.38	16.0	0.601
M ²	12	17.6	18.78	20.6	0.838	11	14.8	15.69	16.4	0.556
M ³	11	15.6	16.70	18.3	0.958	11	12.9	14.15	15.4	0.812

As far as the description is concerned we wish to make a few comments: In M¹ there is 1 specimen and in M² there are 6 specimens with posterior metalophule. In only 2 M¹ the anterior protolophule is missing, in the other specimens it is rather well developed.

Evolution of Neocricetodon and Cricetus

Our results confirm the statement by Agustí (1986), that there are more than one evolutionary lineage within the genus *Neocricetodon*. *N. lucentensis* can in no way be linked to *N. fahlbuschi*, *N. occidentalis*, or *N. plinii*. On the other hand there may be a phyletic relationship between *N. occidentalis* and *N. plinii*. An evolution from *N. fahlbuschi* to *N. plinii* is less probable. In all Central European Late Neogene cricetines the mesolophids of M₁ and M₂ are much better developed than they are in their Southwest European counterparts. Even when their lengths are more or less equal, the mesolophids in Central European populations are clearly higher and thicker.

Table 1. Relation of mean length M₃/mean length M₁ and mean length M₃/mean length M₂.

Locality	LM ₃ /LM ₁	LM ₃ /LM ₂	Species
CR5	0.68	0.80	<i>N. lucentensis</i>
CR17	0.64	0.82	<i>N. lucentensis</i>
CR8	0.66	0.86	<i>N. lucentensis</i>
CR14	0.85	0.98	<i>N. plinii</i>
CR15	0.84	0.98	<i>N. plinii</i>
CR4B	0.82	0.95	<i>N. aff. fahlbuschi</i>
CR2	0.81	0.95	<i>N. aff. fahlbuschi</i>
Polgárdi 2	0.91	1.05	<i>C. kormosi</i>
Polgárdi 4 Upper	0.84	1.00	<i>C. polgardiensis</i>
Polgárdi 4 Lower	0.87	1.02	<i>C. polgardiensis</i>
CR6	0.90	1.04	<i>C. cf. kormosi</i>

Cricetus cf. *kormosi* from Crevillente 6 may be derived from some *Neocricetodon* species, but it is not probable that *N. plinii* be its ancestor. The anteroconid of M_1 in *N. plinii* is fairly well subdivided, whereas in *C. cf. kormosi* it is simple or only slightly subdivided. The species *kormosi* is generally attributed to the genus *Cricetus*. We think this may be an incorrect assumption. The type species of *Cricetus*, *C. cricetus* (L.), is characterized by double protolophules in M^1 and M^2 . In the species *kormosi* and *polgardiensis* the anterior protolophule of M^1 may be absent, and in a few specimens of M^2 of *polgardiensis* it is absent too. In *C. angustidens* from Serrat d'en Vacquer (Perpignan, France) the absence of anterior protolophules in M^1 and M^2 appears to be a common feature. The same is true for a small collection of *C. angustidens* we collected at a new locality near Alcoy (Alicante). In *C. cf. kormosi* from Crevillente 6 the anterior protolophule is sometimes absent or weak in M^1 , and always present in M^2 and M^3 . The anterior protolophule is considered to be a primitive feature. If this is true, the mentioned Late Miocene and Pliocene species cannot be in the ascendance of *C. cricetus*, and probably represent a separate genus, or a separate group within the genus *Cricetus*.

Biostratigraphy

The cricetids found in the various Crevillente localities make it possible to create a local zonation, because the changes are great and easy to define.

In the oldest localities, Crevillente 2 and Crevillente 4B, we find an association of *Neocricetodon occidentalis* and *Hispanomys peralensis*.

The next zone is characterized by the association *N. plinii* sp. nov. and *H. adroveri*. It is best represented in Crevillente 15.

In the next zone *N. plinii* is replaced by *N. lucentensis* sp. nov., and *Hispanomys* is represented by *H. aff. adroveri*, a form related to *H. adroveri*, but certainly not identical to it. The localities are Crevillente 8, 17, and 5.

In the following zone *N. lucentensis* has disappeared, and *N. plinii* is back again. *H. cf. adroveri* continues. This fauna is found in Crevillente 14.

Table 2. Repartition of Cricetidae in the Crevillente localities

Locality	Cricetinae	Cricetodontinae	
CR6	<i>C. cf. kormosi</i>	<i>H. sp.</i>	
CR14	<i>N. plinii</i>	<i>H. cf. adroveri</i>	<i>H. sp.</i>
CR5	<i>N. lucentensis</i>		
CR17	<i>N. lucentensis</i>	<i>H. cf. adroveri</i>	
CR8	<i>N. lucentensis</i>	<i>H. cf. adroveri</i>	
CR15	<i>N. plinii</i>	<i>H. adroveri</i>	<i>H. sp.</i>
CR4B	<i>N. occidentalis</i>	<i>H. peralensis</i>	
CR2	<i>N. occidentalis</i>	<i>H. peralensis</i>	

Finally in Crevillente 6 we find *C. cf. kormosi* and a poorly documented *Hispanomys*.

The most remarkable thing in this zonation is the subsequent appearance, disappearance and reappearance of *N. plinii*. We thoroughly investigated the possibility, that Crevillente 14 should be placed lower in the stratigraphy, below Crevillente 8 and 17. However, the field data show, that Crevillente 14 is stratigraphically higher than Crevillente 17. This may mean, that the localities Crevillente 8, 5, and 17 represent a time interval with different ecological conditions.

We will discuss the biostratigraphy of the Crevillente localities in more detail in our forthcoming publication on the Muridae from the same localities.

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