REVISTA ESPAÑOLA DE PALEONTOLOGÍA, **Extra**, 49-57. 1992

CLASSIFICATION OF EUROPEAN OLIGOCENE CRICETIDS

M. FREUDENTHAL[1], J.I. LACOMBA[2] & M.A. SACRISTÁN[3]

1) Nationaal Natuurhistorisch Museum. Leiden, The Netherlands, and Departamento de Estratigrafía y Paleontología. Univ. Granada, Spain.
2) Departamento de Geología. Univ. Valencia, Spain.
3) Departamento de Paleontología, Univ. Complutense, Madrid, Spain.

ABSTRACT

A proposal is made for a classification of Oligocene European cricetids. Various problems concerning the evolution of *Eucricetodon* and *Pseudocricetodon* are discussed. A new species of *Pseudocricetodon* is described from a level slightly lower than the oldest occurrence of the genus, known so far.

Keywords: Cricetidae (Mammalia), Oligocene, Spain.

RESUMEN

En este trabajo se propone una clasificación de los Cricétidos del Oligoceno de Europa. Se discuten varios problemas relativos a la evolución de *Eucricetodon* y *Pseudocricetodon* y, dentro de este último género, se describe una nueva especie procedente de un nivel más antiguo que la distribución anteriormente conocida del género.

Palabras clave: Cricetidae (Mammalia), Oligoceno, España.

INTRODUCTION

In 1986 we decided to undertake a revision of the cricetid genera *Eucricetodon* Thaler, 1966 and *Pseudocricetodon* Thaler, 1969. Since Montalbán (prov. Teruel, Spain) is the type-locality of the type-species of *Pseudocricetodon,* we found it necessary to carry out new prospections and excavations in the area of Montalbán. Apart from the excavation of the classical site of Montalbán, many new fossiliferous localities were discovered, which yielded a wealth of material, mainly Theridomorpha, Cricetidae, Gliridae, and Eomyidae. Some results have been published already (Freudenthal, 1988, Freudenthal *et al.*, 1990), but it will take much time to study the very large collections available now.

So far our study of the material has been dedicated mainly to the Cricetidae, more precisely to the problem how to distinguish the two genera mentioned above. *Pseudocricetodon* was created as a monospecific genus by Thaler (1969). Hugeney described two new species, *Pseudocricetodon thaleri* in 1969, and *Pseudocricetodon philippi* in 1971. In 1980 the same author transferred *Eucricetodon incertus* (Schlosser, 1884) to the genus *Pseudocricetodon,* and in 1985 Comte did the same with *Eucricetodon moguntiacus* Bahlo, 1972. Apart from these taxonomic adjustments, and in spite of the large number of publications on Oligocene cricetids that have appeared in the past decades (Bahlo, 1975; Brunet, 1979; Comte, 1985; Dienemann, 1987; Hugueney, 1969, 1971; Vianey-Liaud, 1971, 1972, 1974, and many others) the classification of this group remained basically untouched since the work by Mein & Freudenthal (1971). In 1987 Engesser created the subfamily Pseudocricetodontinae and in 1989 Ünay-Bayraktar in her study of Middle Oligocene Turkish rodents published an entirely new concept of the classification of Oligocene cricetids. In this paper we will comment that classification and propose an alternative, that deviates less from the current one.

THE CLASSIFICATION PROPOSED BY ÜNAY-BAYRAKTAR

Ünay-Bayraktar (1989) presents a proposal for a new taxonomic classification of Oligocene cricetids. She states "The philosophy which is at the basis of our classification is that it should lead to a flexible system, a system which is by no means presented as natural or perfect, but which can be easily adapted when new information becomes available". (Op. cit., p. 17). However, the preamble of the International Code of Zoological Nomenclature reads "The object of the Code is to promote stability...". Furthermore she states "The larger part of this classification will be clarified in the discussion of the Thracian representatives of the Muroidea" (op. cit. p. 18). Unfortunately this clarification

https://doi.org/10.7203/sjp.25014

lacks in her paper. We will here discuss some details of Ünay's classification.

Family **Melissiodontidae.**

Ünay-Bayraktar assembles two subfamilies in her family Melissiodontidae: Paracricetodontinae and Melissiodontinae. Unfortunately she gives no arguments for this arrangement. Her only statement related to this subject is (op. cit., p. 38) "We therefore have come to the conclusion that the subfamilies Paracricetodontinae with the genera *Paracricetodon* and *Trakymys* and the subfamily Melissiodontinae with the genera *Melissiodon* and *Edirnella* are closely related and probably constitute a group of family rank". Her opinion that *Paracricetodon* and *Trakymys* are related appears to be perfectly correct, but the grouping of *Melissiodon* and *Edirnella* is less obvious. After Ünay-Bayraktar the best distinctive character for the Melissiodontinae is the antero-lingual cusp (*Melissiodon* cusp) in M^1. This cusp is indeed well-developed in *Melissiodon* and present, though less-developed, in *Edirnella.* However, apart from the question whether this accessory cusp may be attributed such importance, it is not useful as a grouping character, since it appears in *Heterocricetodon* and various *Eucricetodon* with the same degree of development as in *Edirnella,* and it is at least present in other *Eucricetodon* and in *Paracricetodon.*

Ünay's morphological sequence *Paracricetodon - Trakymys - Edirnella - Melissiodon* (op. cit., p. 37, 38) may well be interpreted by placing both *Trakymys* and *Edirnella* in the Paracricetodontinae. The predominance of crests over cusps as seen in *Edirnella* is a development known to happen in various c ricetid groups, and in itself does not present an argument for taxonomic relationship (e.g. the Late Miocene cricetine *Hattomys* has a dental pattern that is possibly more like *Melissiodon* than the one of *Edirnella*).

The Melissiodontinae appear to be a different group that need not even be closely related. Possibly the dental pattern is not a good criterion to solve the problem. According to Schaub (1925) the mandible of *Melissiodon* is quite different from the one of *Paracricetodon.* Skull and mandible characters may be better arguments than dental morphology in solving these taxonomic problems.

Family **Pseudocricetodontidae**

Engesser (1987) created the subfamily Pseudocricetodontinae, with the following diagnosis: "Small to large Oligocene and lower Miocene cricetids with rather lophodont molars. M^1 with large prelobe, straight or even concave labial edge, and often long anterior arm of protocone. M^2 with double protoloph. M_1 mostly with posterior crest of the paraconid and often double mesoloph. M_1 and M_2 mostly without the posterior arm of the hypoconid" (op. cit., p. 991).

Ünay-Bayraktar (1989) raised this subfamily to family rank, and gave a diagnosis for the family Pseudocricetodontidae, that is so vague that it fits almost all cricetids, and a more detailed diagnosis of her subfamily Pseudocricetodontinae: "Small pseudocricetodontids. Crown base of cheek teeth very low. Cusps small relative to the size of the occlusal surface and pointed. Mesoloph(id)s usually well-developed. Anterior arm of protocone and hypocone present in M^1"(op. cit., p. 38).

Then she creates the subfamily Adelomyarioninae, with the genera *Adelomyarion* Hugueney, 1969 and *Kerosinia* Ünay-Bayraktar, 1989, within the family Pseudocricetodontidae Engesser, 1987. Her diagnosis of this new subfamily is:

1) Occlusal surface of the M^2 subquadrate.
2) Longitudinal crests of the M^1, M^2 and M_1, M_2, M_3 near the median axis of the occlusal surface.
3) Anterior end of the longitudinal crest of M^1 and M^2 either connecting to the paracone or showing a tendency to do so.

Argument 1 is of subordinate diagnostic value; it is equally true for a wide variety of other cricetids.

Argument 2 is not true for the upper molars of *Adelomyarion.* The longitudinal crest in the upper molars of *Adelomyarion* is characterized by an oblique position that cannot be said to be either axial or lingual.

Argument 3 is not true for *Kerosinia.* The longitudinal crest of the upper molars in this genus shows the same structure as it does in *Pseudocricetodon* and many *Eucricetodon.*

We think the similarities in dental morphology between *Kerosinia variabilis* ÜNay-Bayrakter, 1989 and various species of *Pseudocricetodon* (e.g. the straight labial border of M^1 and the double mesolophids in M_1) are so great, that *Kerosinia* must be closely related to *Pseudocricetodon.* It is quite possible that they belong to the same genus, in which case *Kerosinia* is a junior synonym.

Adelomyarion, on the other hand, is a quite different taxon. Possibly its most characteristic features are the oblique entoloph, pointing towards the paracone, or connected to this cusp; the interruption, or tendency to interrupt the posterior branch of the protocone, resulting in a strongly oblique sinus, that may in some cases continue into the anterosinus; the straight, oblique or hardly indented outline of M^1 between anterocone and protocone.

In the lower molars the metalophulid of M_1 is frequently absent; in M_2 the mesolophid is often absent; the M_3 is rather short.

Freudenthal & Cuenca Bescós (1984) expressed their doubt as to whether *Adelomyarion* is a cricetid, or a member of a different, hitherto unknown, group of rodents. This problem remains unsolved. There seems to be little doubt, that the subfamily Adelomyarioninae will have to be raised to a higher taxonomic level in the future.

PROPOSED CLASSIFICATION OF OLIGOCENE CRICETIDS

We hereby propose a classification of European Oligocene cricetids, that differs considerably less from the current one than Ünay's proposal, and reflects fairly well our present knowledge of this group (see also Table 1):

Table 1.

Family Cricetidae Murray, 1866
  Subfamily Paracricetodontinae Mein & Freudenthal, 1971
    Paracricetodon Schaub, 1925
    Trakymys Ünay-Bayraktar, 1989
    Edirnella Ünay-Bayraktar, 1989
  Subfamily Eucricetodontinae Mein & Freudenthal, 1971
    Eucricetodon Thaler, 1966
    Eumyarion Thaler, 1966?
    Mirabella de Bruijin, Ünay, Saraç & Klein Hofmeier, 1987?
  Subfamily Pseudocricetodontinae Engesser, 1987
    Tribe Pseudocricetodontini Engesser, 1987
      Pseudocricetodon Thaler, 1969
      Lignitella Ünay-Bayraktar, 1989
      Kerosinia Ünay-Bayraktar, 1989
    Tribe Heterocricetodontini Ünay-Bayraktar, 1989
      Heterocricetodon Schaub, 1925
      Cincamyarion Agustí & Arbiol, 1989

Family Melissiodontidae Stehlin & Schaub, 1951
    Melissiodon Schaub, 1920

Family incertae sedis
  Subfamily Adelomyarioninae Ünay-Bayraktar, 1989
    Adelomyarion Hugueney, 1969.

Family **Cricetidae** Murray, 1866
Subfamily Paracricetodontinae Mein & Freudenthal, 1971

Attributed genera:
Paracricetodon Schaub, 1925
Trakymys Ünay-Bayraktar, 1989
Edirnella Ünay-Bayraktar, 1989

Diagnosis (mainly after Bahlo, 1975). Medium-sized to large cricetids. Ectolophid poorly developed. Metaconid and entoconid connected by a high cingullum ridge along the border of the lower molars. M_1 and M_2 with free hypoconid hind arm. Anteroconid of M_1 poorly developed and anterior metalophulid absent. M_3 on the average longer and broader than M_1. M^2 and M^3 with free anterior arm of the protocone. Posterior part of M^3 little reduced. Mandible almost vertical with respect to the occlusal surface, diasteme flat.

N.B. *Eucricetodon robustus* Agustí & Arbiol, 1989 may belong to the Paracricetodontinae, instead of being an *Eucricetodon*.

Subfamily **Eucricetodontinae** Mein & Freudenthal, 1971

Attributed genera:
Eucricetodon Thaler, 1966
Eumyarion Thaler, 1966?
Mirabella de Bruijn, Ünay, Saraç & Klein Hofmeier, 1987?

Proposed diagnosis: Small to large cricetids, dentition with rather bunodont cusps. Mandible transversally inclined with respect to the occlusal surface, diasteme concave with steep posterior border. Maxilla with short foramen incisivum, not —or only slightly— entering between the M^1.

Lower molars: M_3 smaller than M_1. Posterior part of M_3 generally reduced. Protoconid hind arm in M_1 and M_3 frequently present, in M_1 it may be connected to the metaconid. Anterior metalophulid in M_1 frequently present. Posterolophid of M_1 often forms a wide curve. In M_2 and M_3 the metalophulid is generally placed far forward, and the anterosinusid reduced.

Upper molars: Lingual border of M^1 straight or convex, forming an angle of less than 90° with the posterior border. The prelobe of M_1 may be set off from the rest of the molar, but more frequently the lingual border between anterocone and protocone is smooth.

N.B. *Eumyarion* is possibly an Eucricetodontine; the position of *Mirabella* is by no means clear; we place it here because Ünay-Bayraktar (1989) places it in the same subfamily as *Eumyarion*.

Subfamily **Pseudocricetodontinae** Engesser, 1987

Diagnosis: (modified after Engesser, 1987). Small to large Oligocene and lower Miocene cricetids with rather lophodont molars. M^1 with large prelobe, straight or even concave labial edge, and often long anterior arm of protocone. M^2 with double protolophule. M_1 mostly with a strong ridge descending from the metaconid, along the border of the tooth, into the mesosinusid, without reaching the entoconid. In M_1 the mesolophid is frequently double. M_1 and M_2 nearly always without the posterior arm of the hypoconid. Mandible transversally inclined with respect to the occlusal surface, diasteme concave.

N.B. The diagnosis has been modified, because the terminology applied by Engesser has some terms for the upper and the lower dentition mixed up. Some details have been added.

Tribe **Pseudocricetodontini** Engesser, 1987

Attributed genera:
Pseudocricetodon Thaler, 1969
Lignitella Ünay-Bayraktar, 1989
Kerosinia Ünay-Bayraktar, 1989

Proposed diagnosis: Small Pseudocricetodontinae, foramen incisivum in the maxilla short (posterior border lying before the foremost point of the M^1),

Lower molars: M_3 smaller than M_1. Posterior part of M_3 less reduced than in Eucricetodontinae. Protoconid hind arm in M_1 and M_2 nearly always present, in M^1 nearly always connected to the metaconid. An-

terior metalophulid in M_1 rarely present. Posterolophid of M_1 hardly curved, running straightly towards the entoconid. In M_2 and M_3 the metalophulid is generally more or less transverse, which, combined with a long anterolophulid results in a wide anterosinusid. Posterior branch of the hypoconid hardly ever present.

Upper molars: Lingual border of M^1 straight or concave, forming an angle of about 90° with the posterior border. The prelobe of M^1 is frequently set off from the rest of the molar, the lingual border between anterocone and protocone presenting a sharp angle.

Tribe **Heterocricetodontini** Ünay-Bayraktar, 1989

Attributed genera:
Heterocricetodon Schaub, 1925
Cincamyarion Agustí & Arbiol, 1989

Proposed diagnosis: Medium to large pseudocricetodontines. The foramen incisivum of the maxilla is known in *H. incertus* and in a *Heterocricetodon* from Gaimersheim; in both cases it extends backwards between the M^1. M^2 frequently shows a free anterior branch of the protocone. Third molars not very much reduced.

N.B. Following Daams *et al.* (1989) the genus *Heterocricetodon* includes *Cricetodon incertus* Schlosser, 1884.

N.B. *Cincamyarion* is placed in this group on the basis of dental morphology; the foramen incisivum of the maxilla is not known.

Family **Melissiodontidae** Stehlin & Schaub, 1951

Attributed genus:
Melissiodon Schaub, 1920

Proposed diagnosis: Mandible without a marked masseter triangle, the incisor is not prolonged into the ramus ascendens, but ends below the M_2. The symphysis is very small (mandible characters after Schaub, 1925).

In the dentition the cusps are very much reduced, and the crests predominate. The dental pattern is very complex. Anteroconid of M_1 with one or two cusps. M_3 relatively long. M^1 very large, with two cusps in the anterocone.

Incertae sedis

Subfamily **Adelomyarioninae** Ünay-Bayraktar, 1989

Attributed genus:
Adelomyarion Hugueney, 1969.

Proposed diagnosis: Upper molars with oblique entoloph, pointing towards the paracone, or connected to this cusp; there is a tendency to interrupt the posterior branch of the protocone, resulting in a strongly oblique sinus, that may in some cases continue into the anterosinus; the outline of M^1 between anterocone and protocone is straight and oblique or hardly indented.

In the lower molars the metalophulid of M_1 is frenquently absent; in M_2 the mesolophid is often absent; the M_3 is rather short.

REMARKS ON *EUCRICETODON*

Most authors (Bhalo, 1975; Brunet *et al.*, 1981; Comte. 1985; Dienemann, 1987) distinguish various groups, or evolutionary lineages, within the genus *Eucricetodon.* Roughly these groups could be:
atavus-huberi-huerzeleri-praecursor-collatus-gerandianus and *dubius-hochheimensis-haslachensis.*

Many discussions about this subdivision, and the possible phylogeny of *Eucricetodon* center around the distinction between *E. dubius* (Schaub, 1925) and *E. praecursor* (Schaub, 1925). For that reason a short discussion of the problems concerning these two taxons is given here.

E. dubius and *E. praecursor* are two species of roughly the same size and morphology. The holotype of *E. dubius* is the mandible QT 764 from the Quercy (Lot-et-Garonne, France), kept in the Basel Museum; the holotype of *E. praecursor* is the mandible QT 763 from the Quercy, in the same museum.

Morphologically these two specimens are quite similar. Differences between the holotypes are:

The mandible of *E. praecursor* is moderately inclined with respect to the occlusal surface; the mandible of *E. dubius* is almost vertical, when the occlusal surface is oriented horizontally. The diasteme of *E. praecursor* is possibly deeper than it is in *E. dubius.*

Contrary to the description by Schaub (1925) the incisor of *E. praecursor* bears three ribs, whereas in *E. dubius* it bears two ribs.

In the M_1 of *E. praecursor* the metaconid is connected to the anteroconid by a high cingulum ridge; the metaconid is very much isolated from the protoconid; there is a small mesoconid; the mesolophid is thin and of medium length; the posterior branch of the hypoconid is long and it ends free; in the M_1 of *E. dubius* the metaconid is connected to the anteroconid by a low cingulum ridge; there is no mesoconid, the mesolophid is short; the posterior branch of the hypoconid is long and connected to the entoconid.

In the M_2 of *E. praecursor* the posterior branch of the protoconid is short, the mesoconid is weak, the mesolophid short, the ectomesolophid strongly developed; the posterior branch of the hypoconid is short; in the M_2 of *E. dubius* the posterior branch of the protoconid is long, there is no mesoconid, the mesolophid is of medium length, there is no ectomesolophid; the posterior branch of the hypoconid is not visible, but probably present and fused with the very broad posterolophid.

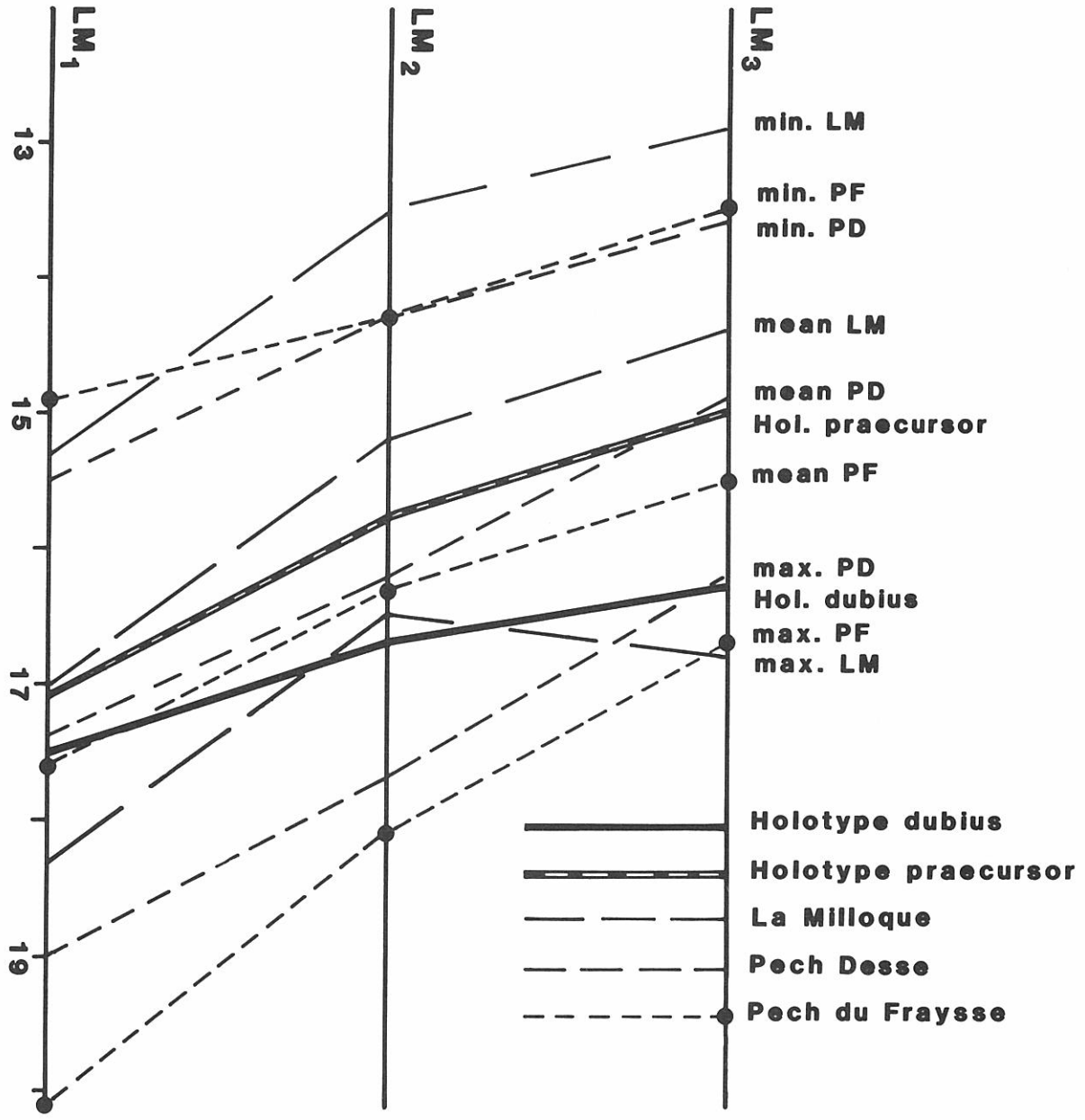


Figure 1. Lengths of M_1, M_2, and M_3 of the holotypes and various populations of *E. praecursos.* Measurements of the two holotype mandibles by the first author; data for Pech Desse and Pech du Fraysse from Compte (1985); data for La Milloque from Brunet (1979).

In the M_3 of *E. praecursor* the posterior branch of the protoconid is short, the mesoconid is weak, the mesolophid absent; the hypolophulid is short (less than half the posterior tooth width); in the M_3 of *E. dubius* the posterior branch of the protoconid is long, there is no mesoconid, the mesolophid is of medium length; the hypolophulid is long (about half the posterior tooth width).

This is the kind of differences that in themselves are not sufficient to distinguish two species. Only when they materialize in statistically reliable samples, can they be used to distinguish species.

The best differences between these two species might be found in the upper molars, but these are not present in Schaub's original material from the Quercy. Schaub's statement that he had been able to distinguish upper molars to match the two holotype mandibles may be one hundred percent correct, but it can, unfortunately, not be proven. The upper molars Schaub attributes to these species come from Puy-de-Montdoury (Puy-de-Dôme, France), and their relation with the two mentioned holotype mandibles from the Quercy is not sure. The interpretation may be inverted, and it is also possible that one or two species more are involved. So, to solve the problem, we will have to try and find sufficiently large samples of similar *Eucricetodon* material.

Brunet (1979) describes *E. praecursor* from La Milloque (Lot-et-Garonne, France) on the basis of 30 to

50 specimens per element, quite a good sample.

Both holotype mandibles (*E. praecursor* and *E. dubius*) fit perfectly well in the morphological and metrical variability of the population from La Milloque. The measurements of the holotype of *E. praecursor* are all slightly larger than the mean values in the sample from La Milloque; the measurements for the holotype of *E. dubius* are slightly smaller than the maximum values for La Milloque. This leads to two conclusions:

1) The two holotype mandibles may well belong to a single species.

2) The supposition (Schaub, 1925; Brunet *et al.*, 1981), that the hind molars in *E. dubius* are relatively less reduced than in *E. praecursor,* is not tenable. This becomes clear in Fig. 1, where the lengths of the molars of the two holotype mandibles are compared with the minimum, mean and maximum of *E. praecursor* from La Milloque, and *E. dubius* from Pech Desse and Pech du Fraysse. Basically all lines are parallel, with the exception of the line for the maxima of the population from La Milloque, where the M_2 is slightly smaller than expected.

Brunet (1979) and Comte (1985) give similar graphs, but instead of giving absolute values, they choose one reference population, drawn as a straight line, and calculate the lines for the other populations in terms of the logarithms of the differences with the reference. This method is not recommendable for various reasons:

Logarithms in this case serve no purpose at all; choosing a reference population obscures the real data, and may produce an undesirable optical impression. Furthermore the graph may be influenced by the accidental underrepresentation of one of the dental elements in the reference population. In Küttigen (reference population in Brunet, 1979, p. 657) only 7 specimens of M^3 are available, not sufficient to calculate a reliable mean value, and M_1 is poorly represented by 11 specimens. In Pech Desse (reference population in Comte, 1985, p. 32) only 10 specimens of M^3 are available. This may mean, that in both cases the lines for all the other populations might take a considerably different shape when a sufficiently large number of specimens were found for each dental element of the reference population.

When the absolute size is taken as the standard, the graph is easily read, one may add his own data without any difficulty, and a change in the data for one of the lines does not influence the other ones.

The largest published samples of *E. dubius* are the ones described by Comte (1985) from Pech Desse and pech du Fraysse Quercy). Both holotype mandibles (*E. praecursor* and *E. dubius*) fit in the morphological and metrical variability of these populations. But, unfortunately these are not homogeneous samples. A simple analysis of the measurement tables shows that at least the M^1 from Pech Desse, and the M^2, M^3, and M_1 from Pech du Fraysse show such high variability values (V' as defined by Freudenthal & Cuenca Bescós, 1984), that almost certainly they must contain various species. So, these samples are not fit to help us in a discussion on the identity of the two species under question.

The German locality of Gaimersheim has yielded a large sample attributed to *E. dubius,* but here again there is sincere doubt about its homogeneity.

In the sample of *E. dubius* from Vivel del Río (Teruel, Spain), described by Hugueney *et al.* (1987) at least two species are represented (personal observation).

If the number of ribs on the lower incisor is a taxonomically valid criterion, it may be necessary to attribute (most of) the populations known as *E. dubius* to *E. praecursor.* However, the difference between two and three ribs is possibly not a diagnostic feature. Possibly *E. dubius* and *E. praecursor* represent one species. There is another argument for this theory:

E. praecursor, according to the table compiled by Brunet & Vianey-Liaud (1987) is restricted to "zone MP 29" with reference locality Rickenbach. *E. dubius* is reported only from older levels.

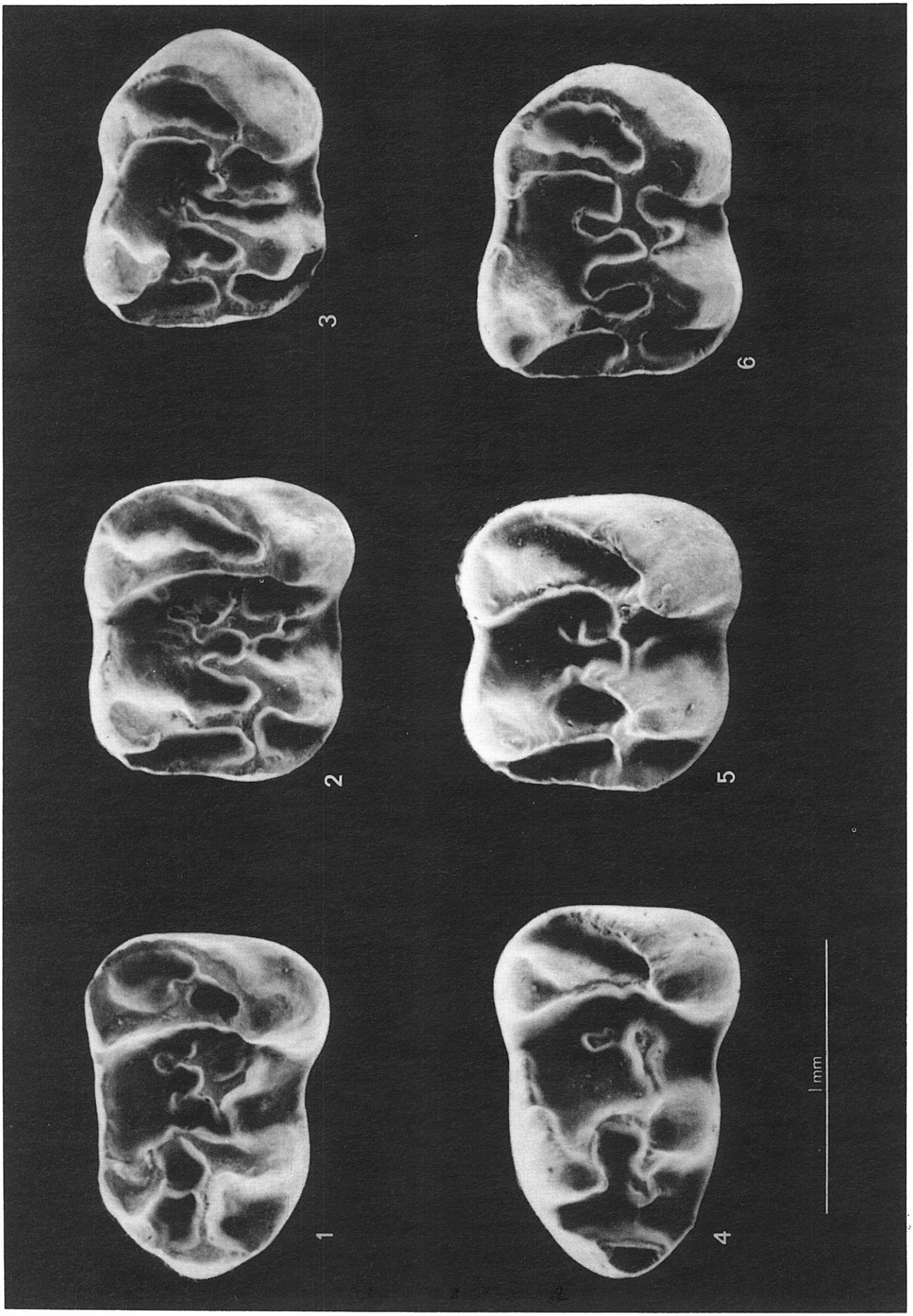
Thanks to the work of the Montpellier research group, today a very large number of localities from the Quercy is known (for an overview see Remy *et al.*, 1987), where *E. dubius* has been reported. Not a single Quercy locality is attributed to the level of Rickenbach. Schaub had one mandible of *E. dubius* (QT 764), and two mandibles of *E. praecursor* (QT 763 and QT 984). It is a very odd chance, that the latter two mandibles should come from a Quercy locality belonging to a stratigraphic level not represented in the vast collections available today.

Our suggestion is therefore that *E. praecursor* and *E. dubius* are synonyms. We prefer to preserve the name *E. dubius,* since it is being used for the Quercy populations. *E. praecursor* is then a synonym of E. *du-*

Plate 1.

Pseudocricetodon sp. from Montalbán 3C
Fig. 1. M_1 sin., MLB3C 61
Fig. 2. M_2 sin., MLB3C 62
Fig. 3. M_3 sin., MLB3C 64

Pseudocricetodon montalbanensis Thaler, 1969 from Montalbán 1D
Fig. 4. M_1 sin., MLB1D 208
Fig. 5. M_2 sin., MLB1D 444
Fig. 6. M_3 sin., MLB1D 504


1
2
3
4
5
6
1 mm

bius. For the material from Rickenbach, La Milloque, etc., that is morphologically different from *E. dubius* a new species name should be created.

REMARKS ON *PSEUDOCRICETODON*

In discussions on the phylogeny of *Pseudocricetodon* it is frequently assumed, that *E. moguntiacus* Bahlo, 1975 from Heimersheim be a descendant of *P. montalbanensis* Thaler, 1969. Thanks to Drs Schmidt-Kittler and Hugueney we had the opportunity to study a collection from Heimersheim; Dr Hugueney had already made a separation of this material into various groups, which made our study a lot easier. We came to the following conclusions:

Bahlo (1975) described over 250 specimens of *E. moguntiacus,* and less than 20 specimens of what he called *Eucricetodon atavus.* Freudenthal (1988) demonstrated, that this *Eucricetodon* is not *E. atavus.* We found a much higher frequency of this *Eucricetodon,* and think, that a considerable part of Bahlo's *E. moguntiacus* collection belongs to his "*E. atavus*"). The remaining *E. moguntiacus* material belongs to two different species of *Pseudocricetodon,* distinguished by their size, and some minor morphological details.

The supposed lineage *P. montalbanensis-moguntiacus* cannot be confirmed nor rejected, until the Heimersheim material be revised in more detail, and the two *Pseudocricetodon* species separated, and morphologically defined. The name *E. moguntiacus* is based on the holotype HLM/Hhm 595, one of the smallest M^2; after dividing the material on the basis of dimensions into two groups, *P. moguntiacus* is roughly of the same size as *P. montalbanensis.* Because of some morphological differences we don't think the two species are identical.

In the M_2 and M_3 of *P. moguntiacus* the protoconid hind arm is longer and more detached from the metaconid than in *P. montalbanensis.* The mesolophid is on the average shorter and of a simpler structure, the ectomesolophid is less developed. The mesoloph of M^1 and M^2 is on the average shorter than in *P. montalbanensis.*

PSEUDOCRICETODON SP. NOV.

So far, the classic level of Montalbán (MLB 1D in our terminology), was the oldest occurrence of *Pseudocricetodon.* We found, however, an obviously new species of this genus in a level slightly lower than the classic one. The material is very poor (1 M_1, 2 M_2 and 2 M_3). Its highly complicated morphology proves that at this level already there must have been at least two lineages of *Pseudocricetodon,* because the new species can by no means be an ancestor of *P. montalbanensis* from MLB 1D, which shows a much more simple morphology. In view of the scarcity of the material we refrain from naming a new species.

Locality: Montalbán 3C
Material: (measurements in units of 0.1 mm) M_1 sin., MLB3C 61, 12.3 × 8.5; M_2 sin., MLB3C 62, 11.5 × 9.8; M_2 dext., MLB3C 63, 11.2 × 9.7; M_3 sin., MLB3C 64, 10.7 × 8.7: M_3 dext., MLB3C 65, 10.7 × 8.5.

This material will be incorporated in the collections of the Departamento de Ciencias de la Tierra, Universidad de Zaragoza.

Description.

M_1: The anteroconid is a transverse crest, the lingual anterolophid closes the anterosinusid; there is a low metalophulid; the hind arm of the protoconid is long, and reaches the metaconid at mid-height. There is a small mesoconid, that bears a mesolophid of medium length, directed towards the protoconid hind arm. The mesoconid bears a second crest, directed posteriorly, that branches into three crests. There is a long and high hypoconid hind arm, that is strongly connected to the entoconid.

M_2: The protoconid hind arm is long, and ends freely in the mesosinusid. Mesoconid and mesolophid are as complex as in M_1 and there is a very strong ectomesolophid. The ectolophid is low, almost interrupted, between mesoconid and hypolophulid. There is no hypoconid hind arm. In the second specimen the mesoconid is somewhat less complex, and the ectolophid is higher.

M_3: The metalophulid is interrupted, and bears various posterior spurs. The protoconid hind arm is very long, and ends freely. There is no mesoconid, the mesolophid is short, the ectomesolophid very strong. The ectolophid is interrupted between protoconid and mesolophid. In the second specimen the protoconid hind arm is shorter, and the ectolophid is low, but not interrupted.

This species differs from all other species of *Pseudocricetodon* by its very complex dental morphology, specially the complex structure of the mesolophid in M_1 and M_2, the presence of a well developed hypoconid hind arm in M_1, and by the nearly or completely interrupted ectolophid in M_2 and M_3. It is furthermore characterized by very well developed ectomesolophids in M_2 and M_3.

ACKNOWLEDGEMENTS

We wish to thank Dr G. Cuenca Bescós (Zaragoza) for her help on many levels, that made the excavations in Montalbán possible.

We are grateful to Dr M. Hugueney (Lyon), who

allowed us to study Oligocene cricetid material in the collections of the University of Lyon, and put many of her own observations at our disposal, and to Dr N. Schmidt-Kittler (Mainz), who allowed us to study cricetid material from Heimersheim.

We highly appreciate the work of two anonymous referees who contributed considerably to the final form of this study.

This work was financially supported by the Diputación General de Aragón, Spain, and the National Museum of Geology and Mineralogy, Leiden, The Netherlands, for which we are most grateful.

REFERENCES

Bahlo, E. 1975. Die Nagetierfauna von Heimersheim bei Alzey (Rheinhessen, Westdeutschland) aus dem Grenzbereich Mittel-Oberoligozän und ihre stratigrafische Stellung. *Abh. Hess. Landesamt Bodenf.,* **71:** 1-182.

Brunet, M. 1979. Les Cricetidae (Rodentia, Mammalia) de la Milloque (bassin d'Aquitaine): horizon repère de l'Oligocène supérieur. *Géobios,* **12, 5:** 653-673.

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

Brunet, M. & Vianey-Liaud, M. 1987. Mammalian Reference Levels MP 21-30. *In:* Schmidt-Kittler, N., 1987. Intern. Symp. on Mammal. Biostratigraphy and Paleoecology of the European Paleogene, Mainz, Febr. 18-21, 1987. *Münchner Geowiss. Abh., A,* **10:** 30-31.

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

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

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

Engesser, B. 1987. New Eomyidae, Dipodidae, and Cricetidae (Rodentia, Mammalia) of the Lower Freshwater Molasse of Switzerland and Savoy. *Eclog. Geol. Helv.,* **80, 3:** 943-994.

Freudenthal, M. 1988. Redescription of *Eucricetodon atavus* (Misonne, 1957) from Hoogbutsel (Belgium). *Bull. Inst. Roy. Sci. Nat. Belgique, Sci. Terre,* **58:** 199-207.

Freudenthal, M. & Cuenca Bescós, G. 1984. Size variation of fossil rodent populations. *Scripta Geol.,* **76:** 1-28.

Freudenthal, M.; Lacomba, J.L.; Martínez-Salanova, J. & Sacristán, A. 1990. Nueva sucesión de niveles con micromamíferos en el Oligoceno de Montalbán (Prov. Teruel, España). *Acta Salmanticensia,* **68:** 133-140.

Hugueney, M. 1969. Les rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Branssat (Allier). *Docum. Lab. Géol. Fac. Sci. Lyon.,* **34:** 1-227, 5 pls.

Hugueney, M. 1971. Pseudocricetodon philippi, nouvelle espèce de Cricétidé (Rodentia, Mammalia) de l'Oligocène moyen de Saint-Martin-de-Castillon (Vaucluse). *C. R. Acad. Sci. Paris, D. 272,* **20:** 2533-2535.

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

Mein, P. & Freudenthal, M. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. *Scripta Geol.,* **2:** 1-37, 2 pls.

Remy, J.A.; Crochet, J.-Y.; Sigé, B.; Sudre, J.; de Bonis, L.; Vianey-Liaud, M.; Godinot, M.; Hartenberger, J.-L.; Lange-Badré, B. & Comte, B. 1987. Biochronologie des phosphorites du Quercy: Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. *In:* Schmidt-Kittler, N., 1987. Intern. Symp. on Mammal. Biostratigraphy and Paleoecology of the European Paleogene, Mainz, Febr. 18-21, 1987. *Münchner Geowiss. Abh., A,* **10:** 169-188.

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

Thaler, L. 1969. Rongeurs nouveaux de l'Oligocène moyen d'Espagne. *Palaeovertebrata,* **2, 5:** 191-207.

Ünay-Bayraktar, E. 1989. Rodents from the middle Oligocene of Turkish Thrace. *Utrecht Micropal. Bull.,* **5:** 1-119, 11 pls.

Vianey-Liaud, M. 1971. Données nouvelles sur l'évolution des genres Eucricetodon et Pseudocricetodon à l'Oligocène en Europe Occidentale. *C. R. Acad. Sci. Paris, D, 273,* **6:** 619-622.

Vianey-Liaud, M. 1972. Contribution à l'étude des Cricetidés oligocènes d'Europe occidentale. *Palaeovertebrata,* **5, 1:** 1-44, 5 pls.

Vianey-Liaud, M. 1974. L'anatomie crânienne des genres *Eucricetodon* et *Pseudocricetodon* (Cricetidae, Rodentia, Mammalia); essai de systématique des Cricétidés oligocènes d'Europe occidentale. *Géol. Mediterr.,* **1, 3:** 111-132.