Cricetidae (Rodentia, Mammalia) from the Upper Oligocene of Mirambueno and Vivel del Río (prov. Teruel, Spain)

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Key words — Oligocene, Rodentia, Spain.
The Cricetidae from a number of Oligocene mammal-bearing localities near Montalbán (prov. Teruel, Spain) are described. The cricetid fauna is characterised by the dominance, both in number of species and in number of specimens, of the subfamily Pseudocricetodontinae. A local faunal zonation on the basis of Cricetidae is given.
Two new species are described: *Eucricetodon martinensis* sp. nov., and *Allocricetodon cornelii* gen. nov., sp. nov.

Contents

Introduction

In this paper the Cricetidae from a number of Upper Oligocene mammal-bearing localities near Montalbán (prov. Teruel, Spain) are described. They are represented by four genera: *Eucricetodon*, *Allocricetodon* gen. nov., *Heterocricetodon*, and *Pseudocricetodon*. The genus *Pseudocricetodon* has been described in a separate paper (Freudenthal et al., 1994). *Melissiodon* is represented in the collection, but it is not studied in this paper; in my opinion this genus belongs to another family (see Freudenthal et al., 1992). The localities are situated near the eastern border of the Calatayud-Teruel Basin, topographical map no 27-19 (492), between the villages of Martín del Río and Vivel del Río, on the southwestern bank of the river Vivel.

A stratigraphic section of the area, with the geographic and stratigraphic position of the localities will be published by Freudenthal, Martínez-Salanova & Sacristán (in prep.).

The material described in this paper will be deposited in the Department of Geology, University of Zaragoza.

Measurements are given in units of 0.1 mm.

Abbreviations	MIR1	Mirambueno 1	MIR4D	Mirambueno 4D
	MIR2A	Mirambueno 2A	PAJ	Pareja
	MIR4B	Mirambueno 4B	VIV	Vivel del Río
	MIR4C	Mirambueno 4C		

The photographs were made on the Zeiss DSM 950 Scanning Electron Microscope of the Granada University.

Taxonomic descriptions

Family Cricetidae Murray, 1866
Subfamily Eucricetodontinae Mein & Freudenthal, 1971
Genus *Eucricetodon* Thaler, 1966

Eucricetodon dubius (Schaub, 1925)
Pl. 1, figs. 1-2.

Synonymy — *Cricetodon praecursor* Schaub, 1925 (see Freudenthal et al., 1992).

Holotype — Mandibula sin. with M_1-M_3, QT 764, Naturhistorisches Museum, Basel.

Type-locality — Quercy (Lot-et-Garonne, France).

Remark — Mayo (1982) states that Schaub did not designate a holotype for *E. dubius*, and designates Au 1206 from Puy-de-Montdoury as lectotype, and QT 764 as paralectotype. However, Schaub (1925, p. 50) speaks of the two type-mandibles, referring himself to *C. dubius* and *C. praecursor*, so he did implicitly designate the mandible QT 764 as holotype, and Mayo's lectotype designation must be rejected.

Localities with *E. dubius* in our area — Vivel del Río, Mirambueno 1, 2A.

Material and measurements — See Table 1, Fig. 1.

This species was reported from Vivel del Río by Hugueney et al. (1987). In our collections from Vivel del Río, as well as in the collection described by Hugueney et al. (1987), it is by far the most frequent cricetid.

Description of the material from Vivel del Río

M_1 — In many specimens the anterolophid is an almost transverse arch that descends from the metaconid along the anterior border, towards the protoconid, without reaching that cusp. In these specimens the anteroconid is hardly indicated, and the anterior wall of the tooth is very blunt. The anterolophulid - if present - is very short. This morphotype is the one figured in Pl. 1, fig. 1, by Brunet et al. (1981, fig. 27), and by Comte (1985, fig. 6j). The entire morphology of these specimens reminds one of a miniature *Paracricetodon*.

In another group of specimens the anteroconid is fairly well marked, the distance between protoconid and anteroconid is longer, and the anterior end of the tooth is pointed (Pl. 1, fig. 2). These specimens resemble the holotype of *E. dubius* more closely.

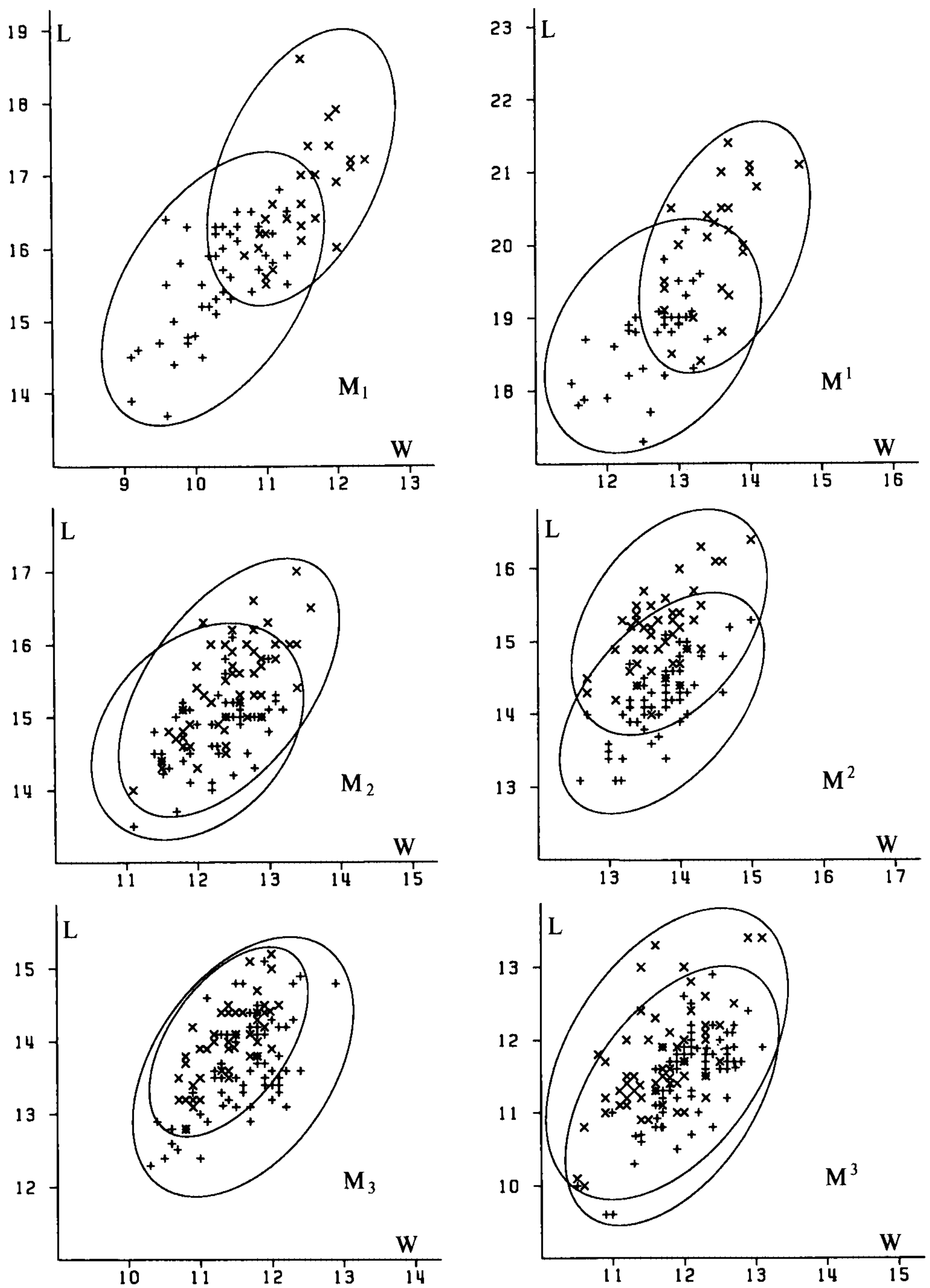


Fig. 1. Length/width diagrams of the molars of *Allocricetodon cornelii* (+) and *Eucricetodon dubius* (×) from Mirambueno 1.

It cannot be excluded, that these two morphotypes represent two different species; further study will be needed to decide whether a clear demarcation between the two can be drawn.

The outline of the tooth is quite characteristic: asymmetrical, with a step-wise increase of width between the protoconid-metaconid pair and the hypoconid-entoconid pair. The entoconid is generally much larger than the metaconid. The anterolophulid is absent or interrupted, rarely complete. The anterior metalophulid is absent or interrupted, less frequently complete. The protoconid hind-arm is connected to the base of the metaconid, or a little bit higher; it rarely ends free. The mesolophid is absent, or short to medium-length; in a few specimens it is double. There may be an ectomesolophid, and a weak mesoconid. The hypoconid hind-arm is long and thick, placed on the posterior part of the hypoconid. The posterosinusid is wide.

M_2 — The protoconid hind-arm is longer and more detached from the metaconid than in M_1. Mesolophid, ectomesolophid, and mesoconid are better developed than in M_1. The hypoconid hind-arm is placed farther backwards, and may be shorter.

M_3 — The protoconid hind-arm is on the average longer and more detached from the metaconid than in M_2. Mesolophid, ectomesolophid, and mesoconid are less developed; the hypoconid hind-arm may be present.

M^1 — The anterocone is broad and simple. The protocone fore-arm never forms a complete anterolophule; the lingual anteroloph may be prolonged and meet the anterior tip of the protocone; this connection should not be interpreted as an anterolophule. The posterior protolophule is complete, and the fore-arm of the protocone rarely forms an anterior protolophule. The mesoloph is placed in the posterior part of the mesosinus; it is of medium length or long, and may reach the molar border. Only in some rare cases there is a mesocone or a second mesoloph. There frequently is a mesostyl. The metalophule is connected to the center of the hypocone, or to its anterior part, not to the entoloph.

M^2 — The protolophule is anterior; a posterior connection, originating from the entoloph has not been observed. The sinus is directed strongly forward; there is no mesocone. The mesoloph has a backward position; it is of medium length or long. There frequently is a mesostyl. The metalophule is connected to the hypocone, less often to the entoloph.

M^3 — The axioloph may be interpreted without any problem as the old entoloph, connected to the protolophule. There is no trace of an old entoloph on the labial wall of the protocone, so this cusp is not 'rotated' (see for a discussion of this morphology Freudenthal & Daams, 1988). The neo-entoloph is frequently absent, low, or interrupted, resulting in a not-reduced sinus, that protrudes deeply, and far forward into the molar. The mesoloph is usually of medium length or long.

Discussion — We found this species also in Mirambueno 2A, where it is the dominant cricetid, and in Mirambueno 1, where it is about as frequent as *Allocricetodon cornelii* gen. nov., sp. nov., to be described hereafter. Morphologically, and in size, these three populations are quite similar.

A few differences with the population from Cournon-les-Souméroux (Brunet et al., 1981) may be noted: in our populations the anterior metalophulid in M_1 seems to be less frequent. In the upper molars there is no mesocone nor a second mesoloph.

In comparison with the population from Gaimersheim (Dienemann, 1987) the mesolophs of the upper molars appear to be longer. It is worthwhile noting, that in the populations described by Dienemann (op. cit., p. 60) the same two morphotypes of M_1 are distinguished, that were mentioned above. The size ranges of the Gaimersheim material are very great. More specifically, the minima for VIV on the one hand and Gaimersheim on the other, are quite similar. The maxima for Gaimersheim are considerably larger than in the population from Vivel. Possibly two species are present in Gaimersheim (see also next paragraph).

Eucricetodon sp. 1, aff. *dubius* (Schaub, 1925)
Pl. 1, fig. 3.

The size range over the length of all M_3 with 'dubius'-morphology from Vivel del Río (V'= 28.0) indicates that possibly two species are present. Three specimens are considerably larger than the rest of the material (see Table 1); they have a posterior

Table 1. Measurements of *E. dubius* and *E.* aff. *dubius*.

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1												
VIV	34	15.0	16.79	18.7	21.96	0.876	37	10.7	11.85	13.1	20.17	0.638
MIR2A	7	15.6	16.80	18.4	16.47	0.909	7	10.6	11.61	13.0	20.34	0.799
MIR1	26	15.5	16.67	18.6	18.18	0.766	27	10.7	11.52	12.4	14.72	0.466
MIR4C	5	15.6	15.90	16.3	4.39	0.308	5	10.3	10.82	11.3	9.26	0.455
M_2												
VIV	36	14.5	15.88	17.2	17.03	0.662	33	11.9	12.87	13.9	15.50	0.620
MIR2A	8	14.7	15.31	16.1	9.09	0.517	8	11.6	12.45	13.2	12.90	0.532
MIR1	51	14.0	15.40	17.0	19.35	0.673	51	11.1	12.45	13.6	20.24	0.562
MIR4C	3	14.0	14.57	15.0	6.90	0.513	3	11.2	11.23	11.3	0.89	0.058
M_3												
VIV	39	12.9	14.69	15.8	20.21	0.772	34	10.9	12.09	13.0	17.57	0.618
VIV	3	16.3	16.77	17.1	4.79	0.416	3	12.4	13.23	14.0	12.12	0.802
MIR2A	4	12.9	13.35	13.9	7.46	0.412	4	10.8	11.43	12.1	11.35	0.531
MIR1	47	12.8	13.98	15.2	17.14	0.534	44	10.7	11.40	12.1	12.28	0.426
MIR4C	1		14.30				1		12.30			
M^1												
VIV	30	18.9	20.59	22.2	16.06	0.974	31	12.8	13.93	14.9	15.16	0.653
MIR2A	9	17.5	19.52	20.8	17.23	1.178	12	11.9	13.24	14.5	19.70	0.675
MIR1	29	18.4	20.05	21.4	15.08	0.816	28	12.6	13.47	14.7	15.38	0.490
MIR4C	2	18.5	19.00	19.5	5.26	0.707	2	12.5	12.75	13.0	3.92	0.354
M^2												
VIV	48	13.7	15.25	16.7	19.74	0.751	50	12.7	14.05	15.6	20.49	0.625
MIR2A	9	14.1	14.69	15.9	12.00	0.540	10	12.4	13.21	14.1	12.83	0.438
MIR1	44	14.0	15.14	16.4	15.79	0.558	45	12.7	13.73	15.0	16.61	0.464
M^3												
VIV	34	11.3	12.59	13.5	17.74	0.532	34	11.6	12.49	13.2	12.90	0.514
MIR2A	9	9.5	11.42	12.3	25.69	0.923	9	10.8	11.59	13.1	19.25	0.732
MIR1	58	10.0	11.70	13.4	29.06	0.720	58	10.5	11.66	13.1	22.03	0.574
MIR4C	1		10.10				1		11.10			

arm of the hypoconid, which is not frequently present in *E. dubius* from the same locality.

V' for the M_3 of the Gaimersheim population is extremely high. It might be interesting to see whether in Gaimersheim the hypoconid hind-arm of M_3 is more frequently present in the larger specimens.

Eucricetodon sp. 2, aff. *dubius* (Schaub, 1925)
Pl. 1, figs. 4-8.

A species resembling *E. dubius* has been found in Mirambueno 4C, where it is a minor component of the fauna. The specimens from MIR4C are of the same size as the smaller specimens from MIR1, MIR2A, and VIV, and this size distribution may mean, that we are dealing with a new species, closely related to *E. dubius*, and on the average smaller.

In a collection of 40 M_1 and 33 M_2 from Vivel the posterior branch of the hypoconid is always present; in *E.* aff. *dubius* from MIR4C it is absent in 1 out of 5 M_1; so, possibly this feature is less developed in *Eucricetodon* sp. 2, aff. *dubius* than in *E. dubius*, but the material is – as yet – insufficient.

Measurements — See Table 1, Figs. 2-7.

Description of the material from Mirambueno 4C

M_1 — There is no anteroconid cusp; the anterolophid forms a continuous arch, firmly connected to the metaconid in 4 out of 5 specimens; the anterior wall of the tooth is very blunt. The anterolophulid is interrupted (4), or complete (1). The anterior metalophulid is interrupted. The protoconid hind-arm ascends to the top of the metaconid. The ectolophid is low. The mesolophid varies between absent and medium-length; one specimen has a second mesolophid. The mesosinusid is blocked by a cingulum ridge descending from the metaconid. The hypoconid hind-arm is very long (4), or absent (1). The posterosinusid is closed by a high posterolophid. The posterior wall of the hypoconid is indented.

M_2 — The anterior metalophulid is complete (2), or interrupted (1). The protoconid hind-arm is long and free. The ectolophid is low, the mesolophid is short or of medium length. The mesosinusid is open. The hypoconid hind-arm is long or very long. The posterolophid closes the posterosinusid at a high level.

M_3 — This specimen is too much worn to permit a description. Its attribution to *E.* aff. *dubius* is not certain.

M^1 — The anterocone is simple; the protocone fore-arm is short; the protolophule is posterior. The sinus points sharply forward; its anterior tip is compressed. The mesoloph is irregular, and of medium length.

M^3 — The axioloph is incomplete; the neo-entoloph is high. The mesoloph is long.

N.B. The incomplete axioloph (= old entoloph) is remarkable, because this is considered to be an advanced feature. In the populations of *E. dubius* described above, that are younger in age, the axioloph is complete, leaving no doubt about its homology with the old entoloph.

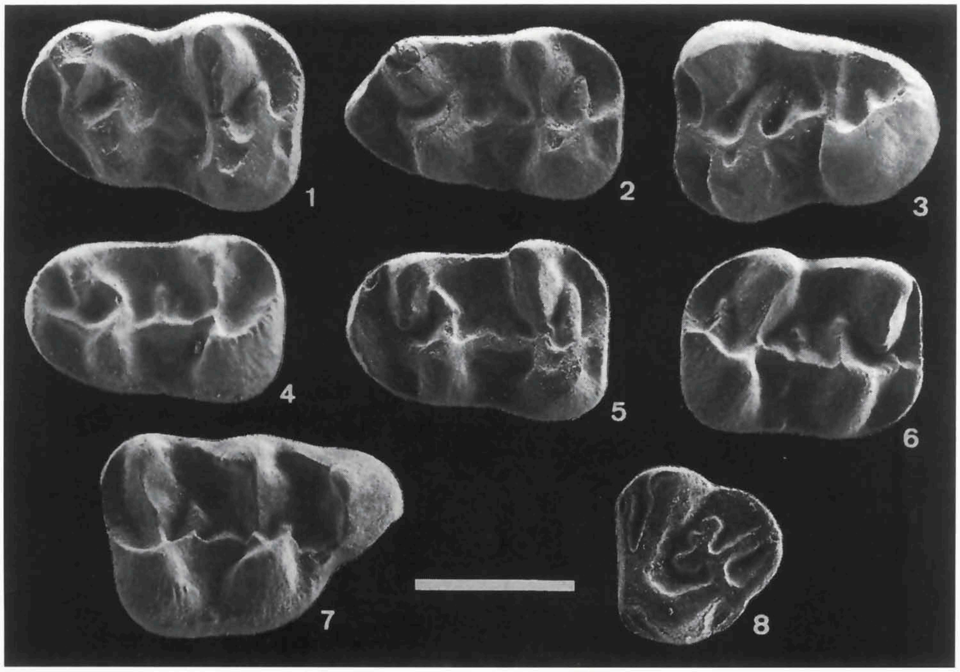


Plate 1

Eucricetodon dubius (Schaub, 1925)
Vivel del Río
Fig. 1. M_1 sin., VIV 8.
Fig. 2. M_1 sin., VIV 5.

Eucricetodon sp. 1, aff. *dubius* (Schaub, 1925)
Vivel del Río
Fig. 3. M_3 sin., VIV 107.

Eucricetodon sp. 2, aff. *dubius* (Schaub, 1925)
Mirambueno 4C
Fig. 4. M_1 sin., MIR4C 107.
Fig. 5. M_1 sin., MIR4C 108.
Fig. 6. M_2 dext., MIR4C 113.
Fig. 7. M^1 dext., MIR4C 117.
Fig. 8. M^3 sin., MIR4C 118.

Scale is 1 mm.

Remark — Direct comparison has made it clear, that the M_1 of *Eucricetodon* sp. from Pareja (Daams et al., 1989, pl. 7, fig. 9; PAJ 743) may be attributed to this species; it has no posterior branch of the hypoconid, but it does have the typical '*dubius*'- morphology. The M^1, PAJ 618, from Pareja (Daams et al., 1989, pl. 7, fig. 8), may belong to this species too.

Eucricetodon martinensis sp. nov.
Pl. 2, figs. 1-12.

Holotype — M^1 sin., MIR4D 142, Departamento de Ciencias de la Tierra, Universidad de Zaragoza.
Type-locality — Mirambueno 4D (Martín del Río, prov. Teruel, Spain).
Age — Early Late Oligocene.

Derivatio nominis — The type-locality is situated in the territory of the village of Martín del Río.

Diagnosis — The molars have massive cusps and narrow valleys. The anterior metalophulid of M_1 is frequently absent. The protoconid hind-arm is moderately developed in M_1, rarely present in M_2, and absent in M_3. The ectolophid of M_1 is oblique. In M^1 the lingual anteroloph often forms a continuous high crest, that reaches the antero-labial tip of the protocone; the metalophule is connected to the center of the hypocone or farther backwards. The sinus of M^1 and M^2 falls down steeply from the entoloph to the molar border, and has no horizontal part. In M^3 the sinus is often very deep, the old entoloph being connected to the anterior part of the protocone, and the neo-entoloph being low or absent.

Differential diagnosis — Three species show similarities with *E. martinensis* sp. nov.: *E. huerzeleri* Vianey-Liaud, 1972, *E. margaritae* Daams et al., 1989, and *E. huberi* (Schaub, 1925).

Table 2. Measurements of *E. martinensis* (MIR4C and MIR4D) and *E. margaritae* (PAJ).

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1												
MIR4D	14	19.5	20.58	21.9	11.59	0.821	13	12.4	13.07	14.2	13.53	0.629
MIR4C	7	19.5	20.49	21.8	11.14	0.720	7	12.5	13.34	14.1	12.03	0.574
PAJ	8	17.8	18.78	20.3	13.12	0.846	11	10.9	12.35	13.3	19.83	0.670
M_2												
MIR4D	13	17.7	18.62	19.8	11.20	0.717	13	14.7	15.52	16.7	12.74	0.656
MIR4C	5	17.3	18.34	18.9	8.84	0.654	5	14.8	15.24	16.0	7.79	0.472
PAJ	10	16.3	16.96	18.2	11.01	0.696	10	12.7	14.04	14.9	15.94	0.622
M_3												
MIR4D	13	14.2	15.85	17.2	19.11	0.816	13	12.3	13.48	14.7	17.78	0.781
MIR4C	12	14.9	15.73	16.8	11.99	0.678	11	12.1	13.35	14.1	15.27	0.650
PAJ	11	13.8	14.86	16.7	19.02	0.870	11	11.4	12.49	13.7	18.33	0.693
M^1												
MIR4D	6	23.3	24.37	26.2	11.72	1.191	5	15.7	16.58	17.2	9.12	0.554
MIR4C	2	22.5	22.85	23.2	3.06	0.495	1	16.2	16.20	16.2		
PAJ	6	22.3	23.32	23.9	6.93	0.598	6	14.8	15.15	15.5	4.62	0.274
M^2												
MIR4D	6	17.6	18.68	19.2	8.70	0.591	6	16.9	17.60	18.4	8.50	0.521
MIR4C	4	16.9	17.43	18.2	7.41	0.574	3	16.1	16.83	17.5	8.33	0.702
PAJ	9	15.6	16.76	17.7	12.61	0.643	9	15.1	15.73	16.6	9.46	0.505
M^3												
MIR4D	12	10.5	12.09	13.6	25.73	0.793	12	12.4	13.67	15.0	18.98	0.778
MIR4C	10	10.9	11.99	12.9	16.81	0.647	9	13.0	13.82	14.4	10.22	0.556
PAJ	10	12.1	13.21	14.3	16.67	0.720	10	13.1	13.91	14.5	10.14	0.465

E. martinensis differs from *E. huerzeleri* by its smaller size, the hardly developed hypoconid hind-arm in the lower molars, and the simple anterocone of M^1.

It differs from *E. margaritae* by its — on the average — larger size, except for M^3 which is on the average smaller; the less developed anterior metalophulid of M_1; the simple or hardly split anterocone of M^1; the more backward position of the metalophule of M^1; the frequently deep sinus of M^3.

It differs from *E. huberi* by its larger size.

The populations from Mirambueno 4C and 4D are morphologically almost identical; the few differences may easily be explained by the small number of specimens available. I will describe the two populations together.

Material and measurements — See Table 2, Figs. 2-7.

Descriptions and comparisons of the material are taken from a data base of morphological descriptions, similar to the one described by Freudenthal et al. (1994). Since the morphologies of *Pseudocricetodon* and *Eucricetodon* are different in many respects, a different set of definitions has to be used. This task is less advanced for *Eucricetodon*, and therefore I do not yet publish the definitions as we did for *Pseudocricetodon*. Tables 6-11 give a selection of features already entered in the data base.

Description of the material from Mirambueno 4C and 4D

M_1 — The anterior metalophulid is generally absent (55%), rarely complete (14%). The protoconid hind-arm is short and free (46%), long and free (9%), connected to the metaconid at a low level (32%), or higher on the metaconid (14%). The sinusid is transverse in most cases (82%). A mesoconid is often developed. The mesolophid is directed obliquely forward (posterolabial-anterolingual), of medium length or long, absent in one case only. A weak ectomesolophid is present in 6 specimens. A very short hypoconid hind-arm is present in 3 specimens.

M_2 — The metalophulid is always connected to the anteroconid. The protoconid hind-arm is absent (83%) or short and free (17%). In 65% of the specimens there is a mesoconid. The mesolophid is of medium length (22%) or long (78%). One specimen has a short hypoconid hind-arm.

M_3 — The metalophulid is directed to the anteroconid (27%), or to the anterolophulid (73%). The protoconid hind-arm is always lacking. The mesolophid is absent (22%), short (26%), of medium length (41%), or long (11%). In 25% of the specimens there is an ectomesolophid.

M^1 — The anterocone is simple (75%), or slightly subdivided (25%). The prelobe is lingually set-off from the protocone in 67% of the cases. In 5 out of 9 specimens the lingual anteroloph is separated from the lingual border, and continues as a high crest to the anterior tip of the protocone; this crest, in my opinion, is not homologous with the anteroloph, though it appears to be so. In most specimens there is a triangle, lingually of the anteroloph, and in front of the protocone (protocone platform); there may be a transverse crest on this platform. The protolophule is nearly always posterior. The metalophule is generally transverse, posterior in one case, and anterior in another one. The posterosinus is open in most cases (86%).

M^2 — The anterior protolophule is always present; in one case there is an interrupted posterior connection, and in another one this connection is complete. The mesoloph is of medium length or long. The metalophule is anterior, but may have a tendency towards a transverse position. The labial border is straight or convex.

M^3 — The lingual anteroloph is absent or weak. The sinus is often deep, and may continue to the junction of protocone and protolophule. The old entoloph is frequently complete, and connected to the protolophule, or, in other words, the protolophule is transversely connected to the entoloph. The axioloph, if present, may be interpreted as the anterior part of this old entoloph, which has lost contact with the hypocone. A (remnant of the) old entoloph, connected to the center of the labial wall of the protocone, is rarely present. The mesoloph is often long and very broad.

Remark — The pattern of the entoloph seems to indicate, that the protocone is not rotated, as frequently seen in *Pseudocricetodon, Allocricetodon* gen. nov., many other species of *Eucricetodon*, and many Miocene Cricetidae (see the discussion on the cricetid M^3 by Freudenthal & Daams, 1988).

Discussion

Apparently *E. martinensis, E. margaritae, E. huberi*, and *E. huerzeleri* form a fairly homogeneous group within the genus *Eucricetodon*. This group is characterised by thick, often crenulated, enamel, and bulky cusps, thick mesoloph(id)s, and frequent presence of a mesoconid or mesocone. In M_1 there is a tendency to enclose a funnel between the protoconid hind-arm, the mesolophid, and the ectolophid; the ectolophid is strongly oblique (anterolabial-posterolingual), and the mesolophid is directed forward, perpendicular to the ectolophid. In M_2 the protoconid hind-arm is rarely present, and in M_3 it is absent. In M^1 the anterocone is a labial cusp with a long and well-developed lingual anteroloph; there may arise a cusp on this anteroloph; the posterosinus is not reduced. In M^3 the old entoloph is frequently preserved, and it may reach far forward to join the protolophule.

On the basis of size one might think, that *E. margaritae* be the ancestor of *E. martinensis*. Such an interpretation is corroborated by the following characters, that are supposedly primitive: the slightly better developed protoconid hind-arm in the M_1 and M_2 of *E. margaritae*; the more anterior position of the metalophule in its M^1, and maybe also in its M^2; the frequently concave labial border of M^2; the size of M^3, that is less reduced in *E. margaritae*

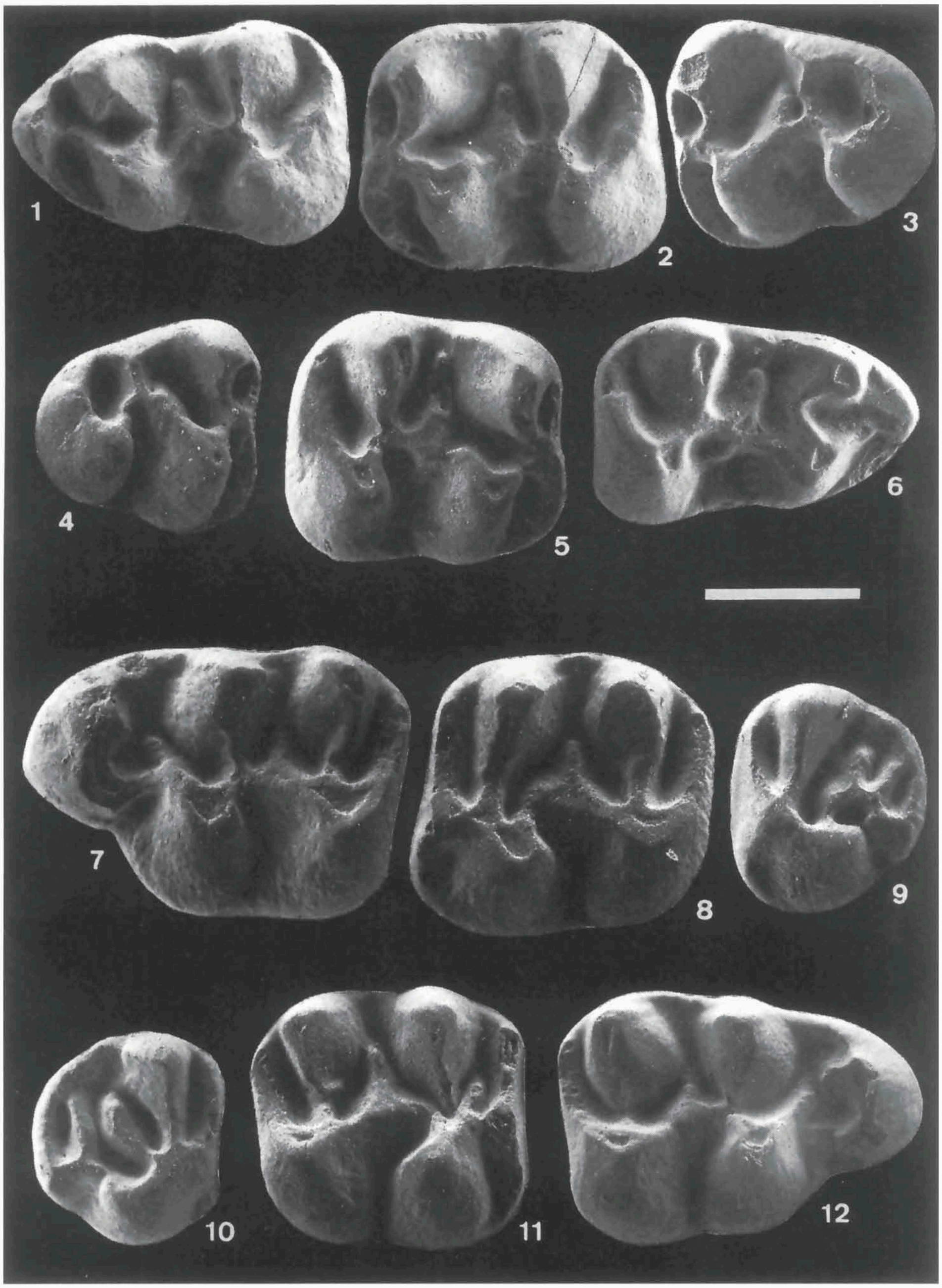
On the other hand *E. margaritae* shows a number of differences with respect to *E. martinensis*, that may be interpreted as derived: the well-developed anterior metalophulid in the M_1 of *E. margaritae*; the always more or less subdivided anterocone of its M^1;

Plate 2

Eucricetodon martinensis sp. nov. from Mirambueno 4D

Fig. 1. M_1 sin., MIR4D 102.
Fig. 2. M_2 sin., MIR4D 19.
Fig. 3. M_3 sin., MIR4D 22.
Fig. 4. M_3 dext., MIR4D 131.
Fig. 5. M_2 dext., MIR4D 119.
Fig. 6. M_1 dext., MIR4D 108.
Fig. 7. M^1 sin., MIR4D 142, holotype.
Fig. 8. M^2 sin., MIR4D 147.
Fig. 9. M^3 sin., MIR4D 155.
Fig. 10. M^3 dext., MIR4D 160.
Fig. 11. M^2 dext., MIR4D 151.
Fig. 12. M^1 dext., MIR4D 145.

Scale is 1 mm.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the normally developed lingual anteroloph of its M^1, that never gives the impression of a longitudinal anterolophule.

The comparison of the M^3 of both species reveals a peculiar situation. The M^3 of *E. martinensis* is on the average smaller than the same element of *E. margaritae*. I think size reduction of the M^3 is an advanced feature. On the other hand, the M^3 of *E. martinensis* has conserved a more primitive dental pattern: the neo-entoloph is often absent or interrupted, and the sinus protrudes into the center of the molar, often towards the anterior tip of the protocone.

Other differences, for which the evolutionary trend is not certain, are: the better developed hypoconid hind-arm in the M_1 and M_2 of *E. margaritae*, and the more forward position of the metalophulid in its M_3.

My conclusion is, that the mixture of primitive and derived features in these two species makes it impossible to place them in an ancestor-descendant relationship. I consider them as two more or less synchronical species, probably with a common ancestor, that should not be much older.

A species that may be close to *E. margaritae* and *E. martinensis* is *E. huberi* (Schaub, 1925). The dimensions of its holotype mandible from Mümliswil are smaller than those of *E. martinensis*.

E. huberi is of the same size as *E. margaritae*. It differs from that species by the construction of the anterior part of M_1: in the holotype of *E. huberi* there is no anterior metalophulid, and the metaconid is connected to the anteroconid through the anterosinusid; in *E. margaritae* the anterior metalophulid is always present, and the connection metaconid-anteroconid does not exist. In the M_2 of *E. huberi* the mesolophid is directed obliquely backwards, whereas in *E. margaritae* this crest is transverse, or directed obliquely forward (from the ectolophid towards the metaconid). The M^1 from Mümliswil, contrary to the figure by Schaub (1925, pl. 4, fig. 2), but in agreement with his description, has a well-developed anterior protolophule, and only an indication of a posterior connection. In *E. margaritae* the posterior protolophule is well developed, and the anterior one absent.

In view of the scarce material of *E. huberi* nothing can be said about its phylogenetic relationships with the two Spanish species.

Subfamily Pseudocricetodontinae Engesser, 1987
Tribe Pseudocricetodontini Engesser, 1987
Genus *Pseudocricetodon* Thaler, 1969

Type-species — *Pseudocricetodon montalbanensis* Thaler, 1969.

In the section of Mirambueno this genus is represented by four species: *P. simplex* Freudenthal, Hugueney & Moissenet, 1994, *P.* aff. *simplex*, *P.* aff. *philippi* Hugueney, 1971, and *P. adroveri* Freudenthal, Hugueney & Moissenet, 1994.

This genus has been extensively studied by Freudenthal et al. (1994), and will not be treated in this paper. The reader is referred to the mentioned study.

Genus *Allocricetodon* gen. nov.

Type-species — *Allocricetodon cornelii* gen. & sp. nov.
Derivatio nominis — Greek 'allos' = different (from).

Diagnosis — Pseudocricetodontinae of medium size. In M_1 there is a crest descending backwards from the metaconid, along the border of the molar, that may reach the entoconid; in most cases there is no anterior metalophulid, and the metaconid is connected to the anteroconid along the molar border. In M_1 and M_2 the posterosinusid is completely closed by a high posterolophid. Protoconid hind-arm in M_3 very well developed. In M^1 the anterolophule is generally incomplete; instead, there is frequently a longitudinal connection between anterocone and paracone. The posterior wall of the metacone in M^1 and M^2 is very steep or vertical, sometimes overhanging. The trapezoid shape of M^2 is caused by a reduction of both hypocone and metacone.

Differential diagnosis — Larger than *Pseudocricetodon* and *Kerosinia*, smaller than *Heterocricetodon* and *Cincamyarion*. Cingulum ridges closing the valleys of the lower molars are better developed than in *Pseudocricetodon*. The metalophulid of M_3 is anterior, and there is a well-developed posterior branch of the protoconid; in *Kerosinia* this branch forms the posterior metalophulid, and the anterior metalophulid is absent.

I create this genus for a group of species, that are closely related to *Cricetodon incertus* Schlosser, 1884. This species has been reported from many European localities. It is, however, not quite clear what exactly is *Cricetodon incertus*. The type-mandible from the Quercy only bears M_2 and M_3, and these teeth are quite worn. Dienemann (1987) gives as measurements: M_2: 15.6 × 13.0; M_3: 14.9 × 12.4. We found a larger value for the length of M_3. Dienemann describes this species from a number of fissure fillings in S. Germany, his richest population being the one from Ehrenstein 7.

In that population the M_1 shows a skew distribution and a large size range (V' = 23.9). Possibly the two specimens with a length around 19.0 (see Dienemann, op. cit., fig. 24) do not belong to *A. incertus*; their size agrees with that of *A. landroveri* (Daams et al., 1989).

In the population from Boujac (Gard, France; Comte, 1985) the size relations between the dental elements are so far away from what is normally found, that there can hardly be any doubt about the heterogeneity of the material. The same is probably true for Mas-de-Pauffié and Pech Desse.

The material from Mirambueno 4C proves, that there exist indeed two synchronical species with the 'incertus'-morphology. The smaller one of these coincides fairly well with the measurements given by Dienemann for *A. incertus*. The larger one is comparable to *A. landroveri* (Daams et al., 1989).

In our locality Mirambueno 1 a third species of this group is found. It is of the same size as the smaller one from MIR4C, and it is impossible to decide to which one belongs the holotype of *A. incertus* (if to any one of the two).

I decided to attribute the MIR4C population to *A. incertus*, and create a new species for the population from MIR1. I must admit, however, that I might have decided the other way as well.

Allocricetodon cornelii sp. nov., has been chosen as the type-species of *Allocricetodon*, because it is the best represented one in our material.

Remark — *Cricetodon murinus* Schlosser, 1884 is a poorly known species. Dienemann (1987) reports that the lower incisor of the holotype has 7 to 8 fine longitudinal lines. This may mean that *C. murinus* is a pseudocricetodontine, and not an eucricetodontine. Dienemann mentions this possibility, and rejects it because of the probable presence of a hypoconid hind-arm in M_1. It is true that this is not a common feature in this group, but it is present in all three genera of this subfamily. Therefore its attri-

Table 3. Measurements of *Allocricetodon landroveri* (#), *A. cornelii* (*), and *A. incertus* (+).

	Length						Width					
	n	min.	mean	max.	V′	σ	n	min.	mean	max.	V′	σ
M_1												
VIV#	2	17.1	17.20	17.3	1.16	0.141	2	10.9	11.20	11.5	5.36	0.424
MIR4D#	31	16.7	18.20	19.5	15.47	0.680	31	11.3	12.27	13.2	15.51	0.548
MIR4C#	23	17.4	18.26	19.3	10.35	0.559	24	11.1	12.16	13.1	16.53	0.545
PAJ#	31	16.4	18.64	20.0	19.78	0.870	33	10.7	12.12	13.4	22.41	0.671
VIV*	3	14.3	14.93	15.6	8.70	0.651	4	10.2	10.50	11.1	8.45	0.408
MIR1*	45	13.7	15.56	16.8	20.33	0.746	45	9.1	10.30	11.3	21.57	0.586
MIR4C+	10	15.3	16.22	16.9	9.94	0.512	10	9.8	10.47	11.0	11.54	0.368
M_2												
VIV#	2	16.1	16.20	16.3	1.23	0.141	2	13.2	13.25	13.3	0.75	0.071
MIR4D#	28	16.2	17.14	18.4	12.72	0.568	27	13.3	14.36	15.4	14.63	0.504
MIR4C#	22	16.1	17.10	18.2	12.24	0.627	22	13.5	14.20	15.3	12.50	0.431
PAJ#	31	15.5	16.65	17.8	13.81	0.602	32	13.0	13.91	15.3	16.25	0.560
VIV*	1		12.00				1		9.50			
MIR2A*	2	13.8	14.20	14.6	5.63	0.566	2	11.7	11.95	12.2	4.18	0.354
MIR1*	47	13.5	14.81	16.1	17.57	0.532	46	11.1	12.25	13.2	17.28	0.529
MIR4C+	17	13.7	14.75	15.7	13.61	0.503	17	11.1	12.11	13.3	18.03	0.543
M_3												
VIV#	1		16.00				1		13.20			
MIR4D#	35	13.6	15.89	17.3	23.95	0.963	35	11.3	13.53	14.7	26.15	0.865
MIR4C#	14	15.1	16.45	17.7	15.85	0.917	13	12.7	13.63	14.6	13.92	0.654
PAJ#	23	14.0	15.51	17.5	22.22	0.860	24	11.8	13.12	14.0	17.05	0.611
VIV*	5	12.7	13.60	14.6	13.92	0.822	6	10.2	11.15	12.3	18.67	0.817
MIR2A*	2	12.2	12.35	12.5	2.43	0.212	2	10.8	10.95	11.1	2.74	0.212
MIR1*	64	12.3	13.65	15.1	20.44	0.668	63	10.3	11.60	12.9	22.41	0.543
MIR4C+	12	13.3	13.89	14.6	9.32	0.450	12	10.6	11.58	12.7	18.03	0.588
M^1												
MIR4D#	14	19.8	21.51	22.9	14.52	0.922	13	13.5	15.01	16.0	16.95	0.860
MIR4C#	16	20.2	21.12	22.7	11.66	0.650	16	13.9	14.81	16.1	14.67	0.586
PAJ#	15	19.5	21.39	22.8	15.60	1.098	23	12.5	14.06	15.4	20.79	0.939
VIV*	2	17.8	18.20	18.6	4.40	0.566	3	11.4	12.10	12.5	9.21	0.608
MIR1*	34	17.3	18.75	20.2	15.47	0.631	39	11.5	12.65	14.1	20.31	0.577
MIR4C+	10	16.9	18.07	19.4	13.77	0.763	10	11.1	12.14	13.0	15.77	0.600
M^2												
VIV	1		16.40				1		16.10			
MIR4D#	29	14.6	16.12	17.2	16.35	0.562	30	14.3	15.91	16.9	16.67	0.658
MIR4C#	19	15.6	16.43	17.4	10.91	0.499	20	15.1	16.10	17.7	15.85	0.639
PAJ#	29	14.0	15.66	17.1	19.94	0.731	25	13.9	15.31	16.5	17.11	0.736
VIV*	5	13.0	14.06	15.0	14.29	0.733	5	12.3	13.26	14.3	15.04	0.757
MIR2A*	3	13.4	14.17	14.9	10.60	0.751	2	12.5	13.25	14.0	11.32	1.061
MIR1*	54	13.1	14.20	15.3	15.49	0.527	53	12.6	13.70	15.0	17.39	0.487
MIR4C+	5	12.9	13.78	14.3	10.29	0.554	5	12.5	12.96	14.1	12.03	0.646
M^3												
MIR4D#	34	12.4	13.67	15.1	19.64	0.650	33	13.1	13.95	15.3	15.49	0.511
MIR4C#	31	12.9	13.65	14.7	13.04	0.494	30	12.5	13.79	15.4	20.79	0.557
PAJ#	22	11.0	12.48	14.0	24.00	1.055	23	11.5	13.11	14.3	21.71	0.762
VIV*	4	10.6	11.25	11.8	10.71	0.520	4	10.4	11.65	12.3	16.74	0.858
MIR2A*	3	12.0	12.23	12.5	4.08	0.252	3	11.5	12.17	12.5	8.33	0.577
MIR1*	68	9.6	11.45	12.9	29.33	0.669	67	10.5	12.04	13.1	22.03	0.527
MIR4C+	17	10.8	11.59	12.5	14.59	0.515	17	10.9	11.96	13.2	19.09	0.533

bution to the Pseudocricetodontinae, in casu *Allocricetodon*, cannot be excluded.

For the description and comparison of the material I created a data base of morphological descriptions, as described by Freudenthal et al. (1994). Since the morphologies of *Allocricetodon* and *Pseudocricetodon* are very close, it turned out to be possible to use the same descriptive tables as the ones used for the latter genus; for the meaning of the descriptive terms the reader is referred to the appendix in Freudenthal et al. (1994).

Allocricetodon cornelii gen. & sp. nov.
Pl. 3, figs. 1-11.

Holotype — M_1 dext., MIR1 8, Departamento de Ciencias de la Tierra, University of Zaragoza.

Type-locality — Mirambueno 1 (Vivel del Río, prov. Teruel, Spain).

Derivatio nominis — Dedicated to my friend and colleague Dr C.F. Winkler Prins (Nationaal Natuurhistorisch Museum, Leiden).

Other localities with *A. cornelii* — Mirambueno 2A, Vivel del Río.

Diagnosis

Lower molars — Cingulum ridges, closing the valleys of the lower molars, well developed, often quite high; in M_1 the lingual anterolophid is very well developed. The anterior metalophulid is nearly always absent. In M_1 the anterolophulid forms an angle with the longitudinal axis of the molar. The mesolophid is of medium length or long; the ectomesolophid is nearly always present, often quite well developed. In M_2 the protoconid hind-arm always ends free; it is nearly always long. The mesolophid is generally absent, less frequently present, and it may even be long. In M_3 there is almost never an ectomesolophid.

Upper molars — The anterocone of M^1 is quite frequently more or less subdivided; the prelobe forms a very marked angle with the border of the protocone. There frequently is a well-developed anterior spur on the paracone, that may reach the anterocone. The sinus of M^1 and M^2 is directed strongly forward in most cases. The connection of the entoloph with the protocone in M^2 is nearly always low, or interrupted.

Differential diagnosis — *A. cornelii* is smaller than *A. landroveri*, and morphologically similar; it is of the same size as *A. incertus*, and morphologically more complicated.

Material and measurements — See Table 3, Fig. 1.

Allocricetodon cornelii from Mirambueno 1

Description (see also Table 12 - 17)

M_1 — The lingual anterolophid is generally high (85%); the anteroconid lies in a central position or somewhat lingually of the axis of the tooth; the anterolophulid is generally oblique, either low or high. The anterior metalophulid is absent in 85% of the specimens. The protoconid hind-arm is nearly always connected to the metaconid,

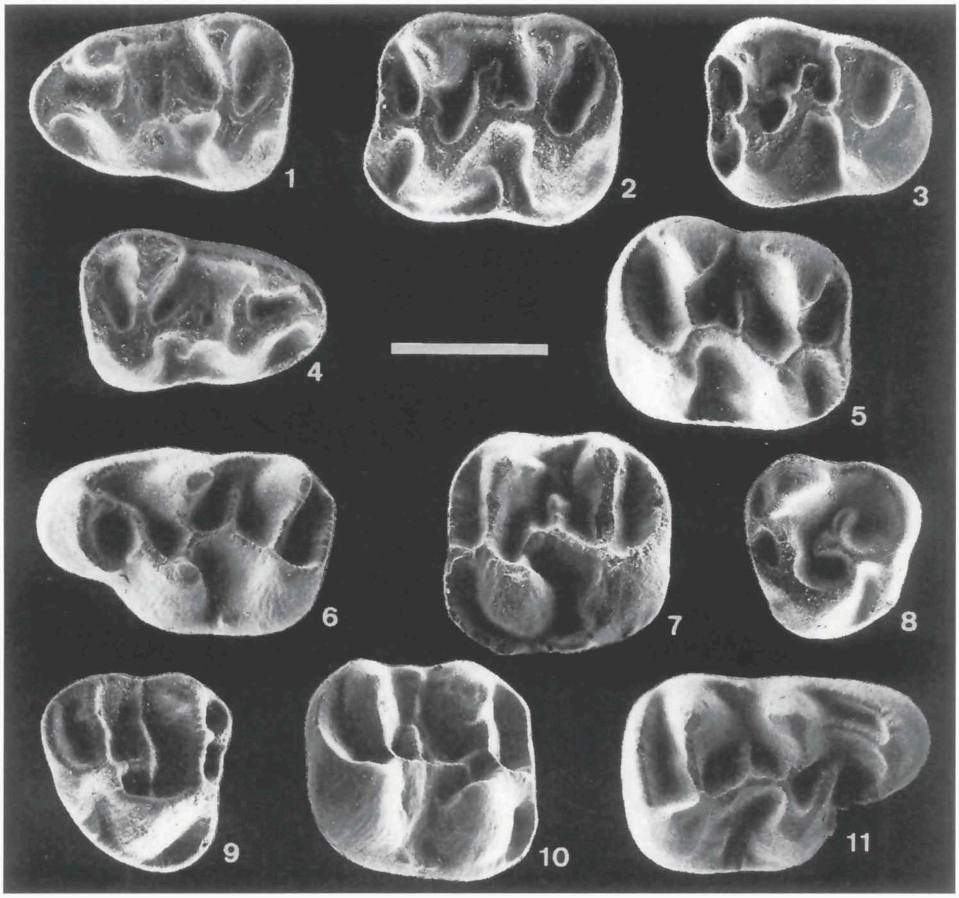

Plate 3

Allocricetodon cornelii sp. nov. from Mirambueno 1
Fig. 1. M_1 sin., MIR1 3.
Fig. 2. M_2 sin., MIR1 12.
Fig. 3. M_3 sin., MIR1 31.
Fig. 4. M_1 dext., MIR1 8, holotype.
Fig. 5. M_2 dext., MIR1 28.
Fig. 6. M^1 sin., MIR1 55.
Fig. 7. M^2 sin., MIR1 68.
Fig. 8. M^3 sin., MIR1 75.
Fig. 9. M^3 dext., MIR1 90.
Fig. 10. M^2 dext., MIR1 74.
Fig. 11. M^1 dext., RGM 417 122.

Scale is 1 mm

either low (45%) or high (50%). The sinusid is transverse (30%) or slightly curved backwards (70%). The ectolophid is longitudinal, with a step-wise connection to the protoconid or the protoconid hind-arm. The mesolophid is of medium length (60%), or long (38%), short in one specimen only; there is no second mesolophid. An ecto-mesolophid is nearly always present (89%). The posterosinusid is firmly closed by the fairly high posterolophid.

M_2 — The protoconid hind-arm is long and free, rarely short and free. The connection of the ectolophid with the protoconid hind-arm is generally high (80%). The mesolophid is absent in 70%, short in 10%, and of medium length in 13% of the specimens. The ectomesolophid is absent in 60% of the cases.

M_3 — The protoconid hind-arm is nearly always long and free. There is no ectomesolophid, except in one specimen.

M^1 — The anterocone is slightly split to deeply split in some 30% of the specimens. The prelobe is broad, and sharply set-off from the protocone. There is a complete anterolophule in 11% of the specimens; in 15% there is a free-ending backward spur on the anterocone; in 40% there is such spur, that is in contact with the paracone. Apart from these 40%, there is an anterior spur from the paracone, either towards the anterostyl (16%), or ending free (10%). The protolophule is posterior, the anterior branch of the protocone is never connected to the anterocone, and hardly ever directed towards that cusp. The sinus is directed strongly forward (76%), or just forward (24%). The entoloph is generally high, but in 38% of the specimens the connection with the protocone is low and step-wise.

M^2 — The lingual anteroloph is well developed; in 62% of the cases it continues along the protocone, and it may separate that cusp from the lingual border. The sinus is like in M^1; in one specimen it is subdivided by a crest from protocone to hypocone (equivalent to the neo-entoloph in M^3). The mesoloph is of medium length or long; in 15% it reaches the border of the molar. In most cases the entoloph-protocone connection is low or interrupted (93%).

M^3 — The protolophule is connected to the anterolophule in the majority of the cases (84%). Generally the sinus is small; it is deep, and the neo-entoloph is absent or interrupted in 9 specimens; in the remainder the neo-entoloph reduces the sinus to a small indentation of the lingual border. The old entoloph is complete in 24%, and totally absent in 56% of the cases.

Allocricetodon cornelii from Mirambueno 2A

The small collection of *A. cornelii* from Mirambueno 2A shows no important differences with the type-population.

Allocricetodon cornelii from Vivel del Río

In most respects this material is identical to the population from Mirambueno 1, though there are some differences: One M^2 has a complete neo-entoloph, and a very long old entoloph, arising from the center of the labial wall of the protocone (terminology of M^3). Three of the 4 specimens of M^3 have a deep sinus; in two of these the neo-entoloph is absent, in the third one it is interrupted. In one specimen the old entoloph is interrupted too, and the sinus continues into the mesosinus.

Discussion

A. cornelii differs from *A. landroveri* from Mirambueno 4C and 4D by: its smaller size; its somewhat better developed mesolophid in M_1, and its less-developed mesolophid in M_2; the total absence of a second mesolophid in M_1; its less developed ectomesolophid in M_2 and M_3; the anterocone of M^1, that may be split; the prelobe of M^1, that is more markedly set-off; its better developed forward paracone spur in M^1; the frequent presence of an entostyl in M^1; the sinus of M^1 and M^2 is more frequently directed strongly forward; its – on the average – shorter mesoloph of M^2; its low or interrupted entoloph-protocone connection in M^2; its less developed old entoloph and axioloph in M^3.

A. cornelii differs from *A. incertus* from Mirambueno 4C by: the better developed cingulum ridges in the lower molars, specially the lingual anterolophid in M_1; the oblique position of the anterolophulid; its better developed ectomesolophid in M_1; its less developed mesolophid of M_2; the anterocone of M^1, that may be split; the prelobe of M^1, that is more markedly set-off; its better developed forward paracone spur in M^1; the sinus of M^1 is more frequently directed strongly forward; the longer lingual anteroloph of M^2, that frequently separates the protocone from the lingual border.

Allocricetodon incertus (Schlosser, 1884)
Pl. 4, figs. 1-6.

Selected synonymy — *Eucricetodon* aff. *atavus* from Pareja (Daams et al., 1989)
Pseudocricetodon incertus from Gandesa and Mina del Pilar 3 (Agustí et al., 1985), p.p.

Holotype — Mandibula sin., with I_1, M_2, and M_3, Bayerische Staatssammlung für Paläontologie, 1879 XV 171 a.

Type-locality — Mouillac (Quercy, France).

Measurements of the holotype — M_2: 15.6 × 12.9; M_3: 15.6 × 12.7.

Remarks — Direct comparison has shown, that the material of *Eucricetodon* aff. *atavus* from Pareja (Daams et al., 1989) belongs to an *Allocricetodon* species, probably to *A. incertus*.

A. incertus is relatively poorly represented in our material. It is astonishing, that it has not been found in Mirambueno 4D, which is nothing but the upper part of the bed of Mirambueno 4C. The faunistic differences between MIR4C and MIR4D will be discussed in another paper (Freudenthal et al., in prep.).

Material and measurements — See Table 3, Figs. 2-7.

Description of the material from Mirambueno 4C

M_1 — The anteroconid is small, placed centrally, and hardly differentiated in the anterolophid arch; only in one case it is a distinct cusp without descending anterolophids. The lingual anterolophid is absent, low, or interrupted. The anterolophulid is complete and longitudinal or oblique. The anterior metalophulid is absent (4), interrupted (3), or complete (3). The protoconid hind-arm is transverse, high, and connected firmly to the metaconid. The ectolophid is longitudinal – or slightly oblique – with a step-wise connection to the protoconid (interrupted in one case). The mesolophid is well developed, a second mesolophid is present in half the specimens. The ectomesolophid is absent, or present as a vague bulge, never as a distinct crest. The posterosinusid is firmly closed by the fairly high posterolophid.

M_2 — The protoconid hind-arm is nearly always long and free. The connection of the ectolophid with the protoconid hind-arm is high (9), low (4), or interrupted (2). The mesolophid is rarely absent (2), more frequently of medium length (10), or long (5). The ectomesolophid is absent in 9 out of 17 specimens; when present it may form a low but distinct crest.

M_3 — The protoconid hind-arm is nearly always long and free, and may reach the lingual cingulum. There is no mesolophid; an ectomesolophid is present in 5 out of 12 specimens.

M^1 — The anterocone is simple in 8 out of 9 specimens. The prelobe is broad; the lingual border of the tooth in front of the protocone is angular or smoothly concave. There is a complete anterolophule in 2 out of 10 specimens; in 2 specimens there is a free-ending backward spur on the anterocone; in one case there is such a spur, that is in contact with the paracone. In another specimen there is a free-ending anterior spur on the paracone. The protolophule is posterior; the anterior branch of the protocone may be curved towards the paracone, or even be connected to that cusp. The sinus is directed strongly forward (4), or just forward (6). The entoloph-protocone connection is high, except for one specimen.

M^2 — The lingual anteroloph is well developed, and surrounds the protocone in one specimen. The sinus is directed strongly forward, just forward, or transverse. The mesoloph is of medium length. The entoloph-protocone connection is low.

M^3 — The protolophule is connected to the anterolophule in the majority of the cases (75%). The sinus is generally small. The old entoloph is complete in 41%, and totally absent in 53% of the cases.

Discussion — The holotype mandible of *A. incertus* shows a peculiar feature: its M_2 and M_3 are of equal length (15.6). In none of our *Allocricetodon* populations this phenomenon is found. The mean length of M_3 is always smaller than the mean length of M_2 (ratio M_3/M_2 varies between 0.87 and 0.96).

In our population of *A. incertus* the maximum for the length of M_2 (15.7) coincides with the length of the holotype M_2 (15.6). Our maximum for the length of M_3 is 14.7, not even near the length of the holotype M_3.

Since the holotype of *Cricetodon incertus* comes from the Quercy, it would be logical to compare our collection with descriptions of Quercy material. However, the material described by Comte (1985) is very poor. That author does describe a somewhat better collection from Boujac (Gard); its attribution to *E. incertus* is not certain. Comparison with the MIR4C population gives the following differences:

There are strong discrepancies in the distribution of length minima, means, and maxima between the populations from MIR4C and Boujac. Probably the Boujac material contains more than one species.

Maybe the mesolophid of M_1 is on the average shorter in the Boujac population. In the M_2 the protoconid hind-arm is frequently curved towards the metaconid; the mesolophid is absent in most specimens. In the M^1 of the Boujac material the longitudinal connection between anterocone and paracone appears to be always present. The posteroloph is widely open in M^1 and M^2. Especially the reduction of the mesolophids may indicate, that the populations from Boujac and Mirambueno 4C do not belong to the same species.

The population of *A. incertus* from Mirambueno 4C is easily distinguished from *A.*

landroveri from the same locality by its size. All dental elements show a distinct size gap in the length/width scatter diagrams (Figs. 2-7). The few doubtful cases are rather easily classified on the basis of the simple morphology of *A. incertus* and the more complex morphology of *A. landroveri*.

The difference between *A. incertus* from Mirambueno 4C and *A. cornelii* from Mirambueno 1 can be summarised as a more complex morphology for *A. cornelii*. In size these two species are identical. Evidently, if they were found together in one single locality, no one would be able to prove the presence of two species. Almost every character found in one population is present in the other one too. Their frequencies, however, are so different, that the existence of two different species is beyond doubt. I will list the differences in a detailed way:

In the M_1 of *A. incertus* the lingual anterolophid is low or interrupted, sometimes absent; in *A. cornelii* this crest is never absent, sometimes low or interrupted, and in the majority of the cases (85%) it forms a high connection between anteroconid and metaconid, sometimes as high as the anteroconid.

In the M_1 of *A. incertus* the anterolophulid is more or less parallel with the longitudinal axis of the molar. In *A. cornelii* the anterolophulid is frequently oblique, making an angle of c. 150° with the axis.

In the M_1 of *A. incertus* there may be an ectomesolophid (40%), but, when present, this crest is considerably less developed than in *A. cornelii*.

The mesolophid of M_2 is much better developed in *A. incertus* than in *A. cornelii*.

The protoconid hind-arm is on the average somewhat longer in the M_3 of *A. incertus*.

The anterocone of M^1 is always simple in *A. incertus*, and may be split in *A. cornelii*. The prelobe of M^1 is more set-off in *A. cornelii*. The forward paracone spur in the

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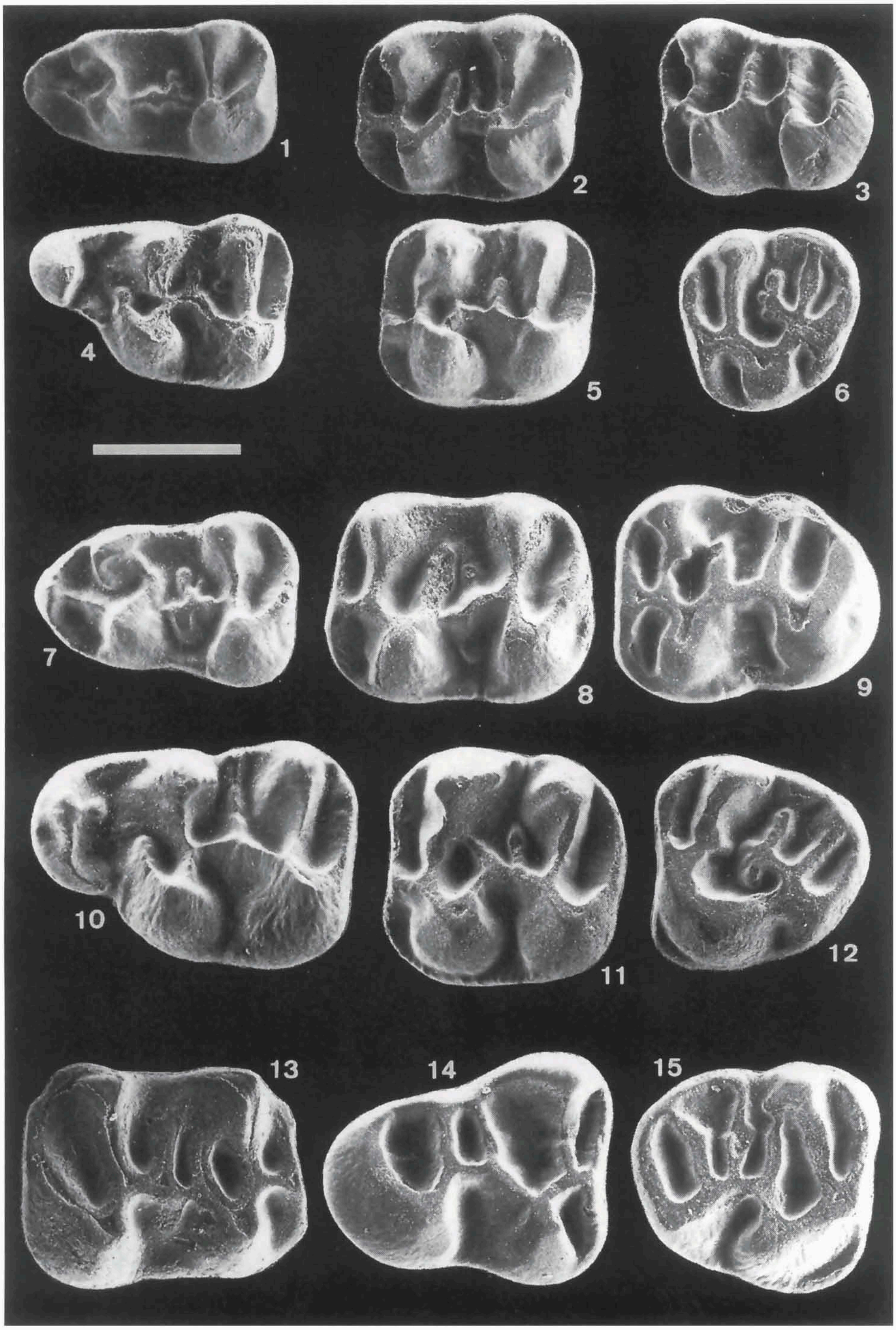
Plate 4

Allocricetodon incertus (Schlosser, 1884) from Mirambueno 4C
Fig. 1. M_1 sin., MIR4C 39.
Fig. 2. M_2 sin., MIR4C 45.
Fig. 3. M_3 sin., MIR4C 55.
Fig. 4. M^1 sin., MIR4C 66.
Fig. 5. M^2 sin., MIR4C 72.
Fig. 6. M^3 sin., MIR4C 1001.

Allocricetodon landroveri (Daams, Freudenthal, Lacomba & Alvarez, 1989) from Mirambueno 4C
Fig. 7. M_1 sin., MIR4C 162.
Fig. 8. M_2 sin., MIR4C 187.
Fig. 9. M_3 sin., MIR4C 215.
Fig. 10. M^1 sin., MIR4C 231.
Fig. 11. M^2 sin., MIR4C 246.
Fig. 12. M^3 sin., MIR4C 267.

Heterocricetodon hausi Engesser, 1987 from Mirambueno 4B
Fig. 13. M_2 dext., MIR4B 35.
Fig. 14. M_3 dext., MIR4B 36.
Fig. 15. M^3 dext., MIR4B 40.

Scale is 1 mm.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M^1 of *A. cornelii* is well developed, and often reaches the anterocone. The sinus is frequently directed strongly forward in *A. cornelii*.

A small collection of *A. incertus* has been recovered from the locality Mirambueno 4B. The scarce material does not permit a thorough comparison, but most features seem to coincide, except for the following: Among three M^1, one has a backward spur on the anterocone, and in two specimens this spur reaches the base of the paracone. This feature occurs in the MIR4C population, but there it is rare.

Lacomba & Morales (1987) have described *A. incertus* from Carrascosa del Campo (Cuenca, Spain). In this population the lingual anterolophid of M_1 is low or interrupted. The anterolophulid is longitudinal (3) or oblique (3). The anterior metalophulid is absent in 6 out of 7 specimens. The mesolophid is short or of medium length. In 3 specimens there is a second mesolophid. The ectomesolophid is absent in half the specimens. In M_2 the mesolophid is short (2) or of medium length (6). In M^1 the anterocone is simple; the lingual wall between prelobe and protocone is not very angular; there is a longitudinal connection between anterocone and paracone in 1 out of 5 specimens. The sinus is directed forward, but not strongly. In M^2 the lingual anteroloph is weak or strong; it never separates the protocone from the lingual border. The sinus is transverse, directed forward, or strongly forward.

None of these characters is decisive for the question whether this population should be attributed to *A. incertus* or *A. cornelii* sp. nov. The distribution of the character states makes *A. incertus* the best choice. Only the anterolophulid of M_1 may be more oblique than in the population from Mirambueno 4C.

Allocricetodon landroveri (Daams, Freudenthal, Lacomba & Alvarez, 1989)
Pl. 4, figs. 7-12.

Selected synonymy — *Pseudocricetodon incertus* from Gandesa and Mina del Pilar 3 (Agustí et al., 1985), p.p.

Holotype — M^1 sin., PAJ 583, Museo Nacional de Ciencias Naturales, Madrid.
Type-locality — Pareja (Guadalajara, Spain).
Age — Early Late Oligocene.
Other localities with *A. landroveri* — Mirambueno 4C and 4D.
Material and measurements — See Table 3, Figs. 2-7.

Description of the material from Mirambueno 4D

M_1 — The lingual anterolophid is generally high (70%); the anteroconid lies in a central position or somewhat lingually of the axis of the tooth; the anterolophulid is oblique, either low or high, less frequently interrupted (15%). The anterior metalophulid is absent in 77% of the specimens. The protoconid hind-arm is nearly always connected to the metaconid, either low (14%) or high (79%). The sinusid is generally directed backwards (90%). The ectolophid is longitudinal or oblique; its connection with the protoconid is either step-wise or smooth. The mesolophid is of medium length (86%), or long (10%), short in one specimen only; there is a second mesolophid in 30% of the cases. An ectomesolophid is nearly always present (84%), and often well developed. The posterosinusid is firmly closed by the fairly high posterolophid.

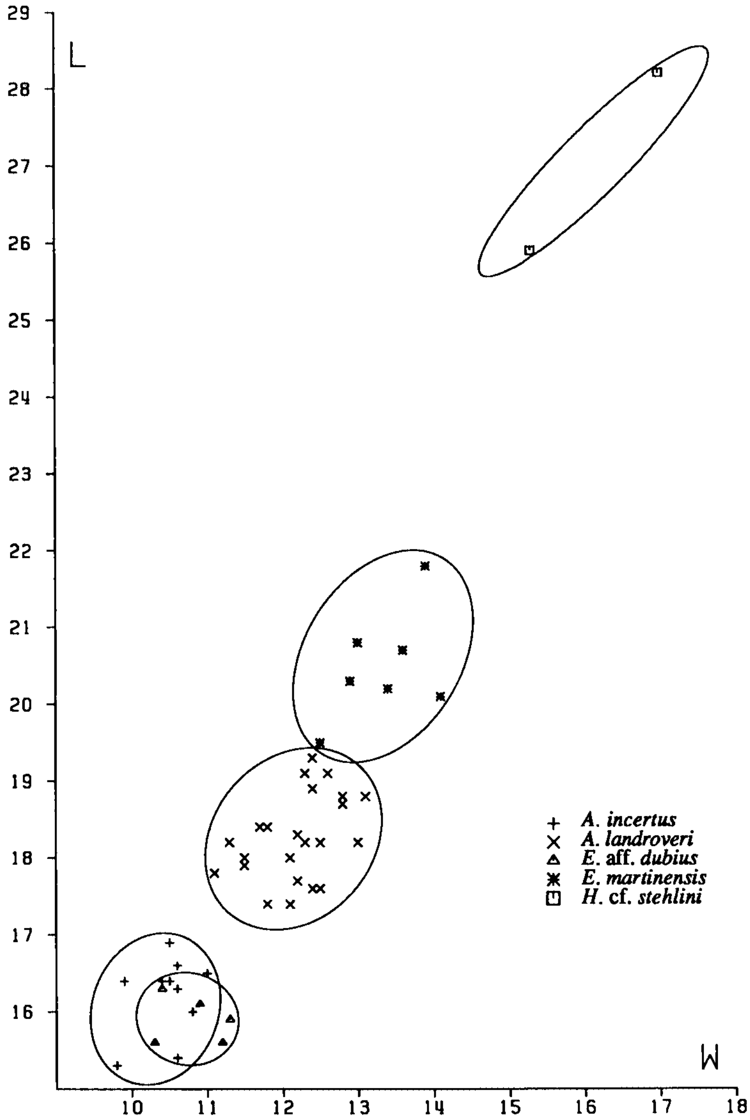

Fig. 2. Length/width diagram of the M_1 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

M_2 — The protoconid hind-arm is long and free (71%), or connected to the metaconid (25%). The connection of the ectolophid with the protoconid hind-arm is high (67%) or low (33%). The mesolophid is absent in 31%, short in 12%, of medium length in 46%, and long in 11% of the specimens. The ectomesolophid is present in 75% of the cases, sometimes well developed. The posterolophid closes the posterosinusid completely.

M_3 — The protoconid hind arm is nearly always long and free, rarely connected to the metaconid. A trace of a mesolophid is present in 2 cases. The ectomesolophid is absent (55%) or present (45%).

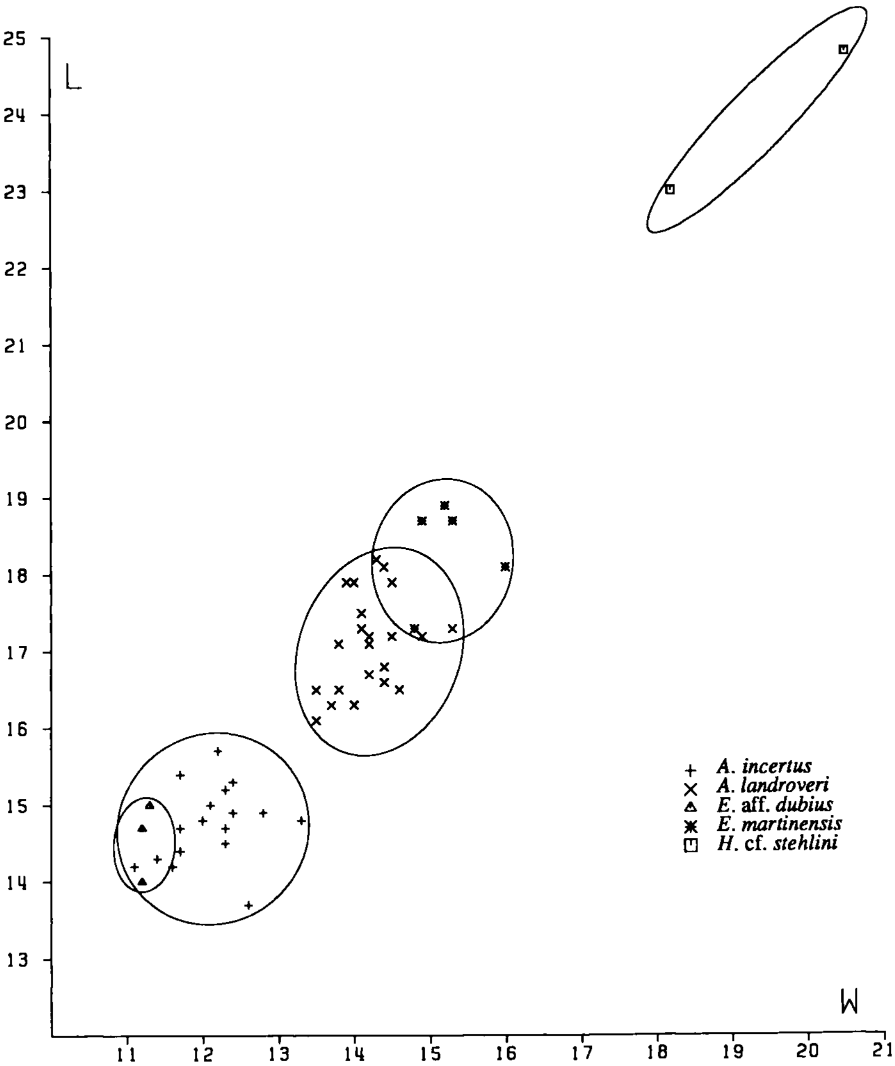

Fig. 3. Length/width diagram of the M_2 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

M^1 — The anterocone is simple. The prelobe is broad, set-off from the protocone (67%) or continuous (33%). The anterolophule is never complete; in 27% there is a free-ending backward spur on the anterocone; in 20% there is such a spur, that is in contact with the paracone. The lingual anteroloph is firmly connected to the protocone, and fairly high in most cases; it may form a protostyl. The protolophule is posterior, interrupted in 2 cases. The anterior branch of the protocone may be directed towards the protocone, or even connected to that cusp. The sinus is directed strongly forward (27%), or just forward (73%). The entoloph-protocone connection is high. The mesoloph is of medium length or long, and may reach the molar border. In more than half the specimens there is a mesostyl, which may form a crest that points towards the mesoloph; in 33% of the cases there is a spur or a connection between

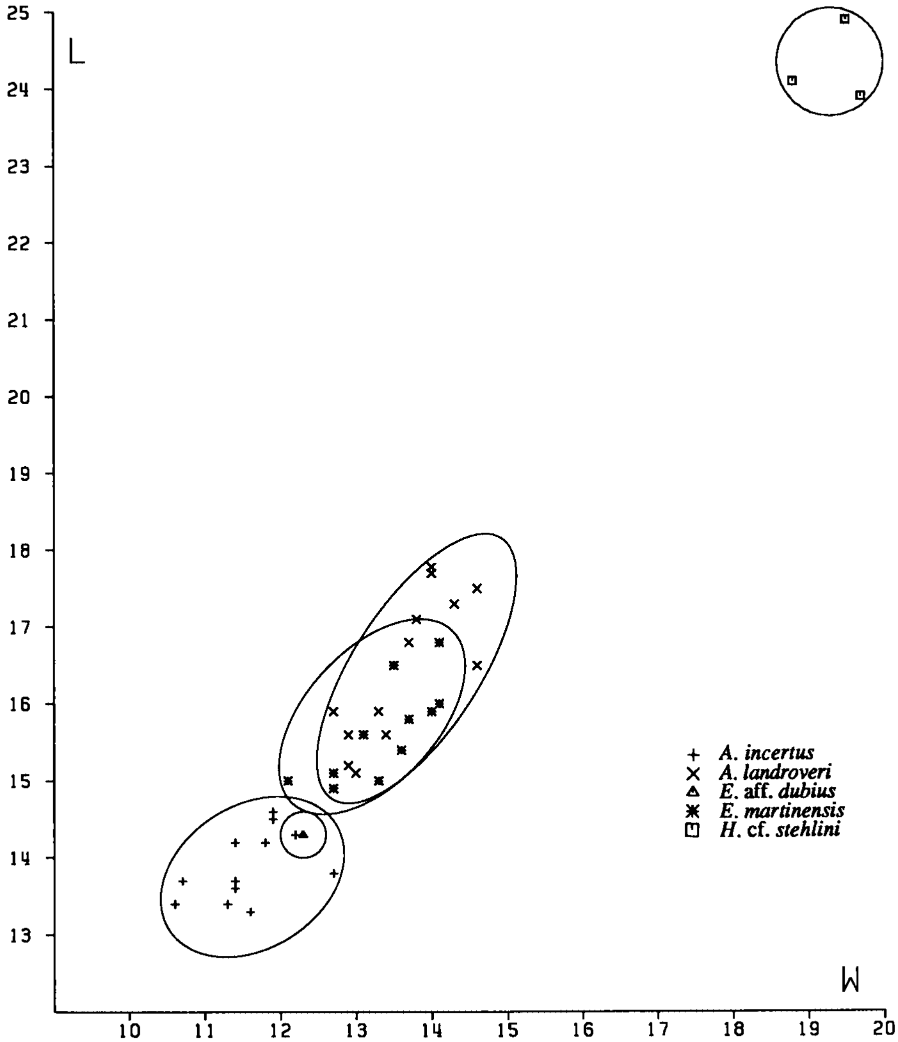

Fig. 4. Length/width diagram of the M_3 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

mesoloph and metalophule. The posterior wall of metacone and metalophule is often very steep, vertical, or even overhanging.

M^2 — The posterior part of the tooth is narrow, due to the reduction of both hypocone and metacone. The lingual anteroloph is well developed; it continues around the protocone in 32% of the cases. There is a complete posterior protolophule in 2 specimens. The sinus is like in M^1; in 2 specimens it is subdivided by a crest from protocone to hypocone (equivalent of the neo-entoloph in M^3). The entoloph-protocone connection is high (69%) or low (31%). The mesoloph is of medium length or long; in 63% it reaches the border of the molar. In 30% of the cases it is more or less connected to the metalophule. The posterior wall of the metacone is often steep or vertical. The posterosinus is more frequently open than in M^1.

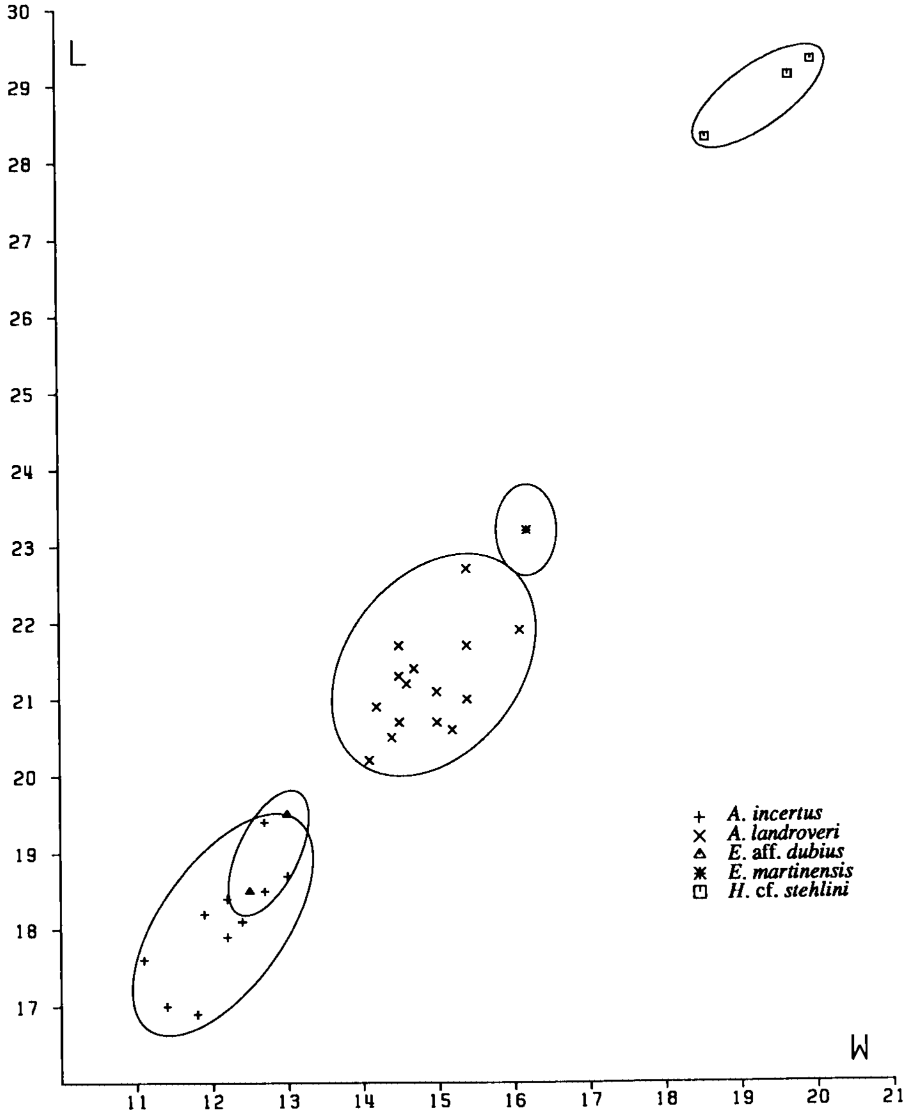

Fig. 5. Length/width diagram of the M^1 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

M^3 — The protolophule is connected to the anterolophule or to the anterocone with equal frequencies. The sinus generally is small; it is deep, and the neo-entoloph is absent or interrupted in 3 specimens; in the remainder the neo-entoloph reduces the sinus to a small indentation of the lingual border. The old entoloph is complete in 64%, and totally absent in 11% of the cases.

Discussion

The populations from Mirambueno 4C and 4D are quite similar in most respects.

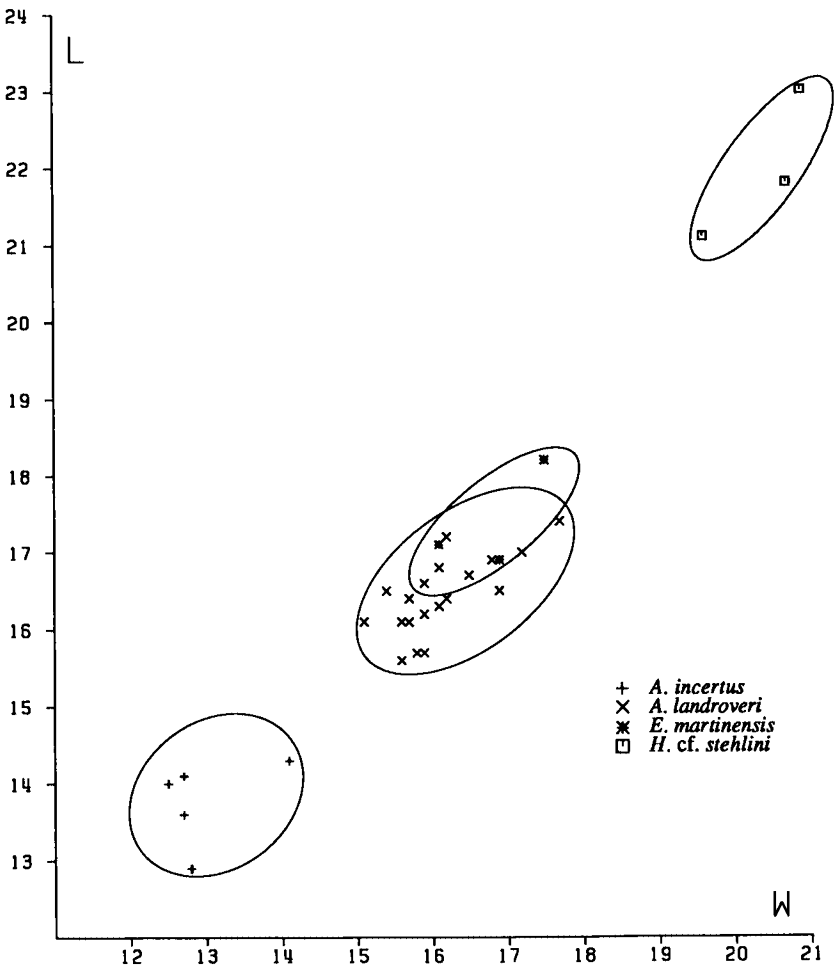

Fig. 6. Length/width diagram of the M^2 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

There are some differences in the frequencies of certain character states, but the overall similarity is such, that these two populations have been listed together in Tables 12-17.

Both populations are similar to the type-population from Pareja. Differences are:

In the M_1 of the population from Pareja the anterior metalophulid is better developed, the protoconid hind-arm is on the average higher, the second mesolophid is more frequent, and there is often a hypoconid hind-arm (29%). The ectolophid of M_2 is on the average lower. In M_3 the ectomesolophid is more frequently present, and the entoconid is on the average smaller. In M^1 there is always a backward spur on the anterocone (and often even two). In M^1 the anterior protolophule is less developed. In M^1 and M^2 the sinus is more strongly directed forward. In M^2 the posterior protolophule is more frequently complete. In M^3 the lingual anteroloph may be absent, the protolophule has a

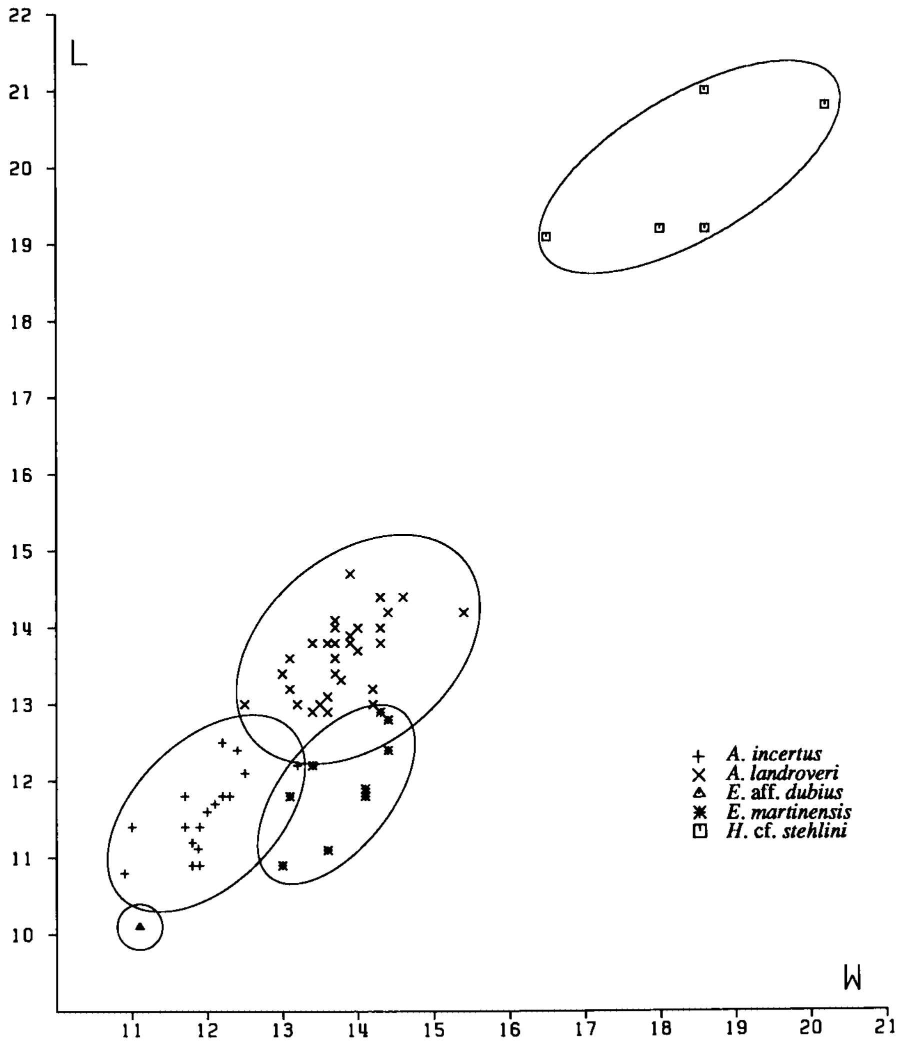

Fig. 7. Length/width diagram of the M^3 of Cricetidae from Mirambueno 4C (except *Pseudocricetodon*).

more forward position, and the second mesoloph is better developed.

Evolutionary trends in this group are not yet known, so it is difficult to say whether a certain character state is primitive or derived. For example it is generally assumed, that the posterior metalophulid is a primitive character, and the anterior connection a derived one; in the Pareja population both the anterior and the posterior metalophulid of M_1 are better developed than in the Mirambueno populations. If one has to decide which one of these populations is more modernised, one may have a slight preference for the one from Pareja, because of the position of the protolophule in M^1 and M^2. However, my provisional conclusion is, that it is not possible to say which one of these populations is more evolved; they are probably more or less synchronical, and the differences observed are due to geographical variations.

Allocricetodon aff. *landroveri*

A small number of specimens from Vivel del Río is attributed to *Allocricetodon landroveri*. Both M_1 have a well-developed mesoconid, in one of these it is even very large. The anterolophulid is not oblique. In one specimen the mesolophid is absent, whereas it is always of medium length or long in the other populations of this species. In both M_2 the protoconid hind-arm is short, the mesolophid absent. In the M^2 there is a second mesoloph.

These features indicate, that the frequencies of character states of this population are probably different from the frequencies of the other populations. For the time being the scarce material leaves no other option than calling it *Allocricetodon* aff. *landroveri*.

Discussion on the genus *Allocricetodon*

In my opinion it is premature to try to establish a phylogeny of the three species now known within the genus *Allocricetodon*. If *A. incertus* from Mirambueno 4C is the ancestor of *A. cornelii* from Mirambueno 1, this lineage is characterised by an increasing complexity of the dental pattern. If, on the other hand, *A. landroveri* is the ancestor of *A. cornelii*, there is no important change in the complexity of the dental pattern, and such a lineage would be characterised by a decrease in size.

It is not probable that *A. landroveri* from Mirambueno 4C and 4D be the ancestor of *A. cornelii* because *A. cornelii* is smaller than *A. landroveri*, and *A.* aff. *landroveri* co-occurs with *A. cornelii* in Vivel del Río. *A. landroveri* from Mirambueno 4C may be the ancestor of *A.* aff. *landroveri* from Vivel del Río, but the latter population is too poor to permit conclusions.

The oldest record of this genus is formed by a few specimens from the classical level of Montalbán (Montalbán 1D), present in our collections. This means that this group appears for the first time almost simultaneously with *Pseudocricetodon*. Unfortunately the material is so poor, that it serves no other purpose than establishing the appearance of the group in the fossil record at a much earlier date than previously assumed.

Freudenthal et al. (1994) state that two species of Pseudocricetodontinae are found in Heimersheim. The smaller one of these two, to which the holotype of *Pseudocricetodon moguntiacus* belongs, may be identical to *P. montalbanensis*. The larger one may belong to *Allocricetodon*.

Tribe Heterocricetodontini Ünay-Bayraktar, 1989
Genus *Heterocricetodon* Schaub, 1925

Type-species — *Heterocricetodon stehlini* Schaub, 1925.

Heterocricetodon stehlini Schaub, 1925

Holotype — Maxilla sin., Q.P. 626, Naturhistorisches Museum, Basel.
Type-locality — Bach (Quercy, France).
Remarks — Four species of very large *Heterocricetodon* have been described: *H.*

stehlini Schaub, 1925, *H. schlosseri* (Schaub, 1925), *H. gaimersheimensis* Freudenberg, 1941, and *H. helbingi* Stehlin & Schaub, 1951. The most recent paper on this group is by Kristkoiz (1992). Although this author accepts the validity of these four species, I feel that the morphological and size differences used to distinguish them cannot be based reliably on the poor material available. I prefer — until better knowledge — to regard them as one single species, *H. stehlini*, the type-species of the genus.

Heterocricetodon cf. *stehlini* Schaub, 1925

In our area *H.* cf. *stehlini* is represented in the localities Mirambueno 4C, Mirambueno 4D, and Mirambueno 1. The material is quite poor.

Material and measurements — See Table 4, Figs. 2-7.

Description of the material from Mirambueno 4C

M_1 — There is no individualised anteroconid in the arch-shaped anterolophid. The anterolophulid is continuous, high or low. The anterior metalophulid is complete. The protoconid hind-arm reaches the top of the metaconid. The mesolophid is long, either double, or branched. The posterolophid closes the posterosinusid.

M_2 — The protoconid hind-arm is connected to the crest descending from the metaconid along the molar border. The mesolophid is of medium length and simple. The posterolophid closes the posterosinusid.

M_3 — The anterior metalophulid is absent in one specimen, transverse in the other ones. The protoconid hind-arm is connected to the crest descending from the metaconid along the molar border. There is no mesolophid. The posterior part of the tooth is narrower than the anterior half.

M^1 — The anterocone is simple. Two specimens have a transverse crest on the anterostyl. The anterior branch of the protocone is long, almost in contact with the posterior spur of the anterocone. There is no protostyl nor a protocone platform. The prelobe is set-off from the protocone by a sharp angle. The protolophule is posterior. The sinus is directed forward. The mesoloph reaches the molar border.

M^2 — The protolophule is posterior plus a long free-ending anterior branch of the protocone. The mesoloph is long, and may reach the molar border. The posterosinus is not closed.

M^3 — The protolophule is double and symmetrical, or the anterior branch is missing. The mesoloph is long, and may reach the molar border. The sinus is deep and directed strongly forward; in one specimen the protocone hind-arm tends to get interrupted. The protocone is reduced to an anterolabial-posterolingual crest.

Description of the material from Mirambueno 4D

The material from MIR4D is similar to that from MIR4C. Differences are:

In M_1 the anterior metalophulid is less developed. In M_2 the protoconid hind-arm is shorter in one specimen. In another specimen the mesolophid is longer. In M^2 the posterosinus is closed.

In view of the scarce material these differences are considered to fall within the normal variation of a species.

Description of the material from Mirambueno 1

The material from MIR1, on the other hand, seems to present some differences, that may be important:

M_1 — The anterior metalophulid is interrupted. The mesolophid is of medium length or long, and may be simple.

M_2 — The protoconid hind-arm is shorter, and hardly connected to the metaconid. There is no mesolophid, or a very thin one.

M_3 — The tooth is hardly reduced posteriorly.

M^1 — The anterocone is simple or split, without a posterior spur. The lingual anteroloph is connected to the anterior branch of the protocone, through a well-developed protostyl. The lingual border of the tooth between protocone and anterocone is smooth and oblique, not angular. The mesoloph is of medium length, or long, with a tendency to get interrupted.

M^3 — There is no anterior protolophule, or an interrupted crest; only the posterior protolophule is complete.

Also in this case the material is very poor. One gets the impression, however, that the populations from MIR4C and MIR4D represent one species, and the one from MIR1 another one.

Heterocricetodon hausi Engesser, 1987
Pl. 4, figs. 13-15.

Holotype — M^2 sin., BUM 5, Naturhistorisches Museum Basel.

Type-locality — Bumbach 1 (Switzerland).

In our area this species has been found in the locality Mirambueno 4B.

Material and measurements — See Table 4.

Description

M_1 — The anterior metalophulid is almost longitudinally directed forward, and then bent towards the anterolophulid in a sharp angle. The protoconid hind-arm is high and transversely connected to the metaconid. The mesolophid is long and branched, the ectomesolophid is short.

M_2 — The protoconid hind-arm is transverse, and strongly connected to the base of the metaconid. The mesolophid is long, in connection with the crest descending from the metaconid.

M_3 — The protoconid hind-arm reaches the molar border; there is no mesolophid.

M^1 — The anterocone is simple; the anterior branch of the protocone is fused to the base of the paracone, and continues towards the anterocone. The posterior protolophule is transverse; the mesoloph is long; the sinus points forwards.

M^3 — The lingual anteroloph is absent, or it forms a low ridge at the antero-lingual base of the protocone. The protolophule is double. The mesoloph is long. There is no metacone.

This material is of about the same size as *H. hausi* from Bumbach 1, maybe slightly smaller, but the measurements are not too reliable, because the material is poorly preserved. The morphological similarity with the material from Bumbach 1 is not perfect. I attribute it to *H. hausi*, mainly on the basis of size.

Table 4. Measurements of *Heterocricetodon* cf. *stehlini* (MIR1, MIR4D, and MIR4C) and *H. hausi* (MIR4B).

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1												
MIR1	2	29.6	29.90	30.2	2.01	0.424	2	15.8	16.15	16.5	4.33	0.495
MIR4D	2	25.1	26.05	27.0	7.29	1.344	1		15.50			
MIR4C	3	25.9	26.97	28.2	8.50	1.159	2	15.3	16.15	17.0	10.53	1.202
MIR4B	1		21.90									
M_2												
MIR1	2	24.7	25.15	25.6	3.58	0.636	3	17.8	18.17	18.7	4.93	0.473
MIR4D	1		23.40				2	17.9	18.20	18.5	3.30	0.424
MIR4C	2	23.0	23.90	24.8	7.53	1.273	3	18.2	19.03	20.5	11.89	1.274
MIR4B	1		18.50				1		14.80			
M_3												
MIR1	1		24.30				1		17.50			
MIR4D	1		22.80				2	16.5	17.55	18.6	11.97	1.485
MIR4C	4	23.8	24.18	24.9	4.52	0.499	3	18.8	19.33	19.7	4.68	0.473
MIR4B	2	17.3	17.85	18.4	6.16	0.778	1		15.30			
M^1												
MIR1	1		29.30				2	18.9	19.00	19.1	1.05	0.141
MIR4C	3	28.3	28.90	29.3	3.47	0.529	4	18.5	19.20	20.0	7.79	0.762
MIR4B	1		21.80									
M^2												
MIR1	1		22.20									
MIR4D	1		21.00									
MIR4C	4	21.1	22.20	23.0	8.62	0.913	3	19.6	20.40	20.9	6.42	0.700
M^3												
MIR1	5	18.7	19.72	20.6	9.67	0.760	4	19.0	19.38	19.9	4.63	0.411
MIR4D	1		18.60				1		18.70			
MIR4C	6	19.1	19.90	21.0	9.48	0.858	5	16.5	18.38	20.2	20.16	1.331
MIR4B	2	15.0	15.50	16.0	6.45	0.707	2	15.3	15.45	15.6	1.94	0.212

Biostratigraphy

The relative frequencies (see Table 5) of the two subfamilies of Oligocene Cricetidae discussed in this paper, Eucricetodontinae and Pseudocricetodontinae, vary considerably, and may serve for stratigraphic purposes.

In the oldest localities known in the area (Olalla 4A, the lower levels of Montalbán) no Pseudocricetodontinae are found, and the Eucricetodontinae are represented by three or four species. In the first locality where *Pseudocricetodon* appears (Montalbán

3C), it is represented by 1.2% of the cricetid specimens, and two species of Eucricetodontinae are present; in the classical level of Montalbán Pseudocricetodontinae and Eucricetodontinae are almost equally frequent, both represented by two species.

In the seven localities studied in this paper thirteen different species of Cricetidae have been recognised (not counting *Melissiodon*). Nine out of these thirteen species belong to the subfamily Pseudocricetodontinae. The other ones belong to the Eucricetodontinae. In the localities MIR4B, MIR4C, and MIR4D Pseudocricetodontinae dominate over Eucricetodontinae not only in number of species, but also in number of specimens. In MIR1 both subfamilies are almost in equilibrium, and the situation is inverted in MIR2A and VIV. In these localities three species of Pseudocricetodontinae and two species of Eucricetodontinae are found; in VIV *Eucricetodon dubius* alone is good for over 75% of the cricetid specimens.

In Spanish localities younger than VIV (e.g. the Ramblian of Navarrete del Río, Valhondo etc.) Cricetidae are represented by Eucricetodontinae only.

Olalla and Montalbán are generally placed in the Lower Oligocene; Vivel del Río on the other hand is considered to be Upper Oligocene, and not even the lowest part of the Upper Oligocene. I place our Mirambueno localities in the lower part of the Upper Oligocene, though the possibility that the upper part of the Lower Oligocene be represented in the oldest levels cannot be denied.

Apparently the early part of the Late Oligocene may be characterised in Spain as the acme of Pseudocricetodontinae. In other areas of Europe this may be the case too.

The localities described in this paper represent a number of faunal zones. On the basis of Cricetidae these zones may be defined as follows:

The oldest zone is represented in Mirambueno 4B; it contains *Heterocricetodon hausi*; *Pseudocricetodon* aff. *simplex*, *Allocricetodon*, and *Eucricetodon* are present, but the collection is not sufficient as yet, to permit a detailed characterization.

The second zone (MIR4C and MIR4D) is characterised by the appearance of *Heterocricetodon* cf. *stehlini*, and by the presence of *Pseudocricetodon simplex*, *Allocricetodon landroveri*, and *Eucricetodon martinensis*. *Allocricetodon incertus* is present in Mirambueno 4C, absent in Mirambueno 4D.

The third zone (MIR1) is characterised by the appearance of *Pseudocricetodon adroveri*, *Allocricetodon cornelii*, and *Eucricetodon dubius*. Pseudocricetodontinae and Eucricetodontinae are almost equally frequent, with a slight advantage for the Pseudocricetodontinae.

In the fourth zone (MIR2A and VIV) the same cricetid species are present as in the previous zone, but *Eucricetodon dubius* is by far the dominant cricetid.

Correlations

Agustí et al. (1987) published a biostratigraphy of the Oligocene of the Ebro and Campins Basins that allows a more or less detailed correlation with our section (see Fig. 8). They correlate Tárrega with the classical level of Montalbán.

Allocricetodon incertus from Gandesa appears to represent two species, if one analyses the measurements given by Agustí et al. (1985). These two species may be *A. incertus* and *A. landroveri*, and Gandesa may be correlated with Mirambueno 4C, or Mirambueno 4C is somewhat older.

Agustí et al. (1987)		This paper
Zones	**Ebro + Campins Basins**	**Central Spain**
Eomys autolensis	Sta Cilia, Autol	
Rhodanomys schlosseri	Torrente de Cinca 68 Ballobar 21	
Rhodanomys transiens	Fraga 7, Ballobar 12 Fraga 6, Fraga 11 Velilla de Cinca	
		Villanueva Rebollar
		Vivel del Río
		Mirambueno 2A
		Mirambueno 1
Eomys aff. *major*	Torrente de Cinca 4 Fraga 4, Les Canotes	
Eomys major	Mina del Pilar, Fraga 2, La Bagarella	
Eomys zitteli	Gandesa	
		Carrascosa
		Pareja, Mirambueno 4C, 4D
		Mirambueno 4B
Theridomys aff. *major*	Can Quaranta, Pla del Pepe	
Theridomys major	Tárrega, Forés 33, Ciutadilla	Montalbán 1D
Theridomys calafensis	Calaf, Fonollosa, Porquerisses, Sta Coloma de Queralt	Olalla 4

Fig. 8. Comparison of Spanish Oligocene sequences.

If that correlation is correct, the zonation by Agustí et al. (1987) does not contain an equivalent of our locality MIR4B. In fact there probably is an important time gap between their *Theridomys* aff. *major* Zone and their *Eomys zitteli* Zone.

In the *Eomys* aff. *major* Zone (Fraga B2, Torre del Compte, Torrente de Cinca 4) appears *Eucricetodon dubius;* in our area this species appears in Mirambueno 1. There seems to be a time gap between Mirambueno 4D and Mirambueno 1, and there may be another one between the *Eomys* aff. *major* Zone and the *Rhodanomys transiens* Zone. Mirambueno 1 and Vivel del Río may represent this time gap in the zonation by Agustí et al.

So, taking the zonation by Agustí et al. (1987) as a basis, Montalbán 1D represents the *Theridomys major* Zone in our area; Mirambueno 4B should be placed in a not yet named zone between the *Theridomys* aff. *major* Zone and the *Eomys zitteli* Zone; Mirambueno 4C and 4D belong to the *Eomys zitteli* Zone, or to a not yet named zone that is somewhat older; Mirambueno 1 and Vivel del Río pertain to the *Eomys major* Zone, or *Eomys* aff. *major* Zone, or to an important gap between the *Eomys* aff. *major* Zone and the *Rhodanomys transiens* Zone.

Mirambueno 4C and 4D are correlatable with Pareja and Alcorisa. Carrascosa is probably somewhat younger.

For a comparison with the zonation presented by Engesser & Mayo (1987) several arguments may be used: *Heterocricetodon hausi* makes MIR4B correlatable with Bumbach 1 to Mümliswil-Hardberg. In MIR4C *Heterocricetodon* is much larger, and the first large *Heterocricetodon* in the Swiss Molasse is described from Wynau 1.

So far not a single molar of *Plesiosminthus* has been found in MIR4B, 4C, and 4D; it seems to appear in MIR1. In the Swiss Molasse this genus appears in Mümliswil-Hardberg. It seems to be a fairly good guess to correlate MIR4C-MIR4D with (part of) the span Bumbach 1 - Wynau 1.

Table 5. Contribution of the different genera to the total cricetid fauna.

	N	*Pseudocricetodon*	*Allocricetodon*	*Heterocricetodon*	*Eucricetodon*
VIV	320	12.5%	8.8%	0.3%	78.4%
MIR2A	81	22.2%	12.3%		65.4%
MIR1	603	0.7%	53.2%	1.5%	44.6%
MIR4D	326	20.9%	54.0%	3.4%	21.8%
MIR4C	503	43.9%	40.0%	5.4%	10.7%
MIR4B	54	59.3%	27.8%	13.0%	*
MLB1D	767	58.8%	0.1%		41.1%
MLB3C	420	1.2%			97.8%
OLA4A	656				100.0%

*) Present in our 1993 collection

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References

Agustí, J., P. Anadón, S. Arbiol & L. Cabrera, 1985. Biozonación mediante Roedores (Mammalia) del tránsito Oligoceno-Mioceno en el sector sureste de la cuenca del Ebro. — Paleont. i Evol., 18: 131-149.

Agustí, J., P. Anadón, S. Arbiol, L. Cabrera, F. Colombo & A. Sáez, 1987. Biostratigraphical characteristics of the Oligocene sequences of North-Eastern Spain (Ebro and Campins Basins). — Münchner Geowiss. Abh., A, 10: 35-42.

Brunet, M., M. Hugueney & Y. Jehenne, 1981. Cournon-les-Souméroux: un nouveau site à vertébrés d'Auvergne; sa place parmi les faunes de l'Oligocène supérieur d'Europe. — Géobios, 14, 3: 323-359.

Comte, B., 1985. Éléments nouveaux sur l'évolution des genres Eucricetodon et Pseudocricetodon (Eucricetodontinae, Rodentia, Mammalia) de l'Oligocène d'Europe occidentale. — Palaeovertebrata, 15, 1: 1-69.

Daams, R., M. Freudenthal, J.I. Lacomba & M.A. Alvarez, 1989. Upper Oligocene micromammals from Pareja, Loranca Basin, prov. of Guadalajara, Spain. — Scripta Geol., 89: 27-56.

Dienemann, A., 1987. Die Gattungen *Eucricetodon* und *Pseudocricetodon* (Rodentia, Mammalia) aus dem Oligozän Süddeutschlands. — Abh. Bayer. Akad. Wiss., math.-naturwiss. Kl., N.F., 165: 1-158, 6 pls.

Engesser, B. & N. Mayo, 1987. A biozonation of the Lower Freshwater Molasse (Oligocene and Agenian) of Switzerland and Savoy on the basis of fossil Mammals. In: N. Schmidt- Kittler (ed.). Intern. Symp. on Mammal. Biostratigraphy and Paleoecology of the European Paleogene, Mainz, Febr. 18-21, 1987. — Münchner Geowiss. Abh., A, 10: 67-84.

Freudenthal, M. & R. Daams, 1988. Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon, Fahlbuschia, Pseudofahlbuschia* nov. gen., and *Renzimys*. In: Freudenthal, M. (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). — Scripta Geol., Spec. Issue 1: 133-252.

Freudenthal, M., M. Hugueney & † E. Moissenet, 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). — Scripta Geol., 104: 57-114, 5 pls.

Freudenthal, M., J.I. Lacomba & M.A. Sacristán, 1992. Classification of European Oligocene cricetids. — Rev. Española Paleont., Extra, 1992: 49-57, 1 pl.

Freudenthal, M., J. Martínez-Salanova & M.A. Sacristán, in prep. Mirambueno, a mammal-bearing section in the Upper Oligocene of Martín del Río (prov. Teruel, Spain). — Scripta Geol.

Hugueney, M., R. Adrover, E. Moissenet & N. Schmidt-Kittler, 1987. Les Mammifères de Vivel del Río (prov. de Teruel, Espagne; Oligocène supérieur): un riche gisement stratifié en comparaison avec des faunes karstiques. In: N. Schmidt-Kittler (ed.). Intern. Symp. on Mammal. Biostratigraphy and Paleoecology of the European Paleogene, Mainz, Febr. 18- 21, 1987. — Münchner Geowiss. Abh., A, 10: 117-130.

Kristkoiz, A., 1992. Zahnmorphologische und schädelanatomische Untersuchungen an Nagetieren aus dem Oberoligozän von Gaimersheim (Süddeutschland). — Abh. Bayer. Akad. Wissensch., math.-naturw. Kl., n.F., 167: 1-137, 3 pls.

Lacomba, J.I. & J. Morales, 1987. Los micromamíferos del Oligoceno superior de Carrascosa del Campo (Prov. Cuenca, España). In: N. Schmidt-Kittler (ed.). Intern. Symp. on Mammal. Biostratigraphy and Paleoecology of the European Paleogene, Mainz, Febr. 18-21, 1987. — Münchner Geowiss. Abh., A, 10: 289-300.

Mayo, N.A., 1982. Bemerkungen zur Systematik und Evolution einiger Theridomyidae und Cricetidae (Rodentia, Mammalia) des Oligozäns: Antwort an M. Vianey-Liaud. — Eclog. Geol. Helv., 75: 697-719.

Schaub, S., 1925. Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. — Abh. Schweiz. Pal. Gesellsch., 45: 1-114, 5 pls.

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Appendix: Distinction between *Allocricetodon cornelii* and *Eucricetodon dubius*

Allocricetodon cornelii and *E. dubius* co-occur in MIR1, MIR2A, and VIV. They may be distinguished by the following features:

M_1 — The posterior branch of the hypoconid is absent in *A. cornelii*, present in *E. dubius*.

M_2 — *E. dubius* has a longer, and longitudinal ectolophid. *A. cornelii* frequently has an ectomesolophid, never a posterior branch on the hypoconid.

M_3 — *E. dubius* has a long M_3. The anteroconid lies labially of the central axis. The protoconid hind-arm is oblique; there often is a mesolophid. The hypolophulid in unworn specimens is very thin.

A. cornelii has a shorter M_3. The anteroconid has a central position. There is a strong, transverse, protoconid hind-arm, no mesolophid. The hypolophulid in unworn specimens is thicker.

M^1 — In *E. dubius* the labial paracone wall bulges out of the labial border of the tooth; the labial border is often convex. The lingual border between anterocone and protocone is straight and oblique, or it may show a sharp angle. The anterocone is isolated. The anterior point of the sinus is frequently compressed. The mesoloph is generally short or of medium length, and placed in the posterior part of the mesosinus. The metalophule is often curved towards the anterior tip of the hypocone. The posterior wall of the metalophule is steep or moderately inclined, visible in occlusal view.

In *A. cornelii* the labial border is straight or concave. The labial border between anterocone and protocone always shows a sharp angle. The anterior point of the sinus is never compressed. The anterocone is frequently connected to the paracone by a longitudinal crest. The mesoloph is frequently long, and placed in the center of the mesosinus. The metalophule is straight towards the anterior tip of the hypocone. The posterior wall of the metalophule is generally vertical, not visible in occlusal view.

M^2 — In *E. dubius* the outline of the tooth is a long rectangle. The sinus is pointing strongly forward, and its anterior point is narrow. The lingual anteroloph is generally poorly developed; the protosinus is just a flat surface, or even absent. The mesoloph is generally short or of medium length, and placed in the posterior part of the mesosinus. The entoloph is long and longitudinal; there is generally no posterior protolophule. The posterior wall of the metalophule is steep or moderately inclined, visible in occlusal view.

In *A. cornelii* the outline of the tooth is rounded quadratic. The sinus is pointing forward, but its anterior point is not very narrow. The lingual anteroloph is generally well developed, and it may surround the protocone. The mesoloph is of medium length or long, and placed in the center of the mesosinus. The entoloph is short and curved; there is a well developed, incomplete, posterior protolophule. The posterior wall of the metalophule is generally vertical, not visible in occlusal view.

M^3 — *E. dubius* has a well-developed axioloph. *A. cornelii* has no axioloph, and frequently a long transverse mesoloph.

Table 6. Character states of M_1 of *E. martinensis* and *E. margaritae.*

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
3	anterolophulid	7		14		21		9	
	3 interrupted	2	28.6	4	28.6	6	28.6	0	0.0
	4 low	4	57.1	9	64.3	13	61.9	8	88.9
	5 complete	1	14.3	1	7.1	2	9.5	1	11.1
5	metalophulid	7		15		22		10	
	2 absent	4	57.1	8	53.3	12	54.5	0	0.0
	3 anterior interrupted	1	14.3	5	33.3	6	27.3	0	0.0
	4 anterior complete	1	14.3	2	13.3	3	13.6	10	100.0
	5 to anteroconid	1	14.3	0	0.0	1	4.5	0	0.0
6	pcd hind-arm	7		15		22		10	
	3 short free	3	42.9	7	46.7	10	45.5	1	10.0
	4 trans to mcd low	2	28.6	3	20.0	5	22.7	1	10.0
	5 trans to mcd high	0	0.0	0	0.0	0	0.0	3	30.0
	6 long free	0	0.0	2	13.3	2	9.1	2	20.0
	7 bent to mcd low	1	14.3	1	6.7	2	9.1	2	20.0
	8 bent to mcd high	1	14.3	2	13.3	3	13.6	1	10.0
8	sinusid	7		15		22		12	
	3 narrow transverse	5	71.4	11	73.3	16	72.7	5	41.7
	4 broad transverse	1	14.3	1	6.7	2	9.1	0	0.0
	5 narrow backwards	1	14.3	1	6.7	2	9.1	4	33.3
	6 broad backwards	0	0.0	2	13.3	2	9.1	3	25.0
9	mesosinusid	7		14		21		10	
	2 open	0	0.0	0	0.0	0	0.0	2	20.0
	3 closed	7	100.0	12	85.7	19	90.5	3	30.0
	4 mesostylid	0	0.0	2	14.3	2	9.5	5	50.0
11	mesoconid	7		14		21		10	
	2 absent	1	14.3	5	35.7	6	28.6	5	50.0
	3 weak	4	57.1	6	42.9	10	47.6	5	50.0
	4 strong	2	28.6	3	21.4	5	23.8	0	0.0
12	mesolophid	7		15		22		11	
	2 absent	0	0.0	1	6.7	1	4.5	0	0.0
	4 medium	3	42.9	7	46.7	10	45.5	3	27.3
	5 long	4	57.1	7	46.7	11	50.0	6	54.5
	6 border	0	0.0	0	0.0	0	0.0	2	18.2
13	ectomesolophid	7		14		21		12	
	2 absent	5	71.4	10	71.4	15	71.4	6	50.0
	3 weak	2	28.6	4	28.6	6	28.6	5	41.7
	4 strong	0	0.0	0	0.0	0	0.0	1	8.3
15	hypoconid branch	7		14		21		9	
	2 absent	6	85.7	12	85.7	18	85.7	2	22.2
	3 short	1	14.3	2	14.3	3	14.3	6	66.7
	4 long	0	0.0	0	0.0	0	0.0	1	11.1

Table 7. Character states of M_2 of *E. martinensis* and *E. margaritae*.

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
6	metalophulid	5		13		18		13	
	4 to anteroconid	5	100.0	13	100.0	18	100.0	11	84.6
	5 to anterolophulid	0	0.0	0	0.0	0	0.0	2	15.4
7	pcd hind-arm	5		13		18		13	
	2 absent	3	60.0	12	92.3	15	83.3	12	92.3
	3 short free	2	40.0	1	7.7	3	16.7	1	7.7
9	sinusid	5		13		18		12	
	3 narrow transverse	0	0.0	4	30.8	4	22.2	2	16.7
	4 broad transverse	0	0.0	1	7.7	1	5.6	2	16.7
	5 narrow backwards	5	100.0	7	53.8	12	66.7	7	58.3
	6 broad backwards	0	0.0	1	7.7	1	5.6	1	8.3
10	mesosinusid	5		12		17		13	
	2 open	2	40.0	5	41.7	7	41.2	10	76.9
	3 closed	3	60.0	7	58.3	10	58.8	3	23.1
12	mesoconid	5		12		17		12	
	2 absent	1	20.0	5	41.7	6	35.3	8	66.7
	3 weak	1	20.0	7	58.3	8	47.1	3	25.0
	4 strong	3	60.0	0	0.0	3	17.6	1	8.3
13	mesolophid	5		13		18		13	
	4 medium	2	40.0	2	15.4	4	22.2	8	61.5
	5 long	3	60.0	11	84.6	14	77.8	5	38.5
14	ectomesolophid	5		12		17		12	
	2 absent	4	80.0	4	33.3	8	47.1	7	58.3
	3 weak	1	20.0	8	66.7	9	52.9	5	41.7
16	hypoconid branch	5		12		17		10	
	2 absent	4	80.0	12	100.0	16	94.1	8	80.0
	3 short	1	20.0	0	0.0	1	5.9	2	20.0

Table 8. Character states of M_3 of *E. martinensis* and *E. margaritae*.

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
6	metalophulid	14		12		26		11	
	4 to anteroconid	4	28.6	3	25.0	7	26.9	7	63.6
	5 to anterolophulid	10	71.4	9	75.0	19	73.1	4	36.4
11	mesolophid	14		13		27		11	
	2 absent	1	7.1	5	38.5	6	22.2	2	18.2
	3 short	3	21.4	4	30.8	7	25.9	4	36.4
	4 medium	8	57.1	3	23.1	11	40.7	4	36.4
	5 long	2	14.3	1	7.7	3	11.1	1	9.1
12	ectomesolophid	14		13		27		12	
	2 absent	11	78.6	9	69.2	20	74.1	7	58.3
	3 weak	1	7.1	4	30.8	5	18.5	5	41.7
	4 strong	2	14.3	0	0.0	2	7.4	0	0.0
13	entoconid	11		13		24		11	
	2 absent	2	18.2	9	69.2	11	45.8	5	45.5
	3 small	5	45.5	1	7.7	6	25.0	3	27.3
	4 large	4	36.4	3	23.1	7	29.2	3	27.3

Table 9. Character states of M^1 of *E. martinensis* and *E. margaritae*.

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
1	anterocone	2		6		8		7	
	2 simple	2	100.0	4	66.7	6	75.0	0	0.0
	3 half-split	0	0.0	2	33.3	2	25.0	1	14.3
	4 bifid	0	0.0	0	0.0	0	0.0	5	71.4
	5 deeply split	0	0.0	0	0.0	0	0.0	1	14.3
2	prelobe	2		7		9		9	
	4 broad set-off	0	0.0	6	85.7	6	66.7	8	88.9
	5 broad continuous	2	100.0	1	14.3	3	33.3	1	11.1
3	anterolophule	2		7		9		8	
	3 ac-spur	0	0.0	1	14.3	1	11.1	0	0.0
	4 pc-spur	0	0.0	2	28.6	2	22.2	1	12.5
	5 ac + pc spurs	2	100.0	2	28.6	4	44.4	5	62.5
	6 complete	0	0.0	2	28.6	2	22.2	1	12.5
	7 double	0	0.0	0	0.0	0	0.0	1	12.5
10	sinus	2		7		9		9	
	2 strong forward	1	50.0	0	0.0	1	11.1	3	33.3
	3 forward	0	0.0	7	100.0	7	77.8	5	55.6
	5 transverse	1	50.0	0	0.0	1	11.1	1	11.1
13	mesoloph	2		6		8		9	
	3 short	0	0.0	2	33.3	2	25.0	2	22.2
	4 medium	1	50.0	4	66.7	5	62.5	6	66.7
	5 long	0	0.0	0	0.0	0	0.0	1	11.1
	6 border	1	50.0	0	0.0	1	12.5	0	0.0
15	metalophule	2		6		8		9	
	2 anterior	0	0.0	1	16.7	1	12.5	8	88.9
	5 transverse	1	50.0	5	83.3	6	75.0	1	11.1
	8 posterior	1	50.0	0	0.0	1	12.5	0	0.0
16	posterosinus	1		6		7		7	
	2 large open	1	100.0	5	83.3	6	85.7	4	57.1
	3 large closed	0	0.0	1	16.7	1	14.3	3	42.9

Table 10. Character states of M^2 of *E. martinensis* and *E. margaritae*.

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
2	protolophule	4		6		10		11	
	3 anterior	2	50.0	6	100.0	8	80.0	6	54.5
	4 anterior plus	0	0.0	0	0.0	0	0.0	3	27.3
	5 transverse	0	0.0	0	0.0	0	0.0	1	9.1
	6 double	1	25.0	0	0.0	1	10.0	0	0.0
	7 posterior plus	0	0.0	0	0.0	0	0.0	1	9.1
	8 posterior	1	25.0	0	0.0	1	10.0	0	0.0
4	sinus	4		6		10		11	
	2 strong forward	4	100.0	2	33.3	6	60.0	5	45.5
	3 forward	0	0.0	4	66.7	4	40.0	5	45.5
	4 subdivided	0	0.0	0	0.0	0	0.0	1	9.1
6	mesoloph	4		6		10		11	
	4 medium	2	50.0	6	100.0	8	80.0	8	72.7
	5 long	2	50.0	0	0.0	2	20.0	3	27.3
11	shape	3		6		9		10	
	2 subrectangular	1	33.3	1	16.7	2	22.2	0	0.0
	3 trapezoid	2	66.7	5	83.3	7	77.8	10	100.0
12	labial border	4		6		10		11	
	2 straight or convex	4	100.0	5	83.3	9	90.0	4	36.4
	3 concave	0	0.0	1	16.7	1	10.0	7	63.6

Table 11. Character states of M^3 of *E. martinensis* and *E. margaritae*.

		MIR4C		MIR4D		MIR4C+4D		PAJ	
		N	%	N	%	N	%	N	%
1	ling. anteroloph	9		10		19		11	
	2 absent	5	55.6	3	30.0	8	42.1	3	27.3
	3 weak	4	44.4	6	60.0	10	52.6	3	27.3
	4 strong	0	0.0	1	10.0	1	5.3	1	9.1
	5 around pc	0	0.0	0	0.0	0	0.0	4	36.4
2	protolophule	7		12		19		8	
	3 to anterocone	4	57.1	9	75.0	13	68.4	6	75.0
	4 to anterolophule	1	14.3	1	8.3	2	10.5	1	12.5
	5 transverse	2	28.6	2	16.7	4	21.1	0	0.0
	6 double	0	0.0	0	0.0	0	0.0	1	12.5
3	sinus	10		12		22		10	
	2 absent	0	0.0	0	0.0	0	0.0	1	10.0
	3 very small	1	10.0	0	0.0	1	4.5	0	0.0
	4 small	2	20.0	6	50.0	8	36.4	7	70.0
	5 deep	7	70.0	6	50.0	13	59.1	2	20.0
4	mesosinus	10		12		22		10	
	2 open	2	20.0	0	0.0	2	9.1	5	50.0
	3 closed	8	80.0	12	100.0	20	90.9	5	50.0
5	mesoloph	10		12		22		10	
	2 absent	2	20.0	1	8.3	3	13.6	0	0.0
	3 short	1	10.0	1	8.3	2	9.1	0	0.0
	4 medium	3	30.0	5	41.7	8	36.4	5	50.0
	5 long	4	40.0	4	33.3	8	36.4	3	30.0
	6 border	0	0.0	1	8.3	1	4.5	2	20.0
6	old entoloph	10		12		22		11	
	2 absent	3	30.0	2	16.7	5	22.7	0	0.0
	3 short spur	0	0.0	0	0.0	0	0.0	1	9.1
	5 long spur	0	0.0	4	33.3	4	18.2	4	36.4
	6 complete	7	70.0	6	50.0	13	59.1	6	54.5
7	axioloph	10		12		22		11	
	2 absent	9	90.0	8	66.7	17	77.3	10	90.9
	3 anterior spur	1	10.0	4	33.3	5	22.7	1	9.1
10	metacone	9		11		20		10	
	2 absent	8	88.9	7	63.6	15	75.0	4	40.0
	3 present	1	11.1	4	36.4	5	25.0	6	60.0

Table 12. Character states of M_1 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	ling. anterolophid	45		10		53		30	
	2 absent	0	0.0	2	20.0	3	5.7	0	0.0
	3 low	5	11.1	4	40.0	5	9.4	11	36.7
	4 interrupted	2	4.4	4	40.0	9	17.0	5	16.7
	5 high	38	84.4	0	0.0	36	67.9	14	46.7
2	lab. anterolophid	45		10		51		35	
	3 short	2	4.4	0	0.0	0	0.0	0	0.0
	4 long	3	6.7	2	20.0	14	27.5	11	31.4
	5 complete	40	88.9	8	80.0	37	72.5	24	68.6
3	anterolophulid	34		10		48		32	
	3 interrupted	0	0.0	0	0.0	6	12.5	2	6.3
	4 low	16	47.1	4	40.0	19	39.6	16	50.0
	5 complete	18	52.9	6	60.0	23	47.9	14	43.8
4	anterosinusid	44		10		53		36	
	2 narrow	2	4.5	1	10.0	11	20.8	0	0.0
	3 wide	42	95.5	9	90.0	42	79.2	36	100.0
5	metalophulid	44		10		54		35	
	2 absent	35	79.5	4	40.0	39	72.2	12	34.3
	3 anterior interrupted	7	15.9	3	30.0	4	7.4	15	42.9
	4 anterior complete	2	4.5	3	30.0	10	18.5	8	22.9
	5 to anteroconid	0	0.0	0	0.0	1	1.9	0	0.0
6	pcd hind-arm	38		10		50		36	
	3 short free	2	5.3	0	0.0	2	4.0	0	0.0
	4 trans to mcd low	10	26.3	1	10.0	9	18.0	0	0.0
	5 trans to mcd high	14	36.8	5	50.0	33	66.0	14	38.9
	7 bent to mcd low	7	18.4	2	20.0	3	6.0	2	5.6
	8 bent to mcd high	5	13.2	2	20.0	3	6.0	20	55.6
7	sinusid	44		10		53		34	
	2 open	0	0.0	0	0.0	4	7.5	6	17.6
	3 closed	40	90.9	10	100.0	49	92.5	27	79.4
	4 ectostylid	4	9.1	0	0.0	0	0.0	1	2.9
8	sinusid	43		10		55		38	
	3 transverse	13	30.2	1	10.0	9	16.4	11	28.9
	4 backwards	30	69.8	9	90.0	46	83.6	27	71.1
9	mesosinusid	42		10		53		39	
	3 closed	3	7.1	0	0.0	0	0.0	0	0.0
	4 mcd ridge open	13	31.0	6	60.0	28	52.8	32	82.1
	5 mcd ridge closed	26	61.9	4	40.0	25	47.2	7	17.9

Table 12. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
10	ectolophid	41		10		54		40	
	2 longitudinal	39	95.1	6	60.0	46	85.2	29	72.5
	3 oblique	0	0.0	2	20.0	8	14.8	7	17.5
	4 curved	1	2.4	0	0.0	0	0.0	1	2.5
	5 interrupted	1	2.4	2	20.0	0	0.0	3	7.5
11	mesoconid	39		10		52		27	
	2 absent	17	43.6	8	80.0	30	57.7	18	66.7
	3 weak	22	56.4	2	20.0	22	42.3	8	29.6
	4 strong	0	0.0	0	0.0	0	0.0	1	3.7
12	mesolophid	42		10		53		34	
	2 absent	0	0.0	1	10.0	0	0.0	0	0.0
	3 short	1	2.4	1	10.0	2	3.8	0	0.0
	4 medium	25	59.5	3	30.0	46	86.8	25	73.5
	5 long	16	38.1	5	50.0	5	9.4	9	26.5
13	2nd mesolophid	42		10		50		34	
	2 absent	42	100.0	6	60.0	32	64.0	5	14.7
	3 short	0	0.0	1	10.0	4	8.0	9	26.5
	4 medium	0	0.0	1	10.0	12	24.0	18	52.9
	5 long	0	0.0	2	20.0	2	4.0	2	5.9
14	ectomesolophid	44		10		56		38	
	2 absent	5	11.4	6	60.0	7	12.5	6	15.8
	3 weak	13	29.5	2	20.0	10	17.9	14	36.8
	4 strong	26	59.1	2	20.0	39	69.6	18	47.4
15	hypolophulid	43		10		52		41	
	2 anterior oblique	1	2.3	1	10.0	3	5.8	3	7.3
	3 anterior transverse	42	97.7	9	90.0	49	94.2	36	87.8
	4 transverse	0	0.0	0	0.0	0	0.0	2	4.9
16	hypoconid branch	45		10		53		38	
	2 absent	45	100.0	10	100.0	49	92.5	27	71.1
	3 short	0	0.0	0	0.0	3	5.7	7	18.4
	5 long connected	0	0.0	0	0.0	1	1.9	4	10.5
17	posterosinusid	44		10		55		38	
	3 closed	44	100.0	10	100.0	55	100.0	38	100.0
18	lab. posterolophid	44		10		55		33	
	2 absent	35	79.5	9	90.0	49	89.1	29	87.9
	3 small	4	9.1	0	0.0	4	7.3	3	9.1
	4 strong	5	11.4	1	10.0	2	3.6	1	3.0

Table 13. Character states of M_2 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	lab. anterolophid	45		17		48		34	
	3 short	0	0.0	1	5.9	3	6.3	1	2.9
	4 to pcd	44	97.8	16	94.1	45	93.8	32	94.1
	5 around pcd	1	2.2	0	0.0	0	0.0	1	2.9
2	anterolophulid	41		17		44		23	
	4 low	6	14.6	0	0.0	0	0.0	0	0.0
	5 complete	35	85.4	17	100.0	44	100.0	23	100.0
3	metalophulid	47		17		50		35	
	3 anterior interrupted	1	2.1	0	0.0	1	2.0	0	0.0
	5 to anterolophulid	46	97.9	17	100.0	49	98.0	35	100.0
4	metalophulid-spur	47		17		46		40	
	2 absent	44	93.6	15	88.2	41	89.1	28	70.0
	3 weak	1	2.1	1	5.9	4	8.7	4	10.0
	4 strong	2	4.3	1	5.9	1	2.2	8	20.0
5	pcd hind-arm	47		17		46		40	
	3 short free	3	6.4	1	5.9	1	2.2	3	7.5
	4 trans to mcd low	0	0.0	0	0.0	1	2.2	5	12.5
	5 trans to mcd high	0	0.0	0	0.0	2	4.3	0	0.0
	6 long free	44	93.6	15	88.2	36	78.3	26	65.0
	7 bent to mcd low	0	0.0	1	5.9	4	8.7	6	15.0
	8 bent to mcd high	0	0.0	0	0.0	2	4.3	0	0.0
6	sinusid	47		17		48		38	
	2 open	0	0.0	0	0.0	0	0.0	4	10.5
	3 closed	47	100.0	17	100.0	47	97.9	34	89.5
	4 ectostylid	0	0.0	0	0.0	1	2.1	0	0.0
7	sinusid	47		17		46		37	
	3 transverse	25	53.2	8	47.1	13	28.3	18	48.6
	4 backwards	22	46.8	9	52.9	33	71.7	19	51.4
8	mesosinusid	47		16		45		39	
	2 open	3	6.4	8	50.0	20	44.4	35	89.7
	3 closed	44	93.6	8	50.0	25	55.6	4	10.3
9	ectolophid	31		15		31		25	
	2 high	25	80.6	9	60.0	20	64.5	9	36.0
	3 low	5	16.1	4	26.7	11	35.5	16	64.0
	4 interrupted	1	3.2	2	13.3	0	0.0	0	0.0
10	mesoconid	47		15		45		36	
	2 absent	46	97.9	11	73.3	43	95.6	29	80.6
	3 weak	1	2.1	3	20.0	2	4.4	7	19.4
	4 strong	0	0.0	1	6.7	0	0.0	0	0.0

Table 13. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
11	mesolophid	47		17		47		39	
	2 absent	33	70.2	2	11.8	10	21.3	1	2.6
	3 short	5	10.6	0	0.0	7	14.9	5	12.8
	4 medium	6	12.8	10	58.8	25	53.2	26	66.7
	5 long	3	6.4	5	29.4	5	10.6	7	17.9
12	mesolophid	47		17		49		40	
	2 simple	47	100.0	17	100.0	49	100.0	39	97.5
	3 branched	0	0.0	0	0.0	0	0.0	1	2.5
13	ectomesolophid	47		17		49		42	
	2 absent	28	59.6	9	52.9	11	22.4	4	9.5
	3 weak	8	17.0	2	11.8	10	20.4	12	28.6
	4 strong	11	23.4	6	35.3	28	57.1	26	61.9
14	hypolophulid	45		17		45		37	
	2 anterior oblique	41	91.1	12	70.6	35	77.8	34	91.9
	3 anterior transverse	4	8.9	5	29.4	10	22.2	3	8.1
15	hypoconidbranch	47		17		46		38	
	2 absent	44	93.6	17	100.0	42	91.3	34	89.5
	3 short	2	4.3	0	0.0	4	8.7	4	10.5
	5 long connected	1	2.1	0	0.0	0	0.0	0	0.0
16	posterosinusid	47		17		45		38	
	2 open	0	0.0	0	0.0	0	0.0	13	34.2
	3 closed	47	100.0	17	100.0	45	100.0	25	65.8
17	lab. posterolophid	45		17		44		37	
	2 absent	28	62.2	11	64.7	35	79.5	27	73.0
	3 small	14	31.1	4	23.5	8	18.2	8	21.6
	4 strong	3	6.7	2	11.8	1	2.3	2	5.4
18	greatest width	42		17		46		30	
	2 anterior	12	28.6	2	11.8	4	8.7	4	13.3
	3 equal	8	19.0	3	17.6	17	37.0	8	26.7
	4 posterior	22	52.4	12	70.6	25	54.3	18	60.0

Table 14. Character states of M_3 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	lab. anterolophid	65		12		44		28	
	3 short	9	13.8	3	25.0	3	6.8	1	3.6
	4 to pcd	56	86.2	9	75.0	41	93.2	27	96.4
2	anterolophulid	61		11		43		25	
	3 interrupted	1	1.6	0	0.0	0	0.0	0	0.0
	4 short	3	4.9	3	27.3	0	0.0	0	0.0
	5 long	57	93.4	8	72.7	43	100.0	25	100.0
3	anterosinusid	64		12		44		27	
	3 narrow	3	4.7	1	8.3	2	4.5	0	0.0
	4 wide	61	95.3	11	91.7	42	95.5	27	100.0
4	metalophulid	62		12		44		30	
	3 anterior interrupted	0	0.0	1	8.3	2	4.5	1	3.3
	4 to anteroconid	3	4.8	3	25.0	3	6.8	4	13.3
	5 to anterolophulid	59	95.2	8	66.7	39	88.6	25	83.3
5	metalophulid-spur	64		12		45		29	
	2 absent	36	56.3	8	66.7	37	82.2	19	65.5
	3 weak	10	15.6	3	25.0	5	11.1	5	17.2
	4 strong	18	28.1	1	8.3	3	6.7	5	17.2
6	pcd hind-arm	65		12		45		31	
	3 short free	3	4.6	1	8.3	1	2.2	0	0.0
	4 trans to mcd low	0	0.0	0	0.0	1	2.2	0	0.0
	6 long free	61	93.8	9	75.0	39	86.7	28	90.3
	7 bent to mcd low	1	1.5	0	0.0	3	6.7	0	0.0
	9 long to border	0	0.0	2	16.7	1	2.2	3	9.7
7	sinusid	64		11		45		29	
	2 open	9	14.1	1	9.1	5	11.1	3	10.3
	3 closed	50	78.1	10	90.9	40	88.9	25	86.2
	4 ectostylid	5	7.8	0	0.0	0	0.0	1	3.4
8	sinusid	59		12		44		25	
	3 narrow transverse	3	5.1	4	33.3	0	0.0	1	4.0
	4 broad transverse	37	62.7	4	33.3	10	22.7	8	32.0
	5 narrow backwards	4	6.8	0	0.0	3	6.8	2	8.0
	6 broad backwards	15	25.4	4	33.3	31	70.5	14	56.0
9	mesosinusid	59		12		44		26	
	2 open	8	13.6	0	0.0	6	13.6	3	11.5
	3 closed	51	86.4	12	100.0	38	86.4	23	88.5
10	mesolophid	64		12		45		30	
	2 absent	62	96.9	12	100.0	43	95.6	28	93.3
	3 short	1	1.6	0	0.0	1	2.2	0	0.0
	4 medium	1	1.6	0	0.0	1	2.2	2	6.7

Table 14. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
11	mesolophid	65		12		45		30	
	2 simple	65	100.0	12	100.0	45	100.0	30	100.0
12	ectolophid	56		12		38		20	
	2 low	1	1.8	0	0.0	3	7.9	2	10.0
	4 complete	55	98.2	12	100.0	35	92.1	18	90.0
13	mesoconid	65		12		44		27	
	2 absent	65	100.0	12	100.0	42	95.5	27	100.0
	3 small	0	0.0	0	0.0	2	4.5	0	0.0
14	ectomesolophid	64		12		45		29	
	2 absent	63	98.4	7	58.3	25	55.6	8	27.6
	3 weak	1	1.6	1	8.3	9	20.0	12	41.4
	4 strong	0	0.0	4	33.3	11	24.4	9	31.0
15	entoconid	53		10		40		22	
	2 absent	4	7.5	1	10.0	0	0.0	2	9.1
	3 small	21	39.6	4	40.0	10	25.0	5	22.7
	4 large	28	52.8	5	50.0	30	75.0	15	68.2
16	hypolophulid	63		12		44		26	
	2 anterior oblique	39	61.9	7	58.3	34	77.3	22	84.6
	3 anterior transverse	23	36.5	5	41.7	10	22.7	4	15.4
	4 transverse	1	1.6	0	0.0	0	0.0	0	0.0
17	posterosinusid	60		12		45		27	
	2 open	2	3.3	0	0.0	0	0.0	1	3.7
	3 half closed	7	11.7	1	8.3	2	4.4	4	14.8
	4 closed	51	85.0	11	91.7	43	95.6	22	81.5
18	shape	60		12		45		20	
	2 short triangle	4	6.7	0	0.0	0	0.0	1	5.0
	3 long triangle	35	58.3	8	66.7	33	73.3	7	35.0
	4 trapezoid	21	35.0	4	33.3	12	26.7	12	60.0

Table 15. Character states of M^1 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	anterocone	32		9		28		19	
	2 simple	22	68.8	8	88.9	28	100.0	17	89.5
	3 half-split	6	18.8	1	11.1	0	0.0	1	5.3
	4 bifid	1	3.1	0	0.0	0	0.0	1	5.3
	5 deeply split	3	9.4	0	0.0	0	0.0	0	0.0
2	prelobe	36		10		32		21	
	2 narrow set-off	0	0.0	0	0.0	1	3.1	0	0.0
	4 broad set-off	36	100.0	8	80.0	24	75.0	19	90.5
	5 broad continuous	0	0.0	2	20.0	7	21.9	2	9.5
3	anterolophule	37		10		30		21	
	2 absent	1	2.7	2	20.0	10	33.3	0	0.0
	3 ac-spur	1	2.7	0	0.0	6	20.0	3	14.3
	4 pc-spur	12	32.4	2	20.0	5	16.7	2	9.5
	5 ac + pc spurs	19	51.4	4	40.0	9	30.0	10	47.6
	6 complete	4	10.8	2	20.0	0	0.0	0	0.0
	7 double	0	0.0	0	0.0	0	0.0	6	28.6
4	forward pac-spur	38		10		32		29	
	2 absent	13	34.2	8	80.0	21	65.6	16	55.2
	3 free	4	10.5	1	10.0	3	9.4	2	6.9
	4 to anterostyl	6	15.8	0	0.0	0	0.0	3	10.3
	5 to anterocone	15	39.5	1	10.0	8	25.0	8	27.6
5	ling. anteroloph	37		10		31		22	
	2 incomplete	1	2.7	1	10.0	3	9.7	1	4.5
	3 complete	33	89.2	7	70.0	23	74.2	15	68.2
	4 protostyl	3	8.1	2	20.0	5	16.1	6	27.3
6	protocone platform	39		10		30		24	
	2 absent	21	53.8	5	50.0	10	33.3	9	37.5
	3 small	8	20.5	4	40.0	14	46.7	6	25.0
	4 large	2	5.1	1	10.0	3	10.0	6	25.0
	5 crest	8	20.5	0	0.0	3	10.0	3	12.5
7	anterosinus	38		10		28		25	
	2 open	14	36.8	3	30.0	4	14.3	3	12.0
	3 closed	24	63.2	7	70.0	24	85.7	17	68.0
	4 anterostyl	0	0.0	0	0.0	0	0.0	5	20.0
8	protolophule	37		9		30		28	
	2 anterior interrupted	0	0.0	0	0.0	0	0.0	2	7.1
	4 anterior plus	0	0.0	1	11.1	2	6.7	0	0.0
	5 transverse	0	0.0	0	0.0	1	3.3	0	0.0
	6 double	0	0.0	0	0.0	4	13.3	1	3.6
	7 posterior plus	3	8.1	3	33.3	11	36.7	3	10.7
	8 posterior interrupted	0	0.0	0	0.0	1	3.3	1	3.6
	9 posterior	33	89.2	5	55.6	11	36.7	21	75.0
	10 absent	1	2.7	0	0.0	0	0.0	0	0.0

Table 15. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
9	sinus	38		10		30		25	
	2 open	5	13.2	6	60.0	9	30.0	14	56.0
	3 closed	13	34.2	1	10.0	20	66.7	7	28.0
	4 entostyl	20	52.6	3	30.0	1	3.3	4	16.0
10	sinus	38		10		32		25	
	2 strong forward	29	76.3	4	40.0	5	15.6	14	56.0
	3 forward	9	23.7	6	60.0	26	81.3	10	40.0
	4 subdivided	0	0.0	0	0.0	0	0.0	1	4.0
	5 transverse	0	0.0	0	0.0	1	3.1	0	0.0
11	entoloph	24		9		20		18	
	2 high	15	62.5	8	88.9	20	100.0	9	50.0
	3 low	9	37.5	1	11.1	0	0.0	9	50.0
12	mesosinus	39		10		31		25	
	2 open	5	12.8	3	30.0	4	12.9	6	24.0
	3 closed	16	41.0	3	30.0	8	25.8	4	16.0
	4 mesostyl	14	35.9	3	30.0	14	45.2	12	48.0
	5 mesostyl crest	4	10.3	1	10.0	5	16.1	3	12.0
13	mesoloph	39		10		31		27	
	2 absent	1	2.6	0	0.0	0	0.0	0	0.0
	3 short	1	2.6	0	0.0	2	6.5	1	3.7
	4 medium	19	48.7	6	60.0	14	45.2	10	37.0
	5 long	4	10.3	2	20.0	3	9.7	9	33.3
	6 border	14	35.9	2	20.0	12	38.7	7	25.9
14	2nd mesoloph	39		10		32		26	
	2 absent	39	100.0	9	90.0	32	100.0	22	84.6
	3 short	0	0.0	1	10.0	0	0.0	4	15.4
15	entomesoloph	39		10		32		24	
	2 absent	39	100.0	10	100.0	32	100.0	24	100.0
16	mesoloph-mc conn	39		10		32		27	
	2 absent	38	97.4	9	90.0	22	68.8	23	85.2
	3 1 crest	1	2.6	1	10.0	10	31.3	4	14.8
17	metalophule	36		9		27		19	
	2 anterior	36	100.0	7	77.8	26	96.3	19	100.0
	3 anterior interrupted	0	0.0	0	0.0	1	3.7	0	0.0
	5 transverse	0	0.0	2	22.2	0	0.0	0	0.0
18	posterosinus	36		10		29		19	
	2 open	15	41.7	3	30.0	11	37.9	8	42.1
	3 closed	21	58.3	7	70.0	18	62.1	11	57.9
19	labial border	36		10		28		19	
	2 hollow	8	22.2	1	10.0	6	21.4	1	5.3
	3 straight	11	30.6	2	20.0	13	46.4	6	31.6
	4 convex	17	47.2	7	70.0	9	32.1	12	63.2

Table 16. Character states of M^2 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	ling. anteroloph	53		5		47		26	
	3 weak	2	3.8	1	20.0	2	4.3	2	7.7
	4 strong	18	34.0	3	60.0	23	48.9	13	50.0
	5 around pc	33	62.3	1	20.0	22	46.8	11	42.3
2	protolophule	54		5		50		32	
	3 anterior	11	20.4	2	40.0	9	18.0	2	6.3
	4 anterior plus	40	74.1	1	20.0	37	74.0	21	65.6
	6 double	2	3.7	2	40.0	4	8.0	9	28.1
	7 posterior plus	1	1.9	0	0.0	0	0.0	0	0.0
3	sinus	53		4		49		28	
	2 open	0	0.0	1	25.0	1	2.0	3	10.7
	3 closed	44	83.0	3	75.0	47	95.9	24	85.7
	4 entostyl	9	17.0	0	0.0	1	2.0	1	3.6
4	sinus	54		5		50		31	
	2 strong forward	41	75.9	3	60.0	18	36.0	24	77.4
	3 forward	12	22.2	1	20.0	24	48.0	7	22.6
	4 subdivided	1	1.9	0	0.0	2	4.0	0	0.0
	5 transverse	0	0.0	1	20.0	6	12.0	0	0.0
5	mesosinus	53		5		50		28	
	2 open	11	20.8	1	20.0	4	8.0	6	21.4
	3 closed	18	34.0	3	60.0	10	20.0	3	10.7
	4 pac-spur	14	26.4	0	0.0	12	24.0	9	32.1
	5 mesostyl	8	15.1	1	20.0	22	44.0	9	32.1
	6 mesostyl crest	2	3.8	0	0.0	2	4.0	1	3.6
6	mesoloph	55		5		50		31	
	2 absent	1	1.8	0	0.0	0	0.0	0	0.0
	3 short	0	0.0	0	0.0	1	2.0	1	3.2
	4 medium	36	65.5	5	100.0	12	24.0	10	32.3
	5 long	9	16.4	0	0.0	3	6.0	4	12.9
	6 interrupted	1	1.8	0	0.0	5	10.0	3	9.7
	7 border	8	14.5	0	0.0	29	58.0	13	41.9
7	2nd mesoloph	55		5		50		31	
	2 absent	54	98.2	5	100.0	49	98.0	29	93.5
	3 short	0	0.0	0	0.0	1	2.0	0	0.0
	4 long	1	1.8	0	0.0	0	0.0	2	6.5
8	mesoloph-mc conn.	55		5		50		31	
	2 absent	48	87.3	4	80.0	39	78.0	20	64.5
	3 1 crest	7	12.7	1	20.0	10	20.0	11	35.5
	4 2 crests	0	0.0	0	0.0	1	2.0	0	0.0

Table 16. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
9	entoloph-pc conn.	42		4		29		16	
	2 high	3	7.1	0	0.0	22	75.9	9	56.3
	3 low	34	81.0	4	100.0	7	24.1	7	43.8
	4 interrupted	5	11.9	0	0.0	0	0.0	0	0.0
10	pc-hc conn.	55		5		50		31	
	2 absent	52	94.5	5	100.0	48	96.0	31	100.0
	3 weak	1	1.8	0	0.0	0	0.0	0	0.0
	4 interrupted	1	1.8	0	0.0	1	2.0	0	0.0
	5 low	0	0.0	0	0.0	1	2.0	0	0.0
	6 complete	1	1.8	0	0.0	0	0.0	0	0.0
11	metalophule	54		5		49		34	
	3 anterior	53	98.1	5	100.0	49	100.0	33	97.1
	5 transverse	1	1.9	0	0.0	0	0.0	0	0.0
	6 double	0	0.0	0	0.0	0	0.0	1	2.9
12	posterosinus	53		5		50		28	
	2 open	32	60.4	0	0.0	8	16.0	9	32.1
	3 closed	21	39.6	5	100.0	42	84.0	19	67.9
13	shape	53		5		49		22	
	2 subrectangular	13	24.5	2	40.0	14	28.6	0	0.0
	3 trapezoid	40	75.5	3	60.0	35	71.4	22	100.0
14	labial border	55		5		47		28	
	2 concave	48	87.3	5	100.0	21	44.7	19	67.9
	3 straight	7	12.7	0	0.0	23	48.9	9	32.1
	4 convex	0	0.0	0	0.0	3	6.4	0	0.0

Table 17. Character states of M^3 of various *Allocricetodon* species.

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
1	ling. anteroloph	68		17		60		20	
	2 absent	4	5.9	0	0.0	0	0.0	5	25.0
	3 weak	15	22.1	3	17.6	4	6.7	6	30.0
	4 strong	35	51.5	9	52.9	36	60.0	7	35.0
	5 around pc	14	20.6	5	29.4	20	33.3	2	10.0
2	protolophule	70		16		62		21	
	2 absent	1	1.4	0	0.0	0	0.0	0	0.0
	3 to anterocone	10	14.3	3	18.8	25	40.3	15	71.4
	4 to anterolophule	59	84.3	12	75.0	37	59.7	6	28.6
	6 double	0	0.0	1	6.3	0	0.0	0	0.0
3	sinus	70		17		63		21	
	2 absent	1	1.4	0	0.0	0	0.0	1	4.8
	3 very small	10	14.3	4	23.5	1	1.6	4	19.0
	4 small	50	71.4	12	70.6	58	92.1	12	57.1
	5 deep	9	12.9	1	5.9	4	6.3	4	19.0
4	neo-entoloph	68		18		61		21	
	2 absent	7	10.3	1	5.6	4	6.6	3	14.3
	3 interrupted	2	2.9	1	5.6	0	0.0	1	4.8
	4 low	1	1.5	0	0.0	6	9.8	1	4.8
	5 high	58	85.3	16	88.9	51	83.6	16	76.2
5	mesosinus	69		16		64		22	
	2 open	2	2.9	4	25.0	1	1.6	2	9.1
	3 closed	67	97.1	12	75.0	63	98.4	20	90.9
6	mesoloph	70		18		65		21	
	2 absent	1	1.4	0	0.0	1	1.5	0	0.0
	3 short	4	5.7	1	5.6	1	1.5	2	9.5
	4 medium	30	42.9	6	33.3	15	23.1	4	19.0
	5 long	17	24.3	5	27.8	12	18.5	10	47.6
	6 border	18	25.7	6	33.3	36	55.4	5	23.8
7	2nd mesoloph	70		18		65		22	
	2 absent	69	98.6	13	72.2	60	92.3	14	63.6
	3 short	0	0.0	1	5.6	2	3.1	2	9.1
	4 long	1	1.4	4	22.2	3	4.6	6	27.3
8	old entoloph	70		17		64		21	
	2 absent	39	55.7	9	52.9	12	18.8	7	33.3
	3 short spur	6	8.6	1	5.9	2	3.1	1	4.8
	4 curved spur	1	1.4	0	0.0	0	0.0	0	0.0
	5 long spur	7	10.0	0	0.0	8	12.5	2	9.5
	6 complete	17	24.3	7	41.2	42	65.6	11	52.4

Table 17. (continued).

		MIR1 *cornelii*		MIR4C *incertus*		MIR4C+D *landroveri*		PAJ *landroveri*	
		N	%	N	%	N	%	N	%
9	axioloph	70		17		63		20	
	2 absent	22	31.4	6	35.3	6	9.5	6	30.0
	3 anterior spur	5	7.1	1	5.9	25	39.7	5	25.0
	4 post. spur short	9	12.9	2	11.8	1	1.6	0	0.0
	5 post. spur long	20	28.6	6	35.3	6	9.5	0	0.0
	6 two spurs	3	4.3	1	5.9	0	0.0	1	5.0
	7 complete	11	15.7	1	5.9	25	39.7	8	40.0
10	centroloph	69		18		67		22	
	2 absent	2	2.9	0	0.0	1	1.5	0	0.0
	3 weak	2	2.9	1	5.6	2	3.0	1	4.5
	4 strong	25	36.2	15	83.3	56	83.6	18	81.8
	5 = metalophule	40	58.0	2	11.1	8	11.9	3	13.6
11	centrocone	69		17		64		19	
	2 absent	58	84.1	14	82.4	60	93.8	12	63.2
	3 present	4	5.8	0	0.0	2	3.1	5	26.3
	4 isolated	2	2.9	0	0.0	0	0.0	0	0.0
	5 on old entoloph	5	7.2	3	17.6	2	3.1	2	10.5
12	metacone	63		16		59		20	
	2 absent	22	34.9	10	62.5	22	37.3	11	55.0
	3 present	41	65.1	6	37.5	37	62.7	9	45.0
13	posterosinus	68		17		65		22	
	2 open	7	10.3	1	5.9	1	1.5	1	4.5
	3 closed	61	89.7	16	94.1	64	98.5	21	95.5