

# The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain)

M. Freudenthal, M. Hugueney & † E. Moissenet

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

M. Freudenthal, Nationaal Natuurhistorisch Museum, Postbus 9517, NL-2300 RA Leiden, The Netherlands, and Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, E-18002, Granada, Spain; M. Hugueney, URA 11 CNRS, Département des Sciences de la Terre, Université Claude Bernard, 43 Bd. du 11 Novembre, F-69622 Villeurbanne, France.

Key words — Oligocene, Rodentia, Spain.

Two new species of *Pseudocricetodon* are described: *P. simplex* sp. nov. is characterised by a simple dental pattern in the lower molars. It has been discovered almost simultaneously in Oligocene beds near Martín del Río (Teruel Basin) and near Alcorisa on the southern border of the Ebro Basin. *P. adroveri* sp. nov. had previously been described from Vivel del Río as *P. aff. thaleri*, and is characterised by a complex dental pattern. These two new species change the current ideas on the evolution of the genus *Pseudocricetodon*.

## Contents

Introduction .....	57
Topographical and geological situation of the localities .....	58
Methods .....	59
Taxonomic descriptions .....	60
<i>Pseudocricetodon montalbanensis</i> Thaler, 1969 .....	62
<i>Pseudocricetodon simplex</i> sp. nov. ....	65
<i>Pseudocricetodon adroveri</i> sp. nov. ....	72
<i>Pseudocricetodon philippi</i> Hugueney, 1971 .....	77
<i>Pseudocricetodontinae</i> from Turkish Thrace .....	81
Phylogeny of <i>Pseudocricetodon</i> .....	82
Conclusions .....	84
Acknowledgements .....	85
Tables .....	86
Appendix: Description of character states .....	101
References .....	114

## Introduction

In the area between Vivel del Río and Martín del Río (Teruel, Spain) a section of Upper Oligocene beds is found, that contains eight fossil mammal localities in superposition, which permit to recognise at least five different faunal zones. In two of these localities, Mirambueno 4C and 4D, discovered in 1991 by M. Freudenthal and M.A. Sacristán, a new species of *Pseudocricetodon* was encountered, that will be described in this paper.

In 1986 E. Moissenet discovered two fossiliferous levels near Alcorisa on the southern border of the Ebro Basin. When we realised that the *Pseudocricetodon* material from Mirambueno and Alcorisa represented the same species, we decided to describe it together.

This new species of *Pseudocricetodon* is not the only point of resemblance between the faunas of Mirambueno 4C, 4D, and Alcorisa; in fact many species found in these localities are identical or very closely related. Therefore, in our opinion, the localities are of almost the same age and represent a clearly distinguishable faunal episode. The Cricetidae other than *Pseudocricetodon* are described in another paper in this same volume; we will describe the entire fauna recovered from Mirambueno 4C and 4D in a future publication.

The material from Mirambueno and Montalbán described in this paper will be deposited in the 'Departamento de Ciencias de la Tierra', University of Zaragoza, except for the specimens with code RGM that are deposited in the collections of the National Museum of Natural History, Leiden, The Netherlands. Part of the material from Vivel del Río, including the figured specimens, will be deposited in the 'Museo de Paleontología', Sabadell.

Measurements are given in units of 0.1 mm.

#### Abbreviations

ALCN	Alcorisa noir	MIR4C	Mirambueno 4C
ALCR	Alcorisa rose	MIR4D	Mirambueno 4D
COD	Coderet	MLB1D	Montalbán 1D
MIR1	Mirambueno 1	MLB3C	Montalbán 3C
MIR2A	Mirambueno 2A	SMC	St Martin-de-Castillon
MIR4B	Mirambueno 4B	VIV	Vivel del Río

FSL	Fac. des Sciences, Université Lyon I
IPS	Instituto de Paleontología, Sabadell
RGM	National Museum of Natural History, Leiden (formerly Rijksmuseum van Geologie en Mineralogie).

The photographs were made on the Zeiss DSM 950 Scanning Electron Microscope of the Granada University, and on the Hitachi S800 of the CMEABG (Centre de Microscopie électronique appliquée à la Biologie et à la Géologie) of the University Claude Bernard Lyon I.

#### Topographical and geological situation of the localities

The localities of Mirambueno and Vivel del Río are situated near the Eastern border of the Calatayud-Teruel Basin, topographical map of Spain, sheet 27-19 (492), Segura de los Baños, 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 et al. (in prep.).

Alcorisa is a little village in Lower Aragón, (topographical map of Spain, sheet 29-19 (494), Calanda). It is situated at the transition of the Iberian Range to the Ebro

Basin. In 1986 mammal remains were discovered by E. Moissenet in Paleogene continental sediments on the southern flank of the Guadalopillo Syncline, between the village and the Gallipuen Anticline, of which the Mesozoic core appears in the 'Cerros de las Umbrias'. The fossiliferous beds consist of greenish-white marls dipping towards the north (Alcorisa noir, code ALCN), and covered by red clays (Alcorisa rose, code ALCR), sandstones, and conglomerates (Fig. 1). All these fluvio-lacustrine deposits are deformed by the main folding episode that took place during the Late Oligocene. The exact position of the locality will be given in a forth-coming paper by Hugueney & Moissenet. Some 800 kg of sediment were washed during the 1991 summer campaign.

### Methods

In view of the large amounts of material collected in the areas of Montalbán and Vivel del Río, one of the authors (M.F.) has written a set of computer programs, in order to create a data base for the morphological descriptions of the specimens. In this paper we will reduce the classical descriptions of the specimens. They are partly replaced by Tables 1-7, that contain between 13 and 19 features per dental element, and for each feature between 2 and 10 character states. For each population, and for

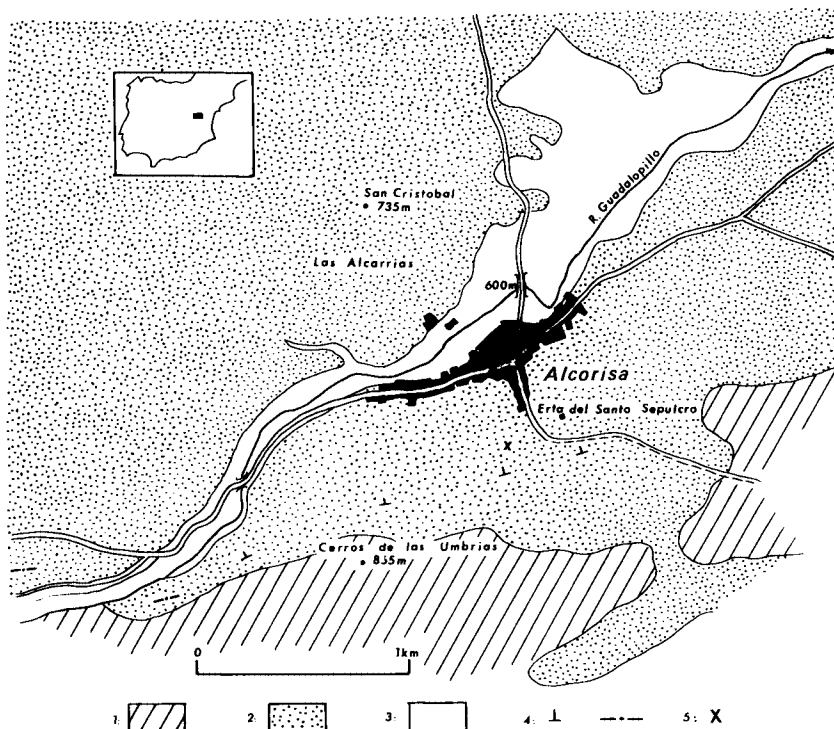


Fig. 1. Location of the Oligocene mammal locality of Alcorisa. 1: Mesozoic rocks of the Iberian Chains. 2: Conglomerates, sandstones, silts and marls of Paleogene age. 3: Quaternary deposits of the Guadalopillo river. 4: Dipping of the Paleogene formations. 5: Oligocene mammal locality of Alcorisa.

each character state, absolute numbers and percentages are given.

Since the value of such a data base depends largely on the objectivity of the choice of the character states, we have tried to define as exactly as possible the meaning of each of the descriptions. These explanations are given in the appendix. For many characters we think we have achieved a reasonable degree of objectivity. Other characters, however, present differences when evaluated by one person or another. This is specially true for the cingulum ridges that may close the valleys of the teeth. In *Pseudocricetodon* these crests are often so tiny that a decision on whether a valley is open or closed is extremely difficult. It may be necessary to revise the definitions of these characters in order to obtain more satisfactory results. The great advantage of our data base is that it makes it possible to visualise, check, and correct the description of each individual specimen at any time. Comparisons between populations are easy; a group of populations may be compared with other populations or other groups, etc.

One should realise that the character states described in Appendix 1 are valid for the genus *Pseudocricetodon* only. A similar data base is being created for the genus *Eucricetodon*, one for the Muridae, and one for the Cricetinae, in which the characters, and the definitions of the character states differ from those for *Pseudocricetodon*.

The terminology of parts of the teeth is given in Fig. 2. A few remarks on terminology should be made: Ünay-Bayraktar (1989, p. 40) calls '**mesoloph**' (between apostrophes) what we call the **mesoloph**, and she calls **genuine mesoloph** what we call **second mesoloph**. On p. 41 ( $M^2$ ) she calls '**mesoloph**' what we call **posterior proto-lophule (plus eventually a second mesoloph)**, and she calls **second 'mesoloph'** what we call the **mesoloph**. Also on p. 41 ( $M_1$ ) she calls **anterosinusid** what we call **protosinusid**.

### Taxonomic descriptions

Family Cricetidae Murray, 1866

Subfamily Pseudocricetodontinae Engesser, 1987

Genus *Pseudocricetodon* Thaler, 1969

Emended diagnosis — Small Pseudocricetodontinae, foramen incisivum in the maxilla short (posterior border lying before the foremost point of the  $M^1$ ).

Lower molars: The ectolophid lies labially of the central axis of the molars. Posterior branch of the hypoconid hardly ever present.  $M_3$  smaller than  $M_1$ . Posterior part of  $M_3$  less reduced than in Eucricetodontinae. Protoconid hind-arm in  $M_1$  and  $M_2$  nearly always present, in  $M_1$  nearly always connected to the metaconid. Anterior metalophulid in  $M_1$  frequently absent. In  $M_1$  the metaconid frequently sends a long spur along the border of the molar towards the entoconid. Posterolophid of  $M_1$  hardly curved, running straightly towards the entoconid. In  $M_2$  and  $M_3$  the metalophulid is generally more or less transverse, which, combined with a long anterolophulid, results in a wide anterosinusid.

Upper molars: Mesolophs well developed, often long. Lingual border of  $M^1$  straight or concave, or very slightly convex, forming an angle of c.  $90^\circ$  with the posterior border. The prelobe of  $M^1$  is frequently set-off from the rest of the molar, the

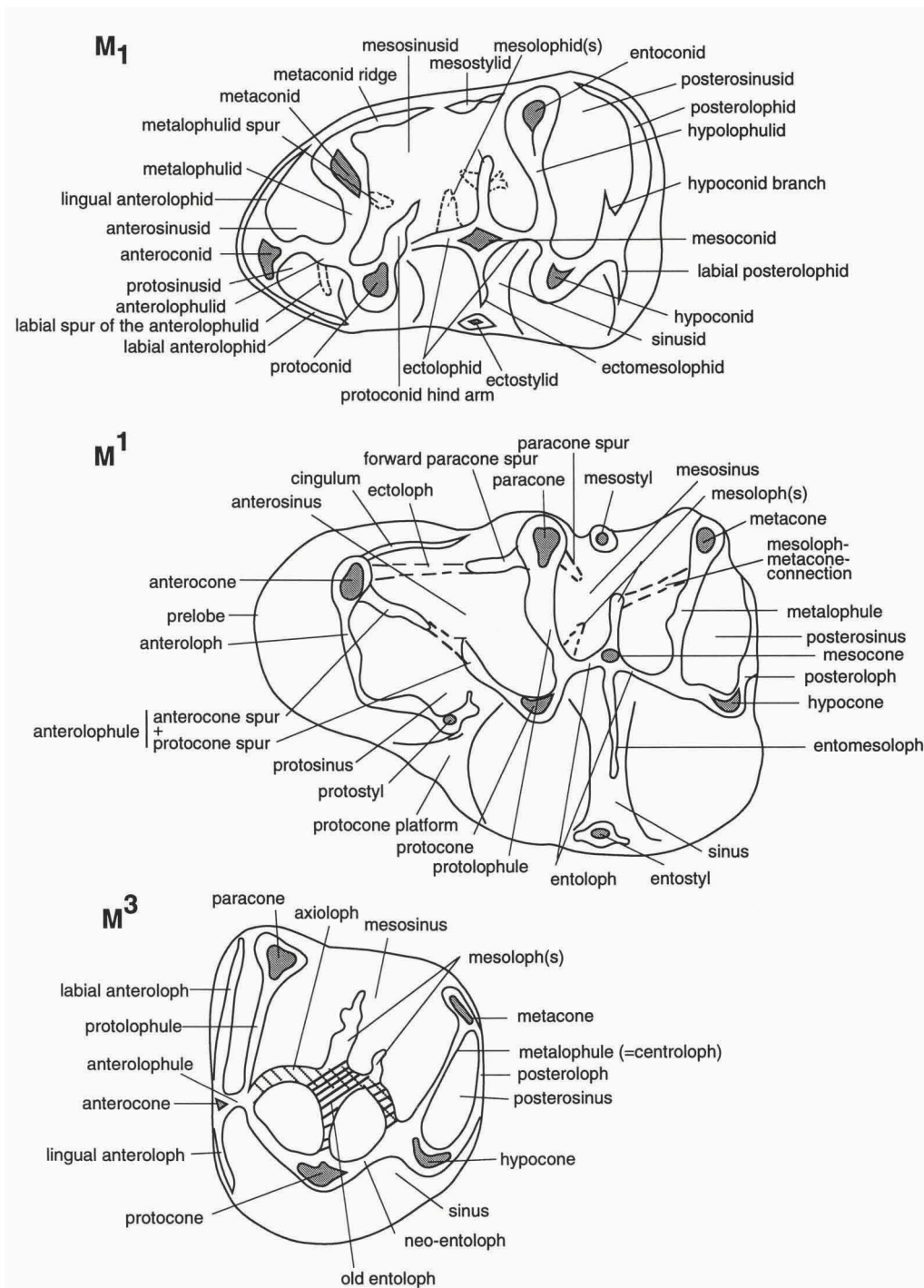


Fig. 2. Terminology of parts of the cheek teeth.

lingual border between anterocone and protocone presenting a sharp angle.

The genus *Pseudocricetodon* was created by Thaler (1969) for a small cricetid from the Lower Oligocene of Montalbán, *Pseudocricetodon montalbanensis*. In the same paper Thaler implied, that *Cricetodon incertus* Schlosser, 1884 belong to this genus too. Since then, a number of species have been described within this genus, or have been transferred to it from other genera. In our opinion the genus contains the following species:

*Pseudocricetodon montalbanensis* Thaler, 1969, type-locality Montalbán;  
*Pseudocricetodon thaleri* (Hugueney, 1969), type locality Coderet;  
*Pseudocricetodon philippi* Hugueney, 1971, type-locality St Martin-de-Castillon;  
*Pseudocricetodon moguntiacus* (Bahlo, 1975), type-locality Heimersheim;  
*Pseudocricetodon* sp. (in Freudenthal et al., 1992) from Montalbán 3C;  
*Pseudocricetodon simplex* sp. nov., type-locality Mirambueno 4C;  
*Pseudocricetodon adroveri* sp. nov., type-locality Vivel del Río.

We exclude from it:

*Eucricetodon incertus* Schaub, 1925;  
*Pseudocricetodon moguntiacus orientalis* Ünay-Bayraktar, 1989;  
*Pseudocricetodon philippi* Hugueney, 1971 in Ünay-Bayraktar, 1989;  
*Pseudocricetodon* (*Lignitella*) *suemengeni* Ünay-Bayraktar, 1989.

Many authors have attributed *Eucricetodon incertus* Schaub, 1925 to the genus *Pseudocricetodon*. Daams et al. (1989) placed it in the genus *Heterocricetodon*. Kristkoiz (1992) considered this to be a premature decision. In another paper in this same volume (Freudenthal, 1994) the position of this species, and several related known and new species will be discussed.

*Pseudocricetodon montalbanensis* Thaler, 1969

Pl. 1, figs. 1-12.

Holotype — M<sup>1</sup> dext., MLBS 505, Museo de Paleontología Miquel Crusafont, Sabadell.

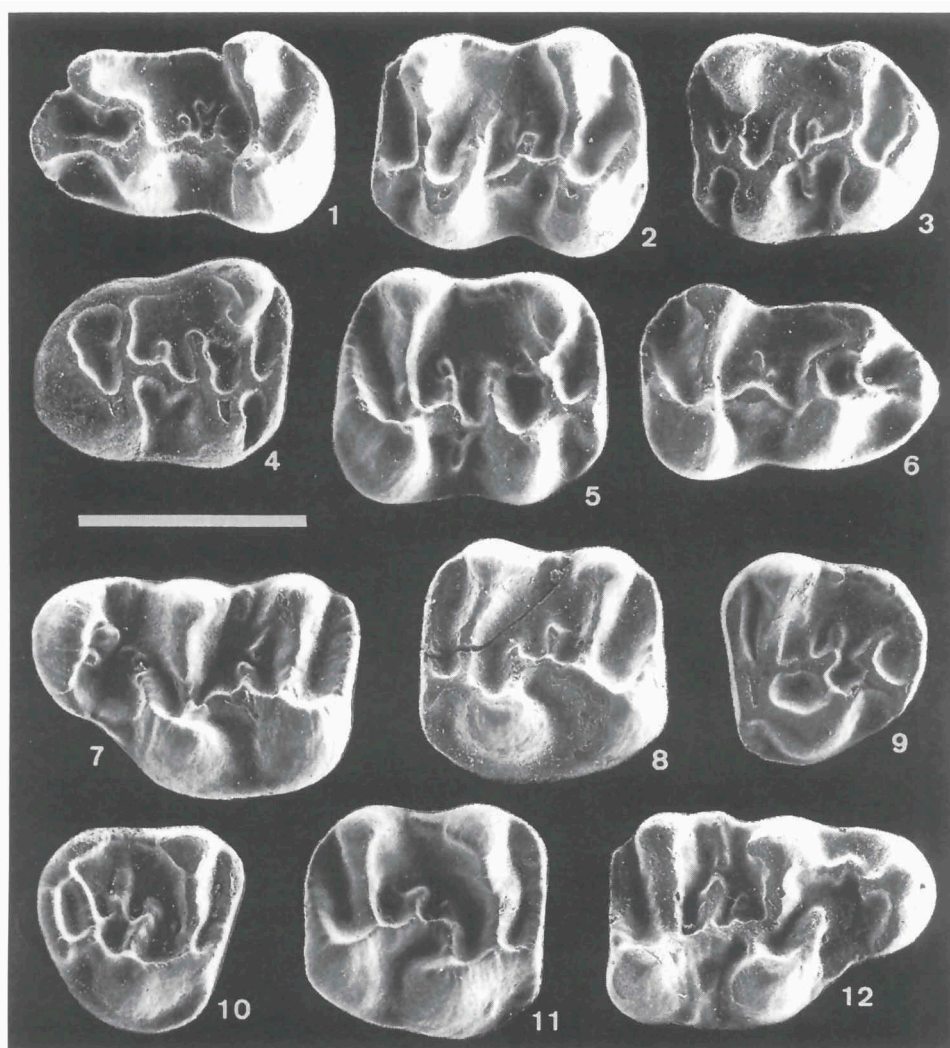
Type-locality — Montalbán (Teruel, Spain).

Translated original diagnosis — Cricetidae from the Oligocene of Europe, differing from *Paracricetodon* by its M<sup>3</sup> that is shorter than M<sup>2</sup>; from *Heterocricetodon* by its mesolophid, that doesn't reach the lingual border, and from *Eucricetodon* by the straight or slightly concave outline of the lingual wall of M<sup>1</sup>.

Emended diagnosis — Apart from the features mentioned in the diagnosis of the genus, the following characters are considered to be important: The dental pattern is fairly complex with well-developed mesolophids, mesolophs, ectomesolophids, and second mesolophs. Sinusid and sinus are generally curved or oblique. In the third molars the metalophulid, resp. protolophule, is generally transverse, not connected to the anterior molar border.

Differential diagnosis — For a comparison with *P. simplex* sp. nov. and *P. adroveri* sp. nov., see hereafter.

It differs from *P. thaleri* (Hugueney, 1969) by its, on the average, smaller size, and its less complex dental pattern. In M<sup>1</sup> the anterolophule is less frequently complete, and the sinus more procumbent.



*Pseudocricetodon montalbanensis* from Montalbán 1D

Fig. 1.  $M_1$  sin., MLB1D 216.

Fig. 2.  $M_2$  sin., MLB1D 405.

Fig. 3.  $M_3$  sin., MLB1D 510.

Fig. 4.  $M_3$  dext., MLB1D 525.

Fig. 5.  $M_2$  dext., MLB1D 457.

Fig. 6.  $M_1$  dext., MLB1D 258.

Fig. 7.  $M^1$  sin., MLB1D 618.

Fig. 8.  $M^2$  sin., MLB1D 709.

Fig. 9.  $M^3$  sin., MLB1D 916.

Fig. 10.  $M^3$  dext., MLB1D 937.

Fig. 11.  $M^2$  dext., MLB1D 753.

Fig. 12.  $M^1$  dext., MLB1D 641.

Scale is 1 mm.

It differs from *P. philippi* by its larger size and more complex dental pattern.

For the difference with *P. moguntiacus* see the discussion hereafter.

Apart from the original description by Thaler (which is restricted to the diagnosis) this species is relatively poorly known. We have collected an extensive material from various localities near Montalbán, which permits us to present a redescription of this species, based on material from the locality Montalbán 1D. This level is the upper part of the bed from which the type-population was obtained.

Material and measurements — See Tables 8 and 9.

#### Description (for full details see Tables 1-6)

$M_1$  — A labial spur on the anterolophulid is rarely present (10%). The protoconid hind-arm is connected to the metaconid at a high level in most specimens (80%). The sinusid is frequently directed backwards (50%). The mesolophid is rarely absent or short (20%), a second mesolophid is present in half the specimens. There may be up to three mesolophid-like structures. An ectomesolophid is frequently present (70%).

N.B. The labial spur on the anterolophulid is rare in this population. The specimen figured by Freudenthal et al. (1992, pl. 1, fig. 4) happens to be one of the few specimens that present this feature well developed.

$M_2$  — A labial spur on the anterolophulid is never present. The mesolophid is hardly ever absent or short, and it is frequently bifurcated. An ectomesolophid is present in almost 90% of the specimens.

$M_3$  — The metalophulid is never connected to the anteroconid. The mesolophid is rarely absent (7%), the ectomesolophid is well developed. The entoconid is large, causing the lingual border of the molar to be concave.

$M^1$  — The anterocone is generally simple (80%). A backward spur on the anterocone indicating the anterolophule is frequent, the anterolophule may be complete. The anterior branch of the protocone is directed antero-labial, hardly ever in contact with the paracone. The sinus is directed forward. The mesoloph is of medium length or long, frequently reaching the molar border, a second mesoloph may be present (25%). In 35% there is a longitudinal connection between mesoloph and metacone. In 11 specimens the anterosinus presents some kind of complexities in the form of extra spurs, small transverse crests, etc.

$M^2$  — The sinus is directed forward, often quite strongly. The mesoloph is of medium length or long; a second mesoloph is present in half the specimens. In 25% there is a longitudinal connection between mesoloph and metacone. In about half the specimens there is a more or less well developed connection between protocone and hypocone, through the sinus, comparable to the neo-entoloph of  $M^3$ . Frequently, the hypocone is hardly reduced, the tooth presenting a subrectangular outline.

$M^3$  — The protolophule is connected to the anterolophule in 75% of the specimens. The old entoloph is present (complete or incomplete) in 75%. The metacone is absent in 60% of the specimens.

Remark — Our material contains a few very small specimens:  $M_2$ , MLB1D 870,  $9.6 \times 8.0$ ;  $M^3$ , MLB1D 925,  $7.7 \times 8.3$ . It cannot be excluded, that they represent another species. The  $M_2$  is characterised by the absence of the anterior metalophulid, a feature not found in any other specimen. In the  $M^3$  the sinus is deep, and the neo-entoloph absent.



Discussion — *P. montalbanensis* differs from *P. moguntiacus* (Bahlo, 1975) from Heimersheim (Rheinhessen, Germany) by: its smaller size; the generally higher protoconid hind-arm in  $M_1$ ; the protoconid hind-arm of  $M_2$  and  $M_3$ , that is generally shorter, and often connected to the metaconid; the better developed mesolophid in  $M_3$ ; the more procumbent sinus in  $M^1$ ; the on the average shorter mesoloph in  $M^2$ ; the somewhat better developed second mesoloph in  $M^2$ .

According to Freudenthal et al. (1992) the population of *P. moguntiacus* from Heimersheim is not homogeneous. A number of specimens should be transferred to *Eucricetodon*, e.g. all  $M_1$  with a hypoconid hind-arm. In the material that we were able to study thanks to the kindness of Professor N. Schmidt-Kittler, we did not find one single  $M_1$  with hypoconid hind-arm.

But, apart from this elimination of a number of *Eucricetodon* specimens, the remaining population may still be heterogeneous. Our measurements seem to indicate that the material possibly contains two species of slightly different size, and morphologically very similar. The holotype HLM-Hhm 595 belongs to the smaller species.

None of the morphological differences listed above is really convincing; *P. moguntiacus* and *P. montalbanensis* are very close, and only the larger dimensions of *P. moguntiacus* present a clear difference. We therefore consider it possible, that the smaller species from Heimersheim (including the holotype of *P. moguntiacus*) is nothing else but *P. montalbanensis*, and *P. moguntiacus* is a junior synonym. The larger species from Heimersheim is a new one, and not yet named. It is larger than *P. montalbanensis*, and morphologically very similar to it.

*Pseudocricetodon simplex* sp. nov.

Pl. 2, figs. 1-11; Pl. 3, figs. 1-12.

Holotype —  $M_1$  sin., MIR4C 288,  $13.8 \times 8.6$ , kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Type-locality — Mirambueno 4C (prov. Teruel, Spain).

Other localities — Mirambueno 4D, Alcorisa noir and Alcorisa rose.

Age — Earliest Late Oligocene.

Diagnosis — Lower molars: In  $M_1$  the posterior branch of the protoconid is connected to the base of the metaconid or ending free; less frequently with a high connection to the metaconid. The sinusid is generally transverse. Second mesolophid rarely present. In  $M_2$  the mesolophid is never bifurcated. In  $M_3$  the mesolophid and mesoconid are absent. The metalophulid is often connected to the anteroconid, though in most cases to the anterolophulid. The posterior branch of the protoconid is nearly always long and free.

Upper molars: There is no connecting crest between mesoloph and metacone. Mesoloph in  $M^1$  and  $M^2$  generally of medium length. In  $M^1$  this mesoloph, together with a transverse crest from the mesostyl, gives the impression of a long, interrupted mesoloph. In  $M^3$  the protolophule is generally connected to the anterior border of the tooth; the mesoloph is well developed; the old entoloph is generally absent, the axioloph nearly always present (complete or incomplete). A small metacone is present.

Differential diagnosis — *P. simplex* differs from *P. philippi* Hugueney, 1971 by its

larger size. It differs from all other species of *Pseudocricetodon* by its more simple dental pattern, specially the absence of the mesolophid in  $M_3$ .

For a comparison with *P. orientalis* see the chapter on Turkish *Pseudocricetodontinae*.

#### *Pseudocricetodon simplex* from Mirambueno 4C

Material and measurements — See Tables 8 and 9, Fig. 3.

Description (for full details see Tables 1-6)

$M_1$  — The protoconid hind-arm is free (22%), or connected to the metaconid, either high (21%) or low (57%). The sinusid is generally transverse (88%). The mesolophid is often absent or short (50%), the second mesolophid is absent in more than 80% of the specimens. The ectomesolophid is present in about half the specimens. A short posterior branch of the hypoconid may be present (19%).

$M_2$  — The mesolophid is often absent or short (44%), never bifurcated. An ectomesolophid is present in more than 90% of the specimens.

$M_3$  — The metalophulid is frequently connected to the anteroconid (30%). The mesolophid is nearly always absent, ectomesolophids are present in 29% only. The entoconid is often reduced or absent, giving the molar a triangular shape.

$M^1$  — The anterocone may be more or less subdivided (38%). A backward spur on the anterocone, indicating the anterolophule is present in 30% only, the anterolophule is never complete. The anterior branch of the protocone is directed antero-labial in about half the specimens, in the other half it is directed to or in contact with the paracone. The sinus is frequently transverse (35%). The mesoloph is of medium length or long, frequently interrupted, so that its labial part forms a separate crest, originating from the mesostyl. The second mesoloph is generally absent (90%). A longitudinal connection between mesoloph and metacone is present in 1 specimen only.

$M^2$  — The lingual anteroloph is well developed, and separates the protocone from the molar border in 26% of the specimens. The sinus is transverse in most cases

#### Plate 2

##### *Pseudocricetodon simplex* from Mirambueno 4C

Fig. 1.  $M_1$  sin., MIR4C 288, holotype.

Fig. 2.  $M_2$  sin., MIR4C 327.

Fig. 3.  $M_3$  sin., MIR4C 360.

Fig. 4.  $M_3$  dext., MIR4C 387.

Fig. 5.  $M_2$  dext., MIR4C 347.

Fig. 6.  $M_1$  dext., MIR4C 305.

Fig. 7.  $M^1$  sin., MIR4C 396.

Fig. 8.  $M^2$  sin., MIR4C 433.

Fig. 9.  $M^3$  sin., MIR4C 463.

Fig. 10.  $M^3$  sin., MIR4C 484.

Fig. 11.  $M^1$  dext., MIR4C 416.

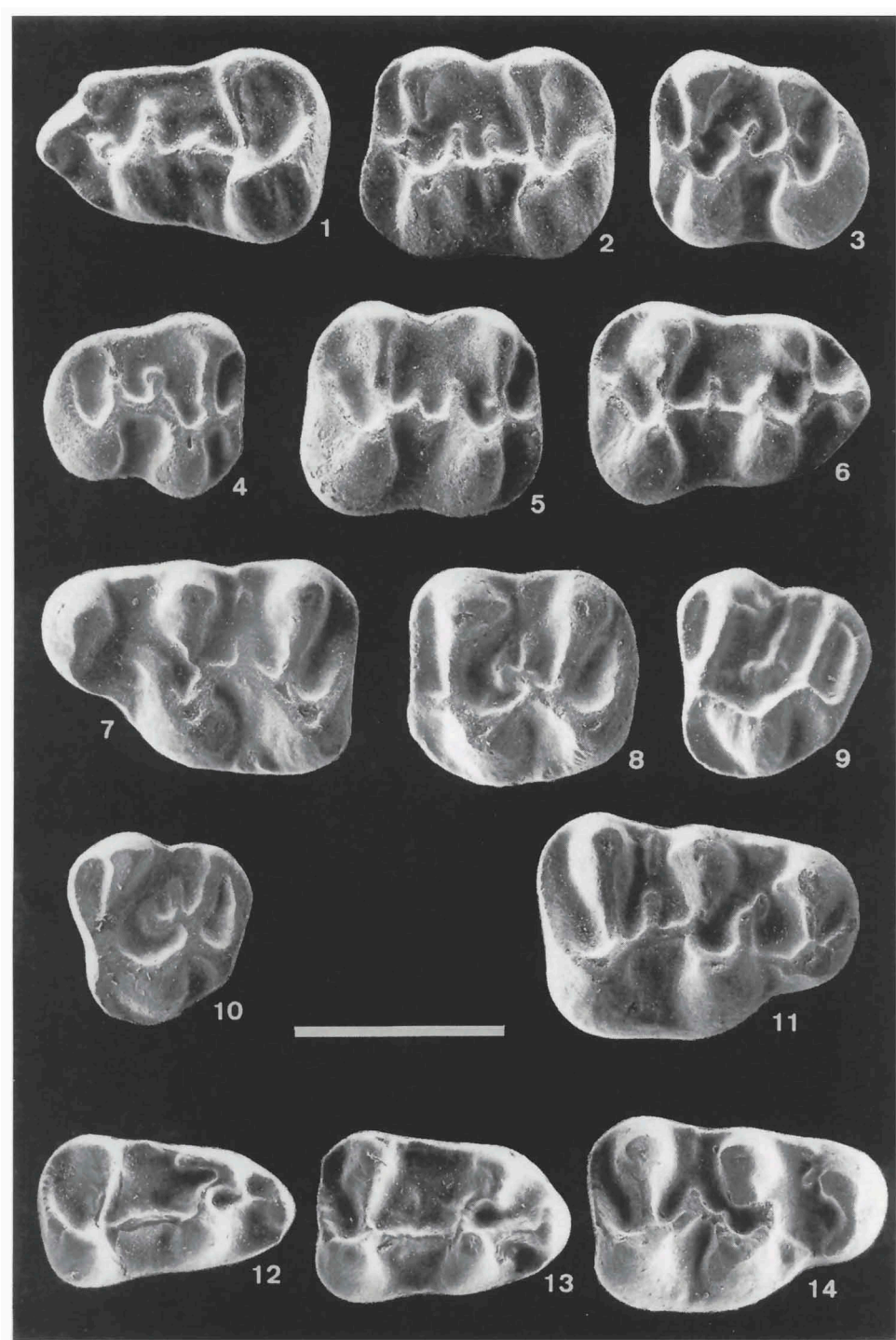
##### *Pseudocricetodon* aff. *philippi* from Mirambueno 4C

Fig. 12.  $M_1$  dext., MIR4C 318

Fig. 13.  $M_1$  dext., MIR4C 319.

Fig. 14.  $M^1$  dext., MIR4C 321.

Scale is 1 mm.



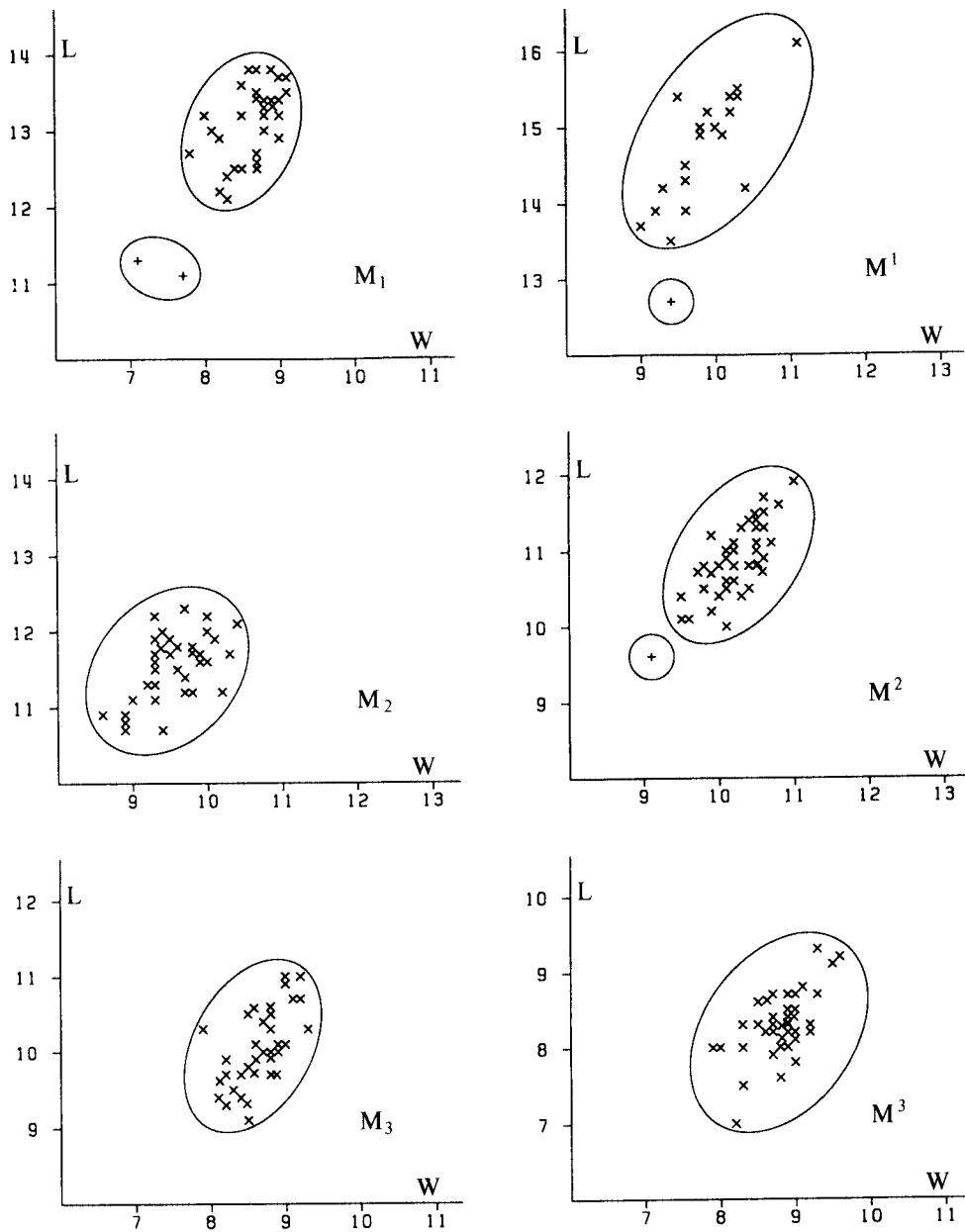


Fig. 3. Length-width diagrams of *Pseudocricetodon simplex* (x) and *P. aff. philippi* (+) from Mirambueno 4C.

(58%). The mesoloph is of medium length (76%) or short (13%), less frequently long, or long and interrupted; a second mesoloph is present in 18% only. A longitudinal connection between mesoloph and metacone is generally absent (92%). A more or less well developed connection between protocone and hypocone, through the sinus, is rarely present (8%). The hypocone is generally reduced, giving the tooth a trapezoid shape (84%).

M<sup>3</sup> — The protolophule is connected to the anterocone in 85% of the specimens. The sinus is generally small, but well developed. The mesoloph is never absent, rarely short. The old entoloph is absent in 70%. The metacone is present in 90% of the specimens.

#### *Pseudocricetodon simplex* from Mirambueno 4D

Material and measurements — See Tables 8 and 9.

Basically this population is identical to the one from Mirambueno 4C. For full details see Tables 1-6. There are some differences:

In MIR4D the anterolophulid of M<sub>1</sub> appears to be better developed. Cingulum ridges all around the molar are somewhat better developed. The protoconid hind-arm of M<sub>2</sub> is on the average longer. In M<sub>3</sub> the metalophulid is more frequently directed forward, and the sinusid is more transverse. The cingulums closing the mesosinusid and posterosinusid of M<sub>3</sub> are better developed. Ectomesolophids are less developed in M<sub>3</sub>.

The sinus of M<sup>1</sup> is more frequently transverse. In M<sup>3</sup> the protolophule is always connected to the anterocone, the mesoloph is on the average shorter, and the metacone is less reduced.

#### *Pseudocricetodon simplex* from Alcorisa

Material and measurements — See Tables 8 and 9, Fig. 4.

For full morphological details see Tables 1-6. Differences between the populations from Alcorisa noir and Mirambueno 4C are:

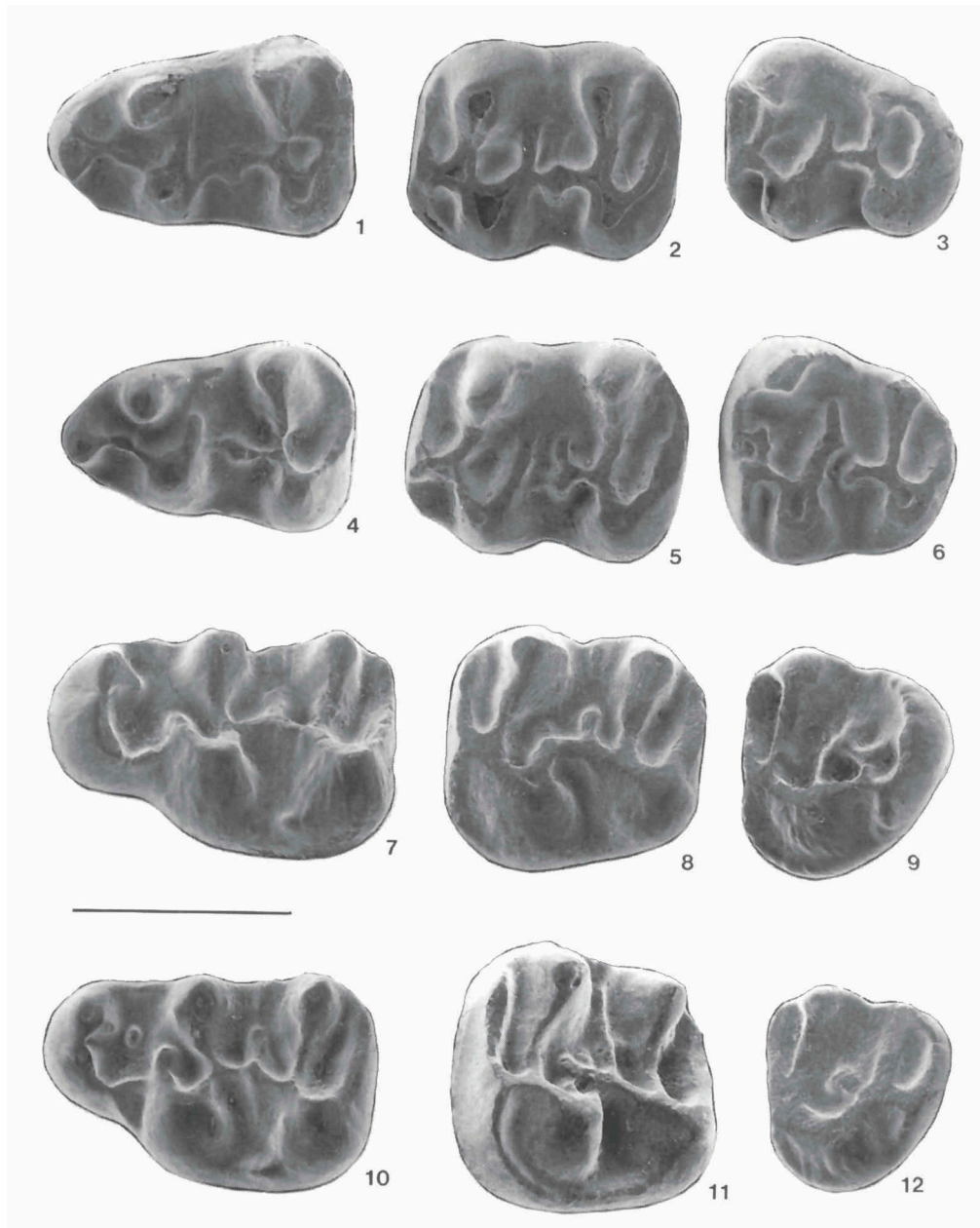
In the M<sub>1</sub> from Alcorisa the anterolophulid and the ectolophid are more frequently interrupted, and the metalophulid more frequently absent. Ectomesolophids are better developed in M<sub>1</sub>, less developed in M<sub>2</sub> and M<sub>3</sub>. The shape of M<sub>3</sub> is more frequently trapezoidal. The sinus of M<sup>2</sup> is less frequently transverse. In M<sup>3</sup> the axioloph is more frequently absent, the metacone is more reduced.

The small collection of *P. simplex* from ALCR, taken from a bed that lies only 10 cm above ALCN, shows no notable differences; perhaps the anterocone of M<sup>1</sup> is more frequently subdivided.

#### Discussion on *Pseudocricetodon simplex*

The populations from MIR4C and MIR4D are highly similar; the one from Alcorisa seems to be a little different. Nevertheless these three populations are attributed to the same species, mainly on the basis of their sharing the characteristic of a simplified dental pattern.

*P. simplex* differs from *P. montalbanensis* Thaler, 1969, *P. moguntiacus* (Bahlo, 1975),



### Plate 3

*Pseudocricetodon simplex* sp. nov. from Alcorisa (noir)

Fig. 1.  $M_1$  sin., ALC 1.

Fig. 2.  $M_2$  sin., ALC 2.

Fig. 3.  $M_3$  sin., ALC 3.

Fig. 4.  $M_1$  sin., ALC 4.

Fig. 5.  $M_2$  sin., ALC 5.

Fig. 6.  $M_3$  sin., ALC 6.

Fig. 7.  $M_1$  sin., ALC 7.

Fig. 8.  $M_2$  sin., ALC 8.

Fig. 9.  $M_3$  sin., ALC 9.

Fig. 10.  $M_1$  sin., ALC 10.

Fig. 11.  $M_2$  sin., ALC 11.

Fig. 12.  $M_3$  sin., ALC 12.

Scale is 1 mm.

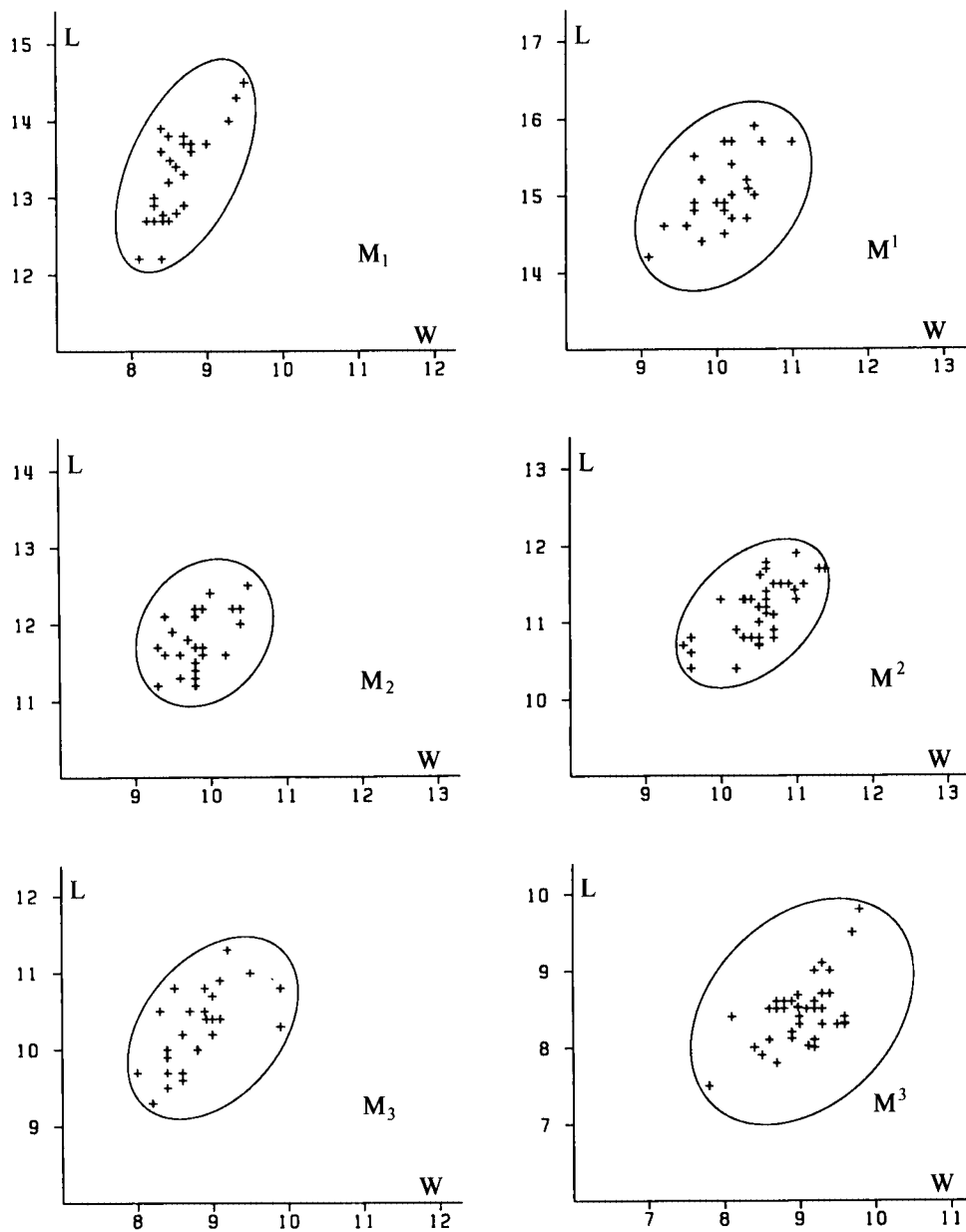


Fig. 4. Length-width diagrams of *Pseudocricetodon simplex* from Alcorisa.

and *P. adroveri* sp. nov. by: the higher anterolophulid in  $M_1$ ; the lower protoconid hind-arm in  $M_1$ ; the more transverse sinus(id)s; the less developed mesoloph(id)s, ectomesolophids, and second mesoloph(id)s; the more procumbent metalophulid in  $M_3$ , and protolophule in  $M^3$ ; the often very long, and free-ending, protoconid hind-arm in  $M_3$ ; the less concave lingual border of  $M_3$ ; the less frequent posterior spur on the anterocone of  $M^1$ ; the anterior branch of the protocone of  $M^1$ , that is more frequently directed towards the paracone; the almost complete absence of a longitudinal connection between mesoloph and metacone in  $M^1$ ; the better developed lingual anteroloph in  $M^2$ ; the better developed mesoloph in  $M^3$ .

It differs from *P. thaleri* (Hugueney, 1969) by the lesser development of accessory crests in all molars; the lesser development of second mesolophids in  $M_1$  and  $M_2$ ; the absence of the mesolophid in  $M_3$ ; the absence of a complete anterolophule in  $M^1$ .

The localities with *P. simplex* are intermediate in age between those with *P. montalbanensis* on the one hand, and those with *P. adroveri* and *P. thaleri* on the other. Whether or not *P. simplex* represents an intermediate phylogenetic step will be discussed in the chapter on Phylogeny of *Pseudocricetodon*.

*Pseudocricetodon* aff. *simplex*

In the locality of Mirambueno 4B, c. 6 m below Mirambueno 4C, we have found a small number of specimens of a *Pseudocricetodon* species. It resembles *P. simplex* from Mirambueno 4B, but in some details it seems to be closer to *P. montalbanensis*. A selection of these features is given in Table 7. Evidently the material is too poor to permit sound conclusions. However, one gets the impression, that some features are frequent in the population from Montalbán 1D, present in MIR4B, and absent in MIR4C.

Furthermore the mean values of the dimensions of this material are smaller than those of *Pseudocricetodon simplex*, and coincide more with those of *P. montalbanensis* (see Tables 8 and 9).

*Pseudocricetodon adroveri* sp. nov.

Pl. 4, figs. 1-12.

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

Holotype —  $M_1$  sin., IPS 7680,  $13.1 \times 8.5$ , figured in Hugueney et al., 1987, pl. 1, fig. 10; this publication Pl. 4, fig. 1. The figured specimens from Vivel del Río will be deposited in the Museo de Paleontología Miquel Crusafont, Sabadell.

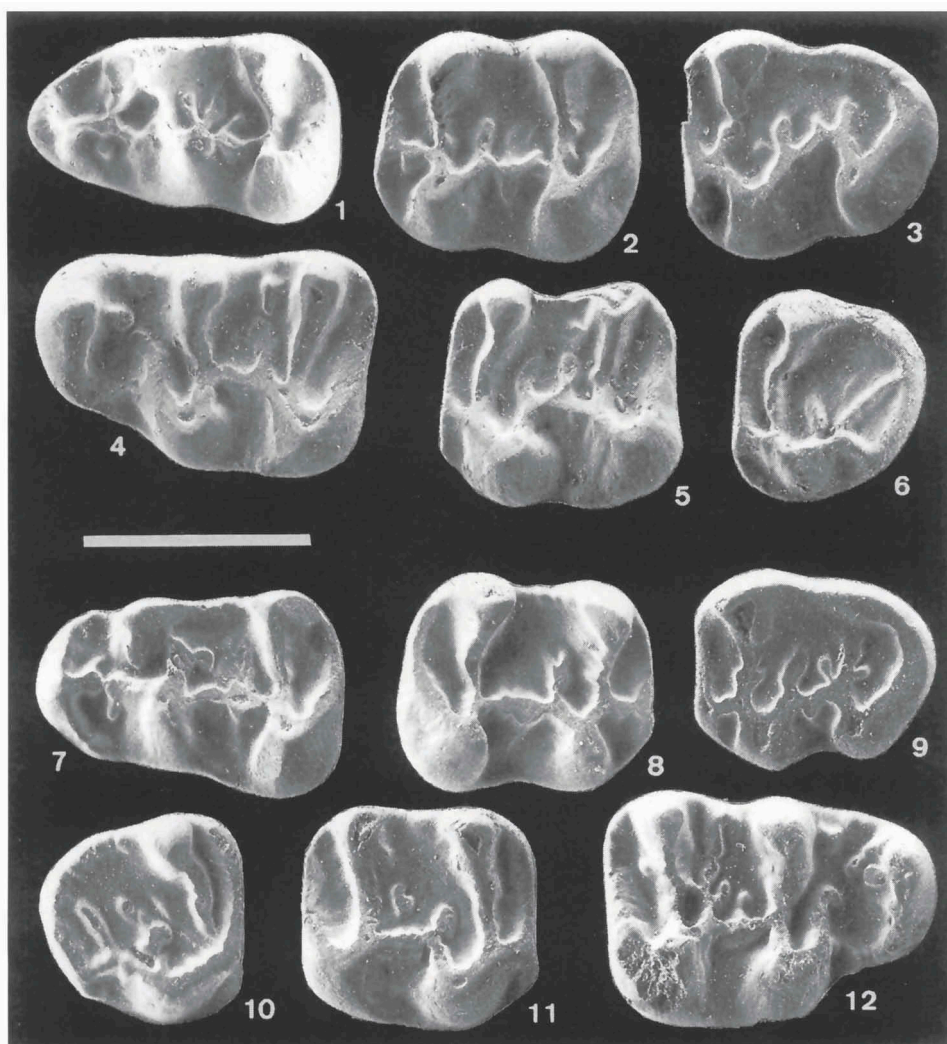
Derivatio nominis — Dedicated to Dr R. Adrover (Paterna), who excavated the type-locality and collected the larger part of the material.

Synonymy — *Pseudocricetodon* aff. *thaleri* in Hugueney et al., 1987.

Age — Late Oligocene.

Diagnosis — Lower molars: There is almost never a posterior branch of the hypoconid. In  $M_1$  the posterior branch of the protoconid is high and connected to the metaconid; mesolophid of medium length or long, less frequently short or absent. Second mesolophid often well developed. In  $M_1$  and  $M_2$  there is frequently a labial spur from the anterolophulid into the protosinusid. In  $M_3$  the mesolophid is rarely absent, the entoconid is well developed.





#### Plate 4

*Pseudocricetodon adroveri* sp. nov.

Vivel del Río

Fig. 1.  $M_1$  sin., IPS 7680, holotype.

Fig. 2.  $M_2$  sin., IPS 7681.

Fig. 3.  $M_3$  sin., IPS 7682.

Fig. 4.  $M^1$  sin., IPS 7683.

Fig. 5.  $M^2$  sin., IPS 7684.

Fig. 6.  $M^3$  sin., IPS 7685.

Scale is 1 mm.

*Pseudocricetodon adroveri* sp. nov.

Mirambueno 2A

Fig. 7.  $M_1$  sin., MIR2A 64.

Fig. 8.  $M_2$  dext., MIR2A 73.

Fig. 9.  $M_3$  sin., MIR2A 77.

Fig. 10.  $M^3$  dext., RGM 417 484.

Fig. 11.  $M^2$  dext., MIR2A 78.

Fig. 12.  $M^1$  dext., RGM 417 494.

Upper molars: Longitudinal connection between mesoloph and metacone frequently present. Anterocone of  $M^1$  simple, with a longitudinal backward spur (or even two such spurs). Dental pattern of  $M^3$  very much simplified; old entoloph present as a transverse spur on the lingual wall of the protocone; axioloph generally missing; metacone hardly ever present.

Differential diagnosis — For the difference with *P. simplex* see the differential diagnosis and the discussion of that species.

*P. adroveri* differs from *P. montalbanensis* by the better developed metalophulid in  $M_1$ ; the better developed labial spur in the protosinusid of  $M_1$  and  $M_2$ ; the more reduced entoconid in  $M_3$ , and metacone in  $M^3$ .

It differs from *P. thaleri* from Coderet by: the less developed metalophulid in  $M_1$ ; the less frequent labial spur in the protosinusid of  $M_1$  and  $M_2$ ; the never complete anterolophule in  $M^1$ , in combination with an anterior branch of the protocone, that is more frequently directed towards the paracone.

*Pseudocricetodon adroveri* sp. nov. from Vivel del Río

Material and measurements — See Tables 8 and 9, Fig. 5.

Description (for full details see Tables 1-6)

$M_1$  — There is frequently a labial spur on the anterolophulid (66%). The metalophulid is absent (11%), interrupted (48%), or complete (41%). The protoconid hind-arm is connected to the metaconid, either high (81%) or low (19%). The mesolophid is short (11%), of medium length (58%), or long (31%); it is often branched. The second mesolophid is absent (15%), short (31%), of medium length (42%), or long (12%). If we count all branches of mesolophid and second mesolophid we get the following result: one mesolophid: 2 specimens; two mesolophids: 9 specimens; three mesolophids: 12 specimens; four mesolophids: 3 specimens. The ectomesolophid is absent in two specimens only, and it is frequently double (35%).

$M_2$  — There is frequently a labial spur from the anterolophulid into the protosinusid (53%). The mesolophid is nearly always of medium length or long, frequently bifurcated. An ectomesolophid is present in 90% of the specimens.

$M_3$  — The metalophulid is connected to the anterolophulid. The protoconid hind-arm always ends free, and it is nearly always long. The mesolophid is absent in 60% of the specimens, an ectomesolophid is present in 80%. The entoconid is generally well developed, the lingual border is concave, giving the molar a trapezoid shape.

$M^1$  — The anterocone is always simple. A backward spur on the anterocone, indicating the anterolophule, is always present, but the anterolophule is never complete. In 44% of the specimens there are even two spurs on the anterocone. The anterior branch of the protocone is generally directed antero-labial, in 27% of the cases directed towards the paracone. The sinus is directed forward (62%) or strongly forward (38%), never transverse. There is nearly always a well-developed protocone platform. The mesoloph is never absent or short, frequently interrupted, so that its labial part forms a separate crest, originating from the mesostyl. The second mesoloph is often present (65%); there may be an entomesoloph (43%). A longitudinal connection between mesoloph and metacone may be present or indicated (43%).

$M^2$  — The sinus is directed forward or strongly forward in most cases (88%). The mesoloph is of medium length (46%) or long (49%), or it reaches the molar border

(6%); a second mesoloph is present in 23% of the specimens. A longitudinal connection between mesoloph and metacone is present in 61%. A connection between protocone and hypocone, through the sinus, is indicated in 16%, and complete in one specimen. The hypocone is generally not reduced, so that the tooth has a subrectangular shape (63%).

M<sup>3</sup> — The protolophule is connected to the anterocone in the majority of the specimens (67%). The sinus is generally small, and may be hardly developed or even absent. The mesoloph is of variable length, absent in 35% of the specimens. The old entoloph is absent in 10% only; the axioloph is absent in 90%. The metacone is generally absent (83%).

*Pseudocricetodon adroveri* sp. nov. from Mirambueno 2A

Material and measurements — See Tables 8 and 9, Fig. 5.

Description (for full details see Tables 1-6)

M<sub>1</sub> — There is frequently a labial spur on the anterolophulid (40%). The metalophulid is absent (17%), interrupted (50%), or complete (33%). The protoconid hind-arm is connected to the metaconid, either high (67%) or low (33%). The mesolophid is absent (17%), short (17%) of medium length (42%), or long (25%), the second mesolophid is nearly always present. The ectomesolophid is absent in one specimen only. There is never a posterior branch of the hypoconid.

M<sub>2</sub> — The labial anterolophid is frequently absent; on the other hand there is nearly always a labial spur from the anterolophulid into the protosinusid. The mesolophid is often absent or short (40%), never bifurcated. An ectomesolophid is present in 80% of the specimens.

M<sub>3</sub> — The labial anterolophid is poorly developed. The metalophulid is connected to the anterolophulid. The mesolophid is nearly always present (83%), an ectomesolophid is present in 50%. The entoconid is generally well developed, the lingual border is concave, giving the molar a trapezoid shape.

M<sup>1</sup> — A backward spur on the anterocone, indicating the anterolophule is always present, but the anterolophule is never complete. In half the specimens there are even two spurs on the anterocone. The anterior branch of the protocone is directed antero-labial, never directed to — or in contact with — the paracone. The sinus is directed forward (62%) or strongly forward (38%), never transverse. The mesoloph is of medium length or long, frequently interrupted, so that its labial part forms a separate crest, originating from the mesostyl. The second mesoloph is generally present (92%); there may be an entomesoloph (23%). A longitudinal connection between mesoloph and metacone may be present or indicated (31%).

M<sup>2</sup> — The lingual anteroloph is frequently absent or weak, and never continues around the protocone. The sinus is transverse in most cases (60%). The mesoloph is of medium length (40%) or long (50%), less frequently short (10%); a second mesoloph is present in 50% of the specimens. A longitudinal connection between mesoloph and metacone is present in 40%. A connection between protocone and hypocone, through the sinus, is never present. The hypocone is generally not reduced, so that the tooth has a subrectangular shape (80%).

M<sup>3</sup> — The protolophule is connected to the anterocone in 9 out of 10 specimens.

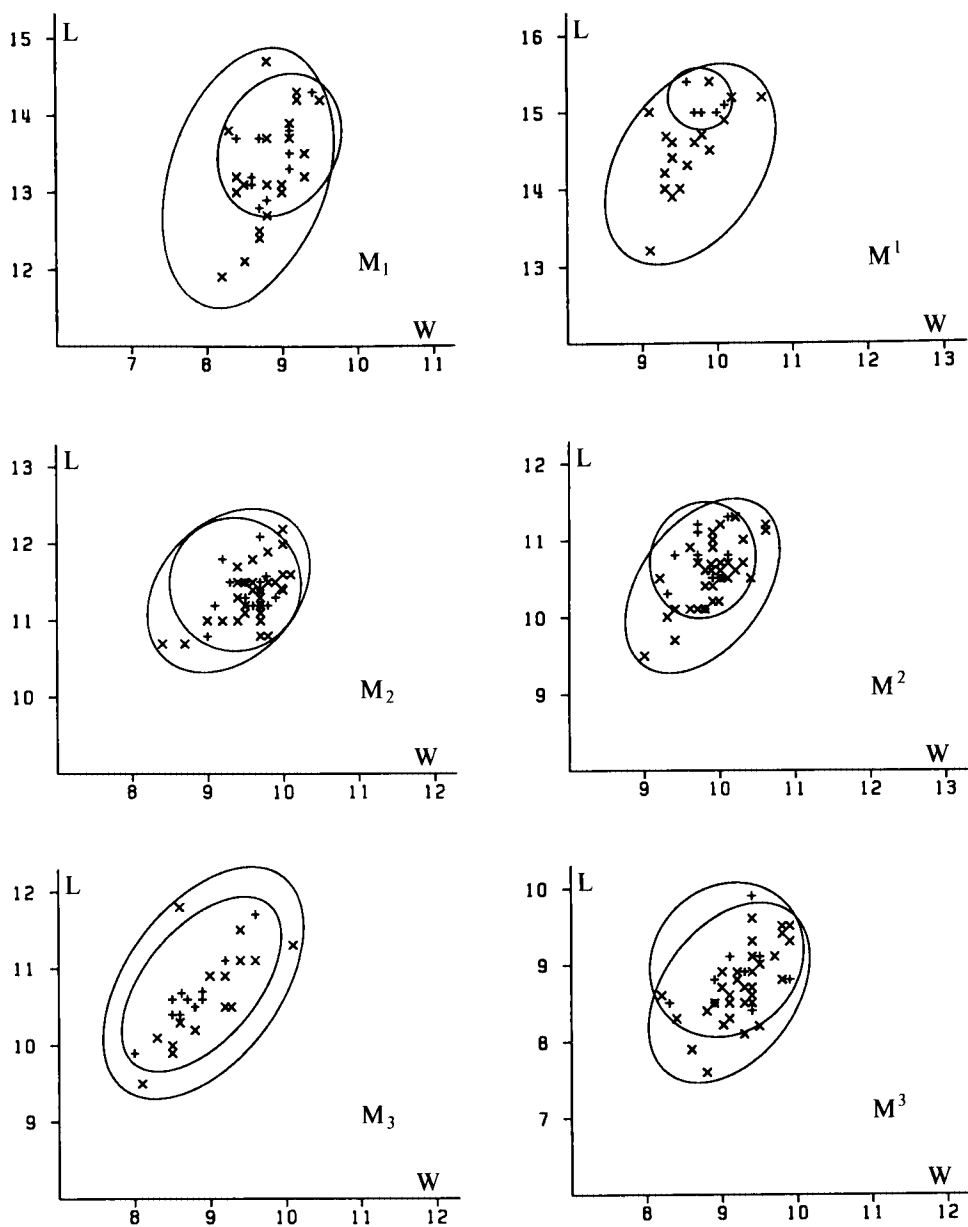


Fig. 5. Length-width diagrams of *Pseudocricetodon adroveri* from Vivel del Río (x) and Mirambueno 2A (+).

The sinus is generally small, but well developed. The mesoloph is generally short or of medium length. The old entoloph is absent in 38%; the axioloph is absent in 63%. The metacone is nearly always absent.

#### Discussion on *Pseudocricetodon adroveri*

Most of the differences between the type-population and the one from MIR2A may be explained by the small number of specimens available. Other differences may have some importance, like e.g. the shorter mesolophid of  $M_2$ , and the longer mesolophid of  $M_3$ ; the less developed ectomesolophid in  $M_3$ , and the more transverse sinus of  $M^2$ .

*P. adroveri* differs from *P. montalbanensis* by: its more reduced  $M_3$  and  $M^3$  in comparison with the  $M_1$  and  $M^1$ ; the better developed labial spur in the anterosinusid of  $M_1$  and  $M_2$ ; the better developed metalophulid in  $M_1$ ; the better developed second mesoloph(id)s, ectomesolophids and entomesolophs in  $M_1$  and  $M^1$ ; the always high ectolophid-protoconid connection in  $M_2$ ; the more complex structure of the mesolophid in  $M_2$ ; the less developed ectomesolophid in  $M_2$  and  $M_3$ ; the more reduced mesolophid and entoconid of  $M_3$ ; the well-developed protocone platform in  $M^1$ ; the less frequently subdivided sinus of  $M^2$ ; the less developed second mesoloph in  $M^2$  and  $M^3$ ; the less frequently complete old entoloph in  $M^3$ ; the hardly ever present, and never complete, axioloph in  $M^3$ ; the more reduced metacone in  $M^3$ .

Summarising we may say, that the  $M_1$  and  $M^1$  of *P. adroveri* show a more complex dental pattern than in *P. montalbanensis*, whereas the  $M_3$  and  $M^3$  are more simplified. The  $M_2$  and  $M^2$  take an intermediate position: in some features they are more complex, in others they are more simple. The dentition of both species shows a gradient of increasing complexity from  $M_3$  to  $M_1$ . In *P. adroveri* this gradient is steeper than in *P. montalbanensis*.

*P. adroveri* differs from *P. thaleri* from Coderet by: its on the average smaller size; the less developed metalophulid in  $M_1$ ; the less frequent labial spur in the protosinusid of  $M_1$  and  $M_2$ ; the less developed second mesolophid in  $M_1$ ; the less developed ectomesolophids in  $M_1$  and  $M_2$ ; the less reduced entoconid in  $M_3$ ; the always simple anterocone of  $M^1$ ; the never complete anterolophule in  $M^1$ ; in combination with an anterior branch of the protocone, that is more frequently directed towards the paracone; the less developed forward spur on the paracone of  $M^1$ ; the less developed posterior protolophule in  $M^2$ ; the less developed second mesoloph in  $M^2$ .

In our opinion most of the differences between *P. montalbanensis*, *P. adroveri*, and *P. thaleri* indicate, that *P. montalbanensis* has the most primitive dental pattern, and that *P. thaleri* is most evolved. *P. adroveri* has a morphologically intermediate position.

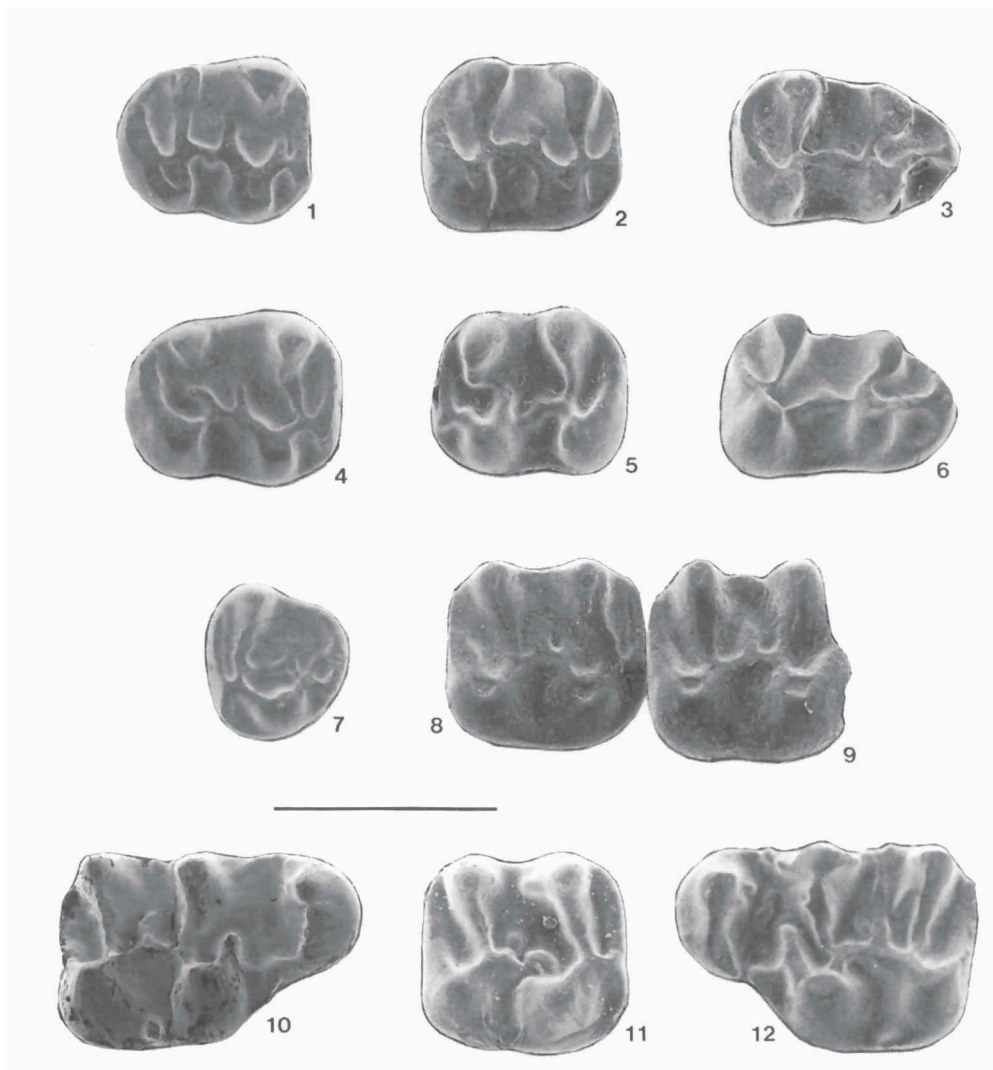
*Pseudocricetodon philippi* Hugueney, 1971

Plate 5, figs. 1-12.

Type-locality — St Martin-de-Castillon (Vaucluse, France).

Holotype —  $M_1$  dext., FSL 97377, Département des Sciences de la Terre, Université Claude Bernard, Lyon (Plate 5, fig. 3).

N.B. The specimens figured on Pl. 5, figs. 1-3 and 7-9 were also figured in



### Plate 5

*Pseudocricetodon philippi* from St Martin-de-Castillon

Fig. 1.  $M_3$  dext., FSL 97381, level C.

Fig. 2.  $M_2$  dext., FSL 97382, level C.

Fig. 3.  $M_1$  dext., FSL 97377, level C, holotype.

Fig. 4.  $M_3$  dext., FSL 97828, level D.

Fig. 5.  $M_2$  sin., FSL 97829, level C.

Fig. 6.  $M_1$  dext., FSL 97827, level D.

Fig. 7.  $M^3$  sin., FSL 97378, level B.

N.B. FSL 97379 and 97380 may belong to the same individual.

Fig. 8.  $M^2$  dext., FSL 97379, level C.

Fig. 9.  $M^1$  dext., FSL 97380, level C.

Fig. 10.  $M^1$  dext., FSL 97825, level C.

Fig. 11.  $M^2$  dext., FSL 97826, level C.

Fig. 12.  $M^1$  sin., FSL 97830, level A.

Scale is 1 mm.

Huguene, 1971, figs. 1-6.

Apart from St Martin-de-Castillon a very small *Pseudocricetodon* has been cited from quite a number of localities: Heimersheim, Balm, Les Chapelins, Gabsheim (Bahlo, 1975, 1976), St Henri (Brunet et al., 1981), Pech-du-Fraysse, Pech Desse (Comte, 1985), Terrenoire (Ducreux et al., 1985), Coulou, Mas-de-Pauffié (Rémy et al., 1987), Kavakdere, Pasaköy, Kocayarma (Ünay-Bayraktar, 1989).

All these populations are poor in specimens. Since new material is available from St Martin-de-Castillon we will pay some attention to this locality.

Six different sites have been sampled at St Martin-de-Castillon. One of these (level C) is the richest, and is the type-locality of *P. philippi*. Level D is more or less equivalent to level C, level E is older, and level 6 is younger. The following description is mainly based on the material from level C.

M<sub>1</sub> — The lingual anterolophid is interrupted or absent; the labial anterolophid is always long. The anterolophulid is always present, generally low. The anterosinusid is wide. The metalophulid is predominantly absent, sometimes anteriorly interrupted, complete in one case only. The protoconid hind-arm is high, either transverse or curved, absent in one specimen. The sinusid is open or closed, always transverse. The mesosinusid is always closed by a crest descending from the metaconid. The ectolophid is longitudinal, sometimes interrupted. The mesoconid is absent or weakly developed. The mesolophid is absent in half the specimens, short or of medium length in the other ones. There is never a second mesolophid. The ectomesolophid is absent or weakly developed. The hypolophulid is anteriorly transverse. There is never a posterior branch of the hypoconid. The posterosinusid is open or closed. The labial posterolophid is weakly developed.

M<sub>2</sub> — The labial anterolophid reaches the protoconid. The anterolophulid is complete except for one specimen. The metalophulid is connected to the anterolophulid, interrupted in one case. The metalophulid spur is absent or weak. The protoconid hind-arm is short, either free, or transversely directed towards the base of the metaconid. The sinusid is generally open, sometimes closed by a weak crest; it is either transverse or directed obliquely backward. The mesosinusid is open or closed. The ectolophid is high, interrupted in 3 cases. The mesoconid is nearly always absent. The mesolophid is simple, generally short, or even absent. The ectomesolophid is present in 2/3 of the specimens, rather strongly developed in 1/3. The hypolophulid is directed somewhat obliquely forward. There is never a posterior branch of the hypoconid. The posterosinusid is open or closed. The labial posterolophid is weakly developed in half the cases. The posterior part of the tooth is generally the broadest.

M<sub>3</sub> — The labial anterolophid always reaches the protoconid. The anterolophulid is long. The anterosinusid is nearly always wide. The metalophulid is directed forward, interrupted in more than half the specimens. The metalophulid spur is absent in most cases. The protoconid hind-arm is very variable, from short, low and free to curved and high. The sinusid is nearly always open, broad, transverse or somewhat oblique backward. The mesosinusid is closed, the mesolophid always absent. The ectolophid is complete, the mesoconid nearly always absent. In half the specimens there is a weak ectomesolophid. The entoconid is always well developed. The hypolophulid is anterior, transverse or slightly oblique. The posterosinusid is open, or half-closed. The shape of the tooth is trapezoid.

M<sup>1</sup> — The anterocone is always simple in level C; in one specimen from level E it is split. The prelobe is broad, continuous or set-off. The anterocone generally presents a short posterior crest, directed towards the anterior branch of the protocone, and in one case the anterolophule is complete. The paracone rarely shows an anterior spur. The lingual anteroloph ends in a protostyl. The protocone platform is generally weak. The anterosinus is closed, and in most cases there is a small anterostyl. The protolophule is posterior; in one specimen from level E there is an anterior connection. The sinus is open, or there is a small entostyl; it is slightly directed forward in the specimens from level C, sometimes subdivided in specimens from other levels. The entoloph is high. The mesosinus is closed by a small crest, and there may be a mesostyl. In one case the mesostyl sends a crest into the mesosinus. The mesoloph is of medium length. There is no second mesoloph nor an entomesoloph. Only one specimen presents a connection between mesoloph and metacone. The metalophule is always anterior, the posterosinus is open, and the labial border is straight.

M<sup>2</sup> — The lingual anteroloph is moderately or strongly developed. The protolophule is anterior with a trace of a posterior connection. The sinus is open or closed, with or without entostyl, weakly directed forward. The closure of the mesosinus is variable; there may be a mesostyl. The mesoloph is short (2), of medium length (8), or long (1). The second mesoloph is absent in all but one specimen. The mesoloph-metacone connection is absent except for one specimen from level E. The entoloph-protocone connection is generally high, sometimes interrupted. One specimen from level E shows a weak protocone-hypocone connection through the sinus. The metalophule is anterior, the posterosinus open. The labial border is more or less concave, the shape of the tooth is subrectangular, or slightly trapezoid.

M<sup>3</sup> — (not represented in level C) The lingual anteroloph is well developed. The protolophule is connected to the anterolophule, tending to be double in one case. The sinus is small, the neo-entoloph high. The mesosinus is closed. The mesoloph is of medium length. There is no second mesoloph. The old entoloph is absent or present. There may be a trace of an axioloph. There is no centrocone, the metacone is small, the posterosinus closed.

Discussion — The following features may be considered to be significant: In M<sub>1</sub> the connections between the main cusps are transverse, the ectolophid is longitudinal and the sinusid is transverse. The mesolophid is absent or short; its position is often marked by a weak mesoconid. Accessory crests (2nd mesolophid, hypoconid branch, etc.) are absent, except for a weak ectomesolophid that is sometimes present. The posterior part of M<sub>3</sub> is little reduced; there is no mesolophid. The dental pattern of M<sup>1</sup> is very simple; the protolophule is posterior. The M<sup>3</sup> is reduced posteriorly, but the main features remain clearly visible.

*Pseudocricetodon* aff. *philippi* Hugueney, 1971

Pl. 2, figs. 12-14.

Locality — Mirambueno 4C.

Material and measurements — See Tables 8 and 9, Fig. 3.

The M<sub>1</sub> are characterised by a very simple dental pattern, specially by a broad mesosinusid, without mesolophid. The protoconid hind-arm is high, and connected



to the metaconid. In one specimen the metalophulid is connected to the anteroconid, and the anterior branch of the protoconid meets this crest, but is subordinate to it; in the other specimen the metalophulid is interrupted. One specimen is very slender, the other one rather plump.

The  $M^1$  are characterised by the absence of the posterior protolophule, the anterior one being complete in one specimen, and indicated in the other one. The sinus is slightly directed forward; the mesoloph is of medium length.

In the  $M^2$  the protolophule is double; the mesoloph reaches the border of the molar, but it is interrupted halfway.

Discussion — This material is attributed to *P. aff. philippi* on the basis of its size; the specimens are smaller than those of *P. simplex* from the same locality (see Fig. 3); they are larger than those of *P. philippi* from St Martin-de-Castillon (Hugueney, 1971), Heimersheim (Bahlo, 1975), and from various Turkish localities (Ünay-Bayraktar, 1989).

In  $M_1$  the metalophulid appears to be better developed, and more forward directed than in the type-population.

The 'primitive' anterior position of the protolophule of  $M^1$  is not known in the type-population of *P. philippi*. It is found, however, in one specimen from St Martin level E, in one or two specimens from Heimersheim, and in one of the two Turkish specimens. The prelobe may be more complicated than in the type-population.

*Pseudocricetodon philippi* is the smallest *Pseudocricetodon* known. Some specimens from St Martin-de-Castillon are rather large and their dental pattern is more complicated (Pl. 5, fig. 12); their attribution to *P. philippi* is not certain.

Brunet et al. (1981) describe *P. philippi* from St Henri (Bouches-du-Rhône, France). These specimens are slightly larger than the type-material, and the dental pattern is very simple.

Comte (1985) mentions seven specimens from Pech-du-Fraysse (Quercy, France) and three teeth from Pech Desse (Quercy, France), larger than the type-material, and with a simpler dental pattern.

Ducreux et al. (1985) mention six teeth from Terrenoire (Alpes-de-Haute-Provence, France), a locality situated in the same basin as St Martin-de-Castillon, and stratigraphically younger. They are slightly larger than the type-material and a little more complicated.

All these populations are poor in specimens, which makes it impossible to assess their relationships, the more so since they seem to present a mixture of primitive and derived characters. One gets the impression, however, that the material attributed to *P. philippi* represents at least two different lineages.

#### *Pseudocricetodontinae* from Turkish Thrace

Ünay-Bayraktar (1989) described a number of *Pseudocricetodontinae* from Turkish Thrace: *Pseudocricetodon moguntiacus orientalis* Ünay-Bayraktar, 1989; *Pseudocricetodon philippi* Hugueney, 1971; *Pseudocricetodon (Lignitella) suemengeni* Ünay-Bayraktar, 1989; *Kerosinia variabilis* Ünay-Bayraktar, 1989.

*Pseudocricetodon (Lignitella) suemengeni* Ünay-Bayraktar, 1989 — In our opinion *Lignitella* should be regarded as a separate genus, distinguished from *Pseudocricetodon* by its sharp, blade-shaped crests and crescentiform, reduced lingual cusps. The anterior

slope of the anterocone of  $M^1$  is very steep. In spite of the excellent quality of the SEM photographs published by Ünay-Bayraktar, these features are not easily recognised. However, the casts of *L. suemengeni*, generously provided by Dr H. de Bruijn (Utrecht), leave no doubt about the differences between *Pseudocricetodon* and *Lignitella*.

The transverse sinus of  $M^1$  and  $M^2$  is frequent in *P. simplex*, and occurs in *P. montalbanensis*, *P. moguntiacus*, and *P. adroveri*; it should not be considered as a distinctive feature of the genus *Lignitella*. *Pseudocricetodon* (*Lignitella*) *suemengeni* Ünay-Bayraktar, 1989 is the type species of the genus *Lignitella*.

*Pseudocricetodon philippi* Hugueney, 1971 — This species is poorly known. All known populations are poor in specimens. Whether they represent one or more species cannot yet be decided. However, the Turkish material is characterised by sharp crests and reduced cusps, and certainly does not belong to *P. philippi*. It may well belong to *Lignitella suemengeni* Ünay-Bayraktar, 1989, since the size differences between these two species are not evident.

*Pseudocricetodon moguntiacus orientalis* Ünay-Bayraktar, 1989 — In view of the doubtful homogeneity of the type-population of *P. moguntiacus*, and the clear morphological identity of the population from Kocayarma, we will treat it as a separate species, and not as a subspecies of *P. moguntiacus*. Some of the most characteristic features of this species are the very sharp and thin crests, and the reduced volume of the cusps, in comparison with W. European forms. It shares the shape of crests and cusps with *Lignitella suemengeni*, and should probably be transferred to the genus *Lignitella*. In other respects the dental pattern of this species appears to be quite close to *P. montalbanensis* and *P. adroveri* sp. nov.

*Kerosinia variabilis* Ünay-Bayraktar, 1989 — Freudenthal et al. (1992) supposed, that *Kerosinia* might be a junior synonym of *Pseudocricetodon*. An important difference between *K. variabilis* and *L. orientalis* from the same locality (whose size distributions overlap largely) is the metalophulid of  $M_3$ . In *K. variabilis* there is hardly ever an anterior metalophulid; the connection between protoconid and metaconid is realised through the posterior branch of the protoconid. In all *Pseudocricetodon* species, as well as in *L. suemengeni*, the metalophulid is anterior, and the posterior branch of the protoconid is long, and ending free. This may be sufficient reason to maintain *Kerosinia* as a separate genus.

Ünay-Bayraktar (1989) places *Kerosinia* in the subfamily Adelomyarioninae. Freudenthal et al. (1992) placed it in the Pseudocricetodontinae. We have not been able to study original material of *Kerosinia*; its position remains — for the moment — unresolved.

### Phylogeny of *Pseudocricetodon* (Fig. 6)

The sections of Montalbán and Mirambueno, with their large number of superposed fossiliferous levels permit to follow the history of *Pseudocricetodon* step by step:

In the oldest levels of Montalbán (MLB3X, MLB3Y) *Pseudocricetodon* is absent.

Freudenthal et al. (1992) described a *Pseudocricetodon* sp. nov. from Montalbán 3C, that represents the oldest occurrence of the genus known so far. The five available teeth show a complex morphology, that excludes the possibility of its being the ancestor of *P. montalbanensis* Thaler, 1969.

The next younger representative of the genus is *P. montalbanensis* from the classical

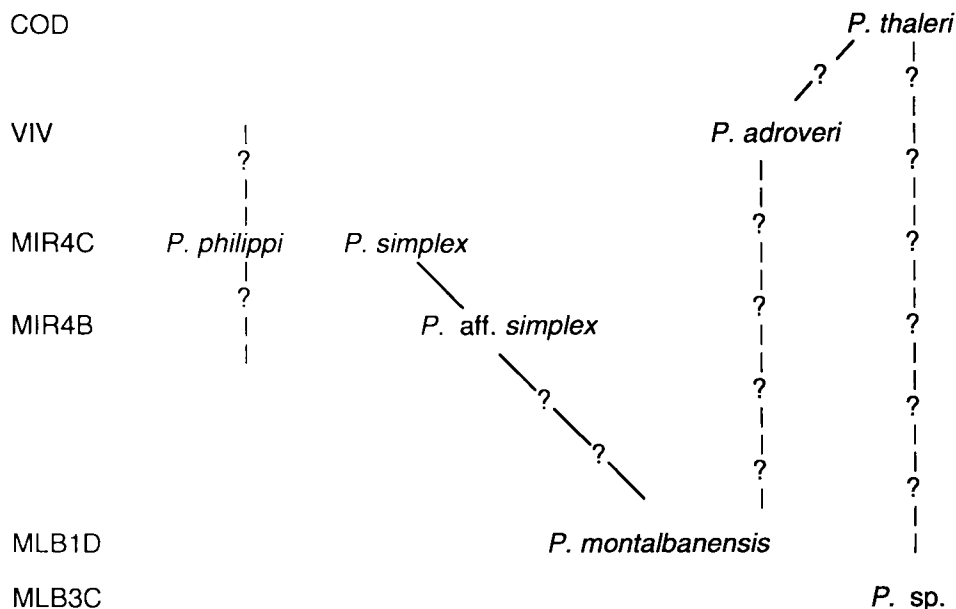


Fig. 6. Possible phylogenetic relationships within the genus *Pseudocricetodon*.

locality of Montalbán (Montalbán 1D; see Freudenthal et al., 1990). This species has a simpler dental pattern than the form from Montalbán 3C, with a number of characters that are considered plesiomorphic. Various authors have considered it to be the ancestor of *P. thaleri* Hugueney, 1969. In view of the geographic vicinity and morphological similarity we think *P. montalbanensis* may be considered to be the ancestor of *P. adroveri* sp. nov. Whether or not this lineage continues towards *P. thaleri* remains to be decided.

On the other hand, on the basis of its stratigraphic position, *P. montalbanensis* may be the ancestor of *P. simplex* sp. nov. The evolution in this hypothetical lineage would be marked by: general simplification of the dental pattern; loss of the backward spur on the anterocone of  $M^1$ ; loss of longitudinal connections between mesoloph and metalophule in the upper molars; reduction of the mesolophid in  $M_1$  and  $M_2$ ; loss of the mesolophid in  $M_3$ .

$M_1$  and  $M_2$  of *P. simplex* are on the average longer than in *P. montalbanensis*, and equal in width; the  $M_3$  are both shorter and narrower than in *P. montalbanensis*. So, if these two species are steps in an evolutionary lineage, *P. simplex* is characterised by a slight size increase, and a relative and absolute reduction of  $M_3$  and  $M^3$ . The size ranges do, however, largely overlap.

An alternative to this interpretation is presented by the small population of *P. aff. simplex* from Mirambueno 4B. This locality is stratigraphically intermediate between Montalbán 1D and Mirambueno 4C (much closer to Mirambueno 4C than to Montalbán 1D). Morphologically the material may be intermediate between *P. montalbanensis* and *P. simplex*, and on this basis a lineage *P. montalbanensis* — *P. aff. simplex* — *P. simplex* seems logical. However, the dimensions of all dental elements of the material from Mirambueno 4B are on the average smaller than those of both *P. montalbanensis*

*nensis* and *P. simplex*. If the above mentioned lineage were true, one would expect the dimensions in the MIR4B population to be intermediate between *P. montalbanensis* and *P. simplex*. Since this is not the case, it is possible that *P. aff. simplex* is the ancestor of *P. simplex*, and that *P. montalbanensis* represents another lineage. The material from Mirambueno 4B is not yet sufficient to come to a sound conclusion. We hope to collect a good sample in the near future.

*P. simplex* is present in Mirambueno 4C and in the next higher level, Mirambueno 4D. It is also found in Alcorisa, but we don't know the exact stratigraphic position of Alcorisa with respect to the Mirambueno localities.

In our next level, Mirambueno 1, *Pseudocricetodon* is practically absent. Then, in Mirambueno 2A, the genus reappears again, represented by *P. adroveri*, a species that is found also in our youngest locality, Vivel del Río, where it was described as *P. aff. thaleri* by Hugueney et al. (1987). It is characterised by a complicated dental pattern. Its ancestor may be either *P. montalbanensis* or *Pseudocricetodon* sp. from Montalbán 3C. *P. thaleri* from Coderet may be related to it.

Apart from these species, that are roughly of the same size, we attribute one more form to the genus *Pseudocricetodon*: *P. philippi* Hugueney, 1971. This species is considerably smaller than all other species of *Pseudocricetodon*. Its morphology is extremely simple. We are not able to say anything about its phylogenetic relationships. Among the material attributed to this species are several populations, that are at the upper size limit of the type-population, or even slightly larger. Their morphology is either more complicated than in the type-population or more simple. The scarcity of the material hampers a decision about the taxonomic identity and relationships of these populations. It seems probable that there exist two lineages of very small *Pseudocricetodon*.

The material described by Ünay-Bayraktar (1989) from Turkish Thrace (*P. moguntiacus orientalis*, *P. philippi*, and *P. (Lignitella) suemengeni*), in our opinion, does not belong to *Pseudocricetodon*. *Lignitella* is a separate genus, comprising two species: *L. suemengeni* and *L. orientalis*. The material described by Ünay-Bayraktar as *P. philippi* belongs to *Lignitella suemengeni*. *Lignitella* represents the Turkish branch of the *Pseudocricetodontinae*.

## Conclusions

The two new species of *Pseudocricetodon* described in this paper extend our knowledge of the genus considerably. They prove, that there are at least four different lineages:

*P. philippi*, the smallest species known, without any evident relationship with the other species.

*Pseudocricetodon* sp. from Montalbán 3C, the oldest known representative, with a highly complicated dental pattern.

*P. simplex*, with a rather simple dental pattern.

*P. adroveri*, with a rather complicated dental pattern. *P. thaleri* may belong to the *adroveri*-lineage.

*P. montalbanensis* may be the ancestor of either *P. simplex* or *P. adroveri*, or of both. *Pseudocricetodon* sp. from Montalbán 3C may be the ancestor of *P. adroveri* and/or *P. thaleri*.

The Turkish *Pseudocricetodontinae* do not belong to the genus *Pseudocricetodon*.

### **Acknowledgements**

The field work in the Mirambueno section was carried out in collaboration with Angelines Sacristán, Javier Martínez, Elvira Martín, and Gloria Cuenca to whom we are greatly indebted.

We are grateful to Joaquin Navarro, and to the mayor of Martín del Río, Francisco Javier Altava, for their help.

This study was financially supported by the National Museum of Natural History, Leiden, the Netherlands, by the 'Diputación General de Aragón', and by a grant of the 'Junta de Andalucía' to the first author.

Table 1. Character states of  $M_1$ .

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 ling. anterolophid	73		37		31		12		25		11		26	
2 absent	11	15.1	17	45.9	11	35.5	1	8.3	8	32.0	0	0.0	0	0.0
3 low	21	28.8	2	5.4	9	29.0	10	83.3	13	52.0	2	18.2	12	46.2
4 interrupted	23	31.5	10	27.0	8	25.8	1	8.3	4	16.0	9	81.8	14	53.8
5 high	18	24.7	8	21.6	3	9.7	0	0.0	0	0.0	0	0.0	0	0.0
2 lab. anterolophid	74		38		31		11		24		11		26	
2 absent	1	1.4	2	5.3	5	16.1	0	0.0	2	8.3	0	0.0	0	0.0
3 short	11	14.9	15	39.5	0	0.0	0	0.0	5	20.8	1	9.1	1	3.8
4 long	50	67.6	18	47.4	25	80.6	8	72.7	12	50.0	10	90.9	14	53.8
5 complete	12	16.2	3	7.9	1	3.2	3	27.3	5	20.8	0	0.0	11	42.3
3 anterolophulid	71		39		33		11		24		11		27	
2 absent	0	0.0	2	5.1	1	3.0	0	0.0	0	0.0	0	0.0	0	0.0
3 interrupted	10	14.1	0	0.0	1	3.0	1	9.1	8	33.3	0	0.0	0	0.0
4 low	42	59.2	1	2.6	11	33.3	1	9.1	6	25.0	5	45.5	23	85.2
5 complete	19	26.8	36	92.3	20	60.6	9	81.8	10	41.7	6	54.5	4	14.8
4 anterosinusid	75		37		33		12		27		11		27	
2 narrow	20	26.7	10	27.0	5	15.2	1	8.3	5	18.5	0	0.0	2	7.4
3 wide	55	73.3	27	73.0	28	84.8	11	91.7	22	81.5	11	100.0	25	92.6
5 metalophulid	76		40		33		14		26		12		27	
2 absent	42	55.3	16	40.0	9	27.3	6	42.9	16	61.5	2	16.7	3	11.1
3 anterior interrupted	23	30.3	12	30.0	8	24.2	2	14.3	5	19.2	6	50.0	13	48.1
4 anterior complete	11	14.5	10	25.0	11	33.3	6	42.9	2	7.7	4	33.3	11	40.7
5 to anteroconid	0	0.0	2	5.0	5	15.2	0	0.0	3	11.5	0	0.0	0	0.0
6 pcd hind arm	76		38		34		13		26		12		27	
3 short free	4	5.3	3	7.9	5	14.7	1	7.7	5	19.2	0	0.0	0	0.0
4 trans to mcd low	5	6.6	12	31.6	14	41.2	8	61.5	7	26.9	0	0.0	4	14.8
5 trans to mcd high	56	73.7	10	26.3	5	14.7	1	7.7	8	30.8	8	66.7	19	70.4
6 long free	1	1.3	3	7.9	3	8.8	2	15.4	3	11.5	0	0.0	0	0.0
7 bent to mcd low	4	5.3	5	13.2	5	14.7	1	7.7	3	11.5	2	16.7	1	3.7
8 bent to mcd high	6	7.9	5	13.2	2	5.9	0	0.0	0	0.0	2	16.7	3	11.1
7 sinusid	76		38		33		13		26		10		27	
2 open	59	77.6	28	73.7	24	72.7	4	30.8	5	19.2	7	70.0	7	25.9
3 closed	8	10.5	4	10.5	4	12.1	9	69.2	18	69.2	3	30.0	19	70.4
4 ectostylid	9	11.8	6	15.8	5	15.2	0	0.0	3	11.5	0	0.0	1	3.7
8 sinusid	76		40		34		14		24		12		25	
3 transverse	34	44.7	12	30.0	30	88.2	13	92.9	20	83.3	6	50.0	12	48.0
4 backwards	42	55.3	28	70.0	4	11.8	1	7.1	4	16.7	6	50.0	13	52.0
9 mesosinusid	77		36		30		12		27		11		23	
2 open	0	0.0	0	0.0	3	10.0	1	8.3	0	0.0	0	0.0	0	0.0
3 closed	0	0.0	1	2.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 mcd ridge open	69	89.6	31	86.1	16	53.3	8	66.7	18	66.7	2	18.2	16	69.6
5 mcd ridge closed	8	10.4	4	11.1	11	36.7	3	25.0	9	33.3	9	81.8	7	30.4

Table 1. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
10 ectolophid	77		40		34		14		25		12		25	
2 longitudinal	66	85.7	38	95.0	33	97.1	13	92.9	19	76.0	12	100.0	24	96.0
3 oblique	2	2.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 curved	2	2.6	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
5 interrupted	7	9.1	1	2.5	1	2.9	1	7.1	6	24.0	0	0.0	1	4.0
11 mesoconid	76		39		33		14		22		12		25	
2 absent	44	57.9	21	53.8	22	66.7	8	57.1	7	31.8	9	75.0	21	84.0
3 weak	17	22.4	14	35.9	8	24.2	4	28.6	5	22.7	3	25.0	3	12.0
4 strong	15	19.7	4	10.3	3	9.1	2	14.3	10	45.5	0	0.0	1	4.0
12 mesolophid	77		39		34		14		24		12		26	
2 absent	6	7.8	0	0.0	7	20.6	3	21.4	6	25.0	2	16.7	0	0.0
3 short	9	11.7	11	28.2	10	29.4	8	57.1	8	33.3	2	16.7	3	11.5
4 medium	52	67.5	27	69.2	15	44.1	3	21.4	10	41.7	5	41.7	15	57.7
5 long	10	13.0	1	2.6	2	5.9	0	0.0	0	0.0	3	25.0	8	30.8
13 2nd mesolophid	77		39		34		13		25		12		26	
2 absent	37	48.1	14	35.9	28	82.4	11	84.6	25	100.0	1	8.3	4	15.4
3 short	12	15.6	12	30.8	4	11.8	2	15.4	0	0.0	2	16.7	8	30.8
4 medium	26	33.8	13	33.3	2	5.9	0	0.0	0	0.0	9	75.0	11	42.3
5 long	2	2.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	11.5
14 ectomesolophid	75		39		32		13		24		12		26	
2 absent	18	24.0	14	35.9	15	46.9	6	46.2	4	16.7	1	8.3	2	7.7
3 weak	18	24.0	10	25.6	10	31.3	6	46.2	6	25.0	4	33.3	10	38.5
4 strong	37	49.3	15	38.5	5	15.6	1	7.7	14	58.3	6	50.0	5	19.2
5 double	2	2.7	0	0.0	2	6.3	0	0.0	0	0.0	1	8.3	9	34.6
15 hypolophulid	76		40		34		14		25		12		25	
2 anterior oblique	4	5.3	4	10.0	2	5.9	0	0.0	1	4.0	3	25.0	2	8.0
3 anterior transverse	66	86.8	34	85.0	31	91.2	13	92.9	24	96.0	8	66.7	21	84.0
4 transverse	5	6.6	2	5.0	1	2.9	1	7.1	0	0.0	1	8.3	2	8.0
5 backwards	1	1.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
16 hypoconid branch	77		39		32		14		24		12		24	
2 absent	75	97.4	37	94.9	26	81.3	12	85.7	14	58.3	12	100.0	21	87.5
3 short	0	0.0	2	5.1	6	18.8	2	14.3	7	29.2	0	0.0	2	8.3
4 long	0	0.0	0	0.0	0	0.0	0	0.0	1	4.2	0	0.0	0	0.0
5 long connected	2	2.6	0	0.0	0	0.0	0	0.0	2	8.3	0	0.0	1	4.2
17 posterosinusid	76		38		31		11		26		11		23	
2 open	0	0.0	2	5.3	2	6.5	0	0.0	1	3.8	0	0.0	1	4.3
3 closed	76	100.0	36	94.7	29	93.5	11	100.0	25	96.2	11	100.0	22	95.7
18 lab. posterolophid	77		37		33		14		22		12		25	
2 absent	56	72.7	26	70.3	32	97.0	13	92.9	22	100.0	12	100.0	20	80.0
3 small	21	27.3	9	24.3	1	3.0	1	7.1	0	0.0	0	0.0	4	16.0
4 strong	0	0.0	2	5.4	0	0.0	0	0.0	0	0.0	0	0.0	1	4.0

Table 2. Character states of  $M_2$ 

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 lab. anterolophid	84		39		35		15		23		13		29	
2 absent	6	7.1	0	0.0	0	0.0	0	0.0	0	0.0	7	53.8	3	10.3
3 short	55	65.5	13	33.3	13	37.1	4	26.7	5	21.7	5	38.5	14	48.3
4 to pcd	23	27.4	26	66.7	21	60.0	11	73.3	18	78.3	1	7.7	12	41.4
5 around pcd	0	0.0	0	0.0	1	2.9	0	0.0	0	0.0	0	0.0	0	0.0
2 anterolophulid	90		40		36		15		23		14		31	
3 interrupted	5	5.6	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 low	3	3.3	1	2.5	0	0.0	0	0.0	0	0.0	0	0.0	1	3.2
5 complete	82	91.1	38	95.0	36	100.0	15	100.0	23	100.0	14	100.0	30	96.8
3 metalophulid	90		41		36		15		25		15		30	
3 anterior interrupted	3	3.3	1	2.4	3	8.3	1	6.7	2	8.0	0	0.0	0	0.0
5 to anterolophulid	86	95.6	40	97.6	33	91.7	14	93.3	23	92.0	15	100.0	30	100.0
6 to protoconid	1	1.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 metalophld-spur	90		41		36		15		25		14		30	
2 absent	67	74.4	29	70.7	35	97.2	15	100.0	24	96.0	12	85.7	16	53.3
3 weak	10	11.1	3	7.3	1	2.8	0	0.0	0	0.0	2	14.3	12	40.0
4 strong	13	14.4	9	22.0	0	0.0	0	0.0	1	4.0	0	0.0	2	6.7
5 pcd hind arm	89		42		36		15		27		15		31	
3 short free	19	21.3	2	4.8	12	33.3	1	6.7	6	22.2	3	20.0	2	6.5
4 trans to mcd low	18	20.2	0	0.0	7	19.4	4	26.7	1	3.7	2	13.3	5	16.1
6 long free	48	53.9	36	85.7	12	33.3	10	66.7	18	66.7	8	53.3	23	74.2
7 bent to mcd low	4	4.5	2	4.8	5	13.9	0	0.0	2	7.4	2	13.3	1	3.2
8 bent to mcd high	0	0.0	2	4.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
6 sinusid	87		42		36		15		25		13		30	
2 open	76	87.4	39	92.9	35	97.2	14	93.3	12	48.0	13	100.0	25	83.3
3 closed	10	11.5	2	4.8	1	2.8	0	0.0	13	52.0	0	0.0	5	16.7
4 ectostylid	1	1.1	1	2.4	0	0.0	1	6.7	0	0.0	0	0.0	0	0.0
7 sinusid	90		42		36		15		28		14		32	
3 transverse	59	65.6	13	31.0	27	75.0	13	86.7	22	78.6	5	35.7	11	34.4
4 backwards	31	34.4	29	69.0	9	25.0	2	13.3	6	21.4	9	64.3	21	65.6
8 mesosinusid	90		42		35		15		26		16		29	
2 open	7	7.8	0	0.0	2	5.7	2	13.3	3	11.5	1	6.3	7	24.1
3 closed	0	0.0	0	0.0	1	2.9	0	0.0	1	3.8	1	6.3	3	10.3
4 mcd ridge open	73	81.1	37	88.1	12	34.3	10	66.7	14	53.8	5	31.3	8	27.6
5 mcd ridge closed	10	11.1	5	11.9	20	57.1	3	20.0	8	30.8	9	56.3	11	37.9
9 ectolophid	89		30		35		14		24		14		32	
2 high	51	57.3	10	33.3	29	82.9	11	78.6	13	54.2	14	100.0	30	93.8
3 low	37	41.6	19	63.3	6	17.1	2	14.3	10	41.7	0	0.0	2	6.3
4 interrupted	1	1.1	1	3.3	0	0.0	1	7.1	1	4.2	0	0.0	0	0.0



Table 2. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
10 mesoconid	89		37		35		15		26		14		31	
2 absent	50	56.2	23	62.2	30	85.7	15	100.0	21	80.8	11	78.6	30	96.8
3 weak	29	32.6	13	35.1	5	14.3	0	0.0	3	11.5	3	21.4	1	3.2
4 strong	10	11.2	1	2.7	0	0.0	0	0.0	2	7.7	0	0.0	0	0.0
11 mesolophid	90		42		36		15		28		15		31	
2 absent	1	1.1	0	0.0	3	8.3	2	13.3	3	10.7	1	6.7	0	0.0
3 short	3	3.3	2	4.8	13	36.1	4	26.7	5	17.9	5	33.3	2	6.5
4 medium	56	62.2	32	76.2	18	50.0	9	60.0	20	71.4	9	60.0	19	61.3
5 long	30	33.3	8	19.0	2	5.6	0	0.0	0	0.0	0	0.0	10	32.3
12 mesolophid	87		40		36		15		26		15		31	
2 simple	60	69.0	34	85.0	36	100.0	15	100.0	26	100.0	10	66.7	6	19.4
3 branched	27	31.0	6	15.0	0	0.0	0	0.0	0	0.0	5	33.3	25	80.6
13 ectomesolophid	90		42		36		15		28		14		32	
2 absent	12	13.3	11	26.2	3	8.3	1	6.7	4	14.3	3	21.4	3	9.4
3 weak	25	27.8	13	31.0	13	36.1	5	33.3	9	32.1	9	64.3	23	71.9
4 strong	53	58.9	18	42.9	20	55.6	9	60.0	15	53.6	2	14.3	6	18.8
14 hypolophulid	90		40		36		15		28		15		32	
2 anterior oblique	44	48.9	26	65.0	7	19.4	4	26.7	19	67.9	8	53.3	15	46.9
3 anterior transverse	46	51.1	14	35.0	29	80.6	11	73.3	9	32.1	7	46.7	17	53.1
15 hypoconid branch	90		40		36		15		28		15		31	
2 absent	87	96.7	40	100.0	34	94.4	14	93.3	27	96.4	15	100.0	28	90.3
3 short	1	1.1	0	0.0	2	5.6	1	6.7	1	3.6	0	0.0	2	6.5
4 long	1	1.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
5 long connected	1	1.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.2
16 posterosinusid	89		39		36		15		29		14		28	
2 open	1	1.1	4	10.3	2	5.6	1	6.7	1	3.4	1	7.1	1	3.6
3 closed	88	98.9	35	89.7	34	94.4	14	93.3	28	96.6	13	92.9	27	96.4
17 lab. posterolophid	85		39		36		15		27		14		31	
2 absent	58	68.2	25	64.1	33	91.7	14	93.3	23	85.2	14	100.0	23	74.2
3 small	27	31.8	14	35.9	3	8.3	0	0.0	4	14.8	0	0.0	8	25.8
4 strong	0	0.0	0	0.0	0	0.0	1	6.7	0	0.0	0	0.0	0	0.0
18 greatest width	88		42		36		15		23		14		29	
2 anterior	3	3.4	0	0.0	2	5.6	0	0.0	1	4.3	0	0.0	1	3.4
3 equal	20	22.7	8	19.0	16	44.4	5	33.3	5	21.7	3	21.4	2	6.9
4 posterior	65	73.9	34	81.0	18	50.0	10	66.7	17	73.9	11	78.6	26	89.7

Table 3. Character states of  $M_3$ 

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 lab. anterolophid	76		28		33		11		24		12		15	
2 absent	1	1.3	0	0.0	0	0.0	0	0.0	1	4.2	0	0.0	0	0.0
3 short	44	57.9	10	35.7	28	84.8	4	36.4	8	33.3	12	100.0	7	46.7
4 to pcd	31	40.8	18	64.3	5	15.2	7	63.6	15	62.5	0	0.0	8	53.3
2 anterolophulid	74		26		33		12		24		12		14	
3 interrupted	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	8.3	0	0.0
4 short	9	12.2	8	30.8	1	3.0	5	41.7	5	20.8	3	25.0	3	21.4
5 long	65	87.8	18	69.2	32	97.0	7	58.3	19	79.2	8	66.7	11	78.6
3 anterosinusid	77		28		33		12		25		12		15	
2 absent	0	0.0	0	0.0	1	3.0	1	8.3	0	0.0	0	0.0	0	0.0
3 narrow	1	1.3	1	3.6	0	0.0	1	8.3	1	4.0	0	0.0	1	6.7
4 wide	76	98.7	27	96.4	32	97.0	10	83.3	24	96.0	12	100.0	14	93.3
4 metalophulid	77		28		33		12		25		12		15	
2 absent	4	5.2	0	0.0	1	3.0	0	0.0	1	4.0	0	0.0	0	0.0
3 anterior interrupted	9	11.7	4	14.3	1	3.0	0	0.0	2	8.0	1	8.3	0	0.0
4 to anteroconid	0	0.0	0	0.0	10	30.3	6	50.0	9	36.0	0	0.0	1	6.7
5 to anterolophulid	62	80.5	23	82.1	21	63.6	5	41.7	13	52.0	10	83.3	13	86.7
6 to protoconid	2	2.6	1	3.6	0	0.0	1	8.3	0	0.0	1	8.3	1	6.7
5 metalophld-spur	77		28		32		12		25		12		15	
2 absent	44	57.1	19	67.9	22	68.8	9	75.0	23	92.0	7	58.3	7	46.7
3 weak	14	18.2	4	14.3	5	15.6	1	8.3	2	8.0	4	33.3	5	33.3
4 strong	19	24.7	5	17.9	5	15.6	2	16.7	0	0.0	1	8.3	3	20.0
6 pcd hind arm	77		28		32		12		25		12		14	
3 short free	8	10.4	0	0.0	0	0.0	2	16.7	2	8.0	1	8.3	2	14.3
4 trans to mcd low	4	5.2	0	0.0	0	0.0	0	0.0	0	0.0	1	8.3	0	0.0
6 long free	58	75.3	26	92.9	29	90.6	10	83.3	23	92.0	10	83.3	12	85.7
7 bent to mcd low	5	6.5	2	7.1	3	9.4	0	0.0	0	0.0	0	0.0	0	0.0
8 bent to mcd high	2	2.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
7 sinusid	76		28		32		11		24		12		15	
2 open	68	89.5	28	100.0	32	100.0	11	100.0	21	87.5	12	100.0	10	66.7
3 closed	8	10.5	0	0.0	0	0.0	0	0.0	3	12.5	0	0.0	5	33.3
8 sinusid	77		27		32		12		25		12		15	
3 narrow transverse	7	9.1	0	0.0	3	9.4	0	0.0	0	0.0	0	0.0	1	6.7
4 broad transverse	9	11.7	4	14.8	16	50.0	11	91.7	13	52.0	3	25.0	3	20.0
5 narrow backwards	21	27.3	5	18.5	2	6.3	0	0.0	0	0.0	2	16.7	3	20.0
6 broad backwards	40	51.9	18	66.7	11	34.4	1	8.3	12	48.0	7	58.3	8	53.3
9 mesosinusid	75		26		30		12		24		12		15	
2 open	34	45.3	6	23.1	10	33.3	1	8.3	10	41.7	5	41.7	2	13.3
3 closed	41	54.7	20	76.9	20	66.7	11	91.7	14	58.3	7	58.3	13	86.7

Table 3. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
10 mesolophid	77		28		31		12		25		12		15	
2 absent	6	7.8	10	35.7	30	96.8	11	91.7	24	96.0	2	16.7	9	60.0
3 short	20	26.0	8	28.6	1	3.2	0	0.0	1	4.0	8	66.7	4	26.7
4 medium	48	62.3	10	35.7	0	0.0	1	8.3	0	0.0	2	16.7	1	6.7
5 long	3	3.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	6.7
11 mesolophid	74		18		31		12		25		12		15	
2 simple	63	85.1	16	88.9	31	100.0	12	100.0	25	100.0	12	100.0	14	93.3
3 branched	11	14.9	2	11.1	0	0.0	0	0.0	0	0.0	0	0.0	1	6.7
12 ectolophid	69		22		31		12		25		12		15	
2 low	23	33.3	2	9.1	0	0.0	0	0.0	1	4.0	0	0.0	0	0.0
3 interrupted	4	5.8	1	4.5	0	0.0	0	0.0	1	4.0	0	0.0	0	0.0
4 complete	42	60.9	19	86.4	31	100.0	12	100.0	23	92.0	12	100.0	15	100.0
13 mesoconid	72		25		31		12		25		12		14	
2 absent	55	76.4	22	88.0	31	100.0	12	100.0	25	100.0	11	91.7	14	100.0
3 small	9	12.5	1	4.0	0	0.0	0	0.0	0	0.0	1	8.3	0	0.0
4 large	8	11.1	2	8.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
14 ectomesolophid	77		27		31		12		25		12		15	
2 absent	7	9.1	9	33.3	22	71.0	11	91.7	22	88.0	6	50.0	3	20.0
3 weak	24	31.2	9	33.3	8	25.8	1	8.3	3	12.0	6	50.0	11	73.3
4 strong	46	59.7	9	33.3	1	3.2	0	0.0	0	0.0	0	0.0	1	6.7
15 entoconid	77		27		30		12		24		12		15	
2 absent	0	0.0	0	0.0	1	3.3	1	8.3	0	0.0	2	16.7	2	13.3
3 small	1	1.3	1	3.7	10	33.3	4	33.3	7	29.2	2	16.7	4	26.7
4 large	76	98.7	26	96.3	19	63.3	7	58.3	17	70.8	8	66.7	9	60.0
16 hypolophulid	76		27		31		12		25		12		15	
2 anterior oblique	55	72.4	12	44.4	14	45.2	3	25.0	7	28.0	7	58.3	10	66.7
3 anterior transverse	18	23.7	13	48.1	17	54.8	9	75.0	18	72.0	1	8.3	2	13.3
4 transverse	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	6.7
5 interrupted	3	3.9	2	7.4	0	0.0	0	0.0	0	0.0	4	33.3	2	13.3
17 posterosinusid	72		26		30		12		25		11		15	
2 open	7	9.7	0	0.0	2	6.7	0	0.0	0	0.0	0	0.0	0	0.0
3 half closed	21	29.2	0	0.0	8	26.7	2	16.7	7	28.0	0	0.0	7	46.7
4 closed	44	61.1	26	100.0	20	66.7	10	83.3	18	72.0	11	100.0	8	53.3
18 shape	76		28		30		12		24		12		15	
2 short triangle	0	0.0	0	0.0	0	0.0	0	0.0	1	4.2	0	0.0	0	0.0
3 long triangle	0	0.0	0	0.0	24	80.0	9	75.0	6	25.0	3	25.0	2	13.3
4 trapezoid	76	100.0	28	100.0	6	20.0	3	25.0	17	70.8	9	75.0	13	86.7

Table 4. Character states of M<sup>1</sup>

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 anterocone	59		33		21		5		23		7		17	
2 simple	47	79.7	27	81.8	13	61.9	3	60.0	19	82.6	5	71.4	17	100.0
3 half-split	10	16.9	6	18.2	4	19.0	0	0.0	1	4.3	2	28.6	0	0.0
4 bifid	2	3.4	0	0.0	4	19.0	2	40.0	3	13.0	0	0.0	0	0.0
2 prelobe	68		34		26		5		24		8		18	
4 broad set-off	33	48.5	20	58.8	11	42.3	3	60.0	15	62.5	5	62.5	13	72.2
5 broad continuous	35	51.5	14	41.2	15	57.7	2	40.0	9	37.5	3	37.5	5	27.8
3 anterolophule	66		34		23		5		23		7		18	
2 absent	0	0.0	0	0.0	1	4.3	1	20.0	6	26.1	0	0.0	0	0.0
3 ac-spur	0	0.0	1	2.9	3	13.0	0	0.0	2	8.7	0	0.0	2	11.1
4 pc-spur	8	12.1	4	11.8	15	65.2	3	60.0	8	34.8	0	0.0	0	0.0
5 ac + pc spurs	47	71.2	25	73.5	4	17.4	1	20.0	6	26.1	3	42.9	8	44.4
6 complete	5	7.6	2	5.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
7 double	6	9.1	2	5.9	0	0.0	0	0.0	1	4.3	4	57.1	8	44.4
4 forward pac-spur	77		34		29		5		25		12		22	
2 absent	56	72.7	24	70.6	22	75.9	5	100.0	19	76.0	9	75.0	14	63.6
3 free	11	14.3	4	11.8	6	20.7	0	0.0	1	4.0	0	0.0	3	13.6
4 to anterostyl	3	3.9	5	14.7	0	0.0	0	0.0	5	20.0	2	16.7	5	22.7
5 to anterocone	7	9.1	1	2.9	1	3.4	0	0.0	0	0.0	1	8.3	0	0.0
5 ling. anteroloph	70		31		28		5		24		10		21	
2 incomplete	5	7.1	1	3.2	3	10.7	1	20.0	2	8.3	0	0.0	0	0.0
3 complete	50	71.4	22	71.0	25	89.3	4	80.0	17	70.8	9	90.0	8	38.1
4 protostyl	15	21.4	8	25.8	0	0.0	0	0.0	5	20.8	1	10.0	13	61.9
6 protocone platform	80		33		28		6		23		10		21	
2 absent	46	57.5	18	54.5	19	67.9	4	66.7	10	43.5	3	30.0	1	4.8
3 small	25	31.3	6	18.2	4	14.3	1	16.7	5	21.7	5	50.0	2	9.5
4 large	7	8.8	2	6.1	0	0.0	0	0.0	4	17.4	1	10.0	14	66.7
5 crest	2	2.5	7	21.2	5	17.9	1	16.7	4	17.4	1	10.0	4	19.0
7 anterosinus	66		34		23		5		24		8		18	
2 open	29	43.9	10	29.4	3	13.0	1	20.0	2	8.3	5	62.5	0	0.0
3 closed	27	40.9	20	58.8	14	60.9	2	40.0	18	75.0	3	37.5	15	83.3
4 anterostyl	10	15.2	4	11.8	6	26.1	2	40.0	4	16.7	0	0.0	3	16.7
8 protolophule	84		34		29		6		25		13		22	
3 anterior	3	3.6	0	0.0	1	3.4	0	0.0	0	0.0	0	0.0	0	0.0
4 anterior plus	1	1.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
5 transverse	1	1.2	0	0.0	2	6.9	0	0.0	0	0.0	0	0.0	0	0.0
6 double	1	1.2	1	2.9	1	3.4	0	0.0	1	4.0	0	0.0	0	0.0
7 posterior plus	2	2.4	2	5.9	11	37.9	1	16.7	11	44.0	0	0.0	6	27.3
8 posterior interrupted	2	2.4	3	8.8	1	3.4	0	0.0	0	0.0	1	7.7	0	0.0
9 posterior	74	88.1	28	82.4	13	44.8	4	66.7	13	52.0	12	92.3	16	72.7
10 absent	0	0.0	0	0.0	0	0.0	1	16.7	0	0.0	0	0.0	0	0.0
9 sinus	83		33		29		5		25		13		22	
2 open	78	94.0	29	87.9	14	48.3	4	80.0	15	60.0	11	84.6	13	59.1
3 closed	1	1.2	2	6.1	4	13.8	0	0.0	4	16.0	0	0.0	2	9.1
4 entostyl	4	4.8	2	6.1	11	37.9	1	20.0	6	24.0	2	15.4	7	31.8

Table 4. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
10 sinus	84		31		29		6		27		13		23	
2 strong forward	20	23.8	2	6.5	3	10.3	0	0.0	2	7.4	5	38.5	9	39.1
3 forward	60	71.4	28	90.3	16	55.2	1	16.7	21	77.8	8	61.5	11	47.8
4 subdivided	2	2.4	1	3.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
5 transverse	2	2.4	0	0.0	10	34.5	5	83.3	4	14.8	0	0.0	3	13.0
11 entoloph	71		23		29		6		22		13		21	
2 high	48	67.6	16	69.6	27	93.1	5	83.3	21	95.5	8	61.5	16	76.2
3 low	16	22.5	7	30.4	2	6.9	1	16.7	1	4.5	1	7.7	5	23.8
4 interrupted	7	9.9	0	0.0	0	0.0	0	0.0	0	0.0	4	30.8	0	0.0
12 mesosinus	80		33		28		6		27		13		21	
2 open	6	7.5	2	6.1	3	10.7	2	33.3	0	0.0	1	7.7	2	9.5
3 closed	4	5.0	4	12.1	3	10.7	0	0.0	2	7.4	3	23.1	9	42.9
4 mesostyl	48	60.0	14	42.4	5	17.9	1	16.7	9	33.3	2	15.4	3	14.3
5 mesostyl crest	15	18.8	9	27.3	8	28.6	1	16.7	13	48.1	4	30.8	6	28.6
6 mesostyl to mesoloph	7	8.8	4	12.1	9	32.1	2	33.3	3	11.1	3	23.1	1	4.8
13 mesoloph	85		34		28		6		27		13		24	
2 absent	1	1.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
3 short	1	1.2	2	5.9	0	0.0	0	0.0	4	14.8	1	7.7	0	0.0
4 medium	40	47.1	27	79.4	23	82.1	2	33.3	18	66.7	3	23.1	4	16.7
5 long	14	16.5	1	2.9	0	0.0	0	0.0	3	11.1	7	53.8	15	62.5
6 interrupted	0	0.0	0	0.0	1	3.6	1	16.7	0	0.0	0	0.0	0	0.0
7 border	29	34.1	4	11.8	4	14.3	3	50.0	2	7.4	2	15.4	5	20.8
14 2nd mesoloph	85		34		30		6		27		13		23	
2 absent	61	71.8	29	85.3	27	90.0	6	100.0	26	96.3	1	7.7	8	34.8
3 short	14	16.5	3	8.8	3	10.0	0	0.0	1	3.7	1	7.7	14	60.9
4 long	10	11.8	2	5.9	0	0.0	0	0.0	0	0.0	11	84.6	1	4.3
15 entomesoloph	84		34		29		6		27		13		23	
2 absent	82	97.6	34	100.0	28	96.6	6	100.0	23	85.2	10	76.9	13	56.5
3 short	1	1.2	0	0.0	1	3.4	0	0.0	2	7.4	2	15.4	5	21.7
4 long	1	1.2	0	0.0	0	0.0	0	0.0	2	7.4	1	7.7	5	21.7
16 mesoloph-mc conn.	83		33		29		5		27		13		23	
2 absent	55	66.3	23	69.7	28	96.6	5	100.0	27	100.0	9	69.2	14	60.9
3 one crest	28	33.7	10	30.3	1	3.4	0	0.0	0	0.0	4	30.8	9	39.1
17 metalophule	83		34		29		5		27		13		23	
2 anterior	80	96.4	34	100.0	29	100.0	5	100.0	27	100.0	13	100.0	23	100.0
3 anterior interrupted	1	1.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 anterior plus	1	1.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
10 absent	1	1.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
18 posterosinus	78		34		28		5		25		12		22	
2 open	6	7.7	4	11.8	10	35.7	0	0.0	11	44.0	7	58.3	22	100.0
3 closed	72	92.3	30	88.2	18	64.3	5	100.0	14	56.0	5	41.7	0	0.0
19 labial border	68		33		23		4		24		7		17	
2 hollow	16	23.5	7	21.2	1	4.3	0	0.0	4	16.7	2	28.6	5	29.4
3 straight	24	35.3	11	33.3	12	52.2	4	100.0	11	45.8	3	42.9	7	41.2
4 convex	28	41.2	15	45.5	10	43.5	0	0.0	9	37.5	2	28.6	5	29.4

Table 5. Character states of  $M^2$ 

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 ling. anteroloph	82		30		39		8		36		10		33	
2 absent	9	11.0	2	6.7	1	2.6	0	0.0	0	0.0	3	30.0	0	0.0
3 weak	51	62.2	14	46.7	14	35.9	0	0.0	17	47.2	4	40.0	17	51.5
4 strong	20	24.4	13	43.3	13	33.3	5	62.5	13	36.1	3	30.0	16	48.5
5 around pc	2	2.4	1	3.3	11	28.2	3	37.5	6	16.7	0	0.0	0	0.0
2 protolophule	82		30		39		9		37		10		33	
3 anterior	5	6.1	1	3.3	2	5.1	1	11.1	3	8.1	0	0.0	3	9.1
4 anterior plus	75	91.5	28	93.3	37	94.9	8	88.9	32	86.5	9	90.0	27	81.8
6 double	1	1.2	0	0.0	0	0.0	0	0.0	2	5.4	1	10.0	3	9.1
7 posterior plus	1	1.2	1	3.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
3 sinus	81		28		38		6		37		10		32	
2 open	72	88.9	20	71.4	19	50.0	1	16.7	13	35.1	10	100.0	22	68.8
3 closed	8	9.9	6	21.4	15	39.5	4	66.7	22	59.5	0	0.0	8	25.0
4 entostyl	1	1.2	2	7.1	4	10.5	1	16.7	2	5.4	0	0.0	2	6.3
4 sinus	81		30		39		9		36		10		32	
2 strong forward	24	29.6	10	33.3	4	10.3	0	0.0	1	2.8	0	0.0	9	28.1
3 forward	30	37.0	14	46.7	13	33.3	1	11.1	30	83.3	4	40.0	19	59.4
4 subdivided	27	33.3	4	13.3	0	0.0	1	11.1	1	2.8	0	0.0	3	9.4
5 transverse	0	0.0	2	6.7	22	56.4	7	77.8	4	11.1	6	60.0	1	3.1
5 mesosinus	79		30		40		7		38		9		33	
2 open	22	27.8	10	33.3	5	12.5	2	28.6	3	7.9	1	11.1	1	3.0
3 closed	10	12.7	3	10.0	8	20.0	1	14.3	5	13.2	2	22.2	14	42.4
4 pac-spur	13	16.5	5	16.7	6	15.0	0	0.0	2	5.3	0	0.0	7	21.2
5 mesostyl	19	24.1	9	30.0	6	15.0	2	28.6	12	31.6	3	33.3	4	12.1
6 mesostyl crest	7	8.9	1	3.3	12	30.0	1	14.3	14	36.8	0	0.0	5	15.2
7 mesostyl to mesoloph	8	10.1	2	6.7	3	7.5	1	14.3	2	5.3	3	33.3	2	6.1
6 mesoloph	80		30		39		9		38		10		33	
3 short	4	5.0	0	0.0	5	12.8	0	0.0	1	2.6	1	10.0	0	0.0
4 medium	58	72.5	12	40.0	31	79.5	6	66.7	25	65.8	4	40.0	15	45.5
5 long	12	15.0	6	20.0	2	5.1	1	11.1	5	13.2	5	50.0	16	48.5
6 interrupted	3	3.8	2	6.7	0	0.0	1	11.1	1	2.6	0	0.0	0	0.0
7 border	3	3.8	10	33.3	1	2.6	1	11.1	6	15.8	0	0.0	2	6.1
7 2nd mesoloph	79		28		39		9		36		10		31	
2 absent	39	49.4	22	78.6	31	79.5	7	77.8	31	86.1	5	50.0	24	77.4
3 short	6	7.6	1	3.6	3	7.7	1	11.1	4	11.1	1	10.0	5	16.1
4 long	34	43.0	5	17.9	5	12.8	1	11.1	1	2.8	4	40.0	2	6.5
8 mesoloph-mc conn.	78		30		39		9		37		10		33	
2 absent	59	75.6	22	73.3	35	89.7	9	100.0	32	86.5	6	60.0	13	39.4
3 one crest	18	23.1	7	23.3	4	10.3	0	0.0	5	13.5	4	40.0	19	57.6
4 two crests	1	1.3	1	3.3	0	0.0	0	0.0	0	0.0	0	0.0	1	3.0

Table 5. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
9 entoloph-pc conn.	60		28		37		9		29		10		28	
2 high	44	73.3	24	85.7	24	64.9	9	100.0	23	79.3	9	90.0	17	60.7
3 low	15	25.0	3	10.7	12	32.4	0	0.0	6	20.7	0	0.0	9	32.1
4 interrupted	1	1.7	1	3.6	1	2.7	0	0.0	0	0.0	1	10.0	2	7.1
10 pc-hc conn.	82		30		39		9		37		10		32	
2 absent	44	53.7	23	76.7	36	92.3	9	100.0	36	97.3	10	100.0	26	81.3
3 weak	26	31.7	2	6.7	1	2.6	0	0.0	0	0.0	0	0.0	5	15.6
4 interrupted	0	0.0	3	10.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
5 low	8	9.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
6 complete	4	4.9	2	6.7	2	5.1	0	0.0	1	2.7	0	0.0	1	3.1
11 metalophule	81		30		39		9		38		10		33	
2 anterior	81	100.0	30	100.0	39	100.0	9	100.0	38	100.0	9	90.0	32	97.0
4 anterior plus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	10.0	0	0.0
5 transverse	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.0
12 posterosinus	78		27		38		7		35		10		33	
2 open	2	2.6	1	3.7	7	18.4	0	0.0	25	71.4	1	10.0	30	90.9
3 closed	76	97.4	26	96.3	31	81.6	7	100.0	10	28.6	9	90.0	3	9.1
13 shape	80		27		38		7		36		10		32	
2 subrectangular	33	41.3	10	37.0	6	15.8	1	14.3	9	25.0	8	80.0	20	62.5
3 trapezoid	47	58.7	17	63.0	32	84.2	6	85.7	27	75.0	2	20.0	12	37.5
14 labial border	80		28		39		7		36		9		32	
2 concave	63	78.8	26	92.9	24	61.5	5	71.4	34	94.4	3	33.3	16	50.0
3 straight	17	21.3	1	3.6	15	38.5	2	28.6	2	5.6	6	66.7	15	46.9
4 convex	0	0.0	1	3.6	0	0.0	0	0.0	0	0.0	0	0.0	1	3.1

Table 6. Character states of M<sup>3</sup>

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1 ling. anteroloph	80		15		38		9		36		10		28	
2 absent	6	7.5	1	6.7	6	15.8	3	33.3	5	13.9	1	10.0	9	32.1
3 weak	31	38.8	11	73.3	23	60.5	4	44.4	17	47.2	5	50.0	16	57.1
4 strong	34	42.5	0	0.0	3	7.9	1	11.1	9	25.0	1	10.0	3	10.7
5 around pc	9	11.3	3	20.0	6	15.8	1	11.1	5	13.9	3	30.0	0	0.0
2 protolophule	80		15		39		9		36		10		30	
2 absent	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	6.7
3 to anterocone	22	27.5	7	46.7	33	84.6	9	100.0	30	83.3	1	10.0	6	20.0
4 to anterolophule	53	66.3	8	53.3	5	12.8	0	0.0	6	16.7	9	90.0	20	66.7
5 transverse	1	1.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	6.7
6 double	4	5.0	0	0.0	1	2.6	0	0.0	0	0.0	0	0.0	0	0.0
3 sinus	77		14		38		9		37		9		30	
2 absent	2	2.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.3
3 very small	25	32.5	3	21.4	4	10.5	1	11.1	2	5.4	1	11.1	9	30.0
4 small	43	55.8	11	78.6	34	89.5	8	88.9	35	94.6	8	88.9	20	66.7
5 deep	7	9.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 neo-entoloph	74		14		36		9		37		8		32	
2 absent	4	5.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
3 interrupted	1	1.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
4 low	10	13.5	0	0.0	1	2.8	0	0.0	1	2.7	0	0.0	0	0.0
5 high	59	79.7	14	100.0	35	97.2	9	100.0	36	97.3	8	100.0	32	100.0
5 mesosinus	79		15		36		10		37		8		31	
2 open	3	3.8	1	6.7	2	5.6	0	0.0	0	0.0	0	0.0	1	3.2
3 closed	76	96.2	14	93.3	34	94.4	10	100.0	37	100.0	8	100.0	30	96.8
6 mesoloph	74		15		36		10		37		8		29	
2 absent	8	10.8	0	0.0	0	0.0	0	0.0	1	2.7	1	12.5	10	34.5
3 short	16	21.6	3	20.0	2	5.6	0	0.0	2	5.4	4	50.0	9	31.0
4 medium	40	54.1	11	73.3	9	25.0	7	70.0	14	37.8	3	37.5	8	27.6
5 long	10	13.5	1	6.7	19	52.8	1	10.0	20	54.1	0	0.0	2	6.9
6 border	0	0.0	0	0.0	6	16.7	2	20.0	0	0.0	0	0.0	0	0.0
7 2nd mesoloph	73		15		35		9		36		8		32	
2 absent	44	60.3	14	93.3	24	68.6	5	55.6	29	80.6	6	75.0	32	100.0
3 short	14	19.2	1	6.7	5	14.3	1	11.1	5	13.9	1	12.5	0	0.0
4 long	15	20.5	0	0.0	6	17.1	3	33.3	2	5.6	1	12.5	0	0.0
8 old entoloph	79		17		37		9		37		8		29	
2 absent	8	10.1	1	5.9	26	70.3	6	66.7	27	73.0	3	37.5	3	10.3
3 short spur	11	13.9	3	17.6	0	0.0	1	11.1	2	5.4	2	25.0	6	20.7
4 curved spur	17	21.5	1	5.9	0	0.0	1	11.1	0	0.0	0	0.0	6	20.7
5 long spur	13	16.5	5	29.4	3	8.1	0	0.0	4	10.8	3	37.5	12	41.4
6 complete	30	38.0	7	41.2	8	21.6	1	11.1	4	10.8	0	0.0	2	6.9



Table 6. (continued).

	MLB1D		HEIM		MIR4C		MIR4D		ALCN		MIR2A		VIV	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
9 axiolph	75		17		37		9		37		8		29	
2 absent	30	40.0	16	94.1	7	18.9	1	11.1	11	29.7	5	62.5	26	89.7
3 anterior spur	31	41.3	0	0.0	4	10.8	0	0.0	5	13.5	1	12.5	0	0.0
4 post. spur short	2	2.7	1	5.9	0	0.0	0	0.0	2	5.4	1	12.5	3	10.3
5 post. spur long	5	6.7	0	0.0	17	45.9	6	66.7	10	27.0	1	12.5	0	0.0
6 two spurs	3	4.0	0	0.0	0	0.0	0	0.0	1	2.7	0	0.0	0	0.0
7 complete	4	5.3	0	0.0	9	24.3	2	22.2	8	21.6	0	0.0	0	0.0
10 centroph	78		13		35		9		37		8		29	
2 absent	1	1.3	1	7.7	1	2.9	0	0.0	0	0.0	0	0.0	0	0.0
3 weak	7	9.0	0	0.0	0	0.0	0	0.0	1	2.7	1	12.5	4	13.8
4 strong	54	69.2	8	61.5	13	37.1	5	55.6	35	94.6	5	62.5	25	86.2
5 = metalophule	16	20.5	4	30.8	21	60.0	4	44.4	1	2.7	2	25.0	0	0.0
11 centrocone	74		17		35		8		37		8		29	
2 absent	60	81.1	16	94.1	34	97.1	8	100.0	31	83.8	7	87.5	26	89.7
3 present	3	4.1	0	0.0	0	0.0	0	0.0	2	5.4	0	0.0	0	0.0
4 isolated	1	1.4	0	0.0	0	0.0	0	0.0	2	5.4	0	0.0	2	6.9
5 on old entolph	10	13.5	1	5.9	1	2.9	0	0.0	2	5.4	1	12.5	1	3.4
12 metacone	71		13		31		8		37		8		30	
2 absent	45	63.4	7	53.8	3	9.7	3	37.5	31	83.8	7	87.5	25	83.3
3 present	26	36.6	6	46.2	28	90.3	5	62.5	6	16.2	1	12.5	5	16.7
13 posterosinus	77		13		34		8		37		8		32	
2 open	3	3.9	2	15.4	1	2.9	0	0.0	0	0.0	0	0.0	1	3.1
3 closed	74	96.1	11	84.6	33	97.1	8	100.0	37	100.0	8	100.0	31	96.9

Table 7. Comparison of some character states for *Pseudocricetodon* from Montalbán 1D, Mirambueno 4B, and Mirambueno 4C.

	MLB1D		MIR4B		MIR4C	
	N	%	N	%	N	%
<b>M<sub>1</sub></b>						
5 metalophulid	63		5		33	
2 absent	36	57.1	4	80.0	9	27.3
3 anterior interrupted	18	28.6	0	0.0	8	24.2
4 anterior complete	9	14.3	1	20.0	11	33.3
5 to anteroconid	0	0.0	0	0.0	5	15.2
<b>M<sub>2</sub></b>						
1 lab. anterolophid	86		3		35	
2 absent	6	7.0	1	33.3	0	0.0
3 short	55	64.0	2	66.7	13	37.1
4 to pcd	25	29.1	0	0.0	21	60.0
5 around pcd	0	0.0	0	0.0	1	2.9
<b>M<sub>3</sub></b>						
10 mesolophid	43		2		31	
2 absent	3	7.0	1	50.0	30	96.8
3 short	7	16.3	1	50.0	1	3.2
4 medium	30	69.8	0	0.0	0	0.0
5 long	3	7.0	0	0.0	0	0.0
13 mesoconid	43		2		31	
2 absent	26	60.5	1	50.0	31	100.0
3 small	9	20.9	1	50.0	0	0.0
4 large	8	18.6	0	0.0	0	0.0
<b>M<sup>1</sup></b>						
3 anterolophule	66		6		23	
2 absent	0	0.0	1	16.7	1	4.3
3 ac-spur	0	0.0	1	16.7	3	13.0
4 pc-spur	8	12.1	1	16.7	15	65.2
5 ac + pc spurs	47	71.2	2	33.3	4	17.4
6 complete	5	7.6	1	16.7	0	0.0
7 double	6	9.1	0	0.0	0	0.0
4 forward pac-spur	77		8		29	
2 absent	56	72.7	7	87.5	22	75.9
3 free	11	14.3	0	0.0	6	20.7
4 to anterostyl	3	3.9	1	12.5	0	0.0
5 to anterocone	7	9.1	0	0.0	1	3.4
6 protocone platform	80		6		28	
2 absent	46	57.5	3	50.0	19	67.9
3 small	25	31.3	3	50.0	4	14.3
4 large	7	8.8	0	0.0	0	0.0
5 crest	2	2.5	0	0.0	5	17.9
<b>M<sup>2</sup></b>						
13 shape	80		6		38	
2 subrectangular	33	41.3	4	66.7	6	15.8
3 trapezoid	47	58.7	2	33.3	32	84.2

Table 8. Measurements of lower molars (\* = *P. philippi*).

	n	min.	mean	max.	V'	$\sigma$		n	min.	mean	max.	V'	$\sigma$
<b>M<sub>1</sub></b>													
COD	15	12.9	13.81	15.2	16.37	0.647		15	8.2	8.96	9.8	17.78	0.504
VIV	23	11.9	13.29	14.7	21.05	0.715		24	8.2	8.83	9.5	14.69	0.357
MIR2A	10	12.8	13.43	14.3	11.07	0.460		12	8.2	8.77	9.4	13.64	0.347
ALC	26	12.2	13.28	14.5	17.23	0.612		26	8.1	8.63	9.5	15.91	0.349
MIR4D	14	12.3	13.06	14.1	13.64	0.483		14	8.2	8.58	9.1	10.40	0.309
MIR4C	32	12.1	13.15	14.2	15.97	0.529		31	7.8	8.64	9.1	15.38	0.340
MIR4C*	2	11.1	11.20	11.3	1.79	0.141		2	7.1	7.40	7.7	8.11	0.424
MIR4B	4	11.5	12.15	12.4	7.53	0.436		5	7.7	8.14	8.7	12.20	0.378
MLB1D	76	11.3	12.41	13.3	16.26	0.540		79	7.6	8.49	9.3	20.12	0.354
SMC*	11	9.0	9.51	10.1	11.52	0.383		12	5.9	6.46	7.1	18.46	0.360
<b>M<sub>2</sub></b>													
COD	13	11.0	11.96	12.9	15.90	0.601		13	8.8	9.92	10.6	18.56	0.596
VIV	30	10.7	11.34	12.2	13.10	0.378		32	8.4	9.56	10.1	18.38	0.384
MIR2A	15	10.8	11.41	12.1	11.35	0.301		15	9.0	9.54	9.9	9.52	0.269
ALC	24	11.2	11.79	12.5	10.97	0.383		25	9.3	9.82	10.5	12.12	0.337
MIR4D	16	11.0	11.79	12.2	10.34	0.310		16	9.5	9.78	10.2	7.11	0.168
MIR4C	36	10.7	11.53	12.3	13.91	0.442		35	8.6	9.55	10.4	18.95	0.429
MIR4B	3	10.8	11.00	11.3	4.52	0.265		2	9.4	9.50	9.6	2.11	0.141
MLB1D	98	9.6	11.00	12.2	23.85	0.444		99	8.0	9.64	10.9	30.69	0.482
SMC*	14	7.5	8.76	10.0	28.57	0.589		14	6.4	7.56	8.9	32.68	0.593
<b>M<sub>3</sub></b>													
COD	4	10.6	11.17	11.6	9.01	0.435		4	8.3	9.27	9.8	16.57	0.670
VIV	15	9.5	10.64	11.8	21.60	0.653		15	8.1	8.97	10.1	21.98	0.545
MIR2A	11	9.9	10.65	11.7	16.67	0.450		12	8.0	8.77	9.6	18.18	0.393
ALC	25	9.3	10.28	11.3	19.42	0.519		25	8.0	8.82	9.9	21.23	0.480
MIR4D	12	9.3	10.42	10.9	15.84	0.463		11	8.5	8.89	9.4	10.06	0.251
MIR4C	35	9.1	10.06	11.0	18.91	0.498		35	7.9	8.65	9.3	16.28	0.342
MIR4B	2	9.4	10.00	10.6	12.00	0.849		2	7.8	8.30	8.8	12.05	0.707
MLB1D	76	9.5	10.52	11.4	18.18	0.425		76	7.7	8.92	9.9	25.00	0.439
SMC*	10	7.3	7.99	9.0	20.86	0.472		10	6.5	6.90	7.9	19.44	0.427

Table 9. Measurements of upper molars (\* = *P. philippi*).

	n	min.	mean	max.	V'	$\sigma$		n	min.	mean	max.	V'	$\sigma$
<b>M<sup>1</sup></b>													
COD	14	14.1	15.00	15.7	10.74	0.491		14	9.3	9.87	10.6	13.07	0.331
VIV	17	13.2	14.51	15.4	15.38	0.557		24	9.1	9.73	10.7	16.16	0.445
MIR2A	5	15.0	15.10	15.4	2.63	0.173		9	9.0	9.73	10.1	11.52	0.328
ALC	24	14.2	15.04	15.9	11.30	0.470		24	9.1	10.08	11.0	18.91	0.433
MIR4D	4	14.2	14.73	15.3	7.46	0.479		6	9.2	9.83	10.2	10.34	0.383
MIR4C	20	13.5	14.73	16.1	17.57	0.701		27	8.8	9.80	11.1	23.12	0.545
MIR4C*	1		12.70					1		9.40			
MIR4B	5	13.1	13.48	13.9	5.93	0.363		8	8.6	9.19	9.7	12.02	0.432
MLB1D	61	12.6	13.89	15.1	18.05	0.596		83	8.6	9.77	10.8	22.68	0.415
SMC*	8	10.5	11.44	12.2	14.98	0.623		13	7.2	7.68	8.5	16.56	0.387
<b>M<sup>2</sup></b>													
COD	8	10.2	10.90	11.7	13.70	0.447		8	9.7	10.16	10.8	10.73	0.370
VIV	33	9.5	10.56	11.3	17.31	0.437		33	9.0	9.88	10.6	16.33	0.367
MIR2A	10	10.1	10.74	11.3	11.21	0.392		10	9.3	9.77	10.1	8.25	0.271
ALC	36	10.4	11.17	11.9	13.45	0.400		37	9.5	10.51	11.3	17.31	0.433
MIR4D	9	10.7	11.09	12.0	11.45	0.476		9	9.9	10.23	10.7	7.77	0.316
MIR4C	40	10.0	10.89	11.9	17.35	0.454		41	9.5	10.23	11.0	14.63	0.361
MIR4C*	1		9.60					1		9.10			
MIR4B	7	10.0	10.34	11.0	9.52	0.351		8	9.4	9.69	10.1	7.18	0.236
MLB1D	85	9.6	10.46	11.3	16.27	0.410		88	9.2	10.04	11.0	17.82	0.408
SMC*	15	7.7	8.36	8.9	14.46	0.295		15	7.1	7.80	8.6	19.11	0.402
<b>M<sup>3</sup></b>													
COD	2	10.1	10.15	10.2	0.99	0.071		2	9.8	9.95	10.1	3.02	0.212
VIV	32	7.6	8.72	9.6	23.26	0.477		32	8.2	9.25	9.9	18.78	0.411
MIR2A	10	8.4	8.91	9.9	16.39	0.436		9	8.3	9.19	9.9	17.58	0.457
ALC	37	7.5	8.46	9.8	26.59	0.436		37	7.8	9.04	9.8	22.73	0.439
MIR4D	10	6.9	8.30	9.1	27.50	0.585		10	8.3	8.77	9.6	14.53	0.427
MIR4C	39	7.0	8.31	9.3	28.22	0.444		39	7.9	8.81	9.6	19.43	0.369
MIR4B	6	7.9	8.23	8.8	10.78	0.350		6	8.4	8.88	9.2	9.09	0.319
MLB1D	84	7.7	8.88	10.2	27.93	0.497		80	8.3	9.26	10.8	26.18	0.514
SMC*	2	6.1	6.55	7.0	13.74	0.636		2	6.9	6.95	7.0	1.44	0.071

## Appendix: Description of character states

### M1 inf.

#### 1: ling. anterolophid

- 2 absent: no lingual cingulum descending from the anteroconid.
- 3 low: a low, complete, connection between anteroconid and metaconid.
- 4 interrupted: a high or low incomplete connection.
- 5 high: a complete connection, that is considerably higher than the bottom of the anterosinusid.

#### 2: lab. anterolophid

- 2 absent: no labial cingulum descending from the anteroconid.
- 3 short: a short crest descending from the anteroconid.
- 4 long: the crest is longer, without reaching the protoconid.
- 5 complete: it reaches the protoconid.

#### 3: anterolophulid

- 2 absent: there is no connection between protoconid and anteroconid.
- 3 interrupted: the crest is interrupted, either between protoconid and metalophulid, or between metalophulid and anteroconid.
- 4 low: the entire crest, or part of it, is clearly lower than the anteroconid.
- 5 complete: the crest is continuous and (almost) as high as the anteroconid.

#### 4: anterosinusid

- 2 narrow: the antero-posterior length is smaller than the a-p length of the anteroconid.
- 3 wide: its length is equal to or larger than the length of the anteroconid.

#### 5: metalophulid

- 2 absent: no anterior metalophulid; the antero-labial wall of the metaconid, or at least its base, is smooth and round.
- 3 anterior interrupted: either from the metaconid, or from the anterolophulid, or from both, a spur indicates the anterior metalophulid.
- 4 anterior complete: the anterior metalophulid is complete (and connected to the anterolophulid).
- 5 to anteroconid: the metalophulid is complete, and connected to the anteroconid.

#### 6: protoconid hind-arm (posterior branch of the protoconid)

- 2 absent: the posterior corner of the protoconid continues smoothly into the ectolophid.
- 3 short free: not longer than the width of the valley between protoconid and metaconid, not connected to the metaconid.
- 4 trans to mcd low: transversely connected to the metaconid at less than half the height of the metaconid.
- 5 trans to mcd high: transversal and at least half as high as the metaconid.
- 6 long free: oblique backwards, surpassing the width of the valley between protoconid and metaconid.
- 7 bent to mcd low: directed obliquely backward, and then curved and connected to the metaconid; less than half the height of the metaconid.
- 8 bent to mcd high: idem, but higher than half the height of the metaconid. In some cases the connection seems to be composed of a protoconid branch and a crest descending from the metaconid.

#### 7: sinusid

- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low cingulum (complete or incomplete) ridge is present.
- 4 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

## 8: sinusid

- 2 forward: the anterior or the posterior border of the sinusid is directed forward.
- 3 transverse: the posterior limit is transverse.
- 4 backwards: the posterior edge is curved backwards.

## 9: mesosinusid

- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low (complete or incomplete) cingulum ridge is present.
- 4 mcd ridge open: a ridge descends from the metaconid, and does not reach the entoconid.
- 5 mcd ridge closed: the ridge from the metaconid meets the entoconid.

## 10: ectolophid

- 2 longitudinal: a more or less longitudinal crest, parting from the lingual part of the protoconid.
- 3 oblique: running straight from the labial part of the protoconid towards the lingual tip of the hypoconid.
- 4 curved: from the labial part of the protoconid, curving towards lingual, and then connecting to the hypoconid.
- 5 interrupted: either not connected to the protoconid, or not connected to the hypoconid.

## 11: mesoconid

- 2 absent: the ectolophid is not swollen.
- 3 weak: the ectolophid is swollen and the base of the mesolophid is broad.
- 4 strong: there is a marked cusp.

## 12: mesolophid

- 2 absent: no trace of a mesolophid.
- 3 short: length less than one third of the distance between ectolophid and the lingual border.
- 4 medium: length between one third and half this distance.
- 5 long: more than half the width of the mesosinusid.
- 6 border: reaching the border of the molar.

## 13: 2nd mesolophid

- 2 absent: there is only one mesolophid.
- 3 short: length less than one third of the distance between ectolophid and the lingual border.
- 4 medium: length between one third and half this width.
- 5 long: more than half this distance.

## 14: ectomesolophid

- 2 absent: no trace of a labial spur on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid.
- 5 double: there are two crests, one of which arises from the mesoconid.

## 15: hypolophulid

- 2 anterior oblique: oblique and placed in front of the hypoconid.
- 3 anterior transverse: transverse, and placed in front of the hypoconid, or on its foremost point.
- 4 transverse: connected to the lingual wall of the hypoconid.
- 5 backwards: connected to the posterior corner of the hypoconid, or to the posterolophid.

## 16: hypoconid branch (posterior branch of the hypoconid)

- 2 absent: there is no crest branching off from the posterolophid.
- 3 short: not longer than two times the enamel thickness.
- 4 long: longer, but not connected to the entoconid.
- 5 long connected: connected to the base of the entoconid.

17: posterosinusid

- 2 open: the posterolophid does not meet the base of the entoconid.
- 3 closed: the posterolophid meets the base of the entoconid.

18: lab.posterolophid

- 2 absent: the posterior wall of the hypoconid is smooth.
- 3 small: the posterior wall of the hypoconid is irregular.
- 4 strong: there is a clear crest that may even enclose a tiny valley.

**M2 inf.**

1: labial anterolophid

- 2 absent: there may be a flat (inclined) surface, but there is no crest.
- 3 short: there is a crest, that does not reach the protoconid.
- 4 to protoconid: it reaches the protoconid base.
- 5 around protoconid: it separates the protoconid from the labial border, at least partly.

2: anterolophulid

- 2 absent: there is no connection between protoconid and anteroconid.
- 3 interrupted: the crest is interrupted, either between protoconid and metalophulid, or between metalophulid and anteroconid.
- 4 low: the entire crest, or part of it, is clearly lower than the anteroconid.
- 5 complete: the crest is continuous and (almost) as high as the anteroconid.

3: metalophulid

- 2 absent: no anterior metalophulid; the antero-labial wall of the metaconid is smooth and round, or the metaconid is fused with the anterolophid.
- 3 anterior interrupted: either from the metaconid, or from the anterolophulid, or from both, a spur indicates the anterior metalophulid.
- 4 complete to anteroconid: the anterior metalophulid is complete and connected to the anteroconid or to the anterolophid.
- 5 complete to anterolophulid: complete, and directed to some spot between anterolophid and protoconid.
- 6 complete to protoconid: complete, and connected to the (anterior corner of) the protoconid.

4: metalophulid spur

- 2 absent: no backward spur on the metalophulid.
- 3 weak: there is a weak backward spur, generally at the transition of metaconid to metalophulid.
- 4 strong: the spur is clearly visible, may be long; not in contact with the protoconid hind-arm, or, if so, clearly distinguishable.

5: protoconid hind-arm (posterior branch of the protoconid)

- 2 absent: the posterior corner of the protoconid continues smoothly into the ectolophid.
- 3 short free: not longer than the width of the valley between protoconid and metaconid, not connected to the metaconid.
- 4 trans to mcd low: transversely connected to the metaconid at less than half the height of the metaconid.
- 5 trans to mcd high: transversal and at least half as high as the metaconid.
- 6 long free: oblique backwards, or transverse; longer than the width of the valley between protoconid and metaconid.
- 7 bent to mcd low: directed obliquely backward, and then curved and connected to the metaconid; less than half the height of the metaconid.
- 8 bent to mcd high: idem, but higher than half the height of the metaconid. In some cases the connection seems to be composed of a protoconid branch and a crest descending from the metaconid.

## 6: sinusid

- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low cingulum ridge (complete or incomplete) is present.
- 4 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

## 7: sinusid

- 2 forward: the anterior or the posterior border of the sinus points forwards.
- 3 transverse: the posterior limit is transverse.
- 4 backwards: the posterior edge is curved backwards.

## 8: mesosinusid

- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low (complete or incomplete) cingulum ridge is present.
- 4 mcd ridge open: a ridge descends from the metaconid, and does not reach the entoconid.
- 5 mcd ridge closed: the ridge from the metaconid meets the entoconid.

## 9: ectolophid

- 2 high: the protoconid-ectolophid connection is continuous.
- 3 low: the ectolophid meets the protoconid at mid-height of its posterior wall.
- 4 interrupted: the ectolophid is separated from the protoconid.

## 10: mesoconid

- 2 absent: the ectolophid is not swollen.
- 3 weak: the ectolophid is swollen and the base of the mesolophid is broad.
- 4 strong: there is a marked cusp.

## 11: mesolophid

- 2 absent: no trace of a mesolophid.
- 3 short: length less than one third of the distance between ectolophid and the lingual border.
- 4 medium: length between one third and half this distance.
- 5 long: more than half this distance.
- 6 border: reaching the border of the molar.

## 12: mesolophid

- 2 simple: a simple crest.
- 3 branched: bifurcated at the top.

N.B. Absent mesolophid is classified under 'simple'.

## 13: ectomesolophid

- 2 absent: no trace of a labial spur on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid, or it is longer than 1/3 of the distance between ectolophid and the labial border.

## 14: hypolophulid

- 2 anterior oblique: oblique and placed in front of the hypoconid.
- 3 anterior transverse: transverse, and placed in front of the hypoconid, or on its foremost point.
- 4 transverse: connected to the lingual wall of the hypoconid.

## 15: hypoconid branch (posterior branch of the hypoconid)

- 2 absent: there is no crest branching off from the posterolophid.
- 3 short: not longer than two times the enamel thickness.
- 4 long: longer, but not connected to the entoconid.
- 5 long connected: connected to the base of the entoconid.



16: posterosinusid

- 2 open: the posterolophid does not meet the base of the entoconid.
- 3 closed: the posterolophid meets the base of the entoconid.

17: lab. posterolophid

- 2 absent: the posterior wall of the hypoconid is smooth.
- 3 small: the posterior wall of the hypoconid is irregular.
- 4 strong: there is a clear crest that may even enclose a tiny valley.

18: greatest width

- 2 anterior: the posterior part of the tooth is considerably broader than the anterior part.
- 3 equal: the tooth is almost rectangular.
- 4 posterior: the anterior part of the tooth is considerably broader than the posterior part.

**M3 inf.**

1: labial anterolophid

- 2 absent: there may be a flat surface descending from the anteroconid, but no crest.
- 3 short: it does not reach the protoconid.
- 4 to protoconid: it reaches the protoconid base.
- 5 around protoconid: it separates the protoconid from the labial border, at least partly.

2: anterolophulid

- 2 absent: there is no connection between protoconid and anteroconid.
- 3 interrupted: the crest is interrupted, either between protoconid and metalophulid, or between metalophulid and anteroconid.
- 4 short: it is complete and runs from protolophulid to anteroconid. The connection with the protoconid is transverse and forms the labial part of the metalophulid. Or, if connected to the protoconid directly, its length is less than the length of the protoconid.
- 5 long: the crest is complete and runs from protoconid to anteroconid, straight or curved.

3: anterosinusid

- 2 absent: there is no anterosinusid.
- 3 narrow: the valley is not wider than the enamel thickness.
- 4 wide: the valley is wider than the enamel thickness.

N.B. Absent only when the metalophulid is fused with the anterolophid; other wise estimate 'narrow' or 'wide'.

4: metalophulid

- 2 absent: no anterior metalophulid; the antero-labial wall of the metaconid is smooth and round, or the metaconid is fused with the anterolophid.
- 3 anterior interrupted: either from the metaconid, or from the anterolophid, or from both, a spur indicates the anterior metalophulid.
- 4 to anteroconid: the anterior metalophulid is complete and connected to the anteroconid.
- 5 to anterolophid: complete, and directed to some spot between anteroconid and protoconid.
- 6 to protoconid: complete, and connected to the (anterior corner of) the protoconid.

5: metalophulid spur

- 2 absent: no backward spur on the metalophulid.
- 3 weak: there is a weak backward spur, generally at the transition of metaconid to metalophulid.
- 4 strong: the spur is clearly visible, may be long, but is not in solid contact with the protoconid hind-arm.

## 6: protoconid hind-arm (posterior branch of the protoconid)

- 2 absent: the posterior corner of the protoconid continues smoothly into the ectolophid.
- 3 short free: not longer than the width of the valley between protoconid and metaconid, not connected to the metaconid.
- 4 trans to mcd low: transversely connected to the metaconid at less than half the height of the metaconid.
- 5 trans to mcd high: transversal and at least half as high as the metaconid.
- 6 long free: oblique backwards, surpassing the width of the valley between protoconid and metaconid.
- 7 bent to mcd low: directed obliquely backward, and then curved and connected to the metaconid. less than half the height of the metaconid.
- 8 bent to mcd high: idem, but higher than half the height of the metaconid. In some cases the connection seems to be composed of a protoconid branch and a crest descending from the metaconid.
- 9 long to border: connected to the cingulum ridge between metaconid and entoconid.

## 7: sinusid

- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low (complete or incomplete) cingulum ridge is present.
- 4 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

## 8: sinusid

- 2 forward: pointing obliquely forward.
- 3 narrow transverse.
- 4 broad transverse.
- 5 narrow backwards.
- 6 broad backwards.

'broad' means: the connection between protoconid and hypoconid is — at least partly — a longitudinal crest.

'narrow' means: there is no longitudinal part in the protoconid-hypoconid connection.

'transverse' means the posterior limit is transverse.

'backwards' means the posterior edge is curved backwards.

## 9: mesosinusid

- 2 open: the cingulum between metaconid and entoconid is interrupted.
- 3 closed: the cingulum between metaconid and entoconid is high and complete.

## 10: mesolophid

- 2 absent: no trace of a mesolophid.
- 3 short: length less than half the distance between ectolophid and the lingual border.
- 4 medium: length about half this distance.
- 5 long: length more than half this distance.
- 6 border: reaching the border of the molar.

## 11: mesolophid

- 2 simple: a simple crest
- 3 branched: bifurcated at the top

N.B. Absent mesolophid is classified under 'simple'.

## 12: ectolophid

- 2 low: a step-wise connection with the protoconid.
- 3 interrupted: not connected to the protoconid.
- 4 complete: a continuous connection with the protoconid.

13: mesoconid

- 2 absent: the ectolophid is not swollen.
- 3 weak: the ectolophid is swollen and the base of the mesolophid is broad.
- 4 strong: there is a marked cusp.

14: ectomesolophid

- 2 absent: no trace of a labial spur on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid, or it is longer than 1/3 of the distance between ectolophid and the labial border.

15: entoconid

- 2 absent: no trace of an entoconid.
- 3 small: a triangular swelling at the lingual end of the hypolophulid.
- 4 large: there is a cusp that rises above the level of the cingulum.

16: hypolophulid

- 2 anterior oblique: oblique and placed in front of the hypoconid.
- 3 anterior transverse: transverse, and placed in front of the hypoconid, or on its foremost point.
- 4 transverse: connected to the lingual wall of the hypoconid.
- 5 interrupted: the entoconid is isolated from the hypolophulid.

17: posterosinusid

- 2 open: the posterolophid is interrupted.
- 3 half closed: the posterolophid is low, before reaching the entoconid.
- 4 closed: the posterolophid is a continuous high crest.

18: shape

- 2 short triangle: lingual border straight, hypoconid smaller than protoconid.
- 3 long triangle: lingual border straight, hypoconid almost as large as protoconid.
- 4 trapezoid: lingual border concave.

**M1 sup.**

1: anterocone

- 2 simple: no trace of subdivision.
- 3 half-split: a slight incision in the wall of the anterocone.
- 4 bifid: two distinct cusps.
- 5 deeply split: split at least at half height of the anterocone.

2: prelobe

- 2 narrow set-off.
- 3 narrow continuous.
- 4 broad set-off.
- 5 broad continuous.

'narrow' means: half as wide (or less) than the tooth width.

'broad' means: more than half as wide as the tooth width.

'set-off' means: the lingual border between anterocone and protocone is angular.

'continuous' means: the lingual border between anterocone and protocone is smooth.

3: anterolophule

- 2 absent: the anterior wall of the protocone is smooth.
- 3 ac-spur: there is a backward spur on the anterocone.
- 4 pc-spur: there is a forward spur on the protocone.
- 5 ac + pc spurs: there are spurs on anterocone and protocone, but no continuous central crest.
- 6 complete: a complete crest between the anterolabial corner of the protocone and the (labial part of the) anterocone.
- 7 double: two posterior crests on the anterocone, either complete or incomplete.

## 4: forward pac-spur

- 2 absent: no spur on the anterior wall of the paracone.
- 3 free: ending free in the anterosinus.
- 4 to anterostyl: connected to the anterostyl.
- 5 to anterocone: a complete crest between paracone and anterocone (anterior ectoloph).

## 5: ling. anteroloph

- 2 incomplete: the anteroloph does not close the protosinus.
- 3 complete: the anteroloph closes the protosinus.
- 4 protostyl: the lingual anteroloph bears a cusp.

## 6: protocone platform

- 2 absent: no flat surface in front of the protocone.
- 3 small: a very small flat surface in front of the protocone, and lingually of the cingulum.
- 4 large: the flat surface is clearly visible.
- 5 crest: a crest on this platform, that may partly surround the protocone.

## 7: anterosinus

- 2 open: labial anteroloph absent or interrupted.
- 3 closed: labial anteroloph continuous towards the paracone.
- 4 anterostyl: the labial anteroloph bears a cusp.

## 8: protolophule

- 2 anterior interrupted: the anterior branch of the protocone skims the paracone or points towards the paracone; there is no posterior protolophule.
- 3 anterior: paracone connected to the anterior branch of the protocone.
- 4 anterior plus: anterior connection plus a trace of a posterior one.
- 5 transverse: paracone connected to the center of the protocone.
- 6 double: anterior and posterior connection complete.
- 7 posterior plus: posterior connection plus a trace of the anterior one.
- 8 posterior interrupted: no anterior connection; the posterior one is incomplete.
- 9 posterior: paracone connected to the posterior corner of the protocone or to the entoloph.
- 10 absent: no connection

N.B. if the anterior branch of the protocone points towards the anterocone it is not considered to be an interrupted anterior connection.

## 9: sinus

- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.
- 4 entostyl: cingulum complete or incomplete, there is an entostyl cusp.

## 10: sinus

- 2 strong forward: the tip of the sinus lies in between protocone and paracone.
- 3 forward: pointing forward, but not entering between protocone and paracone.
- 4 subdivided: strong forward, and the foremost part tends to get separated by a crest.
- 5 transverse: sinus more or less symmetrical.
- 6 backwards: pointing backwards.

## 11: entoloph

- 2 high: complete, smoothly ascending to, or level with protocone.
- 3 low: step-wise connection to protocone or protolophule.
- 4 interrupted: interrupted behind protolophule.

## 12: mesosinus

- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.
- 4 mesostyl: cingulum complete or incomplete, there is a mesostyl cusp.
- 5 mesostyl crest: the mesostyl forms a transverse crest, that is clearly separated from the mesoloph.
- 6 mesostyl to mesoloph: the crest is almost in contact with the tip of the mesoloph.

## 13: mesoloph

- 2 absent: no mesoloph.
- 3 short: shorter than half the distance between entoloph and labial border.
- 4 medium: about as long as half this distance.
- 5 long: longer than half the distance between entoloph and labial border.
- 6 interrupted: mesoloph medium or long, with a detached labial part that does not reach the border.
- 7 border: reaching the labial border.

## 14: 2nd mesoloph

- 2 absent: not a trace of a second mesoloph.
- 3 short: a very small spur on the entoloph, or on the protolophule, in front of the mesoloph.
- 4 long: a clearly visible spur.

## 15: entomesoloph

- 2 absent: no lingual spur on the entoloph.
- 3 short: some trace of an entomesoloph present.
- 4 long: the entomesoloph is more than a mere trace.
- 5 mesocone: there is a mesocone, that bulges into the sinus.

## 16: mesoloph-mc connection

- 2 absent: no longitudinal connection between mesoloph and metacone.
- 3 one crest: a (complete or incomplete) crest between metacone and mesoloph.

## 17: metalophule

- 2 anterior: either oblique, transverse, or curved towards the anterior tip of the hypocone, or towards the entoloph.
- 3 anterior interrupted: idem, but interrupted.
- 4 anterior plus: anterior plus a trace of a posterior connection.
- 5 transverse: towards the center of the hypocone.
- 6 double: both an anterior and a posterior connection.
- 7 posterior plus: posterior plus a trace of a anterior connection.
- 8 posterior: towards the posterior tip of the hypocone.
- 9 posterior interrupted: towards the posterior tip of the hypocone, interrupted.
- 10 absent: no connection.
- 11 to posteroloph: towards the posterior branch of the hypocone.
- 12 curved backward: longitudinal towards the posteroloph.

## 18: posterosinus

- 2 open: the posteroloph does not meet the metacone.
- 3 closed: the posteroloph meets the metacone.

## 19: labial border

- 2 concave: the labial border of the paracone lies lingually of a line connecting the labial borders of anterocone and metacone.
- 3 straight: the borders of the three cusps lie on one straight line.
- 4 convex: the labial border of the paracone lies labially of a line connecting the labial borders of anterocone and metacone.

**M2 sup.****1: lingual anteroloph**

- 2 absent: no anteroloph on the anterior wall of the protocone.
- 3 weak: there is a crest, but no protosinus.
- 4 strong: the anteroloph encircles a protosinus.
- 5 around pc: it is long and separates the protocone from the lingual border.

**2: protolophule**

- 2 anterior interrupted: the anterior connection is interrupted, there is no posterior one.
- 3 anterior: paracone connected to the anterior branch of the protocone, or to its anterior corner.
- 4 anterior plus: anterior connection plus a trace of a posterior one.
- 5 transverse: paracone connected to the center of the protocone.
- 6 double: anterior and posterior connection complete.
- 7 posterior plus: posterior connection plus a trace of the anterior one.
- 8 posterior interrupted: no anterior connection; the posterior one incomplete.
- 9 posterior: paracone connected to the posterior corner of the protocone or to the entoloph.
- 10 absent: no connection

**3: sinus**

- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.
- 4 entostyl: cingulum complete or incomplete, there is an entostyl cusp.

**4: sinus**

- 2 strong forward: the tip of the sinus lies in between protocone and paracone.
- 3 forward: pointing forward, but not entering between protocone and paracone.
- 4 subdivided: strong forward, and the foremost part tends to get separated by a crest.
- 5 transverse: sinus more or less symmetrical.
- 6 backwards: pointing backwards.

**5: mesosinus**

- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.
- 4 pac-spur: (partially) closed by a spur descending from the paracone.
- 5 mesostyl: cingulum complete or incomplete, there is a mesostyl cusp.
- 6 mesostyl crest: the mesostyl forms a transverse crest, that is clearly separated from the mesoloph.
- 7 mesostyl to mesoloph: the crest is almost in contact with the tip of the mesoloph.

**6: mesoloph**

- 2 absent: no mesoloph.
- 3 short: shorter than half the distance between entoloph and labial border.
- 4 medium: about as long as half this distance.
- 5 long: longer than half the distance between entoloph and labial border.
- 6 interrupted: mesoloph medium or long, with a detached labial part that does not reach the border.
- 7 border: reaching the labial border.

**7: 2nd mesoloph**

- 2 absent: not a trace of a second mesoloph.
- 3 short: a small spur, in front of the mesoloph, sprouting from the old entoloph or from the posterior protolophule.
- 4 long: the spur is longer.

8: mesoloph-mc connection

- 2 absent: no longitudinal connection between mesoloph and metacone.
- 3 one crest: 1 longitudinal crest between mesoloph and metacone.
- 4 two crests: 2 longitudinal crests between mesoloph and metacone.

9: entoloph-pc connection

- 2 high: the entoloph is connected to the top of the protocone, either horizontally, or ascending smoothly.
- 3 low: the entoloph is connected to the protocone at mid- height.
- 4 interrupted: the entoloph is not connected to the protocone.

10: pc-hc connection

- 2 absent: the walls and bottom of the sinus are smooth.
- 3 weak: a vague connection between protocone and entoloph or hypocone, through the sinus.
- 4 interrupted: there is a backward spur on the posterior wall of the protocone.
- 5 low: the connection is complete and lower than the entoloph.
- 6 complete: the connection is complete and (almost) as high as the entoloph.

11: metalophule

- 2 anterior: either oblique, transverse, or curved towards the anterior tip of the hypocone, or towards the entoloph.
- 3 anterior interrupted: idem, but interrupted.
- 4 anterior plus: anterior plus a trace of a posterior connection.
- 5 transverse: towards the center of the hypocone.
- 6 double: both an anterior and a posterior connection.
- 7 posterior plus: posterior plus a trace of an anterior connection.
- 8 posterior: towards the posterior tip of the hypocone.
- 9 posterior interrupted: towards the posterior tip of the hypocone, interrupted.
- 10 absent: no connection.
- 11 to posteroloph: towards the posterior branch of the hypocone.
- 12 curved backward: longitudinal towards the posteroloph.

12: posteroloph

- 2 open: the posteroloph does not meet the metacone.
- 3 closed: the posteroloph meets the metacone.

13: shape

- 2 subrectangular: the postero-lingual corner of the tooth is not reduced.
- 3 trapezoid: the postero-lingual corner of the tooth is reduced.

14: labial border

- 2 concave: the labial border of the mesosinus lies lingually of a line connecting the labial borders of paracone and metacone.
- 3 straight: the border of the mesosinus lies in line with a line connecting the labial borders of paracone and metacone.
- 4 convex: the border of the mesosinus lies labially of a line connecting the labial borders of paracone and metacone.

**M3 sup.**

1: lingual anteroloph

- 2 absent: no anteroloph on the anterior wall of the protocone.
- 3 weak: there is a crest, but no protosinus.
- 4 strong: the anteroloph encircles a protosinus.
- 5 around pc: it is long and separates the protocone from the lingual border.

## 2: protolophule

- 2 absent: no lingual connection of the paracone.
- 3 to anterocone: connected to the anterior border.
- 4 to anterolophule: connected to the crest between anterocone and protocone.
- 5 transverse: paracone connected to the center of the protocone.
- 6 double: anterior and posterior connection both more or less complete.

## 3: sinus

- 2 absent: protocone and hypocone connected along the border of the tooth.
- 3 very small: neo-entoloph slightly curved.
- 4 small: about half the transverse width of the protocone.
- 5 deep: neo-entoloph absent or incomplete.

## 4: neo-entoloph

- 2 absent: protocone and hypocone separated by the deeply protruding sinus.
- 3 interrupted: posterior spur on protocone or anterior spur on hypocone or both.
- 4 low: continuous connection lower than protocone and hypocone.
- 5 high: continuous connection as high as protocone and hypocone.

## 5: mesosinus

- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.

## 6: mesoloph

- 2 absent: no individualised mesoloph.
- 3 short: shorter than half the distance between entoloph or axioloph and labial border.
- 4 medium: about as long as half this distance.
- 5 long: longer than half the distance between entoloph and labial border.
- 6 border: reaching the labial border.

## 7: 2nd mesoloph

- 2 absent: not a trace of a second mesoloph.
- 3 short: a small spur, in front of the mesoloph, sprouting from the old entoloph or from the posterior protolophule.
- 4 long: the spur is longer.

## 8: old entoloph

- 2 absent: no spur on the lingual wall of the protocone.
- 3 short spur: spur on the labial wall of the protocone.
- 4 curved spur: spur bent backwards to form posterior axioloph.
- 5 long spur: extends transversely beyond the position of the axioloph (may include the mesoloph).
- 6 complete: curved crest between the labial wall of the protocone and hypocone or neo-entoloph.

## 9: axioloph

- 2 absent: no axioloph; if entoloph complete, then (posterior) axioloph is considered to be absent.
- 3 anterior spur: backward spur on protolophule, or old entoloph bent forwards.
- 4 posterior spur short: forward spur on hypocone or neo-entoloph or centroloph (old entoloph absent). In some cases this is identical to the centrocone. 'short' means: shorter than half the longitudinal width of the mesosinus.
- 5 posterior spur long: idem, but longer than half the longitudinal width of the mesosinus.
- 6 two spurs: both anterior and posterior spur are present (old entoloph absent).
- 7 complete: spurs are connected.



10: centroloph

- 2 absent: no metalophule-like structure.
- 3 weak: a weak crest sprouting from the neo-entoloph or anterior tip of the hypocone in any direction.
- 4 strong: a clearly visible crest, that may contain (part of) the mesoloph, metalophule, and/or ancient entoloph. Difference with the next item is, that it presents some complication, or doubt about its homology.
- 5 = metalophule: the centroloph is identical to the metalophule, without any complications.

11: centrocone

- 2 absent: no cusp in the center of the molar.
- 3 present: a cusp in the center of the molar, connected to the centroloph.
- 4 isolated: a central cusp without any connections.
- 5 on old entoloph: isolated from centroloph, bulge on old entoloph.

12: metacone

- 2 absent: at the position of the metacone the cingulum is a continuous ridge, not forming a cusp.
- 3 present: there is a (small) cusp.

13: posterosinus

- 2 open: the posteroloph does not meet the metacone.
  - 3 closed: the posteroloph meets the metacone.
- N.B. also defined if there is no centroloph or metalophule.

## References

- Bahlo, E., 1975. Die Nagetierfauna von Heimersheim bei Alzey (Rheinhessen, Westdeutschland) aus dem Grenzbereich Mittel/Oberoligozän und ihre stratigrafische Stellung. — Abh. Hess. Landesamt Bodenf., 71: 1-182.
- Bahlo, E., 1976. Gebiszreste von Cricetiden und Theridomyiden (Rodentia) aus dem Mitteloligozän von Gabsheim bei Alzey (Rheinhessen). — Mainz. Geowiss. Mitt., 5: 5-11.
- Brunet, M., M. Hugueney & Y. Jehenne, 1981. Cournon-les-Soumèroux: 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. Lacombe & M.A. Alvarez, 1989. Upper Oligocene micromammals from Pareja, Loranca Basin, prov. of Guadalajara, Spain. — Scripta Geol., 89: 27-56.
- Ducieux, J.-L., M. Hugueney & G. Truc, 1985. La formation des calcaires et lignites de Sigonce (Oligocène moyen, Bassin de Forcalquier, Alpes-de-Haute-Provence): Datation à l'aide des mammifères; reconstitution des milieux de dépôts. — Géobios, 18, 1: 109-114.
- Freudenthal, M., 1994. Cricetidae (Rodentia, Mammalia) from the Upper Oligocene of Mirambueno and Vivel del Río (Teruel, Spain). — Scripta Geol., 104: 1-55, 4 pls.
- Freudenthal, M., J.I. Lacombe, J. Martínez-Salanova & A. Sacristán, 1990. Nueva sucesión de niveles con micromamíferos en el Oligoceno de Montalbán (Prov. Teruel, España). — Acta Salmanticensia, 68: 133-140.
- Freudenthal, M., J.I. Lacombe & 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 (Teruel, Spain). —
- Hugueney, M., 1969. Les rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Branssat (Allier). — Docum. Lab. Géol. Fac. Sci. Lyon, 34: 1-227, 5 pls.
- Hugueney, M., 1971. *Pseudocricetodon philippi*, nouvelle espèce de Cricétidé (Rodentia, Mammalia) de l'Oligocène moyen de Saint-Martin-de-Castillon (Vaucluse). — C. R. Acad. Sci. Paris, D, 272, 20: 2533-2535.
- 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 Paleocology 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.
- Rémy, J.A., J.-Y. Crochet, B. Sigé, J. Sudre, L. de Bonis, M. Vianey-Liaud, M. Godinot, J.-L. Hartenberger, B. Lange-Badré & B. Comte, 1987. Biochronologie des phosphorites du Quercy: Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. — In: N. Schmidt-Kittler (ed.). Intern. Symp. on Mammal. Biostratigraphy and Paleocology of the European Paleogene, Mainz, Febr. 18-21, 1987. — Münchner Geowiss. Abh., A, 10: 169-188.
- Thaler, L., 1969. Rongeurs nouveaux de l'Oligocène moyen d'Espagne. — Palaeovertebrata, 2, 5: 191-207.
- Ünay-Bayraktar, E., 1989. Rodents from the middle Oligocene of Turkish Thrace. — Utrecht Micropal. Bull., 5: 1-119, 11 pls.

Manuscript received 30 November 1993.