Treb. Mus. Geol. Barcelona, 7: 11-93 (1998)

Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France

Matthijs FREUDENTHAL*, Pierre MEIN** and Elvira MARTÍN SUÁREZ***

RESUMEN

FREUDENTHAL, M., MEIN, P. y MARTÍN SUÁREZ, E. Revisión de los Cricetinae (Rodentia, Mammalia) del Mioceno Final y del Plioceno de España y Francia.

En este trabajo se analizan numerosas poblaciones de Cricetinae del Mioceno Final (Vallesiense, Turoliense) y del Plioceno de España y Francia. Se realiza una revisión taxonómica de los distintos géneros y especies atribuidos a esta subfamilia. Se discute la validez de los nombres de géneros empleados para la clasificación del material estudiado. Se reconocen cuatro géneros: *Cricetulodon* Hartenberger, 1966, *Rotundomys* Mein, 1966, *Neocricetodon* Schaub, 1934, y *Apocricetus* nov. gen. En relación con otros géneros reconocidos con anterioridad: *Kowalskia* Fahlbusch, 1969 se considera sinónimo de *Neocricetodon* Schaub, 1934; *Karstocricetus* Kordos, 1987 ha sido considerado sinónimo de *Neocricetodon* Schaub, 1934; *Cricetus* Leske, 1779 incluye únicamente especies actuales y pleistocenas.

Cricetulodon bugesiensis y *Neocricetodon ambarrensis* son especies nuevas, descritas a partir de material del Vallesiense Final de Francia.

Numerosas poblaciones de yacimientos del área estudiada han sido atribuidas a *Cricetus kormosi* Schaub, 1930, or *Cricetus* cf. *kormosi*; en nuestra opinión no están relacionadas con las de Europa central. Para ellas se propone la nueva especie *Apocricetus alberti*.

A partir de alguna especie de *Democricetodon* Fahlbusch, 1964 puede haber derivado el grupo *Cricetulodon* en Europa occidental que dará lugar, posteriormente, a *Rotundomys*.

Neocricetodon coloniza nuestra región en el Vallesiense Final procedente del Este. En una segunda migración, durante el Turoliense Inicial, *Apocricetus* colonizó Europa occidental.

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*Departamento de Estratigrafía y Paleontología. Universidad de Granada, 18071 Granada, Spain; e-mail elvira@goliat.ugr.es, and Nationaal Natuurhistorisch Museum, Postbus 9517, Darwinweg 2, 2333 CR Leiden, The Netherlands; e-mail freudenthal@naturalis.nnm.nl

**Centre des Sciences de la Terre, Université Claude-Bernard Lyon-I, 27-43 Bd. du 11 Novembre, F-69622 Villeurbanne Cedex; e-mail mein@cismsun.univ-lyon1.fr

***Departamento de Estratigrafía y Paleontología. Universidad de Granada, 18071 Granada, Spain; e-mail elvira@goliat.ugr.es

Durante el Turoliense Medio y Final se observan sucesivas apariciones, desapariciones y reapariciones de estos grupos; estos cambios faunísticos parecen relacionarse con acusados cambios climáticos. Después del Messiniense la situación se estabiliza y sólo quedan en nuestra región las especies de *Apocricetus* características de muchas faunas del Plioceno.

Palabras clave: Cricetinae, Rodentia, España, Francia, Mioceno, Plioceno.

ABSTRACT

A large number of populations of Cricetinae from the Late Miocene and the Pliocene of Spain and France is analyzed. After a discussion on the validity of the available genus names, four different genera are recognized: *Cricetulodon* Hartenberger, 1966, *Rotundomys* Mein, 1966, *Neocricetodon* Schaub, 1934, and *Apocricetus* nov. gen. *Cricetulodon bugesiensis* and *Neocricetodon ambarrensis* are new species, recognized in the Late Vallesian of France. *Apocricetus alberti* is a new species name, that replaces most of the previous citations of *Cricetus kormosi* Schaub, 1930, or *Cricetus* cf. *kormosi*, in our area.

The *Cricetulodon* group may be a local evolution, derived from some species of *Democricetodon* Fahlbusch, 1964 in the Early Vallesian, and evolving towards *Rotundomys*. *Neocricetodon*, on the other hand, is interpreted as a group immigrating from the East in the Late Vallesian. A second immigration wave in the Early Turolian brings *Apocricetus* into our area.

During the Middle and Late Turolian we see a continuous appearing, disappearing and re-appearing of these groups, that may be linked to the strong climatic changes of the Messinian. After the Messinian the situation is stabilized, and the only cricetine remaining is *Apocricetus*, characteristic for many Pliocene faunas.

Key words: Cricetinae, Rodentia, Spain, France, Miocene, Pliocene.

INTRODUCTION

Depéret (1890) was the first author who attributed a Neogene European cricetid to the genus *Cricetus* Leske, 1779: *Cricetus angustidens* Depéret, 1890. Schaub (1930) added *Cricetus kormosi*, and Mein & Michaux (1970) described *Cricetus barrierei*. Freudenthal & Kordos (1989) added a fourth species: *Cricetus polgardiensis*.

Cricetus kormosi Schaub, 1930 is not a *Cricetus*, and was transferred to the new genus *Pseudocricetus* by Topachevskii & Skorik, 1992. The type species of *Pseudocricetus* is *P. orienteuropaeus* Topachevskii & Skorik, 1992. The other species attributed to *Pseudocricetus* are *P. antiquus* Topachevskii & Skorik, 1992, and *Cricetus kormosi* Schaub, 1930. If *C. kormosi* is a *Pseudocricetus*, *C. polgardiensis* Freudenthal & Kordos (1989) may be placed in *Pseudocricetus* as well. *Pseudocricetus* is –among other things– characterized by the constant presence of the anterior protolophule in the upper molars, deeply split anteroconid of M_1, and strongly reduced mesolophids.

Cricetus angustidens is not a *Cricetus* either; we think the absence of anterior protolophules, the simple crest-like anteroconid, the deep valleys between protoconid and metaconid, and between protocone and paracone, are sufficient reasons to eliminate

C. angustidens from *Cricetus*; for the same reasons it cannot be placed in *Pseudocricetus*, and we place it in the new genus *Apocricetus*.

Cricetus barrierei Mein & Michaux, 1970 is somewhat smaller, and morphologically very close to *A. angustidens*; we follow the same procedure as before and place it in *Apocricetus* too.

Cricetus kormosi or *Cricetus* cf. *kormosi* has been cited from numerous Western European localities: Crevillente 6, Venta del Moro, Librilla, La Alberca (de Bruijn *et al.*, 1975), Valdecebro 3, Masada del Valle 7 (van de Weerd, 1976), Arenas del Rey (Boné *et al.*, 1978), La Dehesa, Salobreña (Brandy, 1979), La Tour (Aguilar *et al.*, 1982), Molina de Segura 9 (Agustí *et al.*, 1985), Arquillo 1, La Gloria 5, Villastar, Valdecebro 6 (Adrover *et al.*, 1993), etc. In our opinion, in all of these occurrences we are not dealing with *C. kormosi*, but with a species of *Apocricetus*, either *A. plinii* (Freudenthal, Lacomba & Martín Suárez, 1991), or *A. alberti* nov. sp., to be described hereafter.

A second frequently cited cricetine species is *Kowalskia* aff. *fahlbuschi* Bachmayer & Wilson, 1970, e.g. from Crevillente 1, 2, 3, 4 (de Bruijn *et al.*, 1975), Teruel area (van de Weerd, 1976). We revised these occurrences, and came to the conclusion, that they should be attributed to either *Neocricetodon occidentalis* Aguilar, 1982, or to *Apocricetus plinii.*

In this paper we will try to revise a large number of Spanish and French populations that have been attributed to *Neocricetodon*, *Kowalskia*, *Cricetulodon*, *Rotundomys*, *Cricetus kormosi*, *Cricetus barrierei*, and *Cricetus angustidens*, and a number of unpublished populations belonging to the same group of taxons.

Incidentally we will deal with some Central European species, but fundamentally we restrict our analysis to populations from Spain and France, though there is no doubt, that the "*Kowalskia*" populations from Central and Eastern Europe are essential to understand the evolution of this group,

Technical data

Measurements are taken as defined by Freudenthal (1966). The unit of measurement is 0.1 mm; in the measurements tables V' is the variability coefficient as defined by Freudenthal & Cuenca (1984). Terminology of the parts of the cheek teeth is after Freudenthal *et al.* (1994). The specimens with code FSL are kept in the Faculté des Sciences, Université Claude Bernard, Lyon. The specimens with code RGM are kept in the National Museum of Natural History, Leiden. The specimens with code CR22 and PUR4 are kept in the Departamento de Estratigrafía y Paleontología, Universidad de Granada.

Localities

Code	Locality	Studied collections
ACE	Casa del Acero (Murcia, Spain)	Sabadell
ALC	Alcoy (Alicante, Spain)	Lyon
AMB	Ambérieu (Ain, France)	Lyon

Code	Locality	Studied collections
BOT	Botardo (Granada, Spain)	Granada
CARAV	Caravaca (Murcia, Spain)	Utrecht, Lyon
CHABR	Chabrier (Vaucluse, France)	Lyon, Montpellier
CL	Can Llobateres (Barcelona, Spain)	Sabadell
CR	Crevillente (Alicante, Spain)	Leiden, Granada
CUC	Cucalón (Teruel, Spain)	Lyon
DION	Dionay (Isère, France)	Lyon
EICH	Eichkogel (Niederösterreich, Austria)	Vienna
FOURN	Lo Fournas (Pyrénées Orient., France)	Montpellier, Lyon
GLOR	La Gloria (Teruel, Spain)	Lyon
GOR	Gorafe (Granada, Spain)	Granada
KOHF	Kohfidisch (Burgenland, Austria)	Vienna
LIBR	Librilla (Murcia, Spain)	Lyon, Montpellier
LISS	Lissieu (Rhône, France)	Lyon
LOBR	Lobrieu (Vaucluse, France)	Lyon
MOLL	Mollon (Ain, France)	Lyon
Mt.HEL	Mt. Hélène (Pyrénées Orient., France)	Montpellier, Lyon
NGR	Negratín (Granada, Spain)	Granada
PED	Pedregueras (Zaragoza, Spain)	Utrecht
PUR	Purcal (Granada, Spain)	Granada
SERRAT	Serrat d'en Vacquer (Pyr. Orient., France)	Lyon
SETE	Sète (Hérault, France)	Montpellier, Lyon
SIF	Sifón de Librilla (Murcia, Spain)	Granada
SOBL	Soblay (Ain, France)	Lyon
VDM	Venta del Moro (Valencia, Spain)	Lyon
VISO	Fuente del Viso (Albacete, Spain)	Lyon

Uncoded localities

	Alfambra (Teruel, Spain)	Utrecht
	Arquillo (Teruel, Spain)	Lyon
	Castelnou (Pyr. Orientales, France)	Montpellier, Lyon
	Concud (Teruel, Spain)	Utrecht
	Cucuron (Vaucluse, France)	Lyon
	Douvre (Ain, France)	Lyon
	Freiria do Rio Maior (Portugal)	Lisbon
	Hauterives (Drôme, France)	Lyon
	Híjar (Albacete, Spain)	Madrid, Leiden
	La Tour (Basses-Alpes, France)	Montpellier, Lyon
	Loma del Castillo (Teruel, Spain)	Lyon
	Los Mansuetos (Teruel, Spain)	Utrecht
	Masada del Valle (Teruel, Spain)	Utrecht
	Masia del Barbo (Teruel, Spain)	Utrecht
	Montredon (Hérault, France)	Lyon, Leiden
	Port-la-Nouvelle (Aude, France)	Montpellier

Le Soler (Pyrénées Orient., France)	Lyon
Tortajada (Teruel, Spain)	Utrecht
Valdecebro 3 (Teruel, Spain)	Utrecht
Vilafant (Barcelona, Spain)	Sabadell
Villastar (Teruel, Spain)	Lyon
Villeneuve de la Raho (Pyr. Orient., France)	Lyon

VALIDITY OF THE GENUS NAME *NEOCRICETODON*

For a decision on the valid genus name of a variety of Late Miocene Cricetinae the following genera must be considered:

Neocricetodon Kretzoi, 1930
Neocricetodon Schaub, 1934
Epicricetodon Kretzoi, 1941
Neocricetodon Kretzoi, 1951
Rotundomys Mein, 1966
Cricetulodon Hartenberger, 1966
Kowalskia Fahlbusch, 1969

Kordos (1987) revived the name *Neocricetodon* Kretzoi, 1930, and Freudenthal & Kordos (1989) supported this nomenclatorial act. Engesser (1989) rejected this interpretation, because "Kretzoi never gave a description nor a figure nor indicated a collection number of the type of *Neocricetodon schaubi*."

However, Kretzoi (1951) did give a poor, though technically valid, description of *Neocricetodon schaubi*, and therefore the date of publication of *Neocricetodon* sensu Kretzoi is 1951 and not 1930. *Neocricetodon* Kretzoi, 1930 is an unavailable name in the sense of the International Guide of Zoological Nomenclature.

Schaub (1934) was the first to make the name *Neocricetodon* available. The type species of *Neocricetodon* is *Cricetulus grangeri* Young, 1927. *Epicricetodon* Kretzoi, 1941 is a junior synonym of *Neocricetodon*, and *Neocricetodon* Kretzoi, 1951 is a junior homonym of *Neocricetodon* Schaub, 1934. Daxner-Höck *et al.* (1996) gave a detailed review of the history of the name *Neocricetodon*, with which we agree completely.

This does not mean we agree with the interpretation of the physical contents of the genera *Neocricetodon*, *Cricetulodon* and *Kowalskia*, as proposed by Daxner-Höck *et al.* (1996). The validity of the genus name *Neocricetodon* being established, two questions have to be discussed:

1. Is it possible to distinguish between *Neocricetodon* and *Kowalskia* ?
2. Can *Cricetulodon* be distinguished from *Neocricetodon* (or *Kowalskia*) ?

1. Is it possible to distinguish *Neocricetodon* and *Kowalskia* ?

Daxner-Höck *et al.* stated (1996, p.223): "As long as we lack convincing arguments for the individuality of these two genera we should continue to further use the better-defined *Kowalskia*.", and "If this [additional] material proves to be identical to *Kowalskia*, this name will fall in synonymy of *Neocricetodon*..."

But the crucial phrase is "In some morphological features *Neocricetodon grangeri* is similar to *Kowalskia*, in others it is not". No details are given, and there is no differential diagnosis. Our conclusion is, that *Neocricetodon* and *Kowalskia* are identical, unless their difference be proven. The valid name is *Neocricetodon*.

2. Can *Cricetulodon* be distinguished from *Neocricetodon* ?

Daxner-Höck *et al.* (1996) gave an extensive differential diagnosis of *Neocricetodon* and *Cricetulodon*, without defining what species, in their opinion, belong to *Cricetulodon*. In the following analysis of their differential diagnosis we take *Cricetulodon* to contain the species *sabadellensis* Hartenberger, 1966, and *hartenbergeri* (Freudenthal, 1967). According to Daxner-Höck *et al.* the following features are supposed to characterize *Cricetulodon*:

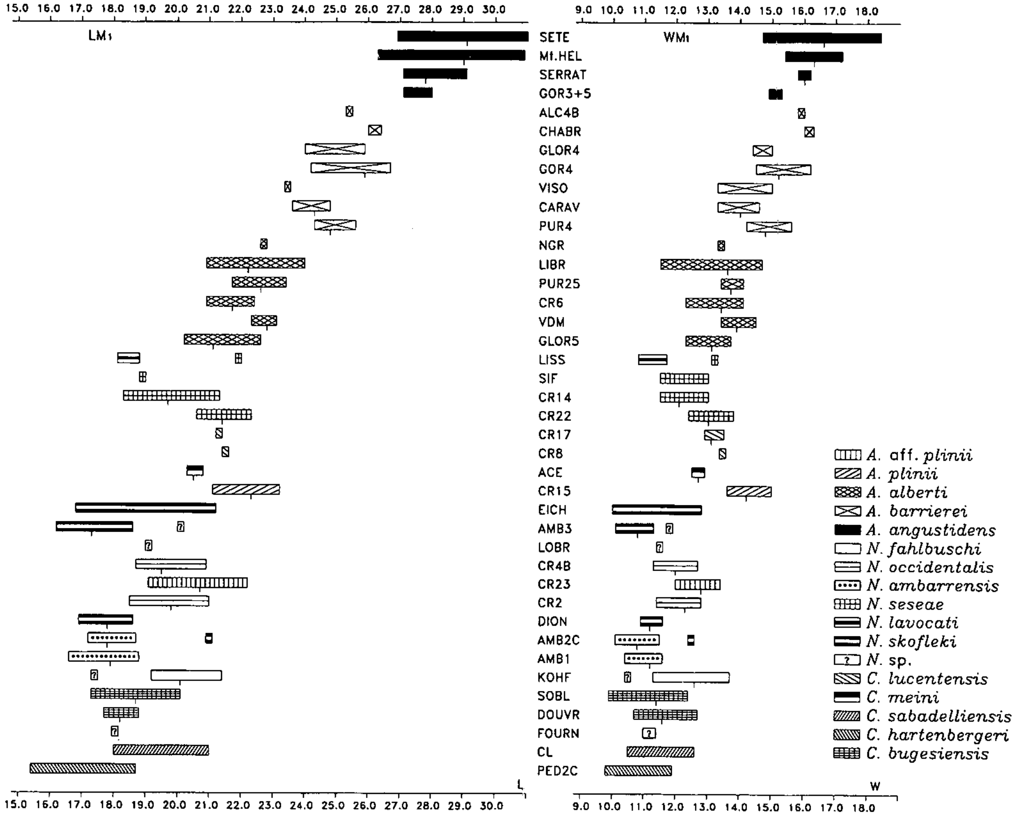

Fig. 1. Ranges of length and width of M_1. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 1. Rangos de longitud y anchura de los M_1. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

Width of sinuses-sinusids - This feature cannot serve to distinguish the two genera; it is difficult to assess, very subjective, and the widest valleys are possibly found in *N. fahlbuschi* (Bachmayer & Wilson, 1970) from Kohfidisch, and not in *Cricetulodon.*

Slender crests and high cusps –Neither in *C. sabadellensis* nor in *C. hartenbergeri* crests and cusps show a difference as compared with the many *Neocricetodon* species.

Anterocone short, asymmetrical, and split posteriorly– As far as the splitting of the anterocone is concerned the two genera are identical. The asymmetrical aspect of the anterocone is not real, but caused by the fact that *C. sabadellensis* generally has a simple anterolophule, connected to the labial anterocone cusp. In many *Neocricetodon* species specimens with a single anterolophule occur, and these show the same asymmetrical aspect. On the other hand the specimens of *C. sabadellensis* with forked anterolophule show an essentially symmetrical anterocone.

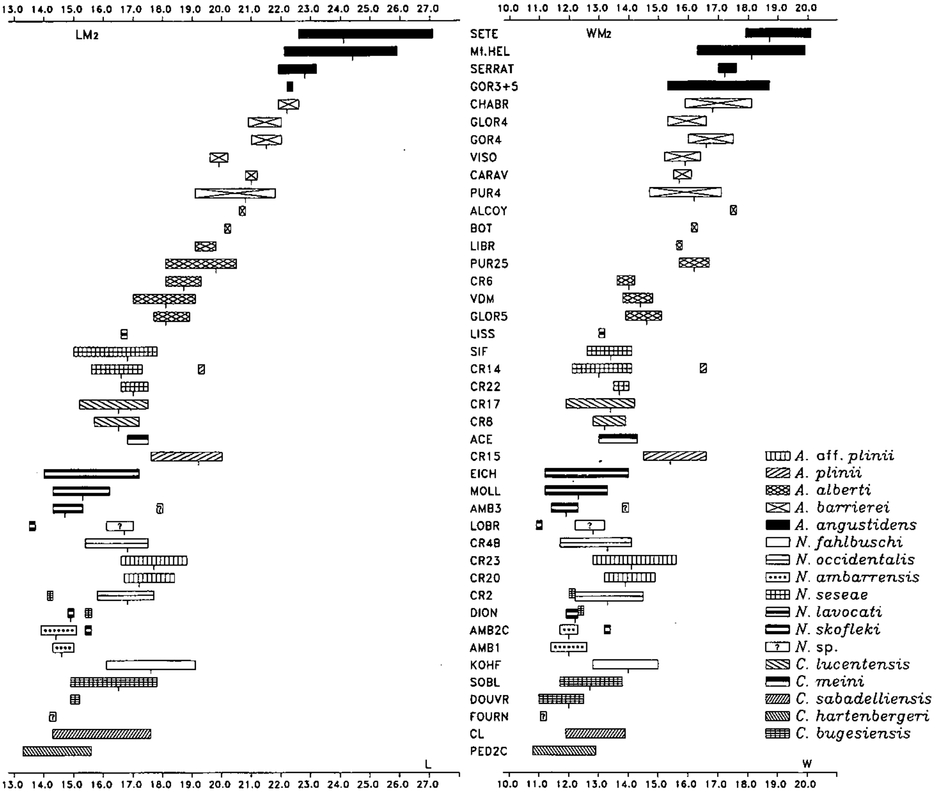

Fig. 2. Ranges of length and width of M_2. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 2. Rangos de longitud y anchura de los M_2. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

Anterolophule simple and strongly built - Forked anterolophules are found in *C. sabadellensis*, though not frequently. Whether or not the frequency of simple/forked anterolophules may serve as a distinctive character will be discussed hereafter.

Strong lingual anteroloph closing the protosinus - No differences are found between *Cricetulodon* and *Neocricetodon.*

Protolophule simple (posterior); if double, the posterior one dominates - The presence of the anterior protolophule of M^1 among the species of the *Cricetulodon/Neocricetodon* complex varies from nearly 100% to almost 0%. In *C. sabadellensis* 35% of the M^1 have this crest, in *C. hartenbergeri* it is present in 88% (6 out of 8 specimens). In *N. fahlbuschi* it is present in 70%, *N. occidentalis* 65%, *N. polonicus* 13%, etc. High and low percentages are found in both genera, and this character has no distinctive value at genus level. In the M^2 of *C. sabadellensis* the anterior protolophule is generally present like in *Neocricetodon.*

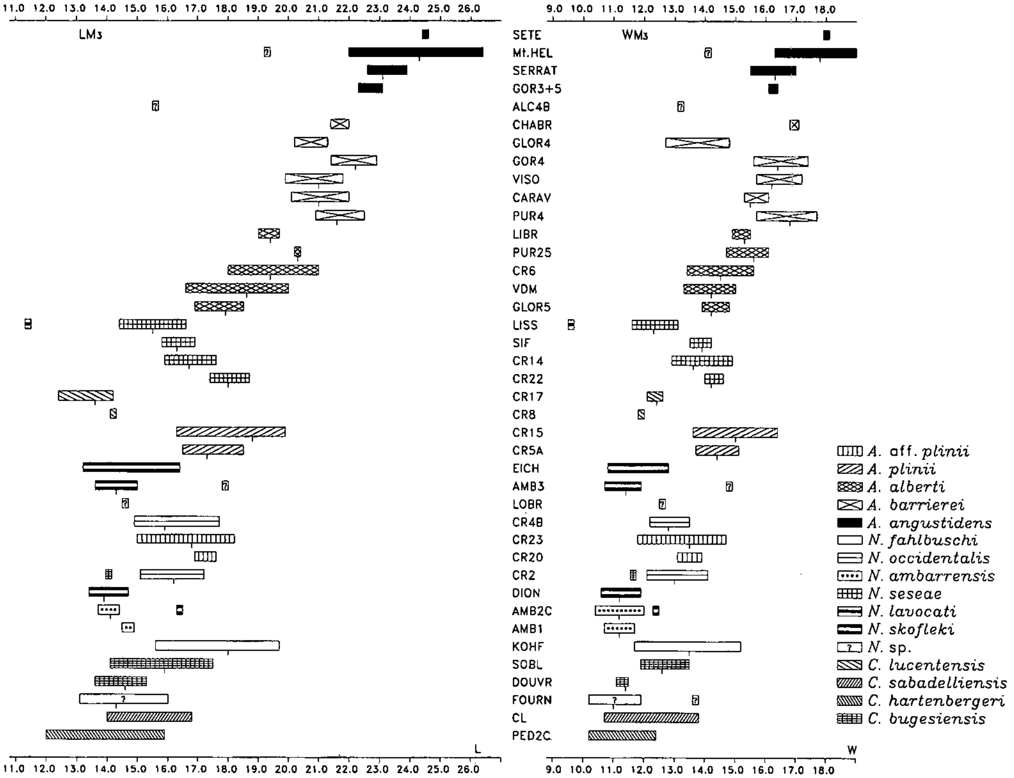

Fig. 3. Ranges of length and width of M_3. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 3. Rangos de longitud y anchura de los M_3. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

Metalophule simple (posterior); if double, the posterior one dominates - The anterior metalophule is absent in the M^1 of *N. polonicus*, and scarce in *C. sabadellensis*, so, better developed in the type-species of *Cricetulodon* than in the type-species of *Kowalskia*. Percentages vary largely throughout the species attributed to *Neocricetodon*, and are not easy to calculate, because they depend partially on the interpretation of the mesoloph/metalophule. In the M^2 of *C. sabadellensis* the anterior metalophule is scarce, like in M^1. In *Neocricetodon* it is variable like in M^1.

Molars 3-rooted - The M^1 of both *Cricetulodon* species are three-rooted. In *Neocricetodon* most populations contain a mixture of three- and four-rooted specimens. The percentage seems to be linked to absolute size and geological age; it is also possible that in eastern populations four-rooted specimens are more frequent than in western populations.

Anterolophulid lingual - Both *Cricetulodon* species have a dominantly lingual anterolophulid in M$_1$. This feature has been reported for *N. fahlbuschi* from Kohfidisch by Bachmayer & Wilson (1980). We revised the type-material of that species,

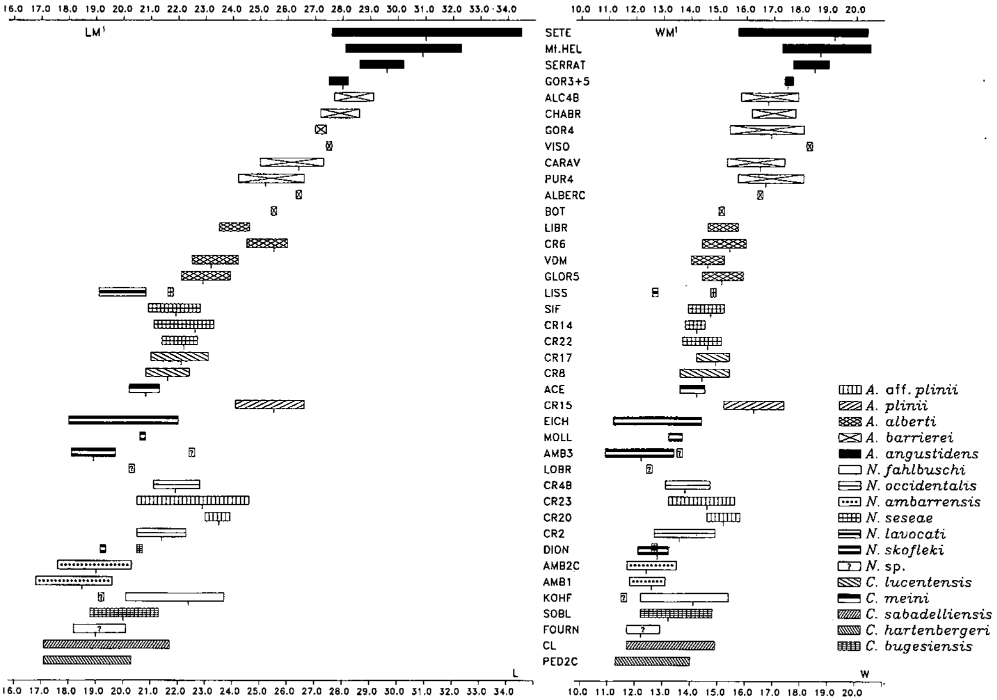

Fig. 4. Ranges of length and width of M^1. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 4. Rangos de longitud y anchura de los M^1. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

and cannot confirm the dominance of lingual anterolophulids. So, the lingual anterolophulid may be present in some *Neocricetodon* species, but its dominance is restricted to the two *Cricetulodon* species.

Metalophid and hypolophid oblique - For this feature no difference has been observed between *Cricetulodon* and *Neocricetodon.*

Mesolophid absent or short - The mesolophid is absent in the M_1 and M_2 of *C. sabadellensis*, in *C. hartenbergeri* it is present in 70% of the M_1 and 60% of the M_2. In the species attributed to *Kowalskia* (=*Neocricetodon*) by Daxner-Höck *et al.* (1996), the mesolophid is better developed, but for example in *N. occidentalis* the percentages for absence and presence are identical to those in *C. hartenbergeri.* Among eastern populations there seems to be a tendency to conserve the mesolophid, whilst it is reduced in western populations. Similar tendencies have been observed in e.g. *Megacricetodon*, and never were a reason to split up that genus.

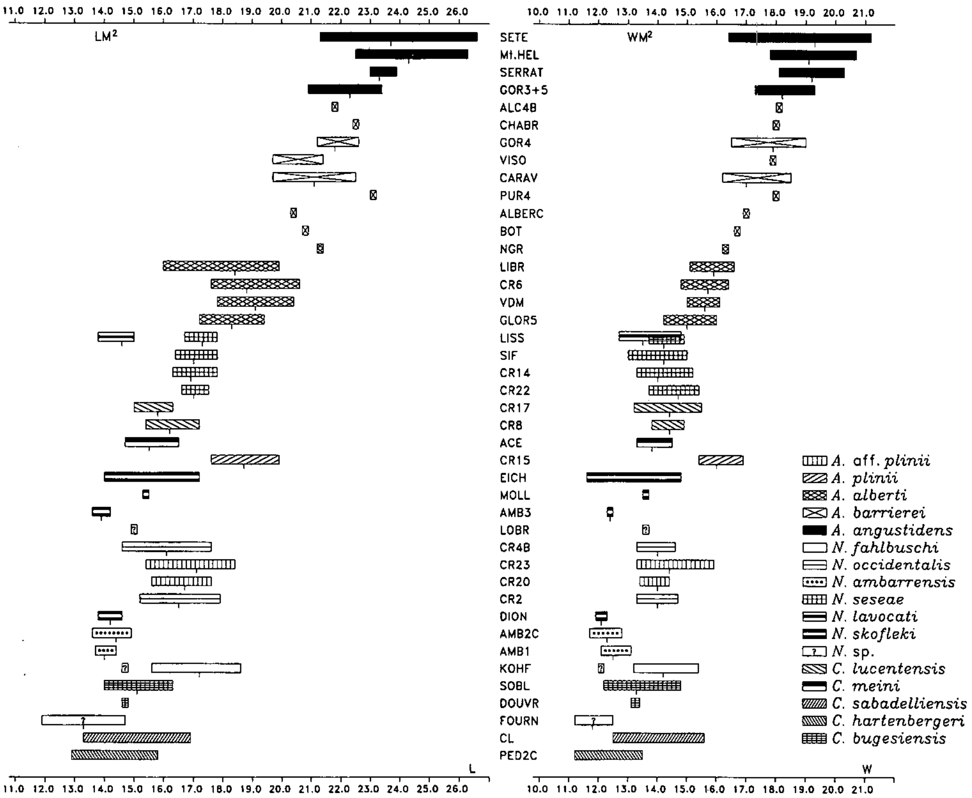

Fig. 5. Ranges of length and width of M^2. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 5. Rangos de longitud y anchura de los M^2. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

M_3 with reduced entoconid - The degree of reduction of the M_3 is quite variable. In some *Neocricetodon* populations (e.g. *N. occidentalis*) it is certainly not less reduced than in *Cricetulodon*.

We think that, among all the features mentioned, only the lingual anterolophulid of M_1 distinguishes *Cricetulodon* from *Neocricetodon*; once this difference is accepted, some other characters may serve as additional arguments.

The main reason, however, to consider *Cricetulodon* and *Neocricetodon* as two separate genera, is of a different nature, and will be discussed in the chapter on *Cricetulodon*.

Our interpretation of the contents of the genera under question is the following:

CRICETULODON Hartenberger, 1966

Type-species: *Cricetulodon sabadellensis* Hartenberger, 1966
Attributed species:
Rotundomys hartenbergeri Freudenthal, 1967
Kowalskia meini Agustí, 1986
Neocricetodon lucentensis Freudenthal, Lacomba & Martín Suárez, 1991
Cricetulodon bugesiensis nov. sp.

ROTUNDOMYS Mein, 1966

Type-species: *Cricetodon montisrotundi* Schaub, 1944
Attributed species:
Rotundomys bressanus Mein, 1975
Rotundomys mundi Calvo *et al.*, 1979
Rotundomys freiriensis Antunes & Mein, 1979

NEOCRICETODON Schaub, 1934

Type-species: *Cricetulus grangeri* Young, 1927
Synonymy: *Epicricetodon* Kretzoi, 1941; *Neocricetodon* Kretzoi, 1951; *Kowalskia* Fahlbusch, 1969; *Karstocricetus* Kordos, 1987
Attributed (European) species:
Neocricetodon schaubi Kretzoi, 1951
Cricetulus lavocati Hugueney & Mein, 1965
Kowalskia polonica Fahlbusch, 1969
Kowalskia magna Fahlbusch, 1969
Kowalskia intermedia Fejfar, 1970
Kowalskia fahlbuschi Bachmayer & Wilson, 1970
Kowalskia moldavica Lungu, 1981
Neocricetodon occidentalis Aguilar, 1982
Karstocricetus skofleki Kordos, 1987
Kowalskia nestori Engesser, 1989
Kowalskia browni Daxner-Höck, 1992
Neocricetodon seseae Aguilar, Calvet & Michaux, 1995
Neocricetodon ambarrensis nov. sp.

PSEUDOCRICETUS Topachevskii & Skorik, 1992

Type-species: *Pseudocricetus orienteuropaeus* Topachevskii & Skorik, 1992
Attributed species:
  Cricetus kormosi Schaub, 1930
  Cricetus polgardiensis Freudenthal & Kordos, 1989
  Pseudocricetus antiquus Topachevskii & Skorik, 1992

APOCRICETUS nov. gen.

Type-species: *Cricetus angustidens* Depéret, 1890
Attributed species:
  Cricetus barrierei Mein & Michaux, 1970
  Neocricetodon plinii Freudenthal, Lacomba & Martín Suárez, 1991
  Apocricetus alberti nov. sp.

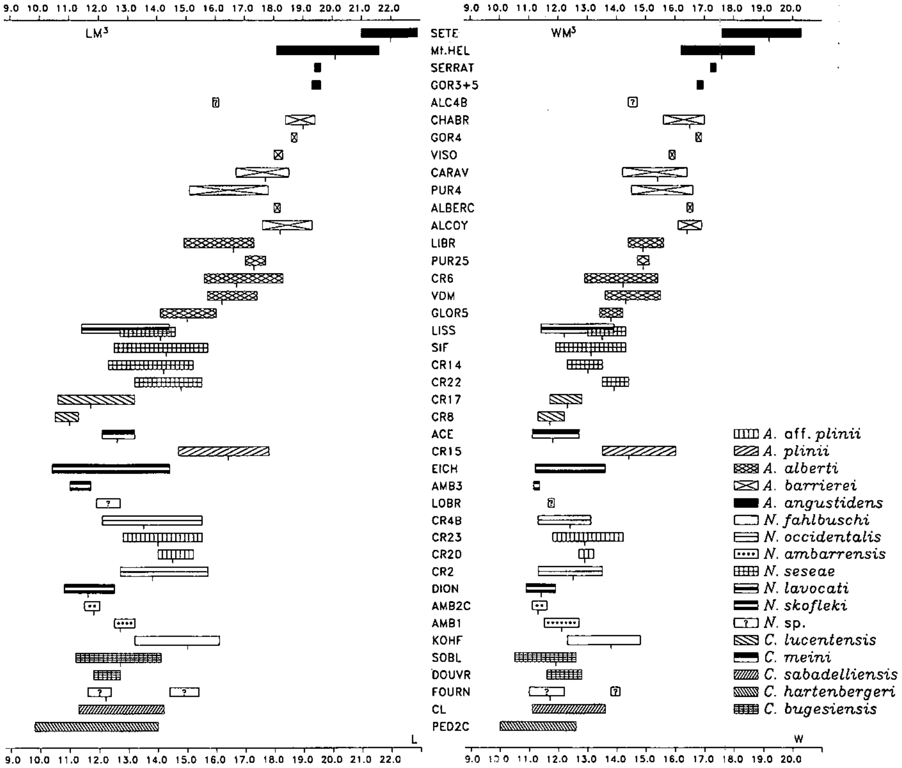

Fig. 6. Ranges of length and width of M³. Arithmetic mean indicated when three or more specimens are available. The material from Chabrier, Hautimagne, Terrats, and Celleneuve is represented under the designation Chabrier.

Fig. 6. Rangos de longitud y anchura de los M³. Se indica la posición de la media aritmética, cuando se dispone de tres o más piezas. El material de Chabrier, Hautimagne, Terrats y Celleneuve se presenta bajo la designación Chabrier.

SYSTEMATIC PALEONTOLOGY

Genus *Cricetulodon* Hartenberger, 1966

Type-species

Cricetulodon sabadellensis Hartenberger, 1966.

Attributed species

Rotundomys hartenbergeri Freudenthal, 1967; *Kowalskia meini* Agustí, 1986; *Neocricetodon lucentensis* Freudenthal, Lacomba & Martín Suárez, 1991; *Cricetulodon bugesiensis* nov. sp.

Emended diagnosis

Cricetinae of small to medium size. The anterolophulid of M_1 is dominantly lingual. Labial spur on the anterolophule of M^1 generally absent, rarely short. There is a tendency to reduce the mesoloph(id)s, the anterosinusid of M_2, and the postero-lingual corner of M_3. The M^1 is almond-shaped, with an almost straight labial border, and a strongly curved lingual border; the most lingual point lies behind the protocone. M^3 round, equally long and broad, often shorter than broad.

Cricetulodon sabadellensis Hartenberger, 1966

Holotype

Maxilla with M^1-M^2 dext., CL 1392, Institut de Paleontologia, Sabadell.

Type-locality

Can Llobateres (Barcelona, Spain).

Other localities

Viladecavalls (various sites), Torrent de Febulines M, Can Purull.

Description

Material from the type-locality:

C. sabadellensis from Can Llobateres was described in detail by Agustí (1981 and 1984). On the basis of Agustí's data, and personal observations, we characterize it as follows:

The anteroconid of M_1 is weakly or strongly subdivided into two cusps, although quite frequently there is no subdivision, or the anteroconid is tripartite. The lingual anterolophulid (80%) dominates strongly over the labial one (1.5%). Mesolophid in M_1 and M_2 generally absent, less frequently short; it is least developed in M_2, and best developed in M_3. The posterolophid closes the posterosinusid at a low level, or leaves that valley open. In M_2 the lingual anterolophid is absent, or –less frequently– small; in M_3 it is better developed, rarely absent. The anterocone of M^1 consists of two cusps connected by a crest; the anterolophule is single. The labial spur on the anterolophule is practically absent. The anterior protolophule is present in 35% of the M^1, 80% of the M^2, and nearly all M^3. The mesoloph of M^1 and M^2 is generally short, less frequently absent or of medium length, rarely long; it is less developed in M^2 than in M^1. Mesoloph of M^3 absent or present; when present it branches of from the anterior metalophule. Posterosinus and posterior metalophule of M^1 and M^2 are nearly always present, in M^3 absent. A small number of M^2 has four roots.

Material from various sites in Catalonia:

The specimen VP 469 (Coll. Sabadell) from Viladecavalls figured by Schaub (1947) is attributed to *Cricetulodon sabadellensis.* (Note that the legends to fig. 2 and fig. 5 in Schaub's paper are interchanged).

Cricetulodon sp. A. from Can Llobateres (Agustí, 1981). Protolophule of M^1 posterior or double (anterior branch low and weak). Anteroconid of M_1 weakly subdivided; no mesolophid in M_1 and M_2, short in M_3. These specimens may be attributed to *C. sabadellensis* (Agustí, pers. comm.).

Cricetulodon sp. B. from Can Purull (Agustí, 1981). Protolophule in M^1 and M^2 double (anterior branch low and weak). M^3 with double protolophule, and a short mesoloph; no mesolophid in M_1 and M_2. These specimens are attributed to *C. sabadellensis* too.

C. sabadellensis is also reported from Torrent de Febulines M, Terrassa. There are two M_1 with bifid anteroconid, smooth anterior wall, two anterolophulids, based on a prelophid. Data from Agustí (1981).

Discussion

The lingual position of the anterolophulid is the main characteristic of the genus. In *C. sabadellensis* it forms an oblique crest from the protoconid to the base of the lingual anteroconid cusp, or halfway up that cusp. When there is a labial anterolophulid it is lower than the lingual one, and does not form an X-shaped structure or a prelophid.

Agustí (1984) came to the conclusion, that there is a correlation between the absence of an anterior protolophule and the presence of a labial spur on the anterolophule, which might mean that these two characters are homologous. Contrary to Agustí's interpretation we think that in that case the anterior protolophule is the original state, and the spur on the anterolophule the derived state. In *Neocricetodon polonicus, N. fahlbuschi, N. occidentalis* (and many others) labial spur and anterior protolophule frequently coexist; may be the spur has not the same origin in *Neocricetodon* as in *Cricetulodon.*

Cricetulodon hartenbergeri (Freudenthal, 1967)

Holotype

M_1 sin., PEC 585, Institut de Paleontologia, Sabadell.

Type-locality

Pedregueras 2C (Zaragoza, Spain).

Other localities

Can Ponsich, Can Petit (Agustí, 1981).

Emended diagnosis

M_1 with bifid anteroconid, and lingual anterolophulid. Anterocone of M^1 subdivided. Mesolophids variable: absent, short, or long. Mesolophs vary between short and long, never absent. Anterior protolophule well-developed. Third molars moderately reduced. M^1 with 3 roots.

For a full description see Freudenthal (1967).

According to Agustí (1981) *C. hartenbergeri* from Can Ponsich is more primitive than the type-population from Pedregueras 2C: It is smaller and the mesoloph(id)s are longer. In M^1 the protolophule is always double, and in M_2 the anterior metalophule is generally present.

Cricetulodon meini (Agustí, 1986)

Holotype

M_1 dext., FCA-237, Institut de Paleontologia, Sabadell.

Type-locality

Casa del Acero (Alicante, Spain).

This species was described as *Kowalskia meini* by Agustí (1986). We transfer it to the genus *Cricetulodon* on the basis of the lingual anterolophulids in M_1, reduced mesoloph(id)s, and reduced M^3.

The size range of *C. meini* from Casa del Acero, as given by Agustí (1986) covers the lower part of the size range of *Neocricetodon occidentalis*, except for M^2 and M^3, that are significantly smaller. This is highly unlikely, since the relation M^1/M^2 is quite constant in this group. We remeasured most of the material, which was kindly put at our disposal by Dr Agustí, and this gave us normal values; the differences with Agustí's measurements are probably due to a different measuring method.

Description

M_1 - The anteroconid forms a smooth crest (1), it is bifid (1), or trifid (1); the splitting is very superficial, and affects both the anterior and posterior wall. The anterolophulid is simple, low, in a lingual position. The mesolophid is short and low (1), long and low (1), or absent (1).

M_2 - Mesolophid absent or long and low.

M_3 - The mandible fragment with $M_{2\text{-}3}$ (Agustí, op. cit., pl. 2, fig. 13) is too large to be attributed to the same species as the rest of the material. We exclude it from *C. meini.*

M^1 - The anterocone is split, but not very deep. The lingual anteroloph is well developed, the labial one is interrupted, or low; the funnel between anterocone and anterolophs is not complete, except in one very worn specimen. The anterior protolophule is complete (4) or interrupted (2). The mesoloph is absent (1), short (2), of medium length (2) or long (1); the medium-length mesoloph forms a badly developed anterior metalophule. There is no posterior metalophule, the metacone being directly connected to the posteroloph. The disposition of the roots is not known.

M^2 - The protocone is not separated from the lingual border. The protolophule is double; the mesoloph is absent (3), of medium length (2), long (1), or it forms an anterior metalophule (4); one specimen has a long mesoloph plus a low anterior metalophule. About half the specimens has a posterior metalophule. The posterolingual corner of the tooth is not very much reduced.

M^3 - The protolophule is double; in two specimens there is a longitudinal crest between protocone and paracone. The protocone is not separated from the lingual border. There may be a very weak cingulum at the anterolingual corner of the tooth (4), but there is no descending lingual anterolophule. The mesoloph is absent (2), or present as a spur on the metalophule (4). The metalophule is well developed. The hypocone and the sinus are larger than in *C. lucentensis.*

Cricetulodon lucentensis (Freudenthal, Lacomba & Martín Suárez, 1991)

Holotype

M_1 dext., RGM 404677, National Museum of Natural History, Leiden, The Netherlands.

Type-locality

Crevillente 17 (Alicante, Spain).

Other localities

Crevillente 8, Crevillente 5.

Description

Short description of the material from Crevillente 17 (for more details see Freudenthal *et al.*, 1991):

Protoconid and protocone are separated from the molar border in the majority of the specimens.

M_1 - Anteroconid simple. Anterolophulid interrupted or simple. Mesolophid absent or long.

M_2 - Anterosinusid generally very small. Mesolophid absent or short.

M_3 - Anterosinusid very small. Mesolophid absent.

M^1 - The anterocone is superficially split. The anterolophule is double and high. The protolophule is double or posterior. The mesoloph varies between absent and long. The posterior metalophule is absent or present. The labial wall is straight. 4 roots.

M^2 - The anterior protolophule is always present; the posterior one is missing in a few cases. The mesoloph is absent or of medium length. The posterior metalophule is absent or present.

M^3 - The protolophule is anterior or double. The mesoloph is absent, short or of medium length. The metalophule is absent, weak, or well-developed.

Discussion

This species is transferred to the genus *Cricetulodon*, because in some cases the anterolophulid of M_1 is clearly lingual (see Freudenthal *et al.*, 1991, pl. 5, fig. 2), and the third molars are strongly reduced. Further characteristics are the reduced anterosinusid of M_2, and the reduced mesolophids, though these reductions are not as strong as they are in *C. sabadellensis*. The M^1 of *C. lucentensis* has 4 roots, a disposition unknown in *C. sabadellensis*. A peculiar feature of the upper molars is the cingulum ridge that separates the protocone from the lingual border.

The first molars of *C. lucentensis* are larger than those of *C. sabadellensis*, the second molars are of the same size, and the third molars are on the average shorter.

In the differential diagnosis of *C. lucentensis* (see Freudenthal *et al.*, 1991) size was given as the difference between *C. lucentensis* and *C. meini*. After measuring the material of *C. meini* there appears to be no size difference between these two species. They are, however, sufficiently different to maintain both species names:

In *C. meini* the protocone is not separated from the lingual border; the funnel between the anterocone cusps of M^1 is incomplete; the hypocone and the sinus of M^3 are larger than in *C. lucentensis*. An ancestor-descendant relationship between *C. meini* and *C. lucentensis* is not impossible.

Cricetulodon bugesiensis nov. sp.
Plate 1, figs. 1-14

Holotype

M_1 sin., FSL 65897, Faculté des Sciences, Université de Lyon.

Type-locality

Soblay (Ain, France; Upper Vallesian, MN10).

Other localities

Douvre, Dionay, Crevillente 2, Lo Fournas 7?.

Derivatio nominis

From Bugey, the region of the Southern Jura, where the type-locality is located.

Diagnosis

Larger than *C. hartenbergeri*, about the size of *C. sabadellensis*. Anterolophulid of M_1 frequently double, with a tendency for the lingual branch to dominate. Anterosinusid in M_2 absent, in M_3 moderately developed. Anterolophule of M^1 simple or forked, labial spur on the anterolophule absent. Mesolophid may be present in M_1, generally absent in M_2 and M_3.

Anterior protolophule absent or present in M^1, present in M^2 and M^3. Mesoloph moderately developed in M^1 and M^2, practically absent in M^3. Anterior metalophule of M^1, when present, formed by the mesoloph. Anterior metalophule in M^2 generally absent; when present, it is a separate crest or it is formed by the mesoloph. Anterior metalophule in M^3 always present. Posterior metalophule in M^1 and M^2 absent or present.

Differential diagnosis

C. bugesiensis differs from the equally large *C. sabadellensis* by the frequently double anterolophulid of M_1, and the less pronounced lingual branch of this anterolophulid. There may be a prelophid (see Freudenthal, 1985).

Description

Material from the type-locality:

M_1 - The anteroconid is superficially split in most of the 21 specimens; in one specimen it is deeply split. The anterolophulid is interrupted, simple, or double. Contrary to the situation in *Neocricetodon occidentalis*, the simple anterolophulid may be connected to the lingual anteroconid cusp, and when it is double the lingual branch tends

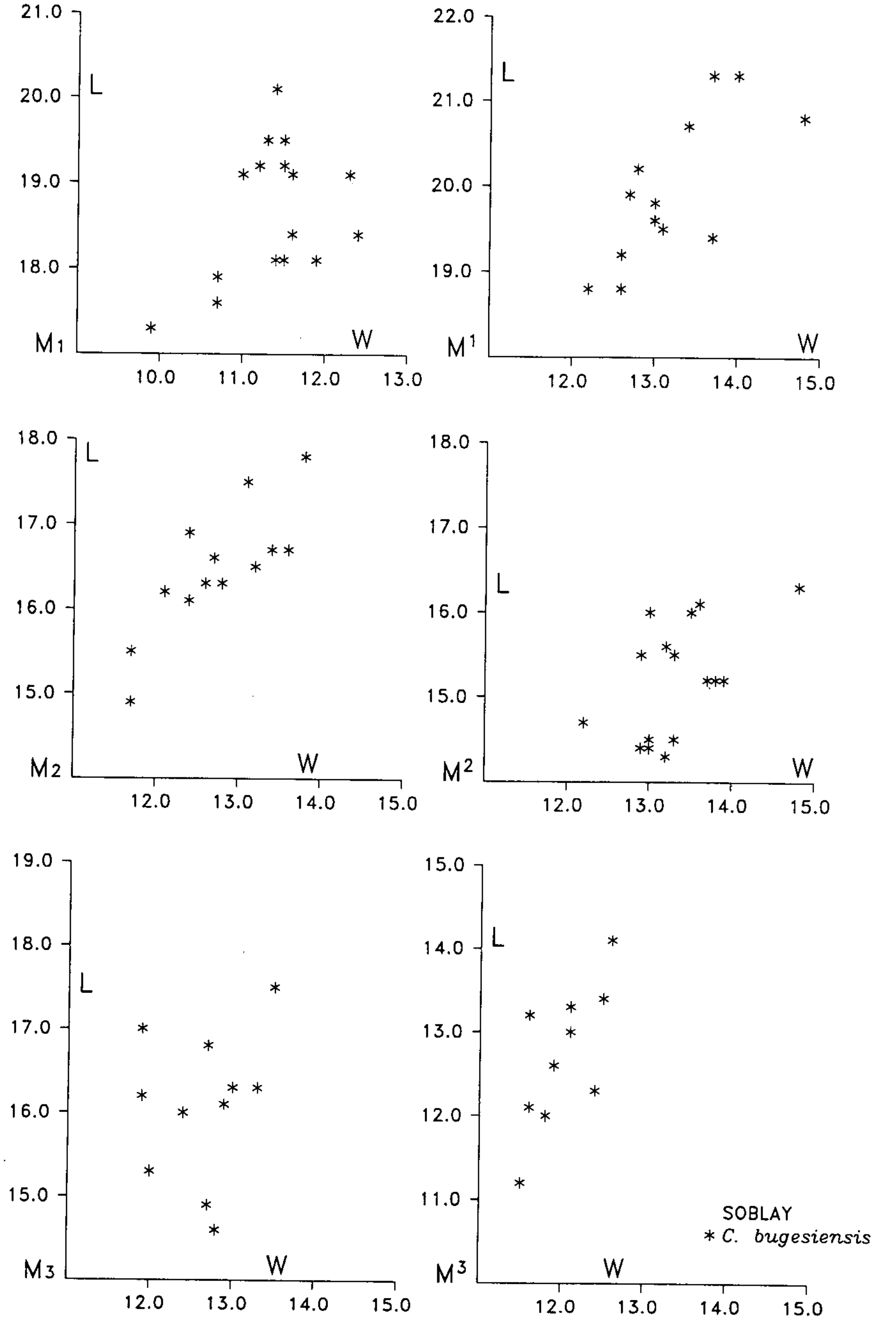

Fig. 7. Length/width diagrams of the molars of *Cricetulodon bugesiensis* nov. sp. from Soblay.

Fig. 7. Diagramas longitud/anchura de los molares de *Cricetulodon bugesiensis* nov. sp. del yacimiento de Soblay.

to dominate. The mesolophid is absent (10), short (3), or it reaches the molar border (6). In one of the specimens one gets the impression, that a half-long mesolophid has been transformed into the hypolophulid.

M_2 - The anterosinusid is absent except for a very small anterosinusid in the largest specimen; in some cases the lingual branch of the anterolophulid forms a weak ridge on the anterior wall of the metaconid (in *N. occidentalis* the lingual branch of the anterolophid frequently forms an anterosinusid). Among 13 specimens the mesolophid is short in three cases, reaching the molar border in another one, and absent in the rest of the specimens.

M_3 - The lingual branch of the anterolophid is much better developed than in M_2, and shows no difference with the situation in *N. occidentalis*. The mesolophid is absent in most cases, and the mesosinusid is frequently open on the lingual border.

M^1 - Anterocone superficially to deeply split. The anterolophule is a simple lingual crest (9), or forked (4). There is a free-ending spur in the anterosinus in only one case (the largest specimen). The protolophule is double (8) or posterior only (6). The mesoloph is absent (1), short (2), of medium length (6), or long (4), and never reaches the molar border. An anterior metalophule is formed by the mesoloph in 5 cases; the posterior metalophule is absent (7) or present (6). On the labial border the metacone protrudes strongly with respect to the paracone.

M^2 - The protolophule is double. The mesoloph is absent (7), short (4), of medium length (3), or long (4). An anterior metalophule is formed by the mesoloph in 3 cases; in 4 cases there is an anterior metalophule plus a mesoloph, and in 9 cases there is no anterior metalophule; the posterior metalophule is absent (6) or present (11).

M^3 - The lingual anteroloph varies between well-developed and almost non-existent. The protolophule is double. The mesoloph is absent (7), or present (3). The anterior metalophule is always present, though very low or interrupted in several cases.

The specimens are on the average larger than those of *C. hartenbergeri*, and smaller than those of *Neocricetodon occidentalis*. In the M_1 of *N. occidentalis* the labial anterolophulid is dominant, and the mesolophid reaches the molar border in most cases. In its M_2 the anterosinusid is rarely absent, and in its M_3 the mesolophid is always present. In the M^1 of *N. occidentalis* there is frequently a free labial spur in the anterosinus, the mesoloph of its M^2 is longer, and in its M^3 this crest is always present.

The dimensions of the Soblay material fall within the range of *Neocricetodon skofleki* from Eichkogel, but there are important differences: In *N. skofleki* the mesoloph(id)s are longer, the labial anterolophulid of M_1 dominates, the anterosinusid of M_2 is present, a long spur in the anterosinus of M^1 is very frequent, the posterior metalophule is always present.

The dimensions of *C. bugesiensis* partly overlap those of the population of *Neocricetodon fahlbuschi* from Kohfidisch. Differences are: In *N. fahlbuschi* the mesoloph(id)s are longer, and a long spur in the anterosinus of M^1 is frequent.

We attribute this population to *Cricetulodon* on the basis of the dominance of lingual anterolophulids, the absence of the anterosinusid in M_2, and the absence of a labial spur on the anterolophule of M^1.

Though the lingual anterolophulids are dominant in M_1 they are not quite comparable with the lingual anterolophulids of *C. sabadellensis*. In *C. bugesiensis* the anterolophulid is more frequently double, and the two branches may arise from a prelophid, whereas in *C. sabadellensis* double anterolophulids are less frequent, and there is no prelophid.

Some fragmentary specimens are larger than the specimens attributed to *C. bugesiensis*. They may represent some species of *Neocricetodon*, though determination of such poor material can not be reliable. Two M_1 have a long and thick mesolophid, and some of the largest specimens attributed to *C. bugesiensis* show a different morphology (see above), and might belong to this *Neocricetodon* too. On the basis of size and the strongly developed mesolophid, we might be dealing with *N. fahlbuschi* or *N. skofleki*.

On the other hand, a third M_1 (estimated length 21.0, width 12.8) has no mesolophid at all, and the lingual anterolophulid dominates over the labial one. This large specimen should be attributed to *Cricetulodon*. So, probably *Neocricetodon* and *Cricetulodon* coexist in Soblay; the *Neocricetodon* is on the average larger, but size ranges overlap.

Material from Douvre:

The material from Douvre is quite poor, but can be attributed to *C. bugesiensis*. It is of the same size.

In M_1 the anterolophulid is double in 3 cases, lingual in 2 cases; the mesolophid is absent (1), long (1), or it reaches the lingual border (3).

In M_2 the anterosinusid is absent (2), very small (1), or small (1); the mesolophid is absent (1), or long (3).

In M_3 the anterosinusid is well developed, and the mesolophid reaches the molar border; in one case there is a longitudinal connection between mesolophid and metaconid.

In the three M^2 the protolophule is double; the mesoloph is long (2), and both anterior and posterior metalophule are present.

In the two M^3 the protolophule is double, and the mesoloph is present. M^3 is short in comparison with the width.

The lingual anterolophulids and the long mesolophids are arguments for attributing this population to *C. bugesiensis*. The population from Douvre shows the same morphological variations as the type-population from Soblay, but frequencies may be different. The small anterosinusid in one of the four M_2 is the only feature not observed in the Soblay population. The mesolophid of $M_{2,3}$ and the mesoloph of M^3 are better developed in Douvre.

Material from Dionay:

Apart from *Neocricetodon skofleki* (Kordos, 1987), a second cricetine is found in the locality of Dionay, represented by an M_2 and an M^1. In the M_2 the mesolophid is absent, whereas it is very well developed in *N. skofleki*; the lingual anterolophid is absent. In the M^1 there is no labial spur on the anterolophule, and a short mesoloph, transformed into an anterior metalophule. Posterior metalophule and posterosinus are well-developed.

These two specimens are attributed to *C. bugesiensis*, though other options cannot be excluded.

Material from Crevillente 2:

A very small M_2, and two very small M_3 are excluded from the *N. occidentalis* population of Crevillente 2. These small specimens have a very much reduced lingual anterolophid (in M_2 almost non-existent), and may be classified as *Cricetulodon bugesiensis*.

Discussion of the genus *Cricetulodon*

C. hartenbergeri is the smallest and oldest species of the known Vallesian and Turolian European cricetines, and shows a mosaic distribution of characters. It may well be derived from some Late Aragonian Spanish *Democricetodon*, or it may represent an immigration from an eastern source, which may be a *Democricetodon* as well.

C. hartenbergeri may well be the ancestor of *C. sabadellensis*, as already supposed by Freudenthal (1967). This evolution is marked by a moderate size increase, development of trilobate anteroconids, reduction of mesoloph(id)s, and reduction of the anterior protolophule.

C. sabadellensis shows an advanced state of several derived characters: tripartition of the anteroconid in M_1, loss of the mesolophids in the lower molars, loss of the anterior protolophule in M^1. The mesoloph of M^1 and M^2 is absent or short, and there is no tendency to form an anterior metalophule. The M^3 is short, and there may be a mesoloph, visible as a spur on the anterior metalophule, but in most specimens the mesoloph is lost.

This advanced morphology, in combination with its old age (Early Vallesian) made us conclude, that *C. sabadellensis* may well be the ancestor of *Rotundomys*, but its advanced morphology makes it impossible that it be the ancestor of any *Neocricetodon* species, or of one of the other *Cricetulodon* species.

The morphology of *C. hartenbergeri*, in which none of the basic characters has suffered an important degree of reduction, makes it a suitable candidate for the ancestry of the later *Cricetulodon* species, *C. bugesiensis* and *C. lucentensis*, but we have not sufficient arguments to confirm or reject this hypothesis. It is not probable, that *C. lucentensis* be derived from *C. bugesiensis*, because in the latter species the anterosinusid of M_2 has already disappeared.

We are not in a position to judge whether *Cricetulodon complicidens* Topachevskii & Skorik, 1992, belongs to *Cricetulodon* or not. Some of the figured M_1 show a dominant labial anterolophulid, and the M^3 are quite reduced. On the other hand mesoloph(id)s, and labial spur of the anterolophule are well developed.

Genus *Rotundomys* Mein, 1966

Type-species

Cricetodon montisrotundi Schaub, 1944

Attributed species

Rotundomys bressanus Mein, 1975; *Rotundomys mundi* Calvo *et al.*, 1979; *Rotundomys freiriensis* Antunes & Mein, 1979; *Rotundomys* sp. nov. Freudenthal, Mein & Martín Suárez (in prep.).

Original diagnosis

"Primitive Cricetinae with cricetodontoid structure, in which all the cusps and crests that connect them have practically the same height, even in unworn teeth." (Translated from French.)

Emended diagnosis

Cricetinae with labial and lingual cusps, and connecting crests equally high. Valleys wide, and metaconid, entoconid, paracone and metacone crest-like. Wear surface turns into a flat, confluent pattern at an early stage of wear. Mesoloph(id)s absent. Posterosinusid not closed by posterolophid in M_1 and M_2, frequently closed in M_3. M^1 with 3 roots.

Rotundomys montisrotundi (Schaub, 1944)

Holotype

M_1 sin., A Mo 849, Naturhistorisches Museum Basel, figured in Mein (1966).

Type-locality

Montredon niveau Depéret (Hérault, France)

Other localities

Can Llobateres, Can Casablanques (Agustí, 1981).

Original diagnosis

"...characteristic is a strong cingulum on the outer side, descending from the protoconid, and closing the sinusid. The metalophulid continues into the hind arm of the protoconid, so that there is no longer a typical longitudinal crest. The metalophulid runs obliquely forward, the labial anterolophid encloses a wide valley at the antero-external corner of the crown." (Translated from German.)

Emended diagnosis

"In all teeth the cusps and crests that connect them have practically the same height; the valleys are closed by low cingulum ridges. No mesolophid, mesoloph only present in M^2 and M^3, connected to the metacone. In M_1 and M_2 the protoconid is directly connected to the entolophid, forming a regularly curved crest. The posterior metalophule is very much backwards, and the metalophulid point strongly forwards." (Translated from French, after Mein, 1966.)

Description

M_1 - Anteroconid and metaconid strongly connected. Their wear surface may remain separated from the rest of the tooth. The anterolophulid may be absent, but it is generally strongly developed, either lingual, central, or labial, lower than the wear surface. The posterolophid is not connected to the entoconid.

M_2 - Lingual anterolophid absent, or forming a small ridge at the base of the metaconid. The posterolophid may reach the base of the entoconid.

M_3 - Lingual anterolophid like in M_2. Ectolophid strongly oblique. The posterolophid may be free from the entoconid, but generally it closes the posterosinusid, and this connection may be high.

M^1 - The anterolophule is single or forked. Anterior protolophule and anterior metalophule absent; posterior protolophule transverse or oblique. In a few cases there is a short mesoloph. The end of the posteroloph forms a small low ridge on the posterior wall of the metacone. In 1 out of 20 specimens there is a posterior metalophule and a very small posterosinus. There sometimes is a very small fourth root in the center of the molar. Generally there are 3 roots, and the internal root may be grooved.

M^2 - The end of the labial anteroloph is low, and often free from the paracone; when connected the connection is very low. There may be a very short mesoloph. In 5 out of 20 specimens there is a posterior metalophule, and a small posterosinus. The internal root may be simple, split at its end, and grooved all over its length, or there are four roots.

M^3 - Labial anteroloph like in M^2. There is sometimes a longitudinal connection between the paracone and the anteroloph, which may be interpreted as an anterior protolophule, which has shifted linguad. It is sometimes difficult to distinguish M^2 and M^3. In M^3 there is a crest from hypocone to metacone (centroloph), that may be either metalophule or mesoloph. In M^2 there is never more than a very small trace of such a crest, in M^3 it is generally complete.

Rotundomys bressanus Mein, 1975

Synonymy

Rotundomys bressanus microtoides Agustí, 1981

Holotype

M^1 sin., FSL 65443, Faculté des Sciences, Université de Lyon.

Type-locality

Soblay (Ain, France).

Other localities

Terrassa, Can Perellada, Santa Margarida, Can Jofresa (Agustí & Gibert, 1982).

Original diagnosis

"Slightly larger than *R. montisrotundi*, higher crowned and with deeper valleys. Entoloph and ectolophid arched, forming sharp re-entrant angles, whilst these crests are smoothly curved at Montredon. Sinus and sinusid deep. The crests that connect the cusps are thickened, and, from a medium state of wear onwards, a continuous, sigmoidal crest runs through the entire tooth. The cingulums that close the valleys in *R. montisrotundi* have almost completely vanished. In the upper molars the posteroloph, which is completely fused with the metalophule, does not continue labially; in the lower molars the posterolophid is short and transverse, and no longer in contact with the entoconid." (Translated from French.)

Discussion

Aguilar (1981) considered *R. bressanus* to be a synonym of *R. montisrotundi*, because the entire range of measurements of *R. bressanus* is contained in the range of his sample of *R. montisrotundi*. Close comparison shows, that *R. bressanus* occupies only the upper part of the range of distribution of *R. montisrotundi*, and that the holotype is larger than any specimen of *R. montisrotundi*.

A relatively easy character to distinguish these two species is the shape of the wear surface of the protoconid and protocone: in *R. montisrotundi* the wear surface of these cusps is an equilateral triangle; in *R. bressanus* the wear surface of the protocone is compressed antero-posteriorly and enlarged transversely, presenting itself as a transverse crest; the wear surface of the protoconid is triangular, but the posterior side of this triangle is concave, giving the labial part of the protocone a transverse crest-like appearance. This goes together with a frequently more labial position of the ectolophid of the lower molars, and a more lingual position of the entoloph of the upper molars of *R. montisrotundi*.

The original diagnosis states that the cingulums that close the valleys have almost completely disappeared. As a general statement this is not true; an important distinctive character of *R. bressanus* is, however, the reduction of the cingulum (=labial anterolophid) between anteroconid and protoconid in M_1, and of the connection between posterolophid and entoconid in M_3.

Agustí (1981) created the subspecies *Rotundomys bressanus microtoides*, but the same author suppressed this subspecies in 1982 (Agustí & Gibert, 1982), maintaining the validity of the species *R. bressanus*.

Agustí & Gibert, 1982 described a number of populations of *R. bressanus* that all are on the average larger than *R. montisrotundi*.

Rotundomys mundi Calvo, Elizaga, López Martínez, Robles & Usera, 1979

Holotype

M^2 dext., H-7, Calvo *et al.*, 1979, fig. 8, 1.

Type-locality

Híjar 1 (Albacete, Spain)

Discussion

Brandy (1979) mentions an M^1 and an M^3 of *R. montisrotundi* (Schaub, 1944) from Híjar. Calvo *et al.* (1979) describe a small collection from the same locality as a new species, *R. mundi.*

Aguilar (1981) considered *R. mundi* to be a synonym of *R. montisrotundi*, and Agustí & Gibert (1982) accepted that interpretation.

The measurements given by Calvo *et al.* coincide perfectly with those of *R. montisrotundi*, and the figured morphotypes of *R. mundi* are present in *R. montisrotundi.* The supposed presence of an anterior protolophule and a double metalophule in *R. mundi* are based on a misinterpretation of the crests: there is no anterior protolophule in M^3, but a connection between paracone and anteroloph, which is distinct from an anterior protolophule; neither is there a double metalophule, since the connection between posteroloph and metacone is not a metalophule.

In spite of this misinterpretation it must be admitted that an M^2 with complete anterior metalophule is rare in Montredon: about 5% according to Aguilar (1981), but, as said in the paragraph on *R. montisrotundi* it is often difficult to distinguish M^2 and M^3, and it is possible that the M^2 morphotype d (and maybe also morphotype e) of Aguilar are in fact M^3. E.g. his specimen MTN 941, (Aguilar, 1981, fig. 15) seems to be an M^3 and not an M^2, so even the percentage of 5% may be exaggerated.

Furthermore, M^3 with a strong connection between anteroloph and paracone, like seen in the specimens from Híjar 1, are unknown in Montredon.

So, there are some arguments in favor of maintaining *R. mundi* as a separate species. In *Rotundomys* sp. (Agustí & Gibert, 1982) from Can Perellada and Can Jofresa the same features seem to be present that distinguish *R. mundi* from *R. montisrotundi.*

Agustí (1981) recognized *R. mundi* in Terrassa, and in 1982 the same author changed it into *Rotundomys* sp. The 1981 interpretation may have been correct, and the material from Can Perellada and Can Jofresa may well belong to *R. mundi* too.

Rotundomys freiriensis Antunes & Mein, 1979

Holotype

M_1 sin., Coll. Centro de Estratigrafia e Paleontologia da Universidade Nova de Lisboa.

Type-locality

Freiria do Rio Maior (Portugal).

Original diagnosis

"*Rotundomys* of small size, characterized by the isolation of the anterolophid of M_1, and by the transverse direction, in the same teeth, of the metalophulids." (Translated from French.)

R. freiriensis is the least typical of the known species of *Rotundomys*, because the anterolophulid of M_1 is lacking, and the typical confluent pattern of the molars of the other species is not formed. It is furthermore characterized by the almost complete loss of the anterior metalophule in M^3, and by the interruption of the hind arm of the protocone in M^2 and M^3.

Discussion on the genus *Rotundomys*

Freudenthal (1967) supposed *Cricetulodon sabadellensis* to be the ancestor of *Rotundomys montisrotundi*. This theory cannot be maintained, if these two species coexist in Can Llobateres, as stated by Agustí (1984). Anyway, in extreme cases they are not easy to distinguish, and their close relationship is beyond doubt.

Mein (1975) considered *R. bressanus* to be derived from *R. montisrotundi*, and we did not find any arguments against this hypothesis.

The youngest species known, *R. freiriensis*, shows several features that make a direct relationship with *R. bressanus* improbable.

A new species of *Rotundomys* from Douvre which may well be the ancestor of *R. montisrotundi* is being described by the present authors, and will be published in a separate paper.

Genus *Neocricetodon* Schaub, 1934

Synonymy

Epicricetodon Kretzoi, 1941; *Neocricetodon* Kretzoi, 1951; *Kowalskia* Fahlbusch, 1969; *Karstocricetus* Kordos, 1987

Type-species

Cricetulus grangeri Young, 1927

Attributed European species

Neocricetodon schaubi Kretzoi, 1951; *Cricetulus lavocati* Hugueney & Mein, 1965; *Kowalskia polonica* Fahlbusch, 1969; *Kowalskia magna* Fahlbusch, 1969;

Kowalskia intermedia Fejfar, 1970; *Kowalskia fahlbuschi* Bachmayer & Wilson, 1970; *Karstocricetus skofleki* Kordos, 1987; *Kowalskia moldavica* Lungu, 1981; *Neocricetodon occidentalis* Aguilar, 1982; *Kowalskia nestori* Engesser, 1989; *Kowalskia browni* Daxner-Höck, 1992; *Neocricetodon seseae* Aguilar, Calvet & Michaux, 1995; *Neocricetodon ambarrensis* nov. sp.

Emended diagnosis

Cricetinae of small to medium size. The anterolophulid of M_1 is dominantly labial. Labial spur on the anterolophule of M^1 frequently well-developed. There is a tendency to maintain the mesoloph(id)s, and the anterosinusid of M_2. The third molars are not very much reduced, and may be elongated.

Neocricetodon lavocati Hugueney & Mein, 1965

Holotype

M^3 sin., FSL 65212, Faculté des Sciences, Université de Lyon. This specimen was described by Hugueney & Mein as an M^2; we now interpret it as an M^3; there is a short mesoloph, based on the anterior metalophule, a common situation in the M^3 of many species, and probably non-existent in M^2. The lingual anteroloph is very small, and does not form a protosinus.

Type-locality

Lissieu (Rhône, France)

Description

The collection from Lissieu has been enlarged considerably since its publication in 1965; for measurements see Fig. 8. It is now clear that, besides the small *N. lavocati*, there is a second, larger, *Neocricetodon* at Lissieu. Two M_1 are smaller than the lower limit of *N. occidentalis* Aguilar, 1982, and are characterized by a long mesolophid, that reaches the molar border; a third specimen reaches the upper size limit of *N. occidentalis*, its anteroconid contains 3 cusps, and it has no mesolophid at all. The mesolophid nearly always reaches the molar border. Some M_3 make a massive impression, due to the fact, that the posterior part is hardly reduced, and almost as broad as the anterior half.

One M_3 is as small as the small specimens from Crevillente 2, that are now attributed to *C. bugesiensis* nov. sp. (see above), and its postero-lingual corner is reduced. A second one, described as Cricetidae sp., (FSL 65216, measurements 11.4 x 9.6, Hugueney & Mein, 1965, pl. 2, fig. 55), is even much smaller. The other nine fall in the size range of *N. occidentalis*. Since we now recognize two species in Lissieu, and *N. lavocati* in our opinion is a very small species, we think, this very small M_3 may

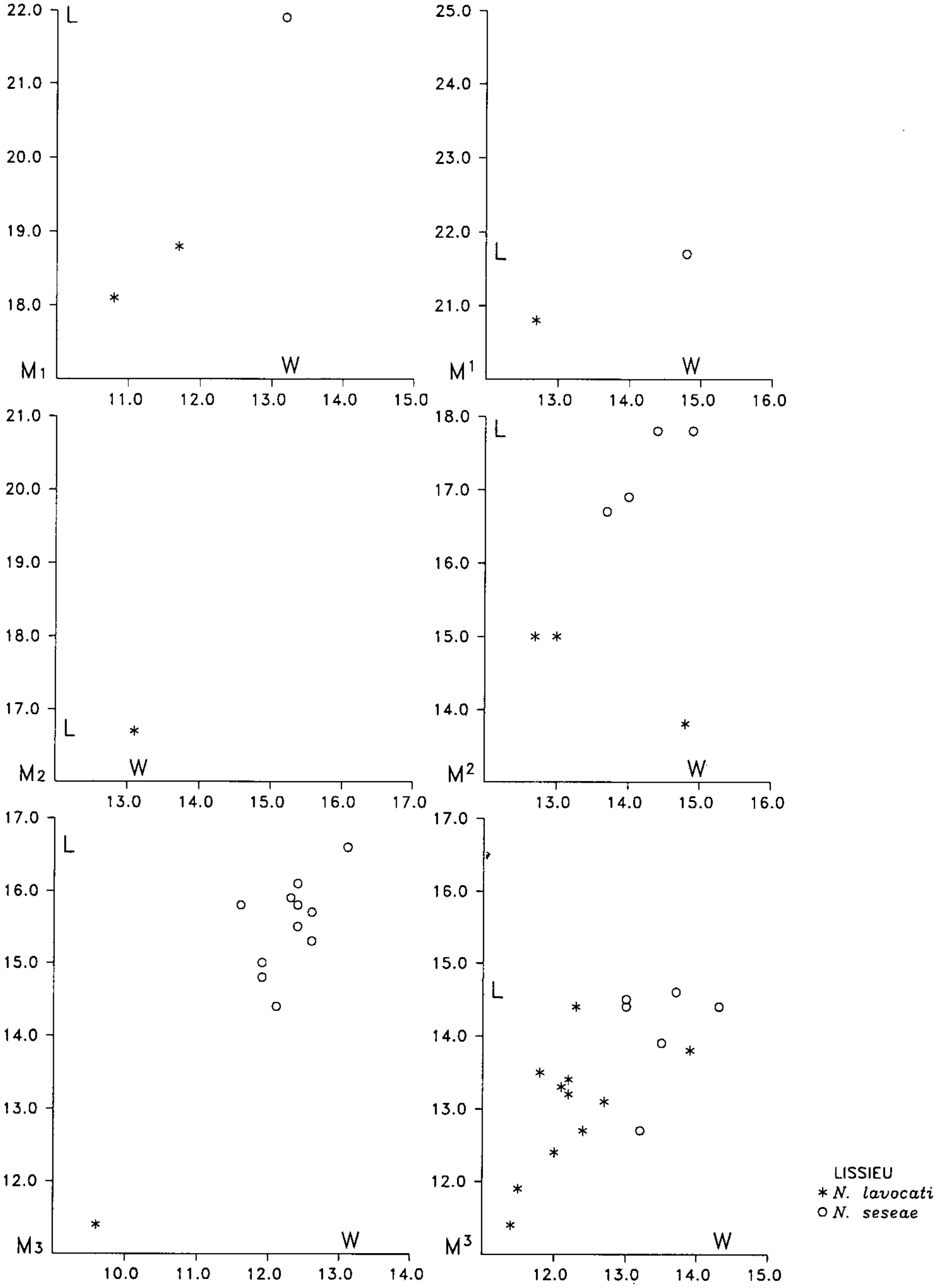

Fig. 8. Length/width diagrams of the molars of *Neocricetodon lavocati* Hugueney & Mein, 1965 and *Neocricetodon seseae* Aguilar, Calvet & Michaux, 1995 from Lissieu.

Fig. 8. Diagramas longitud/anchura de los molares de *Neocricetodon lavocati* Hugueney & Mein, 1965 y *Neocricetodon seseae* Aguilar, Calvet & Michaux, 1995 del yacimiento de Lissieu.

be attributed to *N. lavocati*, and the larger figured specimen (Hugueney & Mein, 1965, pl. 2, fig. 54) belongs to the larger species.

One M^1 has a very long mesoloph, that reaches the molar border and has no contact with the metacone; the other one has a mesoloph of medium length, fused to the metacone. Both have a very long transverse crest in the anterosinus. Their size falls at the lower limit of the range of *N. occidentalis*.

Two M^2 are small, at the lower limit of *N. occidentalis* or smaller; the other ones fall in the upper half of the distribution range of that species. They all have a long and well-developed mesoloph, that is free from the metacone.

The 15 available M^3 can be separated into two groups on the basis of their width. Nine of them are small, and two of these are clearly smaller than the M^3 of *N. occidentalis*, and most of them have a mesoloph; the other ones are larger and have no mesoloph, except for one specimen.

Discussion

The smaller specimens from Lissieu belong to *N. lavocati*, the larger ones cannot be classified reliably; they might represent *N. seseae*.

N. lavocati presents some features that are not commonly found in W. European *Neocricetodon* species; e.g. the very long labial spur of the anterolophule in M^1 is unknown in most Western populations, whereas it is frequent in *N. fahlbuschi* from Kohfidisch, in *N. skofleki* from Eichkogel, and in *N. polonicus* from Podlesice.

As far as the larger species is concerned, tripartite anteroconids are known in *Neocricetodon skofleki* from Tardosbánya. The larger size and the absence of the mesolophid make it improbable that the Lissieu material belong to *N. skofleki*.

The tripartite anteroconid of the large M_1 is known in *A.* aff. *plinii* from CR23, and slightly indicated in one specimen of *N. seseae* from Crevillente 22. We classify this population as *N. seseae*, because *A.* aff. *plinii* is probably older.

Neocricetodon fahlbuschi Bachmayer & Wilson, 1970

Holotype

Maxilla sin. with M^1-M^3, 1970/1393, Museum of Natural History, Vienna, Austria.

Type-locality

Kohfidisch (Burgenland, Austria)

Original diagnosis

Slightly smaller than *Kowalskia magnus*, and larger than *K. polonica*. Posterior paracone spur on M^1.

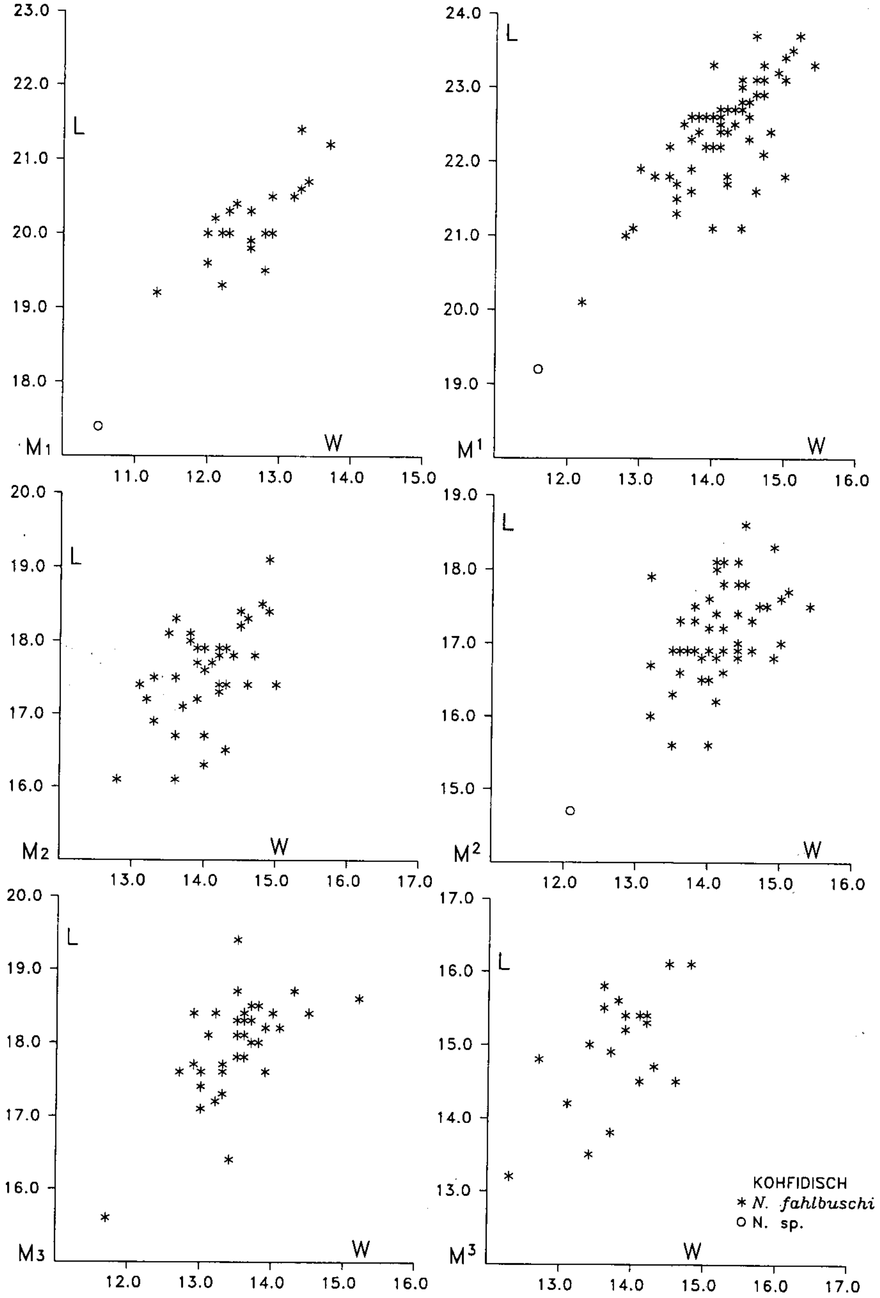

Fig. 9. Length/width diagrams of the molars of *Neocricetodon fahlbuschi* Bachmayer & Wilson, 1970 and *Neocricetodon* sp. 1 from Kohfidisch.

Fig. 9. Diagramas longitud/anchura de los molares de *Neocricetodon fahlbuschi* Bachmayer & Wilson, 1970 y *Neocricetodon* sp. 1 del yacimiento de Kohfidisch.

Emended diagnosis

Neocricetodon of medium size, with hardly subdivided anteroconid in M_1, and well-divided anterocone in M^1. Mesoloph(id)s well-developed, often reaching the molar border. Sinus(id)es wide. Lingual anterolophid absent in M_2, moderately developed in M_3. Spur on the anterolophule of M^1 well-developed. Anterior metalophule absent in M^1, absent or present in M^2. Posterosinus frequently absent in M^1, rarely absent in M^2. M^1 frequently with 4 roots (40 %). M^2 always with 4 roots.

Description

Thanks to the kindness of Dr G. Daxner-Höck we could re-evaluate the type-material of *N. fahlbuschi* from Kohfidisch. The collection is numbered KO 137 1-157. Our measurements give minima and maxima that in most cases do not differ substantially from the values given by Bachmayer & Wilson (1980). The distribution of the measurements, however, is not regular, and a few specimens (a maxillary with M^1-M^2, KO 57, and an isolated M_1, KO 154) are supposed to represent a second, smaller species (see paragraph on *Neocricetodon* sp. 1, hereafter); the remaining material of *N. fahlbuschi* shows a normal range of variation, and appears to be morphologically quite homogeneous.

An unusual high percentage (25-30 %) of the specimens is very much worn, which means that they cannot be used for the morphological description; they are, however, represented in the measurement table.

M_1 - The anteroconid is bifid, never tripartite. The anterolophulid is usually double, less frequently simple; contrary to the observation by Bachmayer & Wilson (1980) the labial branch tends to dominate over the lingual one. The mesolophid is of medium length (3), long (5), or it reaches the lingual border (11). In one specimen a posterior metalophulid is indicated. Another one shows a weak ectomesolophid.

M_2 - The lingual anterolophid is very small (3) or absent (26). The mesolophid is long (5), or it reaches the lingual border (29). In three specimens a rather well-developed posterior metalophulid is observed. Another one shows a weak ectomesolophid.

M_3 - The lingual anterolophid is absent (2), very small (12), or small (15); so it is clearly better developed than in M_2. The mesolophid reaches the lingual border in 29 out of 33 specimens (88%); in 10 of these it sends a branch towards the metaconid. In 4 out of 33 specimens it does not reach the lingual border, and it is in contact with the metaconid. In one specimen a posterior metalophulid is indicated. One specimen shows a strong ectomesolophid. In one specimen the posterolophid is indented.

M^1 - The anterolophule is absent (1), single (22), or d0ouble (15). The labial spur on the anterolophule is present in 62% of the specimens, of medium length (5), long (18), or reaching the molar border (6); it is absent in 17 specimens. The anterolophule spur and the labial branch of the anterolophule are not mutually exclusive: the mentioned spur is present in 8 of the 15 specimens with double anterolophule. The anterior protolophule is absent (14), or present (35).. The numbers observed for the mesoloph differ considerably from those of Bachmayer & Wilson (1980): it is never absent, and may be short (3), of medium length (14), long (24), or reaching the molar border (7). An anterior metalophule is present in one specimen only, and the mesoloph shows no tendency to form one. The posterosinus is absent, small, or well-developed in equal percentages, depending on the development of the posterior metalophule. We have not defined this character in 29 out of a total 63 specimens (46%), due to the peculiar form of the wear surface in this part of the molar. One gets the impression, however, that in a majority of these 29 specimens the posterosinus is absent. There are 3 roots (36), or 4 roots (26).

M^2 - The anterior protolophule is always present. The mesoloph is of medium length (5), long (31), or it reaches the molar border (7). The anterior metalophule (independent of the mesoloph) is absent (16), or present (25). The posterosinus is absent (3), small (3), or well developed (25). There are 4 roots.

M^3 - (15 specimens) The anterior protolophule is always present, double in one case. The mesoloph is always present, somewhat variable in length, but never short. It is based on the metalophule.

Discussion

In several lower molars a posterior branch of the hypoconid or posterior metalophulid is present. In M_1 the valley between protoconid and metaconid tends to be shallow. These are unusual features within this genus, and separate *N. fahlbuschi* from the other species.

Neocricetodon skofleki (Kordos, 1987)
Plate 2, figs. 1-9

Holotype

Mandibula sin. with M_1-M_3, V.86.2, Paleontological Department, Hungarian Natural History Museum, Budapest.

Type-locality

Tardosbánya (Hungary).

Other localities

Eichkogel, Ambérieu 3, Mollon, Ambérieu 2C, Dionay.

Description

Material from Ambérieu 3:

In Ambérieu 3 two species of *Neocricetodon* are recognized: *N. skofleki* and *Neocricetodon* sp. The material of *N. skofleki* is described here; the other species is described later on in the paragraph on *Neocricetodon* sp. 2.

M_1 - The anteroconid is superficially split; one specimen shows a tendency to form multiple cusps. The anterolophulid is labial (1), or double (3). The mesolophid reaches the labial border, forming a mesostylid, in 6 specimens.

M_2 - The lingual branch of the anterolophid is absent (1), or present (2). In one case it forms an anterosinusid. The mesolophid reaches the lingual border and forms a mesostylid. Two specimens have an ectomesolophid.

M_3 - The anterosinusid is small (2), or well-developed (2). The mesolophid is long, without reaching the molar border. In one specimen there is a longitudinal crest between the hypolophulid and the posterolophid, and in a second specimen there is an anterior spur on the posterolophid.

M^1 - The two anterocone cusps are moderately separated, and in one case the anterocone consists of three cusps. There is a long labial spur in the anterolophule in one specimen only. The anterolophule is lingual (1) or double (4). The anterior protolophule is present in all 6 specimens. The mesoloph reaches the lingual border. The anterior metalophule is complete (1), indicated and directed to the mesoloph (3), or absent (1). The posterior metalophule is always present, connected to the posteroloph not far from the hypocone.

M^2 - In all three specimens the protolophule is double, the mesoloph reaches the molar border, and the posterior metalophule is like in M^1. The anterior metalophule is absent (2), or interrupted (1).

M^3 - In the two available specimens the protolophule is double, and the mesoloph forms a spur on the metalophule.

The specimens from Ambérieu 3 are within the lower half of the size range of *N. skofleki* from Eichkogel, and may be attributed to that species, though there are some differences:

- The specimens from Ambérieu 3 are on the average smaller.
- The anterior wall of the anterocon(id) of the M1 appears to be more grooved.
- In M_3 the entoconid seems to be less reduced.
- In M^1 there is no free spur in the anterosinus, except for one case, and in one case there are two parallel anterolophules.

The fact that both Eichkogel and Ambérieu 3 are placed in MN11 corroborates the determination of this population from AMB3 as *N. skofleki*

Material from Mollon:

The population of *Neocricetodon* from Mollon is attributed to *N. skofleki* too. In the five M_2 the mesolophid reaches the lingual border. In both M^1 there is a transverse spur in the anterosinus, which is very long in one case; the mesoloph reaches the labial border. In the single M^2 the mesoloph is long. In the upper molars the anterior metalophule is connected to the mesoloph, complete or interrupted.

Neocricetodon cf. *skofleki* (Kordos, 1987)
Plate 2, fig. 10

Descfiription

Material from Ambérieu 2C:

In Ambérieu 2C two species seem to be present. One of these will be described hereafter as a new species (*N. ambarrensis*); the other one is classified as *N.* cf. *skofleki* (see Fig. 10), and is represented by a relatively big M_1 (21.0 x 12.5), that has its anterolophid subdivided into 3 cusps; the separation between the lingual cusp and the central one is quite deep; there are 3 anterolophulids, a mesolophid that reaches the molar border, and an ectomesolophid, descending from the foremost tip of the hypoconid; the entoconid is connected to the posterolophid by a longitudinal crest that divides the posterosinusid into two valleys.

It comes together with an M_2 (15.5 x 13.3) that is slightly longer, and considerably broader than the rest of the specimens, and an M_3 (16.4 x 12.4), that is both longer and broader. In the M_2 the lingual anterolophid is a thin line on the anterior border of the tooth, the mesolophid reaches the lingual border. In the M_3 the anterosinusid is very small, but there is a clear lingual anterolophid; the mesolophid is of medium length, and there is a strong ectostylid. There is a backward spur on the anterior arm of the hypoconid, and a forward spur on the posterior arm, that form an interrupted longitudinal crest, comparable to the crest observed in M_1. The M_1 is unworn and the M_3 is medium-worn, so they belong to different individuals, which makes it probable, that this crest is significant for the species, and not just an accidental occurrence.

Tripartite anteroconids have been observed in *Cricetulodon sabadellensis* from Can Llobateres, in *Rotundomys* from Montredon, and in *Neocricetodon* populations from Eichkogel, Crevillente 23, and Lissieu.

C. sabadellensis from Can Llobateres and *R. montisrotundi* from Montredon frequently have a tripartite anteroconid, but they never have a long mesolophid; in *A.* aff. *plinii* from CR23 the mesolophid is never long too, and the specimen from Lissieu has no mesolophid. In *N. skofleki* from Eichkogel the anteroconid may consist of three cusps, the mesolophid is long, and there may be a longitudinal crest in the posterosinusid. Our specimens are at the upper size limit of the Eichkogel population. Ambérieu 2C is placed in MN10 and Eichkogel is placed in MN11. The type-locality of *N. skofleki* is Tardosbánya (MN12, Mein, 1990). Such a long vertical range is not usual within this genus. Csákvár, the type-locality of *N. schaubi* is placed in MN10, so one should consider the possibility that we are dealing with that species, but the variability of *N. schaubi* is not known, and the only known M_1 has a bifid anteroconid.

So, by elimination, *N. skofleki* is the only known species that comes into account, but doubt remains because of the large size of the specimens, and because of the long stratigraphic range implied by this occurrence. Kohfidisch and Ambérieu 2C are of about the same age. This means *N.* cf. *skofleki* and *N. fahlbuschi* occur simultaneously. See for further remarks the chapter on phylogeny.

Material from Dionay:

M_1 - The anteroconid is a simple ridge, or superficially subdivided. The anterolophulid is labial (1), or double (5), generally low or interrupted. The mesolophid reaches the molar border (11), or it is of medium length (1). In 8 out of 10 specimens there is an ectomesolophid that descends from the hypoconid.

M_2 - The anterosinusid is small, the mesolophid reaches the lingual border, In two out of five specimens there is an ectomesolophid that descends from the hypoconid.

M_3 - (2 specimens) The anterosinusid is relatively well developed, the mesolophid is long, without reaching the border.

M^1 - The anterolophule is double. There is a long spur in the anterosinus, and a mesoloph that reaches the lingual border. The anterior protolophule is absent (1), or present (2). There is no anterior metalophule, but the metacone tends to become connected to the mesoloph. The posterior metalophule is present.

M^2 - (three specimens) Both protolophule and metalophule are double, the mesoloph is of medium length (1), or it reaches the molar border.

M^3 - In four M^3 the mesoloph is absent, in three specimens it is a short spur on the metalophule, and in two cases it is a long, more or less longitudinal crest.

This material is attributed with doubt to *N. skofleki*. The ectomesolophid is present in a few M_2 from Eichkogel (Daxner-Höck, 1972). In Tardosbánya it occurs in 10% of the M_1 and 7% of the M_2 (Kordos, 1987). In none of the known populations it is as frequent as in Dionay.

A second cricetine from this locality is attributed to *Cricetulodon bugesiensis* nov. sp., described above.

Neocricetodon occidentalis Aguilar, 1982

Holotype

M^1 sin., CR2 63, Instituut voor Aardwetenschappen, Utrecht.

Type-locality

Crevillente 2 (Alicante, Spain).

Other localities

Crevillente 4B, Masia del Barbo 2B, Tortajada A, Alfambra.

Description

Short description of the material from Crevillente 2 (for more details see Freudenthal *et al.*, 1991):

M_1 - Anteroconid simple or superficially split. Anterolophulid simple, connected to the labial cusp of the anteroconid, or forked and connected to each one of the anteroconid cusps. Mesolophid rarely absent or short, generally reaching the molar border, and forming a mesostylid. The posterolophid is connected to the entoconid at mid-height or lower.

M_2 - Anterosinusid present, though very small. The mesolophid may be absent or short, but in most cases it is long, and it frequently reaches the molar border.

M_3 - Anterosinusid present, though very small. The mesolophid is of medium length, or - in most cases - it is long, and it frequently reaches the molar border.

M^1 - The anterocone is superficially or deeply split. The anterolophule is simple or forked; the lingual branch may or may not reach the anterocone. There is no free labial spur on the anterolophule. The protolophule is double or posterior. The mesoloph is of medium length or long, rarely absent. The posterior metalophule is generally present. The labial wall is straight or - more frequently - shows a step-wise offset between paracone and metacone. 3 or 4 roots.

M^2 - The anterior protolophule is always present; the posterior one is missing in a few cases. The mesoloph is of medium length or long, never absent. The posterior metalophule is generally present.

M^3 - The protolophule is always double. The mesoloph varies between absent and long, developed as a spur on the metalophule, and tending to form a connection with the paracone.

A correction has to be made with respect to the description of *N. occidentalis* from Crevillente 2 by Freudenthal *et al.* (1991): A very small M_2 and two very small M_3 are eliminated from *N. occidentalis*, and classified as *Cricetulodon bugesiensis* nov. sp. The lower limit of the size range of *N. occidentalis* for these elements becomes 15.4 and 14.9 respectively (see Figs 1-6).

Material from several localities near Teruel:

Van de Weerd (1976) described *Kowalskia fahlbuschi* Bachmayer & Wilson, 1970 from a number of localities near Teruel: Masia del Barbo 2B, Masada del Valle 2, 5, 6, Alfambra, Tortajada A, Concud Barranco, and Los Mansuetos. We revised this material and came to the conclusion that it may be attributed to either *N. occidentalis* or *A. plinii.*

Masia del Barbo 2B, Tortajada A, and Alfambra, contain *N. occidentalis*; Masada del Valle 2 contains *A.* aff. *plinii*; Concud Barranco, and Los Mansuetos contain *A.* aff. *plinii* or *N. skofleki*, and Masada del Valle 6 contains *A. plinii.*

All these populations are very poor in number of specimens, and a richer material might lead to other conclusions.

Neocricetodon ambarrensis nov. sp.

Plate 3, figs. 1-17

Holotype

M_1 sin., FSL 65907, Faculté des Sciences, Université de Lyon, Pl. 3, fig. 1

Type-locality

Ambérieu 2C (Ain, France; Upper Vallesian, MN10)

Other localities

Ambérieu 1, Cucalón.

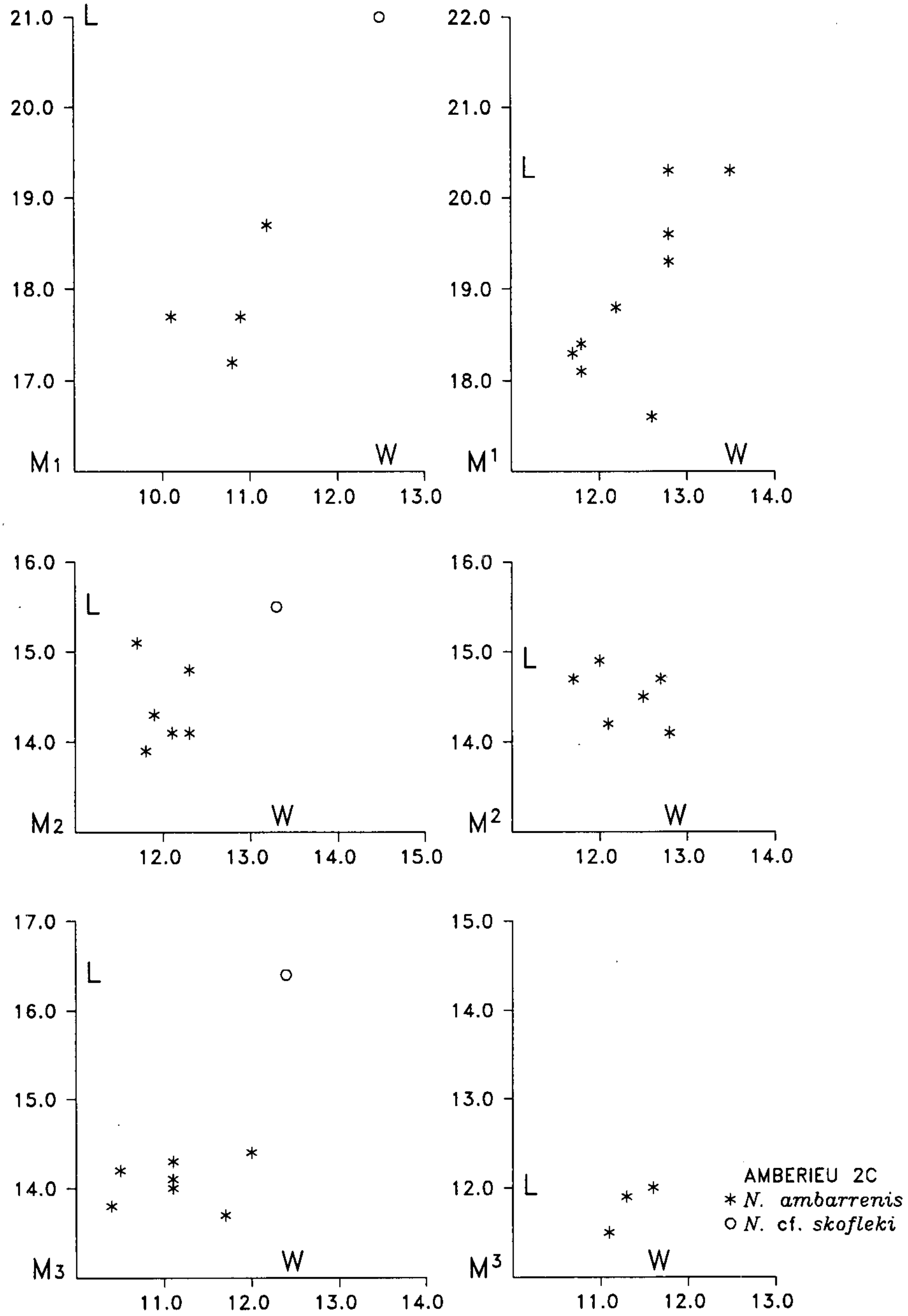

Fig. 10. Length/width diagrams of the molars of *Neocricetodon ambarrensis* nov. sp. and *Neocricetodon* cf. *skofleki* from Ambérieu 2C.

Fig. 10. Diagramas longitud/anchura de los molares de *Neocricetodon ambarrensis* nov. sp. y *Neocricetodon* cf. *skofleki* del yacimiento de Ambérieu 2C.

Derivatio nominis

From the Gallic tribe Ambarri, who, according to Julius Caesar, inhabited the area of the type-locality.

Diagnosis

Small-sized *Neocricetodon* with moderately developed mesoloph(id)s and moderately developed transverse spur in the anterosinus of M^1. M^1 with 3 roots, M^2 with 4 roots.

Differential diagnosis

See Discussion after Cucalón.

Description

Material from Ambérieu 2C:

In AMB2C two species are recognized. One of these is classified as *N. skofleki* (Kordos, 1987). The other one represents a new species, which is smaller than *N. skofleki*, and which we call *N. ambarrensis*. It is also found in Ambérieu 1. For a discussion see after Cucalón.

The M_1 has a superficially split anteroconid. The anterolophulid is labial (2), double (3), or lingual (1). The mesolophid is absent (1), short (1), long (2), or it reaches the molar border (1).

M_2 - The anterosinusid is very small or small, the mesolophid is short (1), or it reaches the molar border (4).

M_3 - The anterosinusid is very small (1), or fairly well developed (7); the mesolophid is absent (1), short (1), or long (6). The mesosinusid is closed by a cingulum ridge.

M^1 - The anterocone is superficially to deeply split. The anterolophule is a simple lingual crest (3), forked and connected to both anterocone cusps (3), or forked with a free labial spur (5); this spur is long in one case. The protolophule is double (8) or posterior only (4). The mesoloph is short (1), of medium length (2), or long (8), and never reaches the molar border. The mesoloph may touch the metacone, but it does not form an anterior metalophule; the posterior metalophule is absent (2) or present (7). The labial border is straight or slightly concave, but the metacone does not protrude like in *C. bugesiensis* nov. sp. from Soblay. There are 3 roots.

M^2 - The protolophule is double. The mesoloph is of medium length (5), or long (3). The anterior metalophule is always present, and exists together with the mesoloph. The posterior metalophule is always present. There are 4 roots.

M^3 - The protolophule is double. The mesoloph is absent. The anterior metalophule is well developed.

It is possible that *Cricetulodon bugesiensis* coexists with *N. ambarrensis* in Ambérieu 2C, since a fragment of M_1 shows a clearly lingual anterolophulid.

Material from Ambérieu 1:

M_1 - The anteroconid is superficially split. The anterolophulid is labial (4), or double (1). The mesolophid is absent (3), short (1), or it reaches the molar border (1).

M_2 - The anterosinusid is small, the mesolophid is short (3), or it reaches the molar border (2).

M_3 - The anterosinusid is very small (1), small (1), or fairly well developed (1); the mesolophid is long (1), or it reaches the lingual border (4). The mesosinusid is closed by a cingulum ridge.

M^1 - The anterocone is rather deeply split. The anterolophule is a simple lingual crest (1), forked and connected to both anterocone cusps (3), or forked with a free labial spur (4); this spur is long in two cases. The protolophule is double (7) or posterior only (2). The mesoloph is absent (2), short (3), of medium length (2), or long (3), and never reaches the molar border. In the specimens without mesoloph there is an anterior metalophule, and the short mesoloph might be called an anterior metalophule as well; the posterior metalophule is absent (1) or present (6). The labial border is straight or slightly concave, but the metacone does not protrude like in the material from Soblay.

M^2 - The protolophule is double, the anterior one being interrupted in one case. The mesoloph is absent (2), of medium length (2), or long (3). The anterior metalophule is always present, independent of the mesoloph. The posterior metalophule is absent (3), or present (4).

M^3 - The protolophule is double. The posterior branch is frequently a longitudinal crest, lingually of the paracone, connecting the anterior protolophule with the protocone hind arm. The anterior metalophule is well developed and bears a mesoloph in 3 cases. In one case there is a thin long mesoloph based on the axioloph, in 3 cases the mesoloph is absent.

Material from Cucalón:

The material consists of 1 M_2 (15.1 x 12.4), 1 M_3 (13.2 x 11.2), 4 M^1 (18.7 x 11.6, - x -, 17.9 x 12.0, 18.6 x 12.3), 4 M^2 (14.7 x 12.1, 13.2 x 11.5, 14.1 x 12.1, 13.8 x 11.9), and 2 M^3 (12.4 x 10.9, 12.9 x 11.3).

The mesolophid of the M_2 is long and vague. The M_3 has a long, high mesolophid that reaches the molar border. In M^1 the anterocone is superficially split, the anterolophule is forked, the anterior protolophule is absent or present, there is no labial spur on the anterolophule, the mesoloph is of medium length, transformed into an anterior metalophule, there is no posterior metalophule. In the M^2 the protolophule is double, the mesoloph is somewhat longer than in M^1, remaining slightly separated from the metacone in 2 of the 3 specimens; in these two cases there is no typical anterior metalophule; the posterior metalophule is absent or present. One of the M^3 is much elongated and has a mesoloph, the other one is more rounded, and has no mesoloph.

Most specimens, except the M^3 are smaller than *Cricetulodon bugesiensis*. They are of the size of *Cricetulodon hartenbergeri*. The M^1 differ from that species by the forked anterolophule, and by the absence of the posterior metalophule (documented in the two unworn specimens), and for the same reasons they differ from *Cricetulodon sabadellensis*.

Neocricetodon sp. 4 from Lo Fournas ‘93 is discarded because it has a labial spur on the anterolophule, and its mesoloph does not form an anterior metalophule.

The specimens are of the size of *N. ambarrensis* or slightly smaller. In *N. ambarrensis* the M^1 generally has a deeply split anterocone, but some specimens have the same morphology as the specimens from Cucalón. The other morphological features of the Cucalón material agree with *N. ambarrensis*, but a reliable determination of this material is not possible, because M_1 is missing, and the other elements are poorly represented.

Discussion

First of all this species must be compared with *Cricetulodon bugesiensis* nov. sp. from Soblay, which is of about the same age and size. Though individual specimens may be difficult to distinguish from *C. bugesiensis*, we think the populations from AMB2C and Soblay cannot represent the same species, because of the following differences:

The anterolophulid of M_1 is predominantly labial.

The anterosinusid of M_2 is better developed, and the mesolophid is on the average longer.

The long spur in the anterosinus of some M^1 is unknown in Soblay.

In Soblay the metacone is displaced lingually with respect to the paracone.

The anterior metalophule of M^2 is always present (predominantly absent in Soblay).

The mesoloph of M^3 is better developed.

The species from Soblay is interpreted as a *Cricetulodon*, and the one from Ambérieu as a *Neocricetodon.*

The specimens are smaller than those of *N. occidentalis*. In the M_1 of *N. occidentalis* the mesolophid reaches the molar border in most cases, and in its M^3 the mesoloph is always present. Morphologically *N. ambarrensis* and *N. occidentalis* are very similar.

The dimensions of *N. ambarrensis* fall within the lower half of the range of *N. skofleki* from Eichkogel. In *N. skofleki* the mesoloph(id)s are longer, a long spur in the anterosinus of M^1 is very frequent, and the posterior metalophule is always present.

N. ambarrensis is clearly smaller than *N. fahlbuschi* from Kohfidisch. Further differences are: In *N. fahlbuschi* the mesoloph(id)s are better developed, and the lingual anterolophid of its M_2 has almost completely disappeared.

Neocricetodon seseae Aguilar, Calvet & Michaux, 1995
Plate 4, figs. 1-7

Holotype

M^1 sin., CTN 29, Université Montpellier II.

Type-locality

Castelnou 1 (Pyrénées Orientales, France).

Other localities

Crevillente 14, 22, 25, Sifón de Librilla, Arquillo 1, Cucuron, Villastar, Lissieu. With doubts: Venta del Moro, La Gloria 5.

Description

Material from Castelnou 1:

Judging from the original description, and from some material we collected ourselves, this locality contains a mixture of faunas of different ages; we think five species of Cricetinae are present, an unusual high number in one locality, and moreover three of these species (*Apocricetus plinii*, *A. barrierei* and *A. angustidens*) are supposed to form a phyletic lineage.

On the basis of size we attribute the two specimens CTN 81 and 82 (Aguilar *et al.*, op. cit., fig. 1d and 1e) to *A. angustidens*, and on the same basis the specimen CTN 79 (*ibidem*, fig. 1c) is attributed to *A. barrierei*. Among our material an M_1, an M^2, and an M^3 appear to belong to *A. plinii*.

N. seseae from Castelnou 1 is characterized by very low anterolophulids in the M_1, well-developed mesolophids, and the presence of a small or very small anterosinusid in M_2.

Our material from CR14 and CR22 is attributed to *N. seseae* on the basis of size and morphology (see hereafter), but that creates doubt about the M_3 figured by Aguilar *et al.*, 1995, pl. 66, fig. 27. That specimen is considerably smaller than our specimens, and the same goes for an M^3 (12.0 x 12.0) present in our material from Castelnou 1. It is quite possible that the M_3 and M^3 from Castelnou 1, described by Aguilar *et al.* (1995), represent *Cricetulodon lucentensis* or *Neocricetodon lavocati*. The most important difference between our material and the type-material of *N. seseae* is the absence of the anterosinusid in M_2, which is small but present in the type material.

Material from Crevillente 14 and Crevillente 22:

In the description of *Apocricetus plinii* from Crevillente 14, Freudenthal *et al.* (1991) expressed some doubt, whether this determination was correct. Martín Suárez & Freudenthal (1994) called it *Neocricetodon* aff. *plinii*.

This doubt is confirmed by the specimens from CR22, a locality that is supposed to be of the same age as CR14, and beyond any doubt younger than the type-locality of *A. plinii*, CR15.

In CR22 four of the seven M_1 have a very long mesolophid, that forms a strong mesostylid in three specimens; in one specimen it is short, and in two specimens it is absent. In six out of eight specimens the anterolophulid is double, in the two others it is strongly labial. In *A. plinii* and in *N. occidentalis* the double anterolophulid is a bifurcation of the anterior part of the anterolophulid; in CR22 the two branches of the anterolophulid originate from a transverse crest, which was called prelophid by Freudenthal (1985). In one specimen there is a very slight indication of a third cuspid in the anteroconid. The M_1 are larger than those of *N. occidentalis*.

In CR14 most M_1 have the same morphology as *A. plinii*, but at least one specimen has the morphology described above (long mesolophid, etc.).

The M_2 from CR14 and CR22 are smaller than those of *A. plinii*.

In CR22 some M_3 are of the same size as in *A. plinii*, others are smaller, and in CR14 most of them are smaller; the larger specimens from CR14 and from CR22 have a well-developed cingulum ridge, that closes the mesosinusid, like in *A. plinii*.

Most M^1 from CR14 have two complete anterolophules, whereas the labial branch is frequently absent or interrupted in *A. plinii*. In CR22 the anterolophule is single, and in one specimen there is a very long transverse labial crest. The mesoloph of M^1 is longer and less connected to the metacone in CR14 and in some specimens from CR22 than it is in *A. plinii*.

The mesoloph of M^2 is longer and less connected to the metacone in CR14 and in some specimens from CR22 than it is in *A. plinii.*

The M^2 and M^3 from CR22 and CR14 are smaller than those of *A. plinii*, and the mesoloph of M^3 is nearly always absent.

We tried to separate two species among this material: one of them would be close to *A. plinii* or *A.* aff. *plinii* and the other one would be more like *N. occidentalis*. It is not possible, however, to separate two taxons unambiguously, due to the scarcity of specimens, and - in CR14 - their poor conservation. Even in a rich collection it may be quite difficult to distinguish them.

Furthermore the M_1 from CR22 are problematic. Their size agrees with that of *A.* aff. *plinii*, but the strong development of the mesolophid excludes their belonging to that species; the strong mesolophids are like in *N. occidentalis*, but the teeth are larger. A characteristic feature is formed by the two parallel anterolophulids, that are based on a prelophid. This is unknown in all cricetine species of similar size, and similar or older age, and characteristic of larger and younger species of the genus *Apocricetus*, like *A. barrierei* and *A. angustidens*. Because these M_1 neither belong to *N. occidentalis* nor to *A.* (aff.) *plinii*, we came to the conclusion that the entire population belongs to another species. For the moment we call it *N. seseae*, because the dimensions agree, and the long mesolophids ending in a mesostylid are present in Castelnou 1 too. In view of the absence of upper molars in the type-population, and the doubt about its homogeneity, this determination can only be provisional. Furthermore the anterosinusid of M_2 in our material seems to be less developed than in the type-material of *N. seseae.*

Differences in comparison with *N. occidentalis* are larger size, the mesolophid of M_2 and M_3 is on the average less developed, and the posterior metalophule of M^2 is less developed. The posterior protolophule may be less developed than the anterior one, and in that respect this material resembles *A.* aff. *plinii* from CR23. We discard their belonging to the same species or lineage, because the mesolophids are much better developed in CR22 than in the older locality CR23.

We attribute this population to *Neocricetodon*, and not to *Apocricetus*, because of the fairly well-developed mesolophids, labial spur on the anterolophule, and rather reduced M^3.

Material from Sifón de Librilla:

We collected *Neocricetodon* material in some new sites along the irrigation canal near Librilla, which we call 'Sifón de Librilla'.

The material from Sifón 1 and 2B is poor. Nevertheless it is clear, that it agrees in size with *N. seseae*. The anteroconid of M_1 is superficially split; the mesolophid is absent in the few M_1 and M_2, that permit observation of this feature; in M_3 it varies between absent and long. In M^1 the anterior protolophule is present; the mesoloph may form the anterior metalophule, or it is longer, and remains more independent; the posterior metalophule is absent. In M^2 the mesoloph is of medium length or long, and there may be an anterior metalophule connected to it; the posterior metalophule is absent or present in equal numbers. The M^1 has three or four roots. In M^3, represented by 7 specimens, the anterior and posterior protolophule are equally well developed and symmetrical; there is no trace of a mesoloph. There are no basic differences with the material from CR14.

Material from Arquillo 1:

M_1 sin., 21.2 x 12.6; M_2 dext., 17.1 x 13.9; M_3 sin., 18.0 x 14.5; M^1 dext., c. 22.8 x.

In the M_1 the anteroconid shows a tendency to tripartition; the anterolophulid is composed of two branches, based on a prelophid, there is no mesolophid. In M_2 there is no lingual anterolophid, and there is a very small trace of a mesolophid. In M_3 there is a vestige of a lingual anterolophid, and in one of the two specimens there is a very low mesolophid. In M^1 there is an anterior protolophule, and a long mesoloph on the anterior wall of the metacone, that does not form a metalophule; there are 4 roots.

Material from Cucuron:

2 M_2 (17.7 x 14.6, 16.8 x 12.2), 2 M_3 (15.0 x 12.9, 13.6 x 11.0), and 2 fragmentary M^1 (- x 13.6, - x 14.4).

Evidently no reliable determination can be given for such a poor material. In M_2 there is no mesolophid in one specimen, a vague mesolophid in the other one; in M_3 it is absent or short. The posterior part of M_3 is strongly reduced. The anterosinusid of M_2 and M_3 is small to fairly well-developed. In M^1 there is an anterior protolophule, a mesoloph plus an anterior metalophule, and a posterior metalophule.

The size is compatible with *N. seseae*, but the small M_3 is too small for that species; it has the size of *C. lucentensis*. In the larger M_3 the labial anterolophid separates the protoconid from the labial border, as in *C. lucentensis*, but this specimen is too large for that species.

Material from Villastar:

Adrover *et al.* (1993) described an M^1 of *Kowalskia lavocati* from Villastar. This specimen is too big in comparison with the specimens from Lissieu, to be ascribed to that species. *N. lavocati* is a very small species, smaller than *N. occidentalis*. The M^1 from Villastar is about as large as the mean value for *N. occidentalis*. We provisionally classify it as *N. seseae*.

Material from Lissieu:

See the paragraph on *Neocricetodon lavocati* from Lissieu.

Material from Venta del Moro and Gloria 5:

For details on Venta del Moro and La Gloria 5 see under *Apocricetus alberti* and *Apocricetus plinii* respectively.

Discussion

The type-population of *Neocricetodon seseae* is poor, and there is some doubt about the homogeneity of the fauna of its type-locality. Most populations attributed here to *N. seseae* are poor in numbers too, and comparisons are therefore difficult. In fact none of these attributions is satisfactorily founded, and only new and abundant material can make it clear, what exactly is *N. seseae*.

Neocricetodon polonicus (Fahlbusch, 1969)
Plate 4, fig. 8-10

Holotype

Mandibula sin. with I, M_1-M_3, MF/822/1, Institute for Systematic Zoology, Krakóv.

Type-locality

Podlesice (NW Krakóv, Poland)

Other localities

Hauterives

Description

This species is documented by 3 specimens from Hauterives, that apparently belong to the same individual. The measurements are: M^1 16.8 x 11.4, M^2 11.8 x 11.2, M^3 10.4 x 10.4

The M^1 has an anterocone that is moderately split from behind; there is a half-long spur on the anterolophule, the protolophule is double, the mesoloph is of medium length, there is no metalophule. In the M^2 the protolophule is double, the mesoloph is long, and the anterior metalophule is fused to the base of the mesoloph; there is no posterior metalophule. In the M^3 the anterior protolophule is stronger than the posterior one; the anterior metalophule is interrupted, and bears a mesoloph. M^1 and M^2 have 4 roots.

Apart from the somewhat shorter mesolophs of M^1 and M^2, there are no differences in comparison with *N. polonicus* from Podlesice.

Neocricetodon sp. 1

Next to *N. fahlbuschi* a second *Neocricetodon* species is recognized in Kohfidisch. It is represented by an M_1 (KO 154, 17.4 x 10.5), and a maxillary, KO 57, with M^1 (19.2 x 11.6) and M^2 (14.7 x 12.1).

These specimens are smaller than *N. fahlbuschi*. It is not clear to what species they might belong.

In the M_1 the anteroconid is simple or very little subdivided, the anterolophulid is labial, and very low, the mesolophid reaches the molar border.

The M^1 has a lingual anterolophule, without labial spur, there is no anterior protolophule, the mesoloph is of medium length, there is no anterior metalophule, and the posterior one is connected to the posteroloph, close to the hypocone.

In the M^2 the protolophule is double, and mesoloph and metalophule are like in M^1.

Neocricetodon sp. 2
Plate 2, figs. 11-14

Apart from *N. skofleki* a larger *Neocricetodon* species is present in Ambérieu 3, represented by four specimens:

In the M_1 the anteroconid is slightly grooved, there are two anterolophulids, that are wide apart; the mesolophid is half-long, and its tip is curved backwards, forming a connection with the entoconid, instead of a hypolophulid. In the M_2 the mesolophid is absent, and in the M_3 it forms part of the hypolophulid. In M_2 the lingual anterolophid is absent, and in the M_3 it vestigial.

One M^1, 22.5 x 13.6, is morphologically identical to the *N. skofleki* specimens, but larger, even larger than the largest specimen from Eichkogel

It is not clear to what species these specimens belong, and we leave them for the moment as *Neocricetodon* sp. The M_2 and M_3 are very much like *Cricetulodon bugesiensis* nov. sp., and the morphology of M_1 is found in at least one specimen from Soblay. Maybe we are dealing with *C. bugesiensis* or a related form, though the M^1 is too big.

Neocricetodon sp. 3

From the locality Lo Fournas 7 we have a small collection, that was kindly put at our disposal by Dr Aguilar, who had already recognized two different species, which he attributed to *Cricetulodon sp.* and *Neocricetodon sp.* respectively.

The *Cricetulodon* may be attributed to *C. bugesiensis* nov. sp. The other species is a *Neocricetodon* of large size (length M^1 22.0 - 24.0). The anterocone of M^1 is slightly split, and there may be a labial spur in the anterosinus. The mesoloph of M^1 and M^2 is long, and M^3 is very short. M_1 and M_2 (1 specimen each) have a long mesolophid; the anteroconid of M_1 is very slightly split. In view of the few number of specimens, and the practical absence of lower molars, we refrain from determining this material.

Neocricetodon sp. 4

A block from Lo Fournas, collected by one of us in 1993 (locality Lo Fournas '93), was at first thought to come from Lo Fournas 7. Study of the cricetine has shown, however, that there is no similarity whatsoever.

M_1 - (2 specimens) The anteroconid is split, the anterolophulid is double or labial, the mesolophid reaches the lingual border.

M_2 - (2 specimens) The anterosinusid is very small or small. The mesolophid reaches the lingual border.

M_3 - The anterosinusid is absent (2), very small (3), small (3), or moderately developed (3). The mesolophid is absent (3), short (2), long (1), or it reaches the molar border (6). In one specimen it has a lingual connection with the metaconid.

M^1 - The anterocone is clearly split. There is a labial spur in the anterosinus which is short (2), or long (7). The anterior protolophule is absent (3), or present (8). The mesoloph is of medium length (4), or long (7), it never reaches the lingual border. The anterior metalophule is absent, the posterior one nearly always present. The metacone is displaced lingually with respect to the paracone, with a step-like shape of the lingual border in most specimens. In one specimen the interior root is split.

M^2 - The anterolophule is double. The mesoloph is long. Both the anterior and the posterior metalophule may be absent or present.

M^3 - The protolophule is anterior, and there is a longitudinal ridge from the anterior protolophule to the entoloph, which should be interpreted as the posterior protolophule. There is a mesoloph based on the entoloph (4), or on the metalophule (1).

This material cannot belong to *Cricetulodon bugesiensis* nov. sp., nor to *Neocricetodon ambarrensis* nov. sp., nor to *N. occidentalis*, because of the long labial spur in the anterosinus of M^1. This feature, the morphology in general, and the fact that at least one of the M^1 has four roots, point towards eastern species like *N. fahlbuschi*, or even more, *N. skofleki* and *N. browni*. Kohfidisch, the type-locality of *N. fahlbuschi* is not much younger than Lo Fournas '93, the type-localities of *N. skofleki* and *N. browni* (Eichkogel and Maramena respectively) are considerably younger. The material from Lo Fournas '93 appears to represent an unknown species with eastern affinities, but we refrain from naming it because there is doubt about the homogeneity of the collection.

Apart from the mentioned material there are two small M^2 with a single metalophule, that is placed on the center of the hypocone. This feature is unknown in *Neocricetodon*, but frequent in species of the Aragonian genus *Megacricetodon* Fahlbusch, 1964. If these specimens are indeed *Megacricetodon* one must come to the conclusion, that the Lo Fournas '93 material is not homogeneous. One of the previously mentioned M_3 without mesolophid may well be *Megacricetodon* too.

There also are two worn M^3 and a fragment of an unworn M^3, representing a rather big species. In one specimen one may observe that there is no anterior protolophule. The M^3 are much broader than the rest of the M^3. A fragmentary M^2 may belong to the same species as these M^3. They do not fit in any species of the supposed age of Lo Fournas '93, and reinforce the idea of heterogeneity of the collection.

Neocricetodon? spp.

We now incorporate in *Neocricetodon* species that are characterized by labial anterolophulids in M_1, long mesoloph(id)s, labial spur on the anterolophule of M^1, elongated third molars, etc. This poses problems for some species that do not fulfill all requisites of the genus diagnosis, like:

Neocricetodon? nestori (Engesser, 1989)

Type-locality

Podere Santa Croce, locality 1 (Tuscany, Italy).

This species shows a mixture of features of the genera *Neocricetodon* and *Cricetulodon*: the well-developed mesoloph(id)s are characteristic of *Neocricetodon*, the reduced M^3 and the sometimes dominant lingual anterolophulid in M_1 (Engesser, 1989, fig. 16D) point towards *Cricetulodon*. The type-locality is supposed to be of Pliocene age (MN13-14), whereas the *Cricetulodon* species known so far are older. We leave this species provisionally in *Neocricetodon*.

Neocricetodon? sp. 5

We include in this species material from Lobrieu, with the following characteristics:

In one M_1 the anteroconid is slightly bifid, in the other one it is tripartite. The anterolophulid is double and the mesolophid reaches the molar border.

In M_2 the lingual anterolophid is small (2); the mesolophid reaches the molar border (4). In two specimens the lingual anterolophid and the mesolophid are absent.

In the M_3 (1 specimen) the anterosinusid is small, and the mesolophid is long.

In the single M^1 the anterolophule is double, there is no spur in the anterosinus, but there is a parastyl. The protolophule is double; the mesoloph is half-long, acting as an anterior metalophule, and there is a mesostyl. The posterior metalophule and the posterosinus are present.

In the M^2 (1 specimen) the mesoloph reaches the molar border, and the anterior metalophule is connected to it mid-way. There is no posterior metalophule. There is a transverse crest in the anterosinus, from the protolophule to the antero-lingual corner of the tooth, and a similar crest is present in one of the M^3.

In two of the M^3 the posterior protolophule forms a longitudinal crest, lingually of the paracone. In one specimen the metacone has disappeared, and the metalophule is just a short crest that ends free.

The M_1, part of the M_2, and the M_3 may be attributed to *N. skofleki*. But M_2 without mesolophid are not reported from Eichkogel or Tardosbánya. They might represent *Cricetulodon bugesiensis* nov. sp. The upper molars also fit better in that species.

Genus *Apocricetus* nov. gen.

Type-species

Cricetus angustidens Depéret, 1890

Attributed species

Cricetus barrierei Mein & Michaux, 1970; *Neocricetodon plinii* Freudenthal, Lacomba & Martín Suárez, 1991; *Apocricetus alberti* nov. sp.

Derivatio nominis

From the Greek word *apo* = away from, and the genus name *Cricetus.*

Diagnosis

Medium to large-sized Cricetinae, practically without mesolophids in M_1 and M_2, with long third molars; in the younger forms the anterior protolophules and posterior metalophules in the upper molars are reduced or absent .

Differential diagnosis

Apocricetus nov. gen. differs from *Neocricetodon* Schaub, 1934 by the loss of the mesolophid in M_1 and M_2, and by the absence of a free labial spur on the anterolophule of M^1.

It differs from *Cricetulodon* Hartenberger, 1966 by the labial or double anterolophulid in M_1, and the long third molars, that tend to become longer in the younger species.

It differs from *Cricetus* Leske, 1779 and *Pseudocricetus* Topachevskii & Skorik, 1992 by the generally crest-like anteroconid of M_1, by the deep valley between protoconid and metaconid of M_1, and the progressive loss of the protolophules in the upper molars.

Remarks

Once the decision is taken to separate *Neocricetodon* and *Cricetulodon* as different genera, it is inevitable to create a new genus for a number of species that are characterized by the loss of the mesolophids in M_1 and M_2, and labial or double anterolophulids in M_1. Incorporating them in one of the mentioned genera would make it impossible to give differential diagnoses for any one of them.

Apocricetus angustidens (Depéret, 1890)

Holotype

Mandibula dext. with M_1-M_3, Pp 75, Musée Guimet d'Histoire Naturelle, Lyon (coll. Donnezan).

Type-locality

Serrat d'en Vacquer (Pyrénées Orientales, France).

Other localities

Mont-Hélène, Sète, Le Soler, Villeneuve de la Raho, Gorafe 3 and 5, Alcoy 4B, Vilafant, Port-la-Nouvelle.

Emended diagnosis

Based on the material from Mont-Hélène: Large *Apocricetus*; M_1 with a crest-like anteroconid, that may show some vestigial subdivision. Mesolophid absent in M_1, present though weak in about 50 % of the M_3. Anterior protolophule rarely present in M^1, more frequent in M^2, and present in about 33 % of the M^3. Posterior metalophule absent in all upper molars.

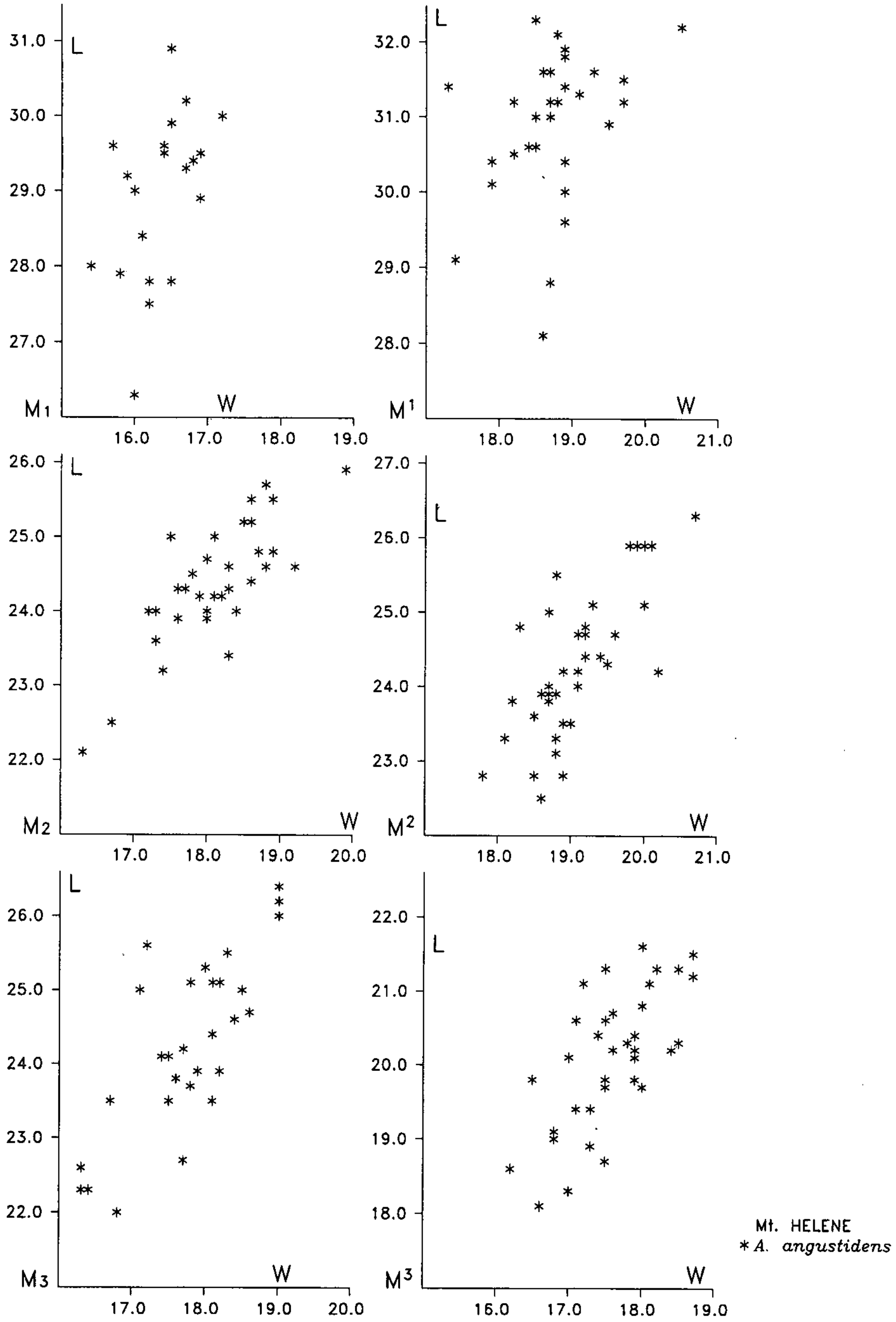

Fig. 11. Length/width diagrams of the molars of *Apocricetus angustidens* (Depéret, 1890) from Mt. Hélène.

Fig. 11. Diagramas longitud/anchura de los molares de *Apocricetus angustidens* (Depéret, 1890) del yacimiento de Mt. Hélène.

Differential diagnosis

Larger than *A. barrierei*, with a better developed cingulum ridge in front of the anterocone of M^1.

Morphological differences with *A. barrierei* can only be defined on a statistical basis; since no rich population of *A. barrierei* is known, it is not possible to give a reliable differential diagnosis on the basis of morphology. An attempt is made, however, in the discussion on *A. barrierei* from Caravaca (see hereafter).

Description

Material from the type-locality:

M_1 - Crest-like anteroconid, smooth or with hardly indicated subdivision. Two anterolophulids, almost equally well developed, and symmetrical, reaching the top of the anteroconid. The anterolophulids may arise from a prelophid (see Freudenthal, 1985), in which case the metalophulid is strongly directed forwards. Mesolophid absent, or short and low, connected to the base of the metaconid.

M_2 - Lingual anterolophid absent, or very weakly developed. Mesolophid absent.

M_3 - Lingual anterolophid weakly developed, or forming an anterosinusid. Mesolophid absent, low and short, or of medium length, not connected to the base of the metaconid.

M^1 - There is a well-developed cingulum ridge in front of the anterocone. Anterior protolophule absent or weakly indicated; posterior metalophule absent. The anterior metalophule is less transverse than it is in Mont-Hélène. The labial border is straight. 4 roots.

M^2 - Lingual anteroloph short and low. Anterior protolophule well-developed or vestigial; posterior metalophule absent; anterior metalophule strong and oblique, no mesoloph.

M^3 - Lingual anteroloph short and low. Anterior protolophule well developed, longitudinal; anterior metalophule strong, no mesoloph.

Hugueney & Mein (1966) stated that the anterior protolophule of the upper molars is absent in the material from Serrat d'en Vacquer, but a renewed observation of the material has shown that it may be present in all three upper molars.

Material from Mont-Hélène:

This locality has yielded a rich collection of *Apocricetus*, called *Cricetus* cf. *angustidens* by Aguilar, Calvet & Michaux (1986). According to these authors it is larger than *Apocricetus angustidens* from its type-locality. We found, that the specimens from Serrat d'en Vacquer fall within the size range of the population from Mont-Hélène, and that a difference of mean values cannot be demonstrated, because of the scarcity of material from the type-locality. We therefore classify the population from Mont-Hélène as *A. angustidens*. It gives a good idea of the morphological and biometrical variability of that species and permits an emended diagnosis (see before).

M_1 - Crest-like anteroconid, smooth or with hardly indicated subdivision. In one specimen the anteroconid is very slightly trifid. There are two anterolophulids, almost equally well developed, and symmetrical, reaching the top of the anterolophid crest, encircling an anterior funnel. In some cases the labial anterolophulid is slightly more transverse than the lingual one. The anterolophulids arise from a prelophid, and the metalophulid is strongly directed forwards. The mesolophid is generally absent, but short in one case.

M_2 - The lingual anterolophid is absent, or very much reduced. The mesolophid is absent in the 34 specimens, attributed to M_2.

M_3 - The lingual anterolophid is absent, or very much reduced. The mesolophid is absent (16), short (4), or long, thin and low (10). M_2 and M_3 are difficult to distinguish, and some specimen may be an M_2, and the occasional presence of a mesolophid in M_2 cannot be denied.

The best criteria to distinguish M_2 and M_3 are the posterior root and the width: specimens with an oblique posterior root are certainly M_3, specimens in which the posterior width is greater than the anterior width are certainly M_2. The average length of M_3 is somewhat larger than of M_2. In a mandible with M_2-M_3 (from Mont-Hélène) the M_3 is slightly longer than the M_2, and this is confirmed in a mandible from Villeneuve de la Raho, where the M_3 is considerably longer.

M^1 - There is a cingulum ridge in front of the anterocone. The three funnels between lingual and labial cusps are equally well developed, and of about the same size. The central funnel is anteriorly open or closed, according to the absence of the anterior protolophule (26), or presence of that crest (4). The anterior metalophule is always present, and seems to be a transformed mesoloph, since it has a transverse position, and is in contact with the anterior wall of the metacone, in front of the wear surface of that cusp. There is no free mesoloph. The posterior metalophule is absent. In most specimens the labial border of the tooth is almost straight. There are 4 roots.

M^2 - The lingual anteroloph is short and low. The anterior protolophule is absent (30) or present (9); in the latter case it may be interrupted. The anterior metalophule is always present, and more oblique and directly connected to the metacone than in M^1. The posterior metalophule is present in one case only, and a trace of such a crest may be observed in a few more specimens.

M^3 - The lingual anteroloph is more reduced than in M^2, and may be absent. The anterior protolophule is absent (22), or present (11); when present, it is often longitudinal, and frequently low or interrupted.

All morphotypes found in the type-population from Serrat d'en Vacquer are observed in the Mont-Hélène material too. The mean dimensions and several morphological features indicate that the Mont-Hélène population is more advanced than the type-population: absence of mesolophid in M_1, lingual anterolophid of M_3 more reduced, less developed anterior protolophule in the upper molars.

Material from Sète:

In the M_1 the anteroconid is slightly subdivided. In M^1 there is a cingulum in front of the anterocone, the anterior metalophule is oblique in one specimen, more transverse in the other one of the same skull; in one (small) specimen the labial border of M^1 is concave.

A maxillary fragment with M^1-M^2 gives measurements that are clearly under the lower limit of the population from Mont-Hélène (M^1, 27.6 x 15.7, M^2, 21.3 x 16.4); the other specimens are within the size range of that population or larger; the total size range of the Sète material is larger than normal in a homogeneous population (see Figs. 1-6). Some M_1 have an anteroconid that is more subdivided than it is in any of the specimens from Mont-Hélène.

Material from Le Soler:

A mandibula sin. with M_1, 30.0 x 15.9, M_2 23.3 x 16.5, M_3 22.8 x 17.4. It is attributed to *A. angustidens* on the basis of size. The slightly tripartite anteroconid, and the presence of a very small trace of a mesolophid in M_1 are not typical of that species.

Material from Villeneuve de la Raho:

A mandibula dext. fragment with M_1, 29.4 x 17.2, and M_2, 25.6 x 19.6; A mandibula dext. fragment with M_2, 22.6 x 18.5, and M_3, 26.3 x 18.6. Both by size and morphology they can be attributed to *A. angustidens.*

Material from Gorafe 3 and 5:

In Gorafe 5 some specimens are slightly below the lower size limit of the population from Mont-Hélène. The M^1 have two very well-developed anterolophules, and no anterior protolophule; the anterocone is almost as broad as the rest of the tooth. This population is classified as *A. angustidens* in spite of the fact that the anterior protolophule of M^2 is present in 2 of the 4 M^2.

In Gorafe 3 the anteroconid of M_1 is crest-like or very superficially subdivided; the two symmetrical anterolophulids arise from a prelophid, and encircle a closed funnel; in one specimen the labial anterolophulid is less developed than the lingual one. there is no mesolophid; the posterolophid descends very deeply, and is connected to the base of the entoconid. In M_2 the mesolophid is of medium length, in M_3 the mesolophid is absent or short. In M^1 the prelobe is slightly narrower than the rest of the tooth. Anterior protolophule and posterior metalophule absent. In M^2 the anterior protolophule absent (2) or present (1); in M^3 the anterior protolophule is absent.

Gorafe 3 represents the same level as Gorafe 5, and the material is attributed to *A. angustidens* too.

Material from Vilafant:

A. barrierei from Vilafant (Agustí, 1981) has a simple anteroconid. We attribute it to *A. angustidens.*

Material from Port-la-Nouvelle:

Two specimens from this locality (an M_1, 27.8 x 17.6, and an M_2, 22.6 x 17.2) are attributed to *A. angustidens*. The majority of the fauna is biostratigraphically considerably older. Apparently two different ages are represented.

Apocricetus barrierei (Mein & Michaux, 1970)
Plate 4, figs. 11-12

Holotype

M^1 dext., FSL 65356, Faculté des Sciences, Université de Lyon.

Type-locality

Chabrier (Vaucluse, France)

Other localities

Hautimagne, Vendargues, Celleneuve, Terrats, Caravaca, Gorafe 4, Purcal 4, Alcoy, Alcoy 4B, Loma del Castillo 1, Fuente del Viso, Botardo, La Alberca, La Gloria 4, La Tour.

Differential diagnosis

In comparison with *A. angustidens* from Mont-Hélène *A. barrierei* is smaller; the cingulum ridge in front of the anterocone is absent or weaker developed. It is larger than *A. alberti* nov. sp. and *A. plinii.*

Description

Type-Material:
The type-material consists of an M_1 with slightly bifid anteroconid, anterolophulid double, low and symmetrical, based on a prelophid, and mesolophid absent; an M_3 without anterosinusid, and with a long mesolophid, that is connected to the base of the metaconid; an M^1 with a weak cingulum ridge in front of the anterocone, strongly separated anterocone cusps, anterolophule double and symmetrical, anterior protolophule and posterior metalophule absent, no mesoloph, straight labial border.

Material from Celleneuve, Hautimagne, Vendargues and Terrats:
Mein & Michaux (1970) mentioned some additional material from Celleneuve, Hautimagne and Vendargues. The material from Celleneuve consists of an M_2 without anterosinusid and mesolophid; an M^1 without cingulum ridge in front of the anterocone, strongly separated anterocone cusps, anterolophule double and symmetrical, anterior protolophule indicated and posterior metalophule absent, no mesoloph; an M^2 without anterior protolophule and posterior metalophule, and without mesoloph; one M^3 without anterior protolophule, and without mesoloph, and two fragmentary M^3 with well-developed longitudinal anterior protolophule.

Among the material from Hautimagne there is an M^3 with a well-developed, longitudinal, anterior protolophule.

A mandible from Vendargues (Mein & Michaux, 1970, pl. 1, fig. 5) shows an M_1 with a slightly subdivided anteroconid, and without mesolophid; an M_2 without lingual anterolophid, and with a trace of a mesolophid; an M_3 without lingual anterolophid, and a somewhat better developed mesolophid.

An M_2 and an M^3 from Terrats show the same morphology as the specimens from Celleneuve.

Mein & Michaux (1970, pl. 1, figs. 2 and 5) figured two M_1 of *A. barrierei* with slightly subdivided anteroconid. The variability of *C. barrierei* is not known due to the scarcity of the material, so we can't be sure that it always has a subdivided anteroconid. In fact, in the following paragraphs we attribute several populations to this species, that have a simple, crest-like anteroconid. We take size as the main criterion to distinguish it from *A. angustidens.*

Mein & Michaux (1970) considered *Cricetus barrierei* to be an intermediate form between *Cricetus kormosi* and *C. angustidens*. We think *A. angustidens* may be a descendant of *A. alberti* nov. sp. The link between these two species may be formed by a number of populations previously assigned to *Cricetus barrierei, C.* cf. *barrierei, C. angustidens, or C.* cf. *angustidens*, and now classified as *A. barrierei.*

Material from Caravaca:

M_1 - Crest-like anteroconid, smooth or with hardly indicated subdivision. Two anterolophulids, almost equally well developed, and symmetrical, reaching the top of the anteroconid, or lower. The anterolophulids arise from a prelophid, and the metalophulid is strongly directed forwards. Mesolophid absent.

M_2 - Anterosinusid absent, mesolophid absent, or short and low, reaching the base of the metaconid.

M_3 - Anterosinusid and mesolophid absent.

M^1 - Cingulum ridge in front of the anterocone absent or weak. Anterior protolophule and posterior metalophule absent or present. Labial border straight. 4 roots.

M^2 - Lingual anteroloph short and low. Anterior protolophule absent or present. Posterior metalophule absent; anterior metalophule strong, no mesoloph.

M^3 - Lingual anteroloph absent or very small. Anterior protolophule present, longitudinal; anterior metalophule strong, no mesoloph.

The specimens from Caravaca are smaller than those of *A. angustidens*. Size ranges do not overlap, when comparing the populations from Caravaca and Mont-Hélène. Morphologically, a useful criterion may be the absence/presence of an anterior protolophule. In *A. angustidens* this crest is present in about 15% of the M^1, 20% of the M^2, and 30% of the M^3 (Mont-Hélène). In *A. barrierei* from Caravaca it is present in 1 out of 5 M^1, 4 out of 6 M^2, and present in the 3 M^3. Another criterion may be the posterior metalophule of M^1; this connection is always absent in the rich population from Mont-Hélène, whereas it is (weakly) present in one specimen from Caravaca.

The anteroconid of M_1 is crest-like, or hardly subdivided, presenting some difference with respect to the type-material of *A. barrierei.*

The section of Caravaca is located quite far from the city of Caravaca, several kilometers South of the village of Almudema, on the road to Lorca. We collected new material in this section, and our sample Almudema 1D contains a small population of *Apocricetus barrierei*. On the average the specimens are larger than those from the classical locality of Caravaca. The anteroconid of M_1 is slightly subdivided in two out of three M_1. Two of the three M_3 have a well-developed mesolophid of medium length. In the six M^2 the anterior protolophule is absent or present in equal numbers, and the same goes for the posterior metalophule. In five of the eight M^3 the anterior protolophule is present, longitudinal, in the other three it is absent. In size this population agrees better with the type-material of *A. barrierei* than the population from the classical site of Caravaca, which is smaller.

Material from Gorafe 4:

In Gorafe 4 the M_1 has a crest-like or very superficially subdivided anteroconid; the two symmetrical anterolophulids arise from a prelophid, and encircle a closed funnel (6) or the labial anterolophulid is less developed than the lingual one (2); there is no mesolophid; the posterolophid descends very deeply, and is connected to the base of the entoconid. In M_2 the mesolophid is absent, the posterolophid is low. In M_3 the mesolophid is absent or short, the posterolophid is low.

In M^1 the prelobe and the rest of the tooth are equally broad, or the prelobe is only slightly narrower. The anterior funnel is complete, the middle funnel is open anteriorly, because the anterior protolophule is absent; the posterior funnel is closed by the posteroloph, the posterior metalophule is absent. In M^2 the anterior protolophule is absent (4) or present (1), the posterior metalophule is absent. In M^3 the anterior protolophule is absent.

Gorafe 4 is stratigraphically lower than Gorafe 3 and 5; its *Apocricetus* is smaller, and therefore attributed to *A. barrierei.*

Material from Purcal 4:

Castillo *et al.* (1990) mentioned a *Cricetus* sp. from Purcal 4 (Granada Basin). This locality lies in a sequence of red and yellow marls, sands and fine conglomerates, dated as transition Mio-Pliocene (Martín Suárez *et al.*, in press). We now have about 20 specimens from this locality, among which 4 M_1 and 5 M^1. The size range partly overlaps *A. angustidens*, but the mean dimensions are smaller. We classify this material as *A. barrierei.* The most important difference in comparison with *A. angustidens* is, that the anterior protolophule of the upper molars is always present (5 M^1, 2 M^2, 1 M^3), and the anteroconid of M_1 is slightly bifid or trifid. In the Caravaca population the anterior protolophule is frequently absent, which probably means that it is a more advanced stage.

Material from Alcoy:

Thaler *et al.* (1965) called the *Apocricetus* from Alcoy *Cricetus* aff. *angustidens* because it is smaller than the true *A. angustidens.* We classify it as *A. barrierei.* We have not been able to locate the original material from Alcoy.

Material from Alcoy 4B:

We collected a small population of *A. barrierei* at a new site near Alcoy (Alcoy 4B, stratigraphically different from, and probably younger than the classical locality of Alcoy); this material is morphologically similar to *A. barrierei*, though some specimens reach the size of *A. angustidens.* M_1 has a crest-like, undivided anteroconid. In M^1 the anterior protolophule and the posterior metalophule are absent or present, and the cingulum ridge in front of the anterocone is weak. M_1 and M^2 fall within the size range of *A. barrierei*, the M^1 are larger, but their morphology is not as advanced as it is supposed to be in *A. angustidens.*

The M_3 and the two M^3 from Alcoy 4B are classified as *Apocricetus* sp.; they are much shorter and narrower than might be expected on the basis of the size of M1 and M2. Apparently they represent another species. In the M_3 the mesolophid is short, and in contact with the base of the metaconid. In the M^3 the mesoloph is absent; the anterior protolophule is either absent, or longitudinally connected to the anteroloph. There is no lingual anteroloph or protosinus.

On the basis of size the two M^3 might be classified as *A. barrierei* since they fall within the size limits of the population from Purcal 4; the M_3 is smaller than it is in any population of *A. barrierei.* This, together with the discrepancy in size between the M1,2 and the M3, led us to classify the M3 as *Apocricetus* sp.

Material from Loma del Castillo 1:

A small collection from Loma del Castillo 1 (MN14, Opdyke *et al.*, 1997) is attributed to *A. barrierei.* M_1 has a low labial anterolophid; the mesolophid absent in M_1 and M_2, of medium length in M_3; the anterior protolophule of M^3 is well-developed, longitudinal.

Measurements - M_1: 24.0 x - ; M_2: 21.0 x 15.9, 20.0 x 14.6; M^3: 17.3 x 14.6.

Material from Fuente del Viso:

Fuente del Viso (MN14, Opdyke *et al.*, 1997) contains *A. barrierei.* M_1 has a crest-like anterolophid, with a very slight indication of 3 cusps in one case; there are two symmetrical anterolophulids, based on a prelophid. The mesolophid is absent in M_1 and M_2, absent or present in M_3. In fresh M_3 one may observe that the anterior arm of the hypoconid is much lower than the posterior branch of the protoconid. In M^1 the bifid anterocone and the two symmetrical anterolophules form a completely closed funnel. The anterior protolophule is absent (1 M^1, 3 M^3), or present (2 M^2, 1 M^3). The mesoloph is absent (submerged in the anterior metalophule), except for a short spur on the metalophule of one of the M^3.

Material from Botardo:

Botardo C - One M^1, 25.5 x 15.1 and one M^2, 20.8 x 16.7 were attributed to *Cricetus* cf. *kormosi* by Martín Suárez (1988). In the M^1 the anterolophule consists of two equally well developed branches; the anterior protolophule is absent; the prelobe is somewhat narrower than the rest of the tooth. In the M^2 the anterior protolophule is present. This material is assigned to *A. barrierei.*

Botardo D - One single M_2, 20.2 x 16.2 agrees in size and morphology with *A. barrierei* from Caravaca.

Botardo C and D probably represent the same level, and are taken together in the Tables.

Material from La Alberca:

A maxilla with worn M^1-M^3 from La Alberca was attributed to "*Cricetus*" *kormosi* Schaub, 1930 by Mein *et al.* (1973). On the basis of size we attribute it to *A. barrierei.* A morphological description is not very useful for this worn specimen, but none of the visible features is in contradiction with the morphology of *A. barrierei.*

Material from La Gloria 4:

Adrover *et al.* (1993) described three species of Cricetinae from various localities in the area of Teruel: *Cricetus* cf. *kormosi*, *Kowalskia lavocati*, and *Cricetus barrierei.* The material from La Gloria 4 is easily distinguished from the other Cricetinae from the area on the basis of size, and it may be attributed to *A. barrierei.*

Material from La Tour:

Aguilar *et al.* (1982) mentioned *Cricetus* cf. *kormosi* from La Tour, based on an M_1 sin. (24.1 x 14.5), and two M^3 (16.8 x 15.0, 17.7 x 14.6).

We have the following additional material: M_2 sin., 19.3 x - ; M_3 sin., 19.5 x 14.7; M^1 sin. plm. 24.9 x 15.8; M^2 dext., 17.7 x - ; M^3 sin., 15.4 x 14.6; M^3 dext., 14.1 x 12.2.

Most of the specimens are within the size limits of *A. barrierei*, but one M^3 in our material is clearly too small for that species. The 2 M^3 in the Montpellier collection have an oblique anterior protolophule.

Apocricetus alberti nov. sp.

Plate 5, figs. 1-5

Objective synonymy

Cricetus cf. *kormosi* - de Bruijn *et al.* (1975); *Cricetus* cf. *kormosi* - Freudenthal *et al.* (1991)

Holotype

M_1, CR6 111, figured in de Bruijn *et al.* (1975), pl. 3, fig. 4. The type collection is stored in the 'Instituut voor Aardwetenschappen', Utrecht.

Type-locality

Crevillente 6 (Alicante, Spain).

Other localities

Venta del Moro, Librilla 2A, 2C, Purcal 23, 24, 25.

Derivatio nominis

Dedicated to our friend and colleague Dr Albert J. van der Meulen (Utrecht).

Diagnosis

Apocricetus with moderately elongated third molars and a simple crest-like anteroconid in M_1. Anterior protolophule of M^1 frequently absent (3 out of 7 specimens), in M^2 nearly always present. M^3 without mesoloph.

Generally the M^1 are banana-shaped, with sinuous borderlines, due to the protruding cusps and indenting valleys.

Differential diagnosis

A. alberti differs from *Pseudocricetus kormosi* and *P. polgardiensis* by the hardly split anteroconid of M_1, and the deep valley between protoconid and metaconid of M_1.

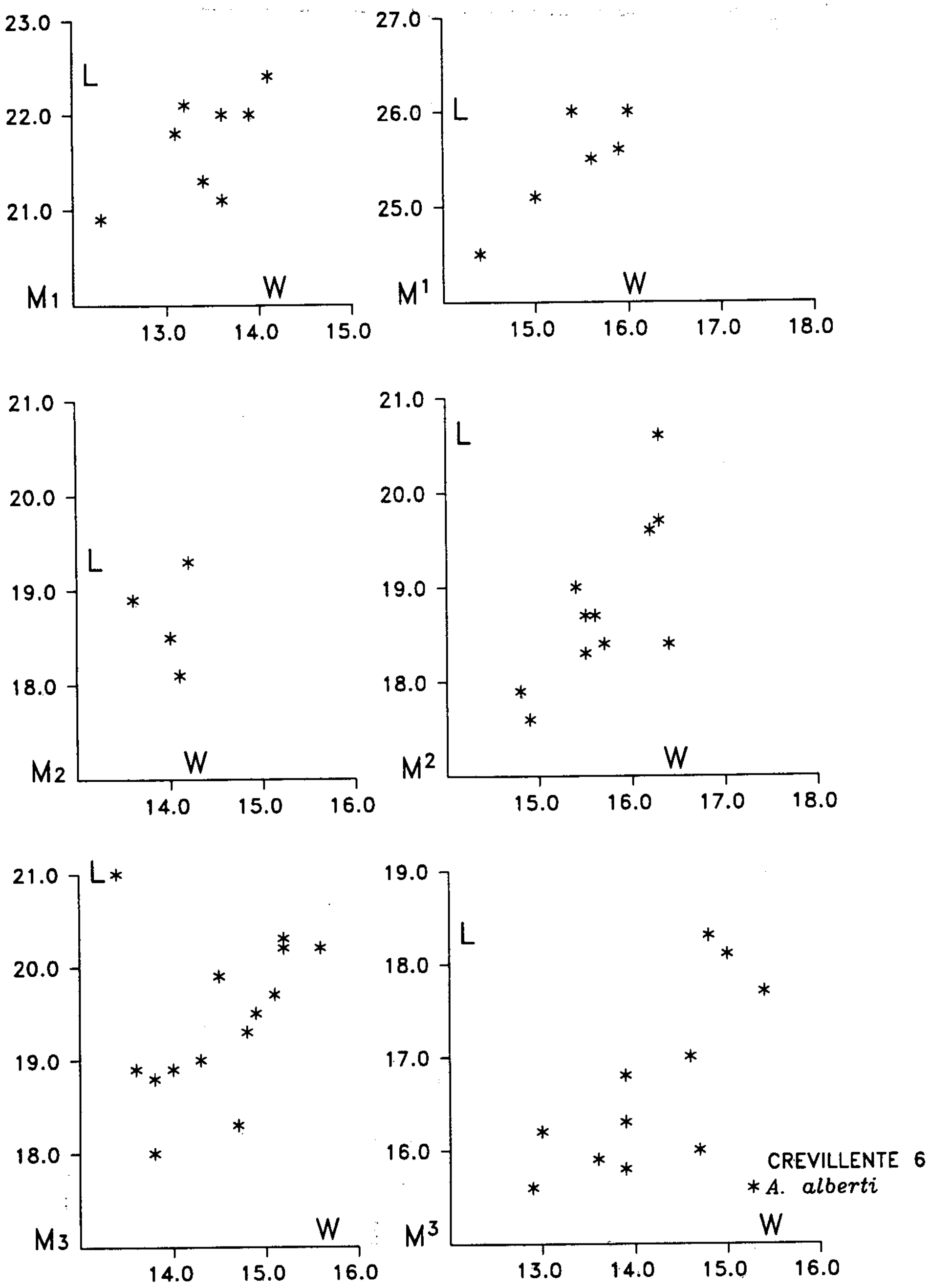

Fig. 12. Length/width diagrams of the molars of *Apocricetus alberti* nov. sp. from Crevillente 6.

Fig. 12. Diagramas longitud/anchura de los molares de *Apocricetus alberti* nov. sp. del yacimiento de Mt. Hélène.

It differs from *A. plinii* by the hardly split anteroconid of M_1, the more pronounced enlargement of M_3, the forked anterolophule with two complete branches of M^1, and the absence of the mesoloph (which is completely converted into an anterior metalophule).

It differs from *A. angustidens* and *A. barrierei* by its smaller size, and by the presence of an anterior protolophule in M^2.

Description

Material from the type-locality:

M_1 - Anteroconid crest-like, in one specimen moderately bifid. Anterolophulid interrupted, simple or double, rather low. In several specimens protoconid and metaconid are not connected, and the two anterolophulids run from the main cusps towards the anteroconid without any connection between them. The labial anterolophulid may be stronger than the lingual one. Mesolophid absent. Frequently the posterolophid does not close the posterosinusid.

M_2 - No anterosinusid. Mesolophid absent; short and connected to the base of the metaconid in one specimen.

M_3 - No anterosinusid. Mesolophid absent (6), very short (2), or long and connected to the metaconid in (4). A hypoconid hind arm is developed in one specimen.

M^1 - Anterocone moderately split. Anterolophules equally well developed and symmetrical. Anterior protolophule absent or present. Anterior metalophule well-developed, and no separate mesoloph. Posterior metalophule absent. 4 roots.

M^2 - Anterior protolophule present. Anterior metalophule well-developed, and no separate mesoloph. Posterior metalophule generally absent (present in 3 specimens). In one small specimen (CR6 185, 17.9 x 14.8) there is no metalophule, and there is a short mesoloph; in this specimen the anterior protolophule is absent too; maybe this specimen represents another species.

M^3 - Anterior protolophule present. Anterior metalophule well-developed, no mesoloph.

Material from Venta del Moro:

The locality of Venta del Moro was described by Aguirre *et al.* (1973), who attribute the cricetine to «*Cricetus*» cf. *kormosi*. This population is now attributed to *A. alberti* nov. sp.

In the M_1 the anteroconid is slightly bifid or trifid; the anterolophulids tend to be parallel, and the lingual one arises directly from the metaconid. In the M_3 the mesolophid is absent (4), or short (5); in one of the latter specimens it forms a low connection with the metaconid. In the upper molars the anterior protolophule is present (3) or absent (1). The mesoloph is completely converted into an anterior protolophule. In the M^2 the anterior protolophule is present, weakly developed in one of the six specimens; the posterior metalophule is absent or present.

One M_2 has a short mesolophid, and another one shows a mesolophid that reaches the border of the molar, like a similar specimen from La Gloria 5. It may represent another species, e.g. *Neocricetodon seseae*, since this feature is unknown in *A. alberti*.

Material from Librilla:

The "*Cricetus kormosi*" population from Librilla is now attributed to *A. alberti* nov. sp. Some specimens may be intermediate in size between *A. alberti* and *A. barrierei* . E.g. an M_1 has a length of 24.0, well over the maximum of *A. alberti* from Crevillente 6, but still considerably smaller than the M_1 of *A. barrierei* from Chabrier. It may be considered as a transitional population between these two species.

We collected a small number of *Apocricetus* specimens in two levels (LIB2A and LIB2C), that are very close to, if not identical with the classical locality. They can be classified as *A. alberti* without any problem. The anteroconid of M_1 is crest-like with a superficial subdivision. The mesolophid is absent in M_1 and M_2, absent or short in M_3. In M^1 (1 specimen) the anterior protolophule is absent, in M^2 and M^3 it is present. The posterior metalophule is absent, or very much reduced. In one of the M_2 in the Montpellier collection a fairly strong ectomesolophid is present.

Material from Purcal 23, 24, 25:

Some 500 m NE of Purcal 4 we took the samples PUR23, PUR24, PUR24A, PUR 25, and PUR25A, from a body of silts and grey sands with gypsum and lignites that is stratigraphically lower than the formation of Purcal 4. All these samples represent the same biostratigraphical level and in the figures they are taken together under the denomination PUR25. In the M_1 the anteroconid is crest-like, with a very superficial subdivision; the mesolophid is absent in M_1, absent or short in M_2, and absent, short, or of medium length in M_3. Of the upper molars only M^3 is represented; the anterior protolophule is always present, the mesoloph is absent. This material is classified as *A. alberti.*

Apocricetus plinii (Freudenthal, Lacomba & Martín Suárez, 1991)

Holotype

M_1 sin., RGM 402101, National Museum of Natural History, Leiden, The Netherlands (Freudenthal *et al.*, 1991, pl. 4, fig. 1).

Type-locality

Crevillente 15 (Alicante, Spain).

Other localities

La Gloria 5, Crevillente 14, Masada del Valle 6, Valdecebro 3, 6.

Description

Material from the type-locality:

Short description (for more details see Freudenthal *et al.*, 1991).

M_1 - Anteroconid superficially split. Anterolophulid simple, connected to the labial cusp of the anteroconid, or forked and connected to each one of the anteroconid cusps. Mesolophid absent. The posterolophid is on the average lower than in *N. occidentalis* Aguilar, 1982.

M_2 - Anterosinusid absent or very small. Mesolophid absent.

M_3 - Anterosinusid absent or very small. Mesolophid absent, short or of medium length.

M^1 - Anterocone superficially or deeply split. Anterolophule simple or double, the labial crest being less developed, and often not connected to the anterocone. Protolophule double or posterior. Mesoloph absent, of medium length, or long. Metalophule anterior or double. The anterior metalophule may be accompanied by a mesoloph. The labial wall is straight or - less frequently - shows a step-wise offset between paracone and metacone. 4 roots.

M^2 - Protolophule double or posterior. Mesoloph absent, of medium length, or long. Metalophule anterior or double. The anterior metalophule may be accompanied by a mesoloph. 4 roots.

M^3 - Protolophule double. Mesoloph absent, short, of medium length, or long, based on the metalophule and not on the entoloph. Anterior metalophule generally well developed.

Normally in Cricetinae M^1 is larger than M_1, and the size ranges of these elements overlap, or at least the upper limit for M_1 coincides with the lower limit for M^1. The dimensions of *A. plinii*, however, show a peculiar distribution: there is an important gap (23.1 for the largest M_1 and 24.1 for the smallest M^1); furthermore the distribution of the M^1 is not homogeneous, and this smallest M^1 is separated from the rest of the specimens (see scatter diagram fig. 4 in Freudenthal *et al.*, 1991). If this smallest specimen belongs to another species, e.g. *A.* aff. *plinii* (see hereafter), the gap would be even greater (from 23.1 to 25.0). The same irregular distribution is found in M^2.

One unmeasurable fragment of M^2 from CR15, RGM 402193, is much bigger (estimated width over 19.0) than *A. plinii*. There is an anterior metalophule, and the metacone is isolated from the posteroloph. The stratigraphically nearest records of such a large cricetine are *A. barrierei* from Alcoy and *Neocricetodon magnus* from Podlesice; both are considerably younger.

Material from Crevillente 14:

One very worn M_2 from Crevillente 14 is considerably larger than the rest of the specimens from that locality. It may represent *A. plinii* or *A. alberti* nov. sp.

Material from La Gloria 5:

Among the material of *Kowalskia fahlbuschi* described by Van de Weerd (1976) the population from Masada del Valle 6 contains *A. plinii.*

A second paper on cricetine material from younger localities near Teruel is by Adrover *et al.* (1993). These authors mentioned *Cricetus* cf. *kormosi* from Arquillo 1, La Gloria 5, Villastar, Valdecebro 3 and 6, and Masada del Valle 7, and described the population from La Gloria 5.

The material from La Gloria 5 may be attributed to *A. plinii* or *A. alberti* nov. sp. It shares with *A. alberti* the hardly split anteroconid of M_1, the more pronounced enlargement of M_3, and the absence of the mesoloph in M^3. It shares with *A. plinii* the asymmetric development of the anterolophule of M^1, and the occasional presence of a separate mesoloph in M^1 and M^2. Valdecebro 3 and 6 are supposed to contain the same species, but the material is very poor. These populations are attributed to *A. plinii*, and seem to be morphologically intermediate between *A. plinii* and *A. alberti*.

One M_2 from La Gloria 5 (18.1 x 14.9) shows a mesolophid that reaches the border of the molar, and therefore doesn't fit in our scheme. We can't be sure whether it is merely a regressive case, or whether this specimen represents another species. The latter possibility is more probable because a similar specimen is found among the *A. alberti* material from Venta del Moro. We might be dealing with *Neocricetodon seseae*.

Apocricetus aff. *plinii* (Freudenthal, Lacomba & Martín Suárez, 1991)

Plate 5, figs. 6-11

In the following a number of populations will be described, that are considered to represent an unnamed species, close to, and maybe the ancestor of, *A. plinii*. We call it for the moment *A.* aff. *plinii*. We refrain from naming it, because we are not absolutely sure, that we are not dealing with a mixture of two species.

Description

Material from Crevillente 23:

M_1 - The anteroconid is superficially to moderately split, sometimes trilobate. The anterolophulid is labial (5), central (2), or double (2). The mesolophid is absent (5), short (3), or it is very thin and reaches the molar border (1). There is always a cingulum ridge, that closes the mesosinusid, and both labial valleys are closed by cingulum ridges too; the anterosinusid is open.

M_2 - The lingual anterolophid forms a ridge on the anterior wall of the molar; it is sometimes absent, and rarely forms an anterosinusid. The mesolophid is absent (17), short (3), of medium length (3), long (2), or it reaches the molar border (1). Cingulum ridges less developed than in M_1.

M_3 - The anterosinusid is better developed than in M_2. The mesolophid is absent (3), short (9), of medium length (14), long (8), or it reaches the molar border (1); it is in contact with the metaconid in a few cases only. The mesosinusid is closed by a cingulum ridge.

M^1 - The anterocone is well split. The anterolophule is simple (10), or forked (2), and it bears a free labial spur in 7 specimens. The anterior protolophule is absent (6), or present (6). In one case the posterior protolophule is very weakly developed. The mesoloph is of medium length or long, either forming an anterior metalophule, or remaining free from the metacone. The posterior metalophule is absent (6), or present (5). 3 or 4 roots.

M^2 - The protolophule is double in 27 specimens; in 2 specimens the posterior branch is weakly developed, and in 1 case it is absent. The mesoloph is of medium length or long, either forming an anterior metalophule, or remaining free from the metacone; in 10 specimens there is a mesoloph plus an anterior metalophule. The posterior metalophule is absent (14), or present (15). 4 roots.

M^3 - The protolophule is anterior (1), or double (29); the posterior branch is often less developed than the anterior one. There is a small trace of a mesoloph, based on the metalophule, in 2 cases only. The metalophule is absent in 3 cases, well-developed in the rest.

Material from various sites near Teruel:

Among the material of *Kowalskia fahlbuschi* described by Van de Weerd (1976), the population from Masada del Valle 2 contains *A.* aff. *plinii*. Concud Barranco and Los Mansuetos contain *Apocricetus* aff. *plinii* or *Neocricetodon skofleki.*

Discussion

The main distinctive features of *A.* aff. *plinii* from CR23 with respect to *A. plinii* from CR15 are:

- The specimens of *A.* aff. *plinii* are on the average smaller.
- The predominantly simple anterolophulid of M_1.
- The mesolophid, that may be present in M_1 and M_2.
- The better developed anterior protolophule, and the less developed posterior protolophule.
- The better developed posterior metalophule.
- In M^2 there is frequently a mesoloph plus an anterior metalophule.
- The absence of the mesoloph in M^3.

We attribute this population to *Apocricetus*, and not to *Neocricetodon*, because of the pronounced reduction of the mesolophids, and a certain degree of elongation of the M^3.

Freudenthal *et al.* (1991) supposed that CR20 and CR23 contained *Neocricetodon occidentalis*, and postponed the study of these localities, because they lie stratigraphically between CR2 and CR4B, and there were no apparent faunistic differences between the latter two localities. However, we have now come to the conclusion that - at least part of - the *Neocricetodon* material from CR20 and CR23 is intermediate in size between *N. occidentalis* and *A. plinii*, and the M_2 have a morphology that reminds one more of *A. plinii* than of *N. occidentalis*. This may be explained in two ways: either there is one species, that shows some morphological features of *N. occidentalis*, but that is closer to *A. plinii*, or these localities contain a mixture of two species.

The smaller one would be of the same size as *N. occidentalis*, and morphologically similar. There are, however, some differences: mesolophids are on the average shorter, the anterior protolophule of M^1 and the posterior metalophule of M^2 are more frequently absent, and in M^3 the mesoloph is always missing.

The larger one would resemble *A. plinii*, but it is on the average smaller, more specifically its M^1 fills the gap in the size ranges between *N. occidentalis* and *A. plinii.* Furthermore the anteroconid of M_1 may be more deeply split, and shows three cusps in several cases; occasionally there is a short, high mesolophid in M_1 and M_2; in M^1 the labial wall is concave, due to the strongly labial position of the metacone; the M^3 has no mesoloph. In M^3 the anterior protolophule is always present, the posterior one, however, may be more weakly developed, or even absent.

In reality, however, we have not managed to separate two species, and for the moment we describe the population from CR23 as one single species, which we call provisionally *A.* aff. *plinii*. The large size range for some of the elements may mean that some of the smaller specimens belong to *N. occidentalis.*

We have considered the possibility that this population belong to *Neocricetodon seseae* from Castelnou 1, and in fact some specimens from Castelnou 1 may represent the same species, since, in our opinion, the population of *N. seseae* is not homogeneous. Anyway, our material cannot be attributed to *N. seseae*, because of the rather deeply split anterocone, the absence of mesostyl(id)s, the closure of the mesosinusid of M_2, etc.

Freudenthal *et al.* (1991) noted that in CR4B the mesolophid of M_1 is either long or absent, and that there are no intermediate cases, and tried to explain this by the mechanism of reduction of the mesolophid. The new data from CR20 and CR23 offer another explanation: the population from CR4B may in reality be a mixture of two species: *N. occidentalis* and *A.* aff. *plinii*. In that case one would expect the larger specimens to have the morphology of *A.* aff. *plinii*, and the smaller specimens to have the morphology of *N. occidentalis*. In reality, however, the two largest specimens have a long mesolophid, and in the smallest specimen the mesolophid is absent.

PHYLOGENY

The oldest species treated in this paper is *Cricetulodon hartenbergeri*. It may be derived from some species of *Democricetodon*, either a Spanish one, or an immigrant from the East. It gives rise to three evolutionary lineages: *C. sabadellensis*, *C. bugesiensis* nov. sp., and *C. lucentensis*.

In our opinion *C. hartenbergeri* is the ancestor of the lineage *C. sabadellensis*, that continues towards *Rotundomys montisrotundi*. However, Agustí (1984) mentioned the co-existence of *Cricetulodon* and *Rotundomys* in Can Llobateres. If this is true, these species represent two lineages, whose dichotomy lies probably shortly before the age of Can Llobateres.

Characteristics of this lineage are increase of hypsodonty, the forming of a flat wear surface with equally high crests and cusps, the loss of the mesolophid in M_1 and M_2, loss of the anterosinusid in M_2, the reduction of the anterior protolophule, and of the mesoloph.

C. hartenbergeri may also be the ancestor of *C. bugesiensis*, through size increase, and a simplification of the dental pattern: reduction of the mesolophid, loss of the anterosinusid in M_2, reduction of the anterior protolophule in M^1, reduction of the posterior metalophule in M^1 and M^2, and reduction of the mesoloph of M^2.

C. meini from Casa del Acero may be the ancestor of *C. lucentensis* from Crevillente 17. The presence of a lingual anteroloph in M^3 is an argument against this hypothesis, but anyway these two species are closely related. The origin of this lineage may be *C. hartenbergeri* too.

Within the genus *Rotundomys* one might construe the lineage *R. freiriensis* - *R. montisrotundi* - *R. bressanus* - *R. mundi*, on the basis of their geological age. However, the possible occurrence of *R. montisrotundi* in Can Llobateres makes this doubtful, and the filiation *R. bressanus* - *R. mundi* is not evident either. Furthermore, in the oldest species, *R. freiriensis*, entoloph and metalophule are more reduced than they are in younger species. In fact the only well-documented species is *R. montisrotundi*; the other species are isolated points in a possibly complex group, and looking for phylogenetic relationships may be premature.

The first appearance of the genus *Neocricetodon* in our area is *N. ambarrensis* nov. sp. from Ambérieu 1 and 2C. It has conserved several morphological features, that have already disappeared in the preceding *Cricetulodon* species. For that reason we don't think there is a phylogenetic relationship between them, and we suppose *N. ambarrensis* to be an immigrant from the East.

This first occurrence coincides in time with *N. fahlbuschi* from Kohfidisch. It seems reasonable to suppose, that they both belong to the same immigration wave, the source of which lies farther East.

In Ambérieu 2C a second species of *Neocricetodon* is found, and the same goes for Kohfidisch. In both cases the material is very poor; in the case of Kohfidisch it is a small species, of the size of *N. ambarrensis*, but we refrain from classifying it. In the case of Ambérieu 2C it is a large species, of the size of *N. fahlbuschi*, but with some morphological characters, that differ from that species. We classify it as *N. skofleki*, though this may turn out to be incorrect. Anyway, the immigration of a diversified group of *Neocricetodon* species at the time represented by Ambérieu 2C/Kohfidisch (Late Vallesian, MN10) seems to be proven.

N. occidentalis, known from the levels of CR2 and CR4B probably belongs to this same wave; it may be derived either from *N. ambarrensis* or from *N. fahlbuschi*, and it may lead towards *N. seseae*. We will not try to reconstruct evolutionary lineages within the genus *Neocricetodon*, because in our opinion this is a typically Central and East European group with a marginal distribution in our area. E.g. *N. lavocati* from Lissieu, with its long spur on the anterolophule of M^1 is not easily connected with one of the known Western European species, whereas it fits in perfectly in the morphology of Eastern species. As a general rule we may say, that the Western populations have a more simple dental pattern than the Eastern ones, where mesoloph(id)s and transverse spurs suffer hardly any reduction.

Apocricetus aff. *plinii* might be derived from *N. occidentalis*, but this is not very probable: it would mean a very sudden change in size and morphology, and in CR4B *N. occidentalis* is present, after the appearance of *Apocricetus* aff. *plinii*. We therefore think, that *A.* aff. *plinii* represents a second immigration wave, dated as Early Turolian (MN11), that gives rise to the lineage *A.* aff. *plinii* - *A. plinii* - *A. alberti* nov. sp. - *A. barrierei* - *A. angustidens*. This lineage is well documented, for most steps fairly rich populations are available, morphological changes and size increase are gradual, to such an extent that the specific attribution is sometimes arbitrary.

This does not mean, that all populations fit perfectly on one line. E.g. In *A.* aff. *plinii* (CR23) the mesoloph of M^3 has disappeared, whereas it is present in the M^3 of *A. plinii* (CR15). Nor is the distribution of the species continuous: *A.* aff. *plinii* is present in CR23, absent in CR4B, and the lineage reappears in CR15 with *A. plinii*. Then it is absent again in CR8 and CR17, and it reappears in CR6 with *A. alberti*. After CR6 this lineage is almost constantly present, and constitutes almost the only cricetine in the area.

This intermittent distribution is certainly linked to the important climatic changes that take place at the end of the Miocene. The time span between CR2 and CR6 roughly covers the Middle and Late Turolian (latest Tortonian and Messinian), a period of important climatic changes. The constant presence, and more continuous evolution of the younger part of the *Apocricetus* lineage coincides with the more constant climatic conditions of the Pliocene.

The intermittent distribution of the first part of the lineage may well explain the fact, that some morphological features do not change gradually: a species disappears from the area, and repopulation takes place from a slightly different source. The geographical distribution of the species was probably fragmentary.

A peculiar occurrence is *Neocricetodon polonicus* in Hauterives: contemporaneous faunas (Early Pliocene, MN14) in our area contain *A. barrierei*, and such small Cricetinae are usually much older. On the other hand, Hauterives is almost of the same age as Podlesice, the type-locality of *N. polonicus*; this species represents another immigration, at least in our area, not directly linked with earlier occurrences of *Neocricetodon*. The typical Pliocene cricetine in our area is *Apocricetus*, while in Central Europe *Neocricetodon* continues.

ACKNOWLEDGMENTS

We are indebted to Dr J.-P. Aguilar for giving us access to the Montpellier collections, and discussing details concerning these collections. Thanks are due to Dr J. Agustí for giving us access to the original material of *C. meini*, and for valuable comments on the Cricetinae from Vallés-Penedés. Dr G. Daxner-Höck enabled us to revise the type-material of *N. fahlbuschi*. Thanks to Dr A.J. van der Meulen we could study the Cricetinae in the collections of Utrecht University. The photographs were made on the Zeiss DSM 950 Scanning Electron Microscope of Granada University.

This study was carried out within the frame-work of the project "Cambios climáticos en el Sur de España durante el Neógeno" of the R. Areces Foundation, and project PB94-1265 of the DGICYT.

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	Length						Width					
	n	min.	mean	max	V'	σ	n	min.	mean	max.	V'	σ
M_1	3	20.3	20.53	20.8	2.43	0.252	3	12.5	12.70	12.9	3.15	0.200
M_2	2	16.8	17.15	17.5	4.08	0.495	2	13.0	13.65	14.3	9.52	0.919
M^1	6	20.2	20.83	21.3	5.30	0.383	6	13.6	14.20	14.5	6.41	0.352
M^2	8	14.7	15.45	16.5	11.54	0.689	10	13.3	13.84	14.5	8.63	0.406
M^3	6	12.1	12.60	13.2	8.70	0.400	6	11.1	11.80	12.7	13.45	0.678

Table 1. Material and measurements of *Cricetulodon meini* (Agustí, 1986) from Casa del Acero (Murcia, Spain)

Tabla 1. Material y medidas de *Cricetulodon meini* (Agustí, 1986) de Casa del Acero (Murcia, España).

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1	16	17.3	18.67	20.1	14.97	0.786	16	9.9	11.37	12.4	22.42	0.611
M_2	13	14.9	16.46	17.8	17.74	0.753	13	11.7	12.73	13.8	16.47	0.675
M_3	12	14.1	15.93	17.5	21.52	1.015	11	11.9	12.65	13.5	12.60	0.545
M^1	14	18.8	19.96	21.3	12.47	0.828	13	12.2	13.20	14.8	19.26	0.705
M^2	17	14.0	15.14	16.3	15.18	0.722	17	12.2	13.28	14.8	19.26	0.587
M^3	10	11.2	12.72	14.1	22.92	0.844	11	10.5	11.87	12.6	18.18	0.590

Table 2. Material and measurements of *Cricetulodon bugesiensis* nov. sp. from Soblay (Ain, France)

Tabla 2. Material y medidas de *Cricetulodon bugesiensis* nov. sp. de Soblay (Ain, Francia)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1	22	19.2	20.15	21.4	10.84	0.547	21	11.3	12.61	13.7	19.20	0.576
M_2	39	16.1	17.55	19.1	17.05	0.678	38	12.8	14.03	15.0	15.83	0.531
M_3	36	15.6	18.00	19.7	23.23	0.743	35	11.7	13.50	15.2	26.02	0.585
M^1	58	21.0	22.42	23.7	12.08	0.674	59	12.8	14.19	15.4	18.44	0.569
M^2	48	15.6	17.15	18.6	17.54	0.665	49	13.2	14.16	15.4	15.38	0.505
M^3	21	13.2	14.98	16.1	19.80	0.805	20	12.3	13.80	14.8	18.45	0.619

Table 3. Material and measurements of Neocricetodon fahlbuschi Bachmayer & Wilson, 1970 from Kohfidisch (Burgenland, Austria)

Tabla 3. Material y medidas de Neocricetodon fahlbuschi Bachmayer & Wilson, 1970 de Kohfidisch (Burgenland, Austria)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1	4	17.2	17.83	18.7	8.36	0.629	6	10.1	10.77	11.5	12.96	0.572
M_2	6	13.9	14.38	15.1	8.28	0.467	6	11.7	12.02	12.3	5.00	0.256
M_3	7	13.7	14.07	14.4	4.98	0.256	9	10.4	11.21	12.0	14.29	0.528
M^1	9	17.6	18.97	20.3	14.25	0.967	11	11.7	12.43	13.5	14.29	0.546
M^2	7	13.6	14.39	14.9	9.12	0.449	6	11.7	12.30	12.8	8.98	0.434
M^3	4	11.5	11.75	12.0	4.26	0.238	3	11.1	11.33	11.6	4.41	0.252

Table 4.- Material and measurements of Neocricetodon ambarrensis nov. sp. from Ambérieu 2C (Ain, France).

Tabla 4. Material y medidas de Neocricetodon ambarrensis nov. sp. de Ambérieu 2C (Ain, Francia)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1	21	26.3	28.96	30.9	16.08	1.086	20	15.4	16.34	17.2	11.04	0.460
M_2	34	22.1	24.39	25.9	15.83	0.831	33	16.3	18.11	19.9	19.89	0.732
M_3	29	22.0	24.28	26.4	18.18	1.193	29	16.3	17.76	19.0	15.30	0.776
M^1	30	28.1	30.89	32.3	13.91	1.004	30	17.3	18.72	20.5	16.93	0.651
M^2	37	22.5	24.28	26.3	15.57	0.984	38	17.8	19.08	20.7	15.06	0.629
M^3	35	18.1	20.10	21.6	17.63	0.940	35	16.2	17.59	18.7	14.33	0.625

Table 5.- Material and measurements of Apocricetus angustidens (Depéret, 1890) from Mont-Hélène (Pyrénées Orientales, France).

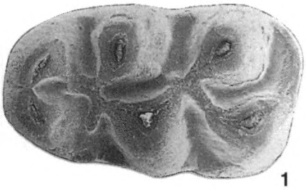
Tabla 5. Material y medidas de Apocricetus angustidens (Depéret, 1890) de Mont-Hélène (Pyrénées Orientales, Francia).

Plate 1 / Lámina 1

Cricetulodon bugesiensis nov. sp. from Soblay
1. M_1 sin., FSL 65897 Holotype / Holotipo
2. M_2 sin., FSL 65899
3. M_3 sin., FSL 65901
4. M_3 dext., FSL 65902
5. M_2 dext., FSL 65900
6. M_1 dext., FSL 65898
7. M^1 sin., FSL 65903
8. M^2 sin., FSL 65903
9. M^3 sin., FSL 65903
10. M^3 dext., FSL 65906
11. M^2 dext., FSL 65905
12. M^1 dext., FSL 65904

Cricetulodon bugesiensis nov. sp. from Dionay
13. M_2 sin., FSL 65924
14. M^1 sin., FSL 65925

Scale represents 1 mm / Escala 1 mm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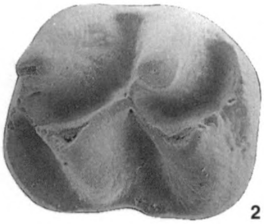
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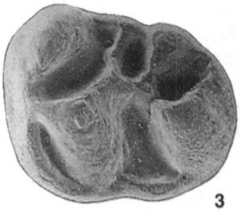
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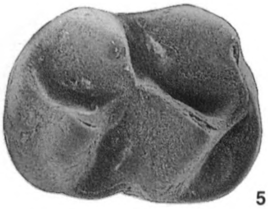
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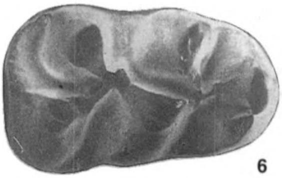
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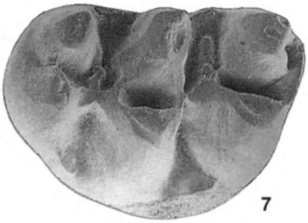
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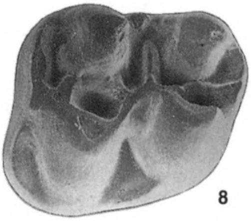
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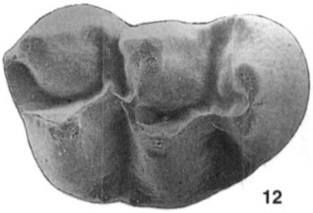
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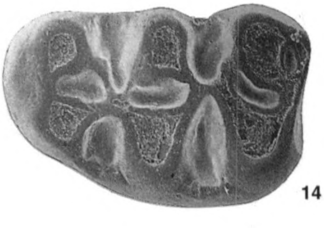
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Plate 2 / Lámina 2

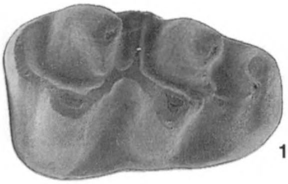
Neocricetodon skofleki (Kordos, 1987) from Ambérieu 3
1. M_1 dext., FSL 65931
2. M_2 dext., FSL 65932
3. M_3 sin., FSL 65933
4. M^3 dext., FSL 65936
5. M^2 dext., FSL 65935
6. M^1 dext., FSL 65934

Neocricetodon skofleki from Mollon
7. M_2 sin., FSL 65937
8. M^1 sin., FSL 65938
9. M^2 sin., FSL 65939

Neocricetodon cf. *skofleki* from Ambérieu 2C
10. M_1 sin., FSL 65926

Neocricetodon sp. 2 from Ambérieu 3
11. M^1 sin., FSL 65930
12. M_1 sin., FSL 65929
13. M_2 dext., FSL 65927
14. M_3 dext., FSL 65928

Scale represents 1 mm / Escala 1 mm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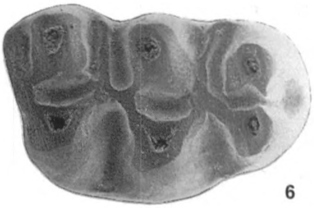
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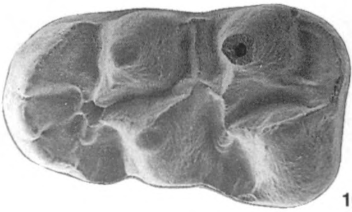
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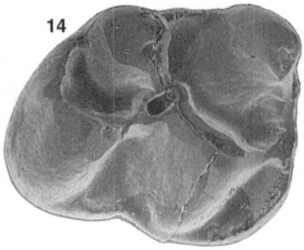

Plate 3 / Lámina 3

Neocricetodon ambarrensis nov. sp. from Ambérieu 2C
1. M_1 sin., FSL 65907 Holotype / Holotipo
2. M_2 sin., FSL 65909
3. M_3 sin., FSL 65911
4. M_1 sin., FSL 65908
5. M_2 sin., FSL 65910
6. M_3 dext., FSL 65912
7. M^1 sin., FSL 65913
8. M^2 sin., FSL 65915
9. M^3 sin., FSL 65917
10. M^1 sin., FSL 65914
11. M^2 dext., FSL 65916
12. M^3 sin., FSL 65918

Neocricetodon ambarrensis nov. sp. from Cucalón
13. M_2 dext., FSL 65919
14. M_3 sin., FSL 65920
15. M^1 sin., FSL 65921
16. M^2 sin., FSL 65922
17. M^3 sin., FSL 65923

Scale represents 1 mm / Escala 1 mm


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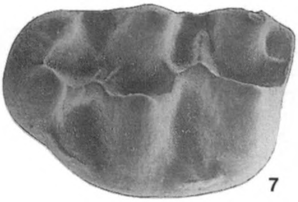
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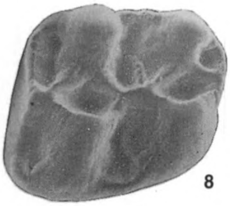
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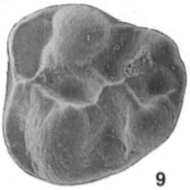
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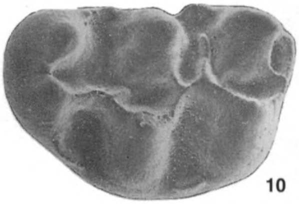
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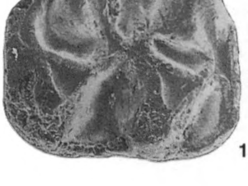
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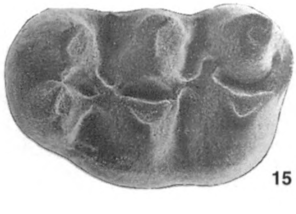
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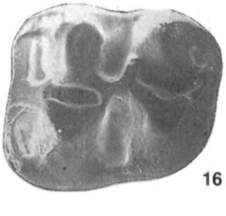
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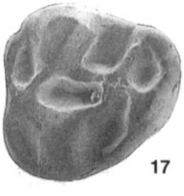
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Plate 4 / Lámina 4

Neocricetodon seseae Aguilar, Calvet & Michaux, 1995 from Crevillente 22
1. M_1 sin., CR22 1
2. M_1 sin., CR22 2
3. M^3 sin., CR22 17
4. M^1 sin., CR22 10

Neocricetodon seseae Aguilar, Calvet & Michaux, 1995 from Crevillente 14
5. M^2 sin., RGM 402085
6. M_1 sin., RGM 402900
7. M^1 sin., RGM 402073

Neocricetodon polonicus (Fahlbusch, 1969) from Hauterives
8. M^3 dext., FSL 65940
9. M^2 dext., FSL 65940
10. M^1 dext., FSL 65940

Apocricetus barrierei (Mein & Michaux, 1970) from Purcal 4
11. M_1 sin., PUR4 1
12. M^1 dext., PUR4 14

Scale represents 1 mm / Escala 1 mm


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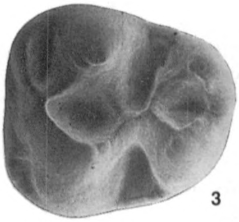
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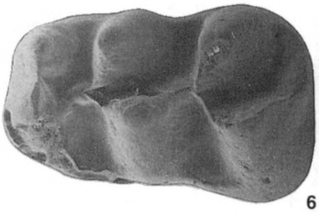
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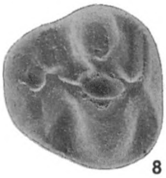
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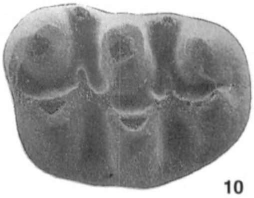
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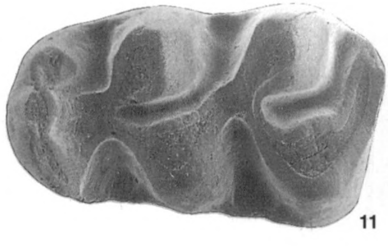
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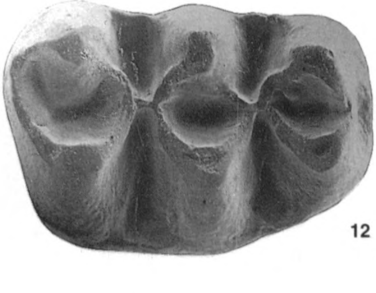
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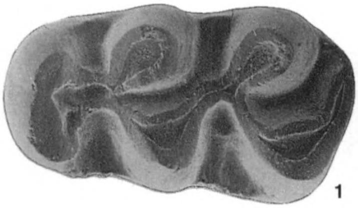
Plate 5 / Lámina 5

Apocricetus alberti nov. sp. from Venta del Moro
1. M_1 sin., FSL 65941
2. M_2 sin., FSL 65942
3. M_3 sin., FSL 65943
4. M^2 sin., FSL 65944
5. M^3 sin., FSL 65945

Apocricetus aff. *plinii* (Freudenthal, Lacomba & Martín Suárez, 1991) from Crevillente 23
6. M_1 sin., RGM 413822
7. M_1 dext., RGM 413826
8. M^1 dext., RGM 413880
9. M^1 sin., RGM 413877
10. M^2 sin., RGM 413894
11. M^3 dext., RGM 413924

Scale represents 1 mm / Escala 1 mm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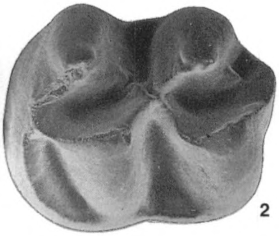
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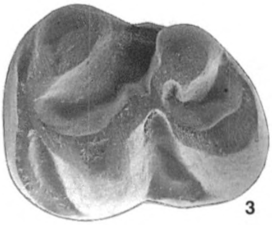
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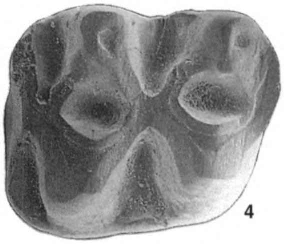
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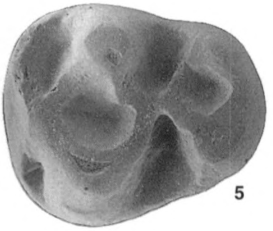
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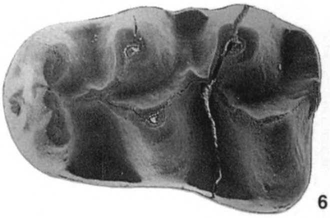
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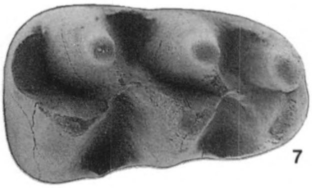
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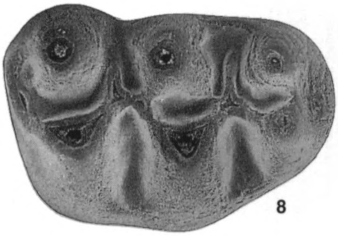
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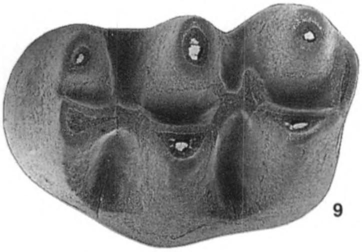
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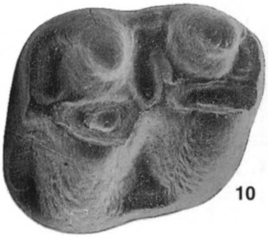
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