The Early Oligocene rodent fauna of Olalla 4A (Teruel, Spain)

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Key words — Oligocene, Mammalia, Spain.
The rodent fauna of the locality Olalla 4A is composed of Theridomorpha, Cricetidae, Gliridae, and Sciuridae. A new genus of Cricetidae is described: *Atavocricetodon*, with three new species: *Atavocricetodon atavoides* sp. nov., *A. nanoides* sp. nov., and *A. minusculus* sp. nov. Two new species of Gliridae are described: *Gliravus olallensis* sp. nov. and *Bransatoglis parvus* sp. nov. Comparison with Montalbán led to the description of yet another new species from that locality: *A. hugueneyae*. Discussion of the Olalla fauna shows that it must be younger than the 'Grande Coupure' and older than the classical locality of Montalbán, in other words Early Oligocene.

Contents

Introduction

The locality Olalla 4 was discovered by M. Freudenthal and R. Daams in 1981, and important samples were taken in 1986 and 1987. In 1987 a sample was taken just above the fossiliferous bed; that sample was called Olalla 4B; since than I use the designation OLA4A for what was previously OLA4.

The locality has been mentioned in the Correlation tables of the Mainz Symposium (Schmidt-Kittler, ed., 1987), and in a table published by Alvarez Sierra et al. (1987). The Sciuridae were published by Cuenca Bescós & Canudo (1992).

A total of 5000 kg of sediment has been processed, which has yielded a collection of thousands of rodent teeth. In this paper the Cricetidae and Gliridae are studied in detail. The faunal list is updated as far as the Theridomorpha, Sciuridae and Eomyidae are concerned.

The Cricetidae are compared with those from the classical locality of Montalbán.

In view of the large amounts of material and the subtle differences between the species, this was done by means of a data base of morphological descriptions (see Freudenthal et al., 1994).

Most of the material will be stored in the collections of the Museum of Paleontology of the University of Zaragoza.

Measurements are given in units of 0.1 mm.

Terminology of the cheek teeth of the Cricetidae is after Freudenthal et al. (1994), that of the Gliridae after de Bruijn (1967).

Abbreviations:

HB	Hoogbutsel (Belgium)
OLA4A	Olalla 4A (Teruel, Spain)
MLB1D	Montalbán 1D (Teruel, Spain)
RGM	Rijksmuseum van Geologie en Mineralogie, now National Museum of Natural History, Leiden, The Netherlands.

Methods

A data base has been created that contains the measurements and the morphological description of each one of the cricetid specimens used in this paper. The evident advantage of such an approach is that at any moment one can verify previously made descriptions, improve them if necessary, change them if the definitions of character states are changed, and comparisons between populations, or groups of populations are easily performed.

This method was used by Freudenthal et al. (1994) for the genus *Pseudocricetodon*, and by Freudenthal (1994) for the genera *Allocricetodon* and *Eucricetodon*. At the time of those publications the data base for *Eucricetodon* was still in a preliminary stage, and definitions of character states were not yet sufficiently precise. Therefore only part of the characters was used in the 1994 paper. By now the morphological data base for *Eucricetodon* is well advanced, and reliable definitions have been found for most character states. The actual descriptions of the material are given in Tables 4-9, that are taken directly from the data base; the explanation of the character states is given in the Appendix; this is a copy of the 'on-screen' help, available during the execution of the data base program.

For a number of features the definitions are not yet reliable, and these features are not used in the analysis.

Comparison of the appendix with the one for *Pseudocricetodon* (Freudenthal et al., 1994) shows that there are a number of differences. These are partly due to a further refinement of the definitions, but others are caused by the differences in morphology between *Pseudocricetodon* and *Eucricetodon*. E.g. in the upper molars of *Pseudocricetodon* a second mesoloph and a mesoloph-metacone connection are common features, whereas these are absent or of no importance in *Eucricetodon*.

I created a similar data base for Gliridae, the data of which are used in this paper, but the character states are not yet fully defined. It is obvious that fusion of the data bases for Cricetidae and Gliridae is useless. Whether those for *Pseudocricetodon* and *Eucricetodon* should be fused is not yet clear. So, for the moment I maintain three separate data bases, that work with the same program, but use different definitions and create different kinds of data.

This entire approach is meant to get morphological descriptions with a high degree of objectivity, a goal that is achieved for many features, whilst for other features it is not achieved at all. Whether good results are obtained depends largely on the choice of the features and the definition of the character states, but in the end the human observation is what counts.

Taxonomic descriptions

Family Cricetidae Murray, 1866
Subfamily Eucricetodontinae Mein & Freudenthal, 1971

The Eucricetodontinae, as proposed by Mein & Freudenthal, 1971, contained all European Oligocene Cricetidae, except *Paracricetodon* and *Melissiodon*. Freudenthal et al. (1992) reduced it to the genera *Eucricetodon*, *Eumyarion*, and *Mirabella* with a question mark for the latter two, the only certain component of the Eucricetodontinae being *Eucricetodon*.

The type-species of *Eucricetodon* is *E. collatus* (Schaub, 1925), which together with the species *gerandianus*, *infralactorensis*, *aquitanicus*, and *longidens* forms a homogeneous group.

Mein & Freudenthal (1971) had doubts about the generic attribution of the other Eucricetodontinae, and listed them as Eucricetodontinae incertae sedis. In fact they form at least three different groups: the *atavus*-group, the *dubius*-group and the *huerzeleri*-group. These groups may in the end turn out to be different genera. That decision is now taken for the *atavus*-group and I propose the new genus *Atavocricetodon*.

Genus *Atavocricetodon* gen. nov.

Type-species — *Atavocricetodon atavoides* sp. nov.

Diagnosis — Eucricetodontinae of very small to medium size, with relatively low-crowned cheek teeth, with thin enamel, relatively small cusps, and long crests. Lower molars with or without hypoconid hind arm. M_1 with protoconid hind arm frequently connected to the metaconid. Upper molars generally with a posterior protolophule and an anterior metalophule. M^1 generally without a complete anterolophule. Old entoloph on M^3 frequently present, or even complete, neo-entoloph fully developed.

Other species attributed:
Cricetodon murinus Schlosser, 1884
Cricetodon huberi Schaub, 1925
Cricetodon atavus Misonne, 1957
Eucricetodon nanus Peláez-Campomanes, 1995
Atavocricetodon hugueneyae sp. nov.
Atavocricetodon nanoides sp. nov.
Atavocricetodon minusculus sp. nov.

Atavocricetodon atavus from Hoogbutsel (Belgium) is the geologically oldest cri-

cetid known in Europe. It has been reported from a number of Early Oligocene localities like Montalbán (Vianey-Liaud, 1971), Heimersheim (Bahlo, 1975), a large number of fissure fillings in S. Germany (Dienemann, 1987), Quercy (Vianey-Liaud, 1972), etc. None of these populations seems to be identical to the type-population (Freudenthal, 1988). In Spain we now have *Atavocricetodon* populations from about twenty different localities in the Calatayud-Teruel Basin, from Valdecollares (Cuenca), and from several localities in the Ebro Basin.

Analysis of the morphological differences between the populations from the many superposed levels at Montalbán may give some clue to the evolutionary trend(s) in *Atavocricetodon*, and decide whether or not it is ancestral to some species of *Eucricetodon*.

Atavocricetodon atavoides sp. nov.
Pl. 1, figs. 1-12.

Type-locality — Olalla 4A (Teruel, Spain).

Holotype — M_1 sin., OLA4 8, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Derivatio nominis — The name is based on the resemblance with *A. atavus*.

Age — Early Oligocene.

Diagnosis — *Atavocricetodon* of large size; M_1 with nearly always complete anterolophulid and metalophulid; ectolophid generally longitudinal (80%); generally with ectomesolophid (65%); hypoconid hind arm nearly always present. M_2 generally with mesolophid of medium length or long (85%); ectomesolophid absent (45 %) or present; hypoconid hind arm frequently absent (50%). M_3 frequently with ectomesolophid (54%). M^1 rarely with complete anterolophule. M^2 generally with low protocone-entoloph connection (70%); lingual border concave (50%), or straight-convex (50%). M^3 with well-developed old entoloph (58% complete).

Differential diagnosis — *Atavocricetodon* of large size, larger than *A. nanoides* and *A. minusculus* from the same locality. Larger than *A. nanus*, and on the average larger than *A. atavus* from Hoogbutsel.

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

Description — See Tables 4-9.

Comparison of *A. atavoides* from OLA4A with *A. atavus* from HB:

M_1 — The anteroconid nearly always has a descending cingulum ridge on both sides; the anterolophulid is generally complete, never absent; the metalophulid is better developed, generally complete; the protoconid hind arm is frequently lower, or detached from the metaconid and directed backwards; the mesolophid is better developed, never absent; the ectomesolophid and the hypoconid hind arm are better developed.

M_2 — The protoconid hind arm is more detached from the metaconid; the sinusid is more frequently closed; the ectolophid is on the average higher; the mesoconid is less developed; the mesolophid, the ectomesolophid, and the hypoconid hind arm are better developed.

M_3 — The labial anterolophid is longer; the protoconid hind arm is longer and

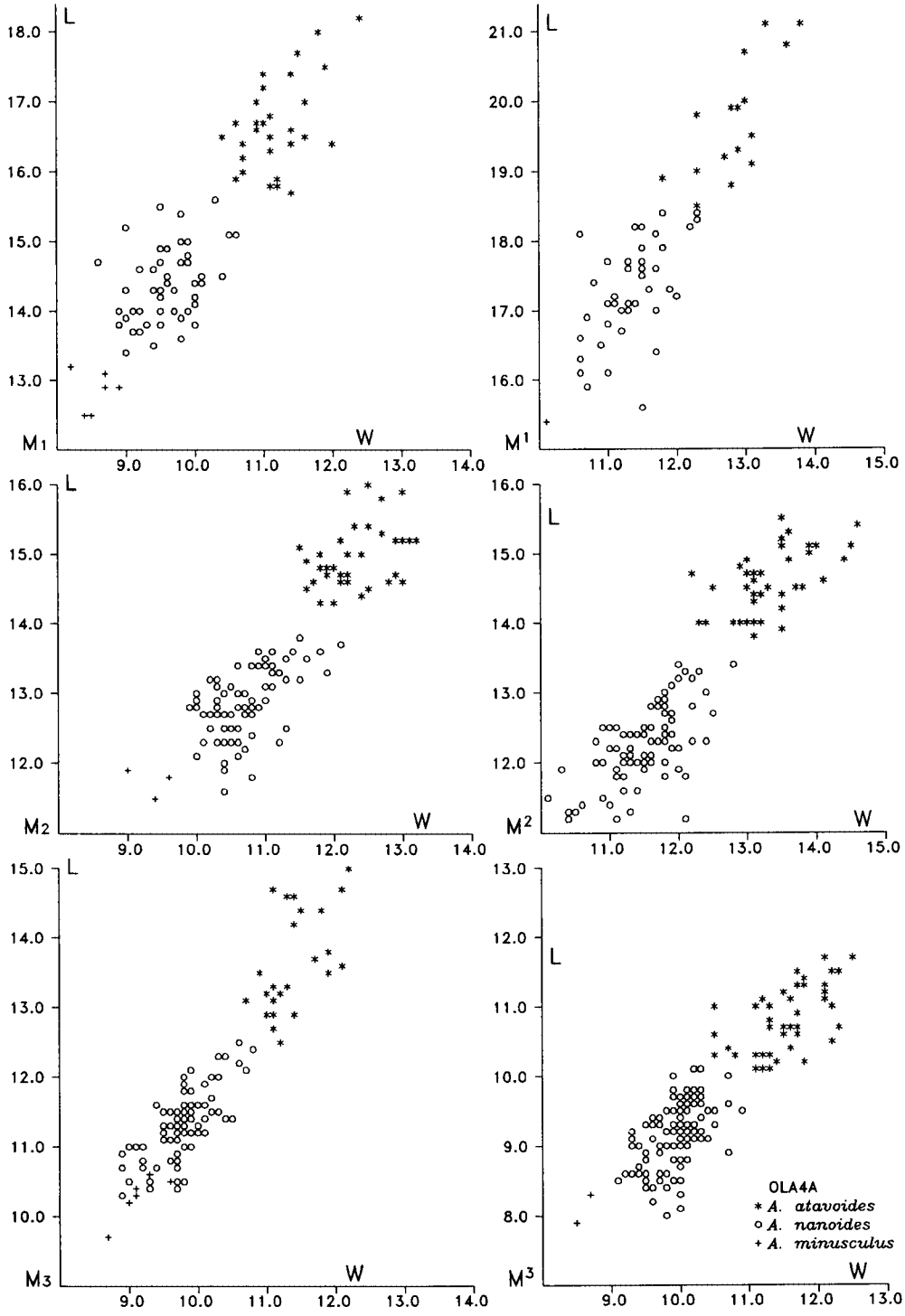

Fig. 1. Length/width diagrams of the Cricetidae molars from Olalla 4A.

more detached from the metaconid; the mesosinusid is more often closed; the mesolophid is nearly always absent; the ectomesolophid is better developed; the entoconid is larger; the posterosinusid is more closed.

M^1 — The anterocone is never split; the prelobe is more frequently set-off from the rest of the tooth; the anterolophule is less frequently complete; there is hardly ever an anterior protolophule; the sinus is more closed; there is never a posterior metalophule.

M^2 — The lingual anteroloph is better developed, frequently continuing around the protocone; the sinus is more frequently closed by a cingulum ridge; the labial border is often straight or convex, whereas it is nearly always concave in *A. atavus*.

The connection of the entoloph with the protocone is clearly higher than it is in *A. atavus*. Not only is the percentage of low connections higher in the HB material, but the low connections are clearly lower in HB than in OLA4A (this difference is not expressed in the character state table).

M^3 — The lingual anteroloph is less developed; the mesosinus is more frequently closed; the mesoloph is well developed, whereas it is generally absent in *A. atavus*. The old entoloph is generally absent, and never complete, in *A. atavus*; in *A. atavoides* it is present in 80 % of the cases, very often complete. The anterior spur of the axioloph is frequently present in *A. atavus*, always absent in *A. atavoides*.

Comparison of *A. atavoides* from OLA4A with *A. hugueneyae* sp. nov. from MLB1D:

M_1 — The anterolophulid is better developed. The protoconid hind arm is on the average lower; in MLB1D it is directed backwards in only one specimen, whereas a long backward crest is frequent in OLA4A. The sinusid is more frequently closed, and the mesosinusid more frequently open; the ectolophid is more longitudinal; the ectomesolophid and the hypoconid hind arm are better developed.

M_2 — The protoconid hind arm is more often detached from the metaconid; the mesosinusid is more frequently closed; the mesoconid, the mesolophid, the ectomesolophid, and the hypoconid hind arm are better developed. The hypolophulid is more oblique.

M_3 — The protoconid hind arm is longer; the ectomesolophid and the entoconid are better developed; the hypolophulid is more oblique.

M^1 — The prelobe is more frequently set-off from the rest of the tooth; there is hardly ever an anterior protolophule; the sinus is more often strongly proverse and more closed; there is never a connection between protocone and hypocone through the sinus; the metalophule is always anterior.

M^2 — There is more frequently a (trace of a) posterior protolophule; the sinus is never subdivided in the MLB1D material; in OLA4A the mesosinus is less frequently closed; the entoloph-protocone connection is lower.

M^3 — The sinus is on the average slightly smaller; the mesoloph is on the average longer; the centroloph is always present; there is less frequently a metacone cusp.

Comparison of *A. atavoides* from OLA4A with *A. nanoides* sp. nov. from OLA4A:

M_1 — The anteroconid nearly always has a descending cingulum ridge on both sides, whereas in *A. nanoides* the lingual cingulum is frequently missing. The protoconid hind arm is on the average lower; the mesoconid is less developed; the meso-

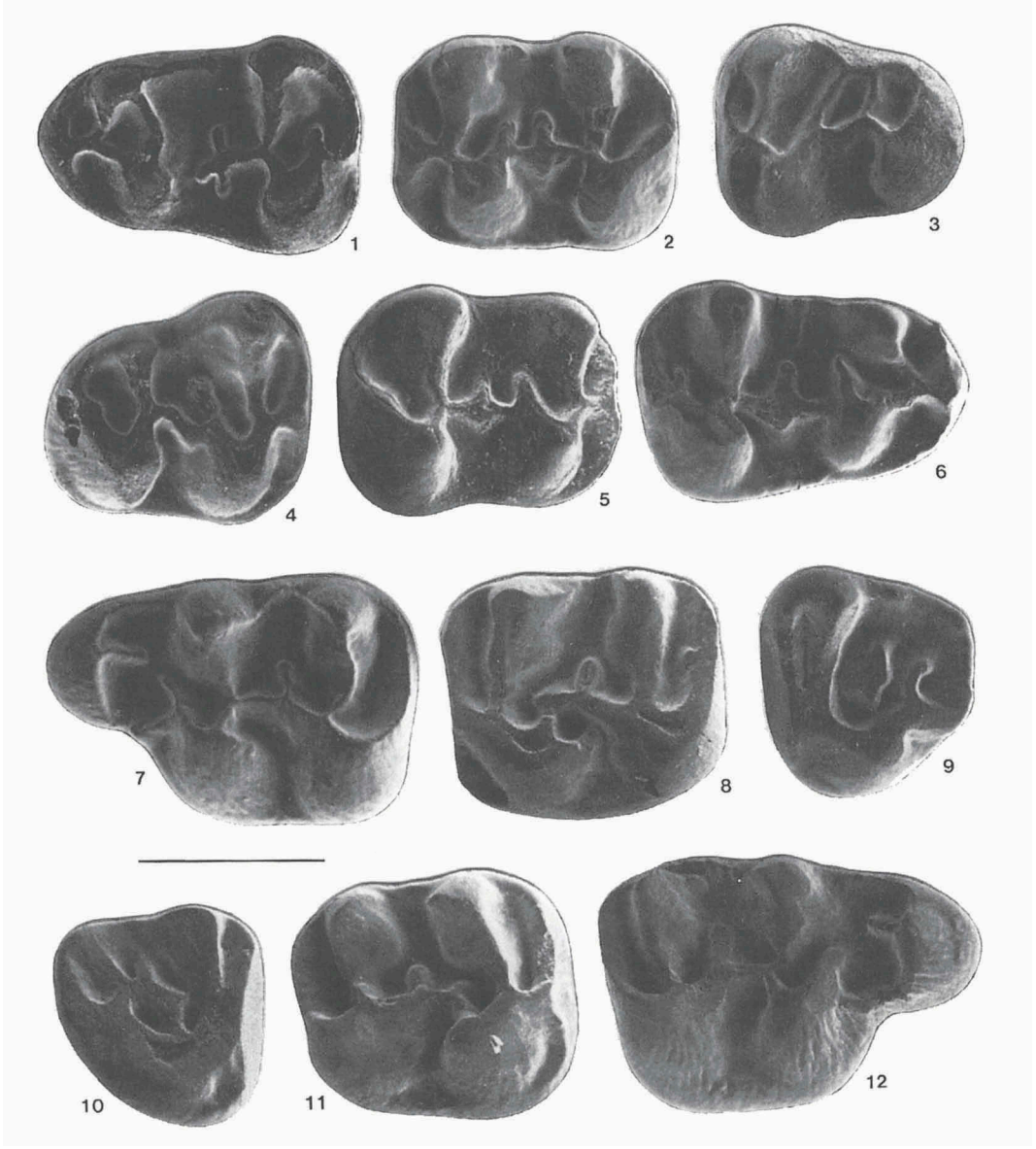

Plate 1

Atavocricetodon atavoides sp. nov. from Olalla 4A

Fig. 1. M_1 sin., OLA4 8, holotype.
Fig. 2. M_2 sin., OLA4 105.
Fig. 3. M_3 sin., OLA4 254.
Fig. 4. M_3 dext., OLA4 343.
Fig. 5. M_2 dext., OLA4 202.
Fig. 6. M_1 dext., OLA4 63.
Fig. 7. M^1 sin., OLA4 404.
Fig. 8. M^2 sin., OLA4 569.
Fig. 9. M^3 sin., OLA4 656.
Fig. 10. M^3 dext., OLA4 743.
Fig. 11. M^2 dext., OLA4 579.
Fig. 12. M^1 dext., OLA4 427.

The scale represents 1 mm.

lophid is on the average slightly longer; the hypoconid hind arm is better developed.

M_2 — The anterosinusid is always large; the protoconid hind arm is longer, never absent; the mesosinusid is more closed; the mesoconid is less developed; the mesolophid, the ectomesolophid, and the hypoconid hind arm are better developed.

M_3 — The ectomesolophid is slightly better developed; the outline of the tooth is more frequently trapezoidal.

M^1 — The sinus is more often strongly proverse and more closed; the mesoloph is always present; the metalophule is always anterior.

M^2 — The lingual anteroloph is on the average better developed, and runs around the protocone quite frequently; there is more often a (trace of a) posterior protolophule; the sinus is more frequently closed, and is subdivided in a number of cases; the entoloph-protocone connection is on the average lower; there is more frequently a (complete or partial) connection between protocone and hypocone, through the sinus.

M^3 — The mesoloph is on the average longer, and may even reach the molar border, which is never the case in *A. nanoides*. The old entoloph appears to be better developed, and connected to the protocone in a more forward position. Quantification of this latter feature has not been made.

Comparison of *A. atavoides* from OLA4A with *A. nanus* from MLB1D:

M_1 — The anteroconid nearly always has a descending cingulum ridge on both sides, whereas in *A. nanus* the lingual cingulum is frequently missing. The anterolophulid and metalophulid are better developed; the sinusid and mesosinusid are more frequently closed; the mesoconid is less developed; the mesolophid is on the average longer; the ectomesolophid and the hypoconid hind arm are better developed.

M_2 — The anterosinusid is always large; the metalophulid is never connected to the anteroconid; the protoconid hind arm is more often long; the mesosinusid is more frequently closed; the mesoconid is less developed; the mesolophid, the ectomesolophid, and the hypoconid hind arm are better developed; the hypolophulid is more oblique.

M_3 — The labial anterolophid is shorter; the anterolophulid is better developed; the anterosinusid is always wide; the metalophulid is less directed forward; the protoconid hind arm is more detached from the metaconid, but on the average shorter than in *A. nanus*; the sinusid is wider; the ectomesolophid and the entoconid are better developed; the hypolophulid is more oblique.

M^1 — The anterocone is never split; the prelobe is more frequently set-off from the rest of the tooth; the sinus is more often strongly proverse and more frequently closed; there is never a connection between protocone and hypocone through the sinus; the mesosinus is more often closed; the metalophule is always anterior.

M^2 — The lingual anteroloph is better developed. There is more frequently a trace of a posterior protolophule in OLA4A, but, on the other hand, the posterior protolophule is more frequently complete in MLB1D; apparently this feature does not give coherent results. The sinus is more frequently closed in OLA4A, and it is on the average more proverse. The entoloph-protocone connection is significantly lower; the labial border is more frequently straight or convex.

M^3 — The lingual anteroloph is better developed, and frequently separates the protocone (partly) from the lingual border. In a few specimens a deep sinus and a low or interrupted neo-entoloph are found, which is not the case in Montalbán 1D. The mesoloph, the old entoloph, and the centroloph are considerably better developed.

Comparison of *A. atavoides* from OLA4A with *A. nanus* from Valdecollares:

M_1 — The metalophulid is better developed; the mesoconid is less developed; the mesolophid is longer; the hypoconid hind arm is better developed.

M_2 — The mesolophid is never absent. The hypoconid hind arm is better developed.

M_3 — The protoconid hind arm is longer.

M^1 — The mesoloph is longer; the metalophule is never directed backwards.

M^2 — There is more frequently a (trace of a) posterior protolophule; the mesoloph is on the average longer, but this may be untrue, due to a difference in interpretation: Peláez-Campomanes (1995) mentions an overwhelming majority of short mesolophs, whereas I would interpret three of the five figured specimens as having a mesoloph of medium length (1/3 to 1/2 the width of the mesosinus).

M^3 — The series of specimens figured (Peláez-Campomanes, 1995, pl. 5, figs. 6-17) makes it clear that in OLA4A the mesoloph and the old entoloph are considerably better developed. The centroloph may be missing in *A. nanus* from Valdecollares, and is always present in our material.

Atavocricetodon hugueneyae sp. nov.
Pl. 2, figs. 1-12.

Type-locality — Montalbán 1D (Teruel, Spain).

Holotype — M_1 sin., MLB1D 205, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Derivatio nominis — In honor of Dr M. Hugueney, as a token of friendship and gratitude.

Age — Early Oligocene.

Diagnosis — *Atavocricetodon* of large size. M_1 with frequently incomplete anterolophulid (50%) and generally complete metalophulid (80%); ectolophid generally oblique (60%); generally with ectomesolophid (80%); hypoconid hind arm present (50%) or absent. M_2 generally with mesolophid absent or short (80%); ectomesolophid absent; hypoconid hind arm frequently absent (67%). M_3 never with ectomesolophid. M^1 never with complete anterolophule. M^2 generally with high protocone-entoloph connection (80%); lingual border generally straight or convex (67%). M^3 with well-developed old entoloph (44% complete).

Differential diagnosis — *Atavocricetodon* of large size, larger than *A. nanus* and *A. minusculus* from the same locality. Larger than *A. nanoides* from OLA4A, and on the average larger than *A. atavus* from Hoogbutsel.

Material and measurements — See Table 1, Fig. 2.

Description — See Tables 4-9.

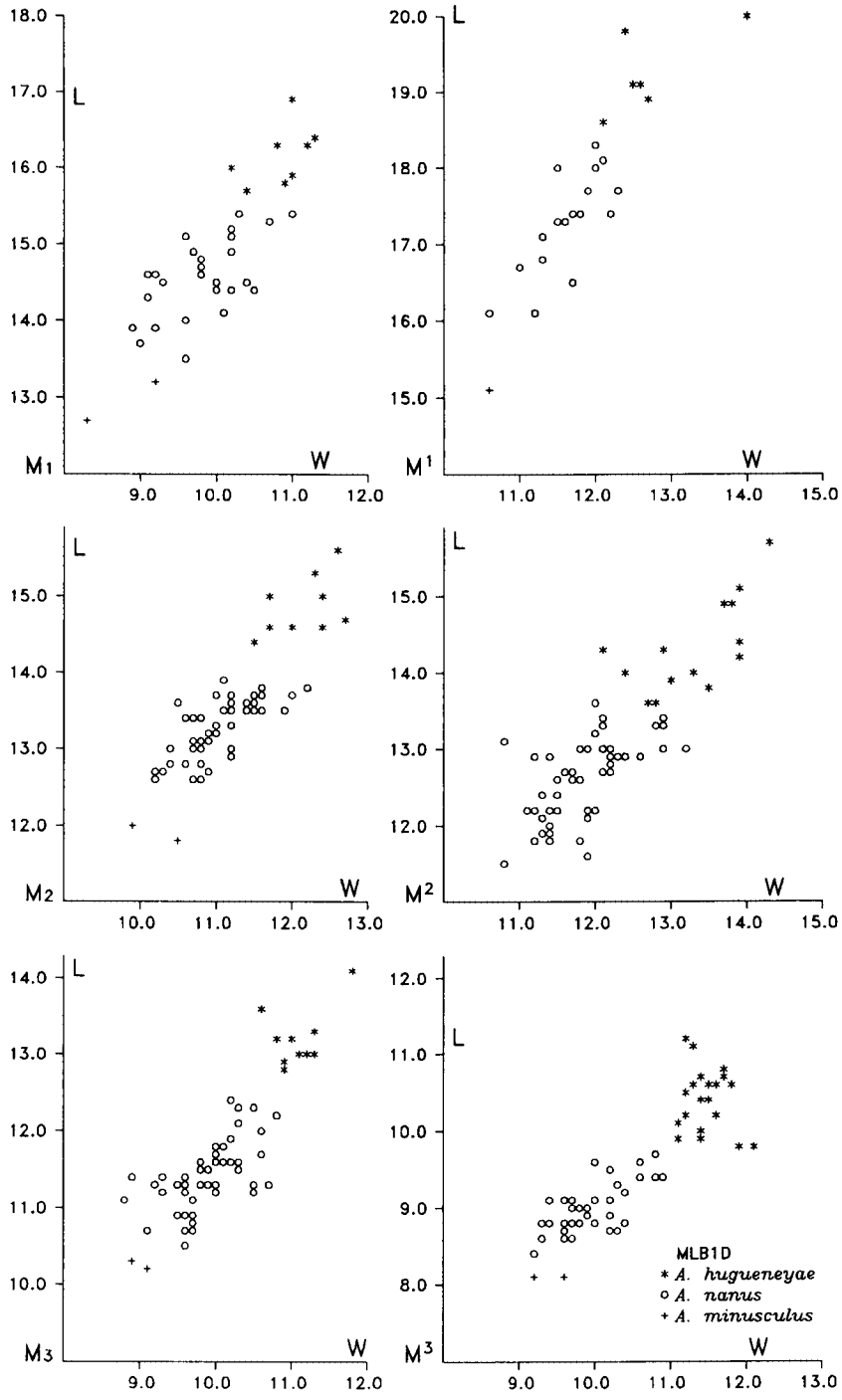

Fig. 2. Length/width diagrams of the Cricetidae molars from Montabán 1D.

Comparison of *A. hugueneyae* from MLB1D with *A. atavus* from HB:

M_1 — The anteroconid nearly always has a descending cingulum ridge on both sides; the anterolophulid is better developed; the protoconid hind arm is lower; the mesosinusid is more frequently closed; the ectolophid is more oblique; the mesoconid and the mesolophid are better developed; the ectomesolophid and the hypoconid hind arm are less developed.

M_2 — The mesosinusid is more frequently open; the mesoconid is less developed; the mesolophid and the ectomesolophid are less developed; the hypolophulid is less oblique.

M_3 — The labial anterolophid is longer; the protoconid hind arm is shorter; the sinusid, mesosinusid and posterosinusid are more often closed; the mesolophid is always absent; the hypolophulid is less oblique; the shape of the tooth is more often trapezoidal.

M^1 — The prelobe is more frequently set-off from the rest of the tooth; the anterolophule is never complete; the sinus is more frequently closed and less proverse; there is more frequently a connection between protocone and hypocone through the sinus.

M^2 — The lingual anteroloph is better developed; there is less frequently a trace of a posterior protolophule; the mesosinus is more frequently closed; the entoloph-protocone connection is higher; the labial border is more frequently straight or convex.

M^3 — The lingual anteroloph is less developed; the sinus is on the average smaller; the mesosinus is more frequently closed; the mesoloph is better developed. The old entoloph is very frequently present, often complete. The anterior spur of the axioloph is frequently present in *A. atavus*, always absent in *A. hugueneyae*.

Comparison of *A. hugueneyae* from MLB1D with *A. atavoides* from OLA4A: See before.

Comparison of *A. hugueneyae* from MLB1D with *A. nanus* from MLB1D:

M_1 — The lingual cingulum of the anteroconid and the metalophulid are more developed; the protoconid hind arm is less frequently directed obliquely backwards; the sinusid and the mesosinusid are less frequently open; the hypoconid hind arm is less frequently absent, but when present in *A. nanus*, it is better developed than in *A. hugueneyae*.

M_2 — The anterosinusid is always large; the protoconid hind arm is less frequently detached from the metaconid; the mesoconid and the ectomesolophid are always absent; the hypoconid hind arm is better developed.

M_3 — No important differences have been observed; maybe the anterolophulid is somewhat better developed.

M^1 — The prelobe is more frequently set-off from the rest of the tooth; the anterolophule is never complete; there is more frequently (a trace of) an anterior protolophule; the sinus is more frequently closed; there is more frequently a connection between protocone and hypocone through the sinus.

M^2 — The lingual anteroloph is better developed; the sinus is more frequently closed and more strongly proverse; the mesosinus is more frequently closed; the entoloph-protocone connection is higher; the labial border is more frequently straight or convex.

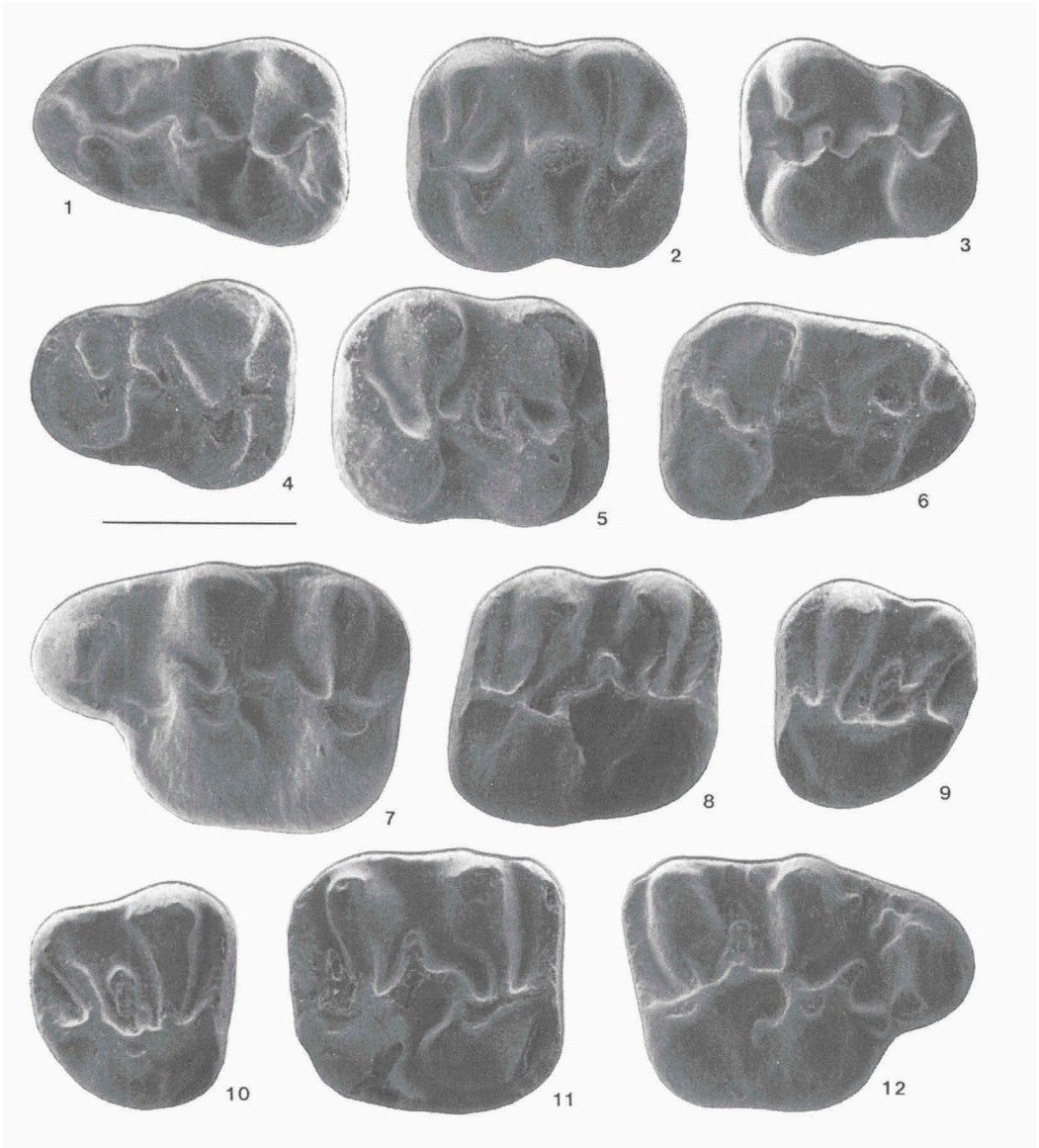

Plate 2

Atavocricetodon hugueneyae sp. nov. from Montalbán 1D

Fig. 1. M_1 sin., MLB1D 205, holotype.
Fig. 2. M_2 sin., MLB1D 161.
Fig. 3. M_3 sin., MLB1D 539.
Fig. 4. M_3 dext., MLB1D 119.
Fig. 5. M_2 dext., MLB1D 159.
Fig. 6. M_1 dext., MLB1D 5.
Fig. 7. M^1 sin., MLB1D 51.
Fig. 8. M^2 sin., MLB1D 789.
Fig. 9. M^3 sin., MLB1D 109.
Fig. 10. M^3 dext., MLB1D 111.
Fig. 11. M^2 dext., MLB1D 832.
Fig. 12. M^1 dext., MLB1D 67.

The scale represents 1 mm.

M^3 — The sinus is on the average somewhat smaller; the mesoloph, the old entoloph and the centroloph are better developed.

Comparison of *A. hugueneyae* from MLB1D with *A. nanoides* sp. nov. from OLA4A: See under *A. nanoides* sp. nov.

Comparison of *A. hugueneyae* from MLB1D with *A. nanus* from MLB1D: See under *A. nanus*.

Comparison of *A. hugueneyae* from MLB1D with *A. nanus* from Valdecollares:

M_1 — The metalophulid is better developed; the mesoconid is less developed; the mesolophid is longer; the hypoconid hind arm is better developed.

M_2 — The mesolophid is never absent, frequently of medium length.

M_3 — The protoconid hind arm is longer.

M^1 — The mesoloph is longer; there is never an entostyl.

M^2 — See the remark on the mesoloph under *A. atavoides* from OLA4A.

M^3 — See *A. atavoides* from OLA4A.

Atavocricetodon nanoides sp. nov.
Pl. 3, figs. 1-12.

Type-locality — Olalla 4A (Teruel, Spain).

Holotype — M_1 sin., OLA4 28, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Derivatio nominis —— The name is based on the resemblance with *A. nanus*.

Age — Early Oligocene.

Diagnosis — *Atavocricetodon* of medium size; M_1 with generally complete anterolophulid (75%) and metalophulid (75%); ectolophid generally oblique (75%); generally with ectomesolophid (60%); hypoconid hind arm generally present (75%). M_2 with or without ectomesolophid (57% / 43%); hypoconid hind arm nearly always absent. M_3 generally with ectomesolophid (80%). M^1 rarely with complete anterolophule. M^2 with high or low protocone-entoloph connection (50% / 50%); lingual border generally concave (65%). M^3 with well-developed old entoloph (42% complete).

Differential diagnosis — *Atavocricetodon* of medium size, smaller than *A. atavoides* sp. nov., larger than *A. minusculus* from the same locality. On the average smaller than *A. atavus* from Hoogbutsel.

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

Description — See Tables 4-9.

Comparison of *A. nanoides* from OLA4A with *A. atavoides* from OLA4A: See under *A. atavoides*.

Comparison of *A. nanoides* from OLA4A with *A. hugueneyae* from MLB1D:

M_1 — The lingual cingulum of the anteroconid is less developed; the anterolophulid is better developed; the protoconid hind arm is lower, and more frequently detached from the metaconid; the sinusid is less frequently open; the mesosinusid is

more frequently open; the ectolophid is more frequently longitudinal; the ectomesolophid and the hypoconid hind arm are better developed.

M_2 — The anterosinusid may be small; the protoconid hind arm is more frequently detached from the metaconid; the mesosinusid is less open; the mesoconid, the mesolophid and the ectomesolophid are better developed; the hypoconid hind arm is less developed; the hypolophulid is more often oblique.

M_3 — The protoconid hind arm is longer; the sinusid is more frequently open; the ectomesolophid and the entoconid are better developed; the hypolophulid is more often oblique; the shape of the tooth is nearly always a long triangle, not trapezoidal.

M^1 — The anterolophule may be complete; there is less frequently (a trace of) an anterior protolophule; the sinus is less frequently closed; there is never a connection between protocone and hypocone through the sinus; the mesosinus is more frequently open.

M^2 — The lingual anteroloph is less developed; the sinus and mesosinus are less frequently closed; the mesoloph is on the average shorter; the entoloph-protocone connection is lower; there is less frequently a protocone-hypocone connection through the sinus; the labial border is more frequently concave.

M^3 — There is less frequently a metacone cusp.

Comparison of *A. nanoides* from OLA4A with *A. atavus* from HB:

M_1 — On the anteroconid the cingulums are better developed; the anterolophulid is better developed; the metalophulid is less developed; the protoconid hind arm is lower and more frequently oblique; the mesoconid and the mesolophid are better developed.

M_2 — The protoconid hind arm is lower and more detached from the metaconid; the sinusid is more frequently closed; the ectolophid is on the average higher; the ectomesolophid is better developed; the hypolophulid is less frequently oblique; the hypoconid hind arm is less developed.

M_3 — The labial anterolophid is longer; the protoconid hind arm is longer and more detached from the metaconid; the mesolophid is on the average shorter; the mesosinusid is more frequently closed; the ectomesolophid is better developed; the entoconid is larger; the posterosinusid is more often closed; the shape of the tooth is more triangular.

M^1 — The anterocone is always simple; the anterolophule is less frequently complete; there is less frequently (a trace of) an anterior protolophule; the mesoloph is shorter or even absent.

M^2 — There is less frequently a (trace of a) posterior protolophule; the sinus is never subdivided; the mesosinus is more frequently open; the mesoloph is shorter; the connection of the entoloph with the protocone is higher; there is hardly ever a protocone-hypocone connection through the sinus; the labial border is often straight or convex, whereas it is nearly always concave in *A. atavus*.

M^3 — The sinus is often smaller; the mesosinus is more frequently closed; the mesoloph and the old entoloph are better developed; the anterior spur of the axioloph is frequently present in *A. atavus*, always absent in *A. nanoides*.

Comparison of *A. nanoides* from OLA4A with *A. nanus* from Valdecollares:

M_1 — The metalophulid is better developed; the mesoconid is less developed; the

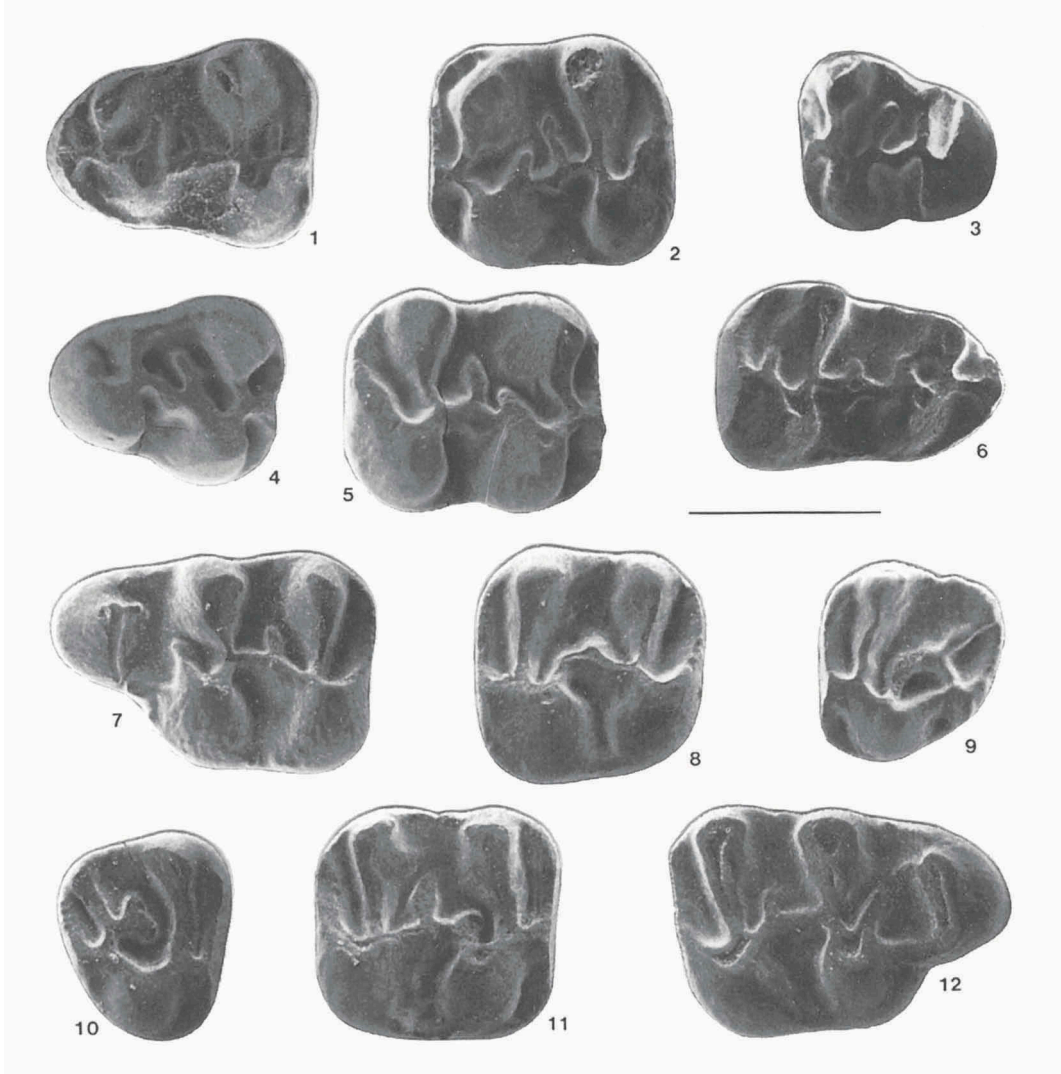

Plate 3

Atavocricetodon nanoides sp. nov. from Olalla 4A

Fig. 1. M_1 sin., OLA4 28, holotype.
Fig. 2. M_2 sin., OLA4 101.
Fig. 3. M_3 sin., OLA4 251.
Fig. 4. M_3 dext., OLA4 272.
Fig. 5. M_2 dext., OLA4 125.
Fig. 6. M_1 dext., OLA4 41.
Fig. 7. M^1 sin., OLA4 401.
Fig. 8. M^2 sin., OLA4 507.
Fig. 9. M^3 sin., OLA4 653.
Fig. 10. M^3 dext., OLA4 696.
Fig. 11. M^2 dext., OLA4 531.
Fig. 12. M^1 dext., OLA4 416.

The scale represents 1 mm.

mesolophid is longer; the hypoconid hind arm is longer; the labial posterolophid is better developed.

M_2 — The mesolophid is longer; the hypoconid hind arm is less developed.

M_3 — The protoconid hind arm is longer and more detached from the metaconid.

M^1 — The mesoloph is longer; the metalophule is never posterior.

M^2 — See the remark on the mesoloph in the comparison of *A. atavoides* with *A. nanus* from Valdecollares.

M^3 — The mesoloph and the old entoloph are better developed. The centroloph may be missing in *A. nanus* from Valdecollares, and is always present in OLA4A.

Comparison of *A. nanoides* from OLA4A with *A. nanus* from MLB1D:

M_1 — The labial cingulum on the anteroconid is better developed; the anterolophulid is more frequently complete; the anterolophulid and the metalophulid are better developed; the protoconid hind arm is on the average lower; the sinusid and the mesosinusid are more frequently closed; the ectolophid is more often longitudinal; the ectomesolophid is better developed; the hypolophulid is less frequently oblique; the hypoconid hind arm is more frequently present, but in MLB1D, when present, it is on the average longer.

M_2 — The anteroconid is less developed; the protoconid hind arm is more frequently detached from the metaconid; the mesosinusid is less frequently open; the mesoconid, the mesolophid, and the ectomesolophid are better developed.

M_3 — The anteroconid and the anterolophulid are better developed; the labial anterolophid is less developed; the anterosinusid is on the average wider; the metalophulid is less directed forward; the protoconid hind arm is more detached from the metaconid, but on the average shorter than in *A. nanus*; the sinusid is wider; the entoconid is better developed; the hypolophulid is more often oblique; the shape of the tooth is nearly always a long triangle, not trapezoidal.

M^1 — The anterocone is always simple; the prelobe is more frequently set-off from the rest of the tooth; the sinus is more often closed; there is never a connection between protocone and hypocone through the sinus; the metalophule is more frequently forward directed.

M^2 — The sinus is more frequently strongly proverse; the mesoloph is on the average shorter; the entoloph-protocone connection is lower; the labial border is less frequently concave.

M^3 — The lingual anteroloph, the mesoloph, the old entoloph, and the centroloph are on the average better developed; the centrocone is much less developed.

Atavocricetodon minusculus sp. nov.
Pl. 4, figs. 1-14.

Type-locality — Olalla 4A (Teruel, Spain).

Holotype — M_1 sin., OLA4 48, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Other localities — Valdecollares ?, Montalbán 1D.

Diagnosis and differential diagnosis — The smallest *Atavocricetodon* known so far.

Material and measurements — See Table 1, Figs. 1, 2.

Description of the material from Olalla 4A

M_1 — The anteroconid is small (1), with a labial cingulum ridge (2), or with two cingulum ridges (3). The anterolophulid is interrupted (1) or complete (5). The metalophulid is interrupted (2), complete (3), or connected to the anteroconid (1). The protoconid hind arm is short and connected to the base of the metaconid (1), short and connected higher on that cusp (2), long and connected to the metaconid (1), or long and free (2). The sinusid is half closed (2) or closed (3), either transverse (4) or curved backwards (2). The mesosinusid is partly closed by a ridge descending from the metaconid. The ectolophid is longitudinal (4), oblique (1), or interrupted (1). The mesoconid is absent (1) or weak (5). The mesolophid is absent (2), short (3), or of medium length (1). There is no ectomesolophid. The hypolophulid is transverse to the ectolophid (6), or transverse to the hypoconid (1). The hypoconid hind arm is absent (5), short (1), or long (1).

M_2 — The lingual anterolophid is long. The labial anterolophid is short (2), or connected to the protoconid (1). The anterolophulid is complete. The anterosinusid is large. The metalophulid is connected to the anterolophulid. The protoconid hind arm is short and free (1), or long and free (2). The sinusid is half closed (2), or closed (1); either transverse (1) or curved backwards (2). The mesosinusid is open (2), or partly closed by a ridge descending from the metaconid (1). The ectolophid is high (2) or low (1). The mesoconid is absent (2) or weak (1). The mesolophid is absent (1), short (1), or of medium length (1). The ectomesolophid is absent (2) or weak (1). The hypolophulid is anterior, either oblique (2) or transverse (1). The hypoconid hind arm is absent.

M_3 — The anteroconid is absent (1) or small (4). The lingual anterolophid is short (2) or long (3). The labial anterolophid is short (4), or connected to the protoconid (1). The anterolophulid is long. The anterosinusid is wide (5). The metalophulid is anterior interrupted (2), or directed to the anteroconid (3). The protoconid hind arm is long and free, reaching the molar border in one case. The sinusid is open (5) or closed (1), either transverse (2) or directed backwards (3). The mesosinusid is closed. The mesolophid and the ectomesolophid are absent. The entoconid is small (2) or large (1). The hypolophulid is anterior oblique (1), anterior transverse (3), or transverse (1). The posterosinusid is open (2) or closed (2). The shape of the tooth is a short triangle (1), or a long triangle (5).

A total of six M_3 from OLA4A are attributed to this species. Some of them are clearly smaller than the M_3 of *A. nanoides*, others are as large as the small specimens of that species. One cannot be sure that the separation has been made correctly. The smallest specimen is completely worn and cannot be described. The other ones have either an interrupted metalophulid, or this crest is short, and connected to the middle of the lingual anterolophid. In 2 out of 6 specimens the labial anterolophid is much reduced, the protoconid lies near the anterior border, and the anterolophulid is not longitudinal, but oblique/transverse towards the anteroconid that lies lingually of the central axis. In several specimens the posterolophid is absent or low.

M^1 — The anterocone is simple. The prelobe is set-off from the rest of the tooth. The anterolophule is formed by a protocone spur only. The lingual anteroloph bears

a protostyl. The protocone platform is absent. The anterosinus is open. The protolophule is posterior. The sinus is open, and strongly directed forward. There is no protocone-hypocone connection through the sinus. The mesosinus is open. The mesoloph is absent. The metalophule is anterior. The labial border is convex.

M^3 — The lingual anteroloph is absent or strong. The protolophule is directed towards the anterolophule. The sinus is very small or small. The neo-entoloph is high. The mesosinus is closed. The mesoloph is absent or of medium length. The old entoloph is absent or complete. The axioloph is a long posterior spur or formed by the old entoloph. The centroloph is strong. The centrocone is present. The metacone is present. The posterosinus is closed.

Description of the material from Montalbán 1D

M_1 — The anteroconid is small. The anterolophulid is low, either interrupted or complete. The metalophulid is absent or connected to the anteroconid. The protoconid hind arm is short and connected to the base of the metaconid, or long and connected higher on that cusp. The sinusid is open or half closed; its posterior border is transverse. The mesosinusid is open or partly closed by a ridge descending from the metaconid. The ectolophid is longitudinal or oblique. The mesoconid is absent or strong. The mesolophid is of medium length. There is no ectomesolophid. The hypolophulid is connected to the ectolophid. The hypoconid hind arm is absent or long.

M_2 — The lingual anterolophid is long, the labial anterolophid is connected to the protoconid. The anterolophulid is complete. The anterosinusid is large. The metalophulid is connected to the anterolophulid. The protoconid hind arm is long and free. The sinusid is open and transverse. The mesosinusid is open. The ectolophid is high. The mesoconid is absent. The mesolophid is short. The ectomesolophid is absent. The hypolophulid is anterior transverse. The hypoconid hind arm is absent.

M_3 — The anteroconid is small. The lingual anterolophid is long. The labial anterolophid is connected to the protoconid, or continues around it. The anterolophulid is long or double. The anterosinusid is narrow or wide. The metalophulid is connected to the anteroconid or to the anterolophulid. The protoconid hind arm is long and connected to the base of the metaconid, or it reaches the border of the molar. The sinusid is half closed, and transverse. The mesosinusid is closed. The mesolophid and the ectomesolophid are absent. The entoconid is small. The hypolophulid is anterior, either oblique or transverse. The posterosinusid is closed. The shape is a short triangle, or trapezoidal.

M^1 — The anterocone is simple. The prelobe is smoothly continuous with the rest of the tooth. The anterolophule is formed by a protocone spur and an anterocone spur. The lingual anteroloph is complete. The protocone platform is absent. The anterosinus is closed. The protolophule is posterior plus a trace of an anterior one. The sinus is open, and directed forward. There is no protocone-hypocone connection through the sinus. The mesosinus is open. The mesoloph is short. The metalophule is absent. The labial border is convex.

M^3 — The lingual anteroloph is weak or strong. The protolophule is directed towards the anterolophule. The sinus is small. The mesosinus is closed. The mesoloph is absent. The old entoloph is a short spur on the protocone, or it is complete. The axioloph is absent, or formed by the old entoloph. The centroloph is strong. The

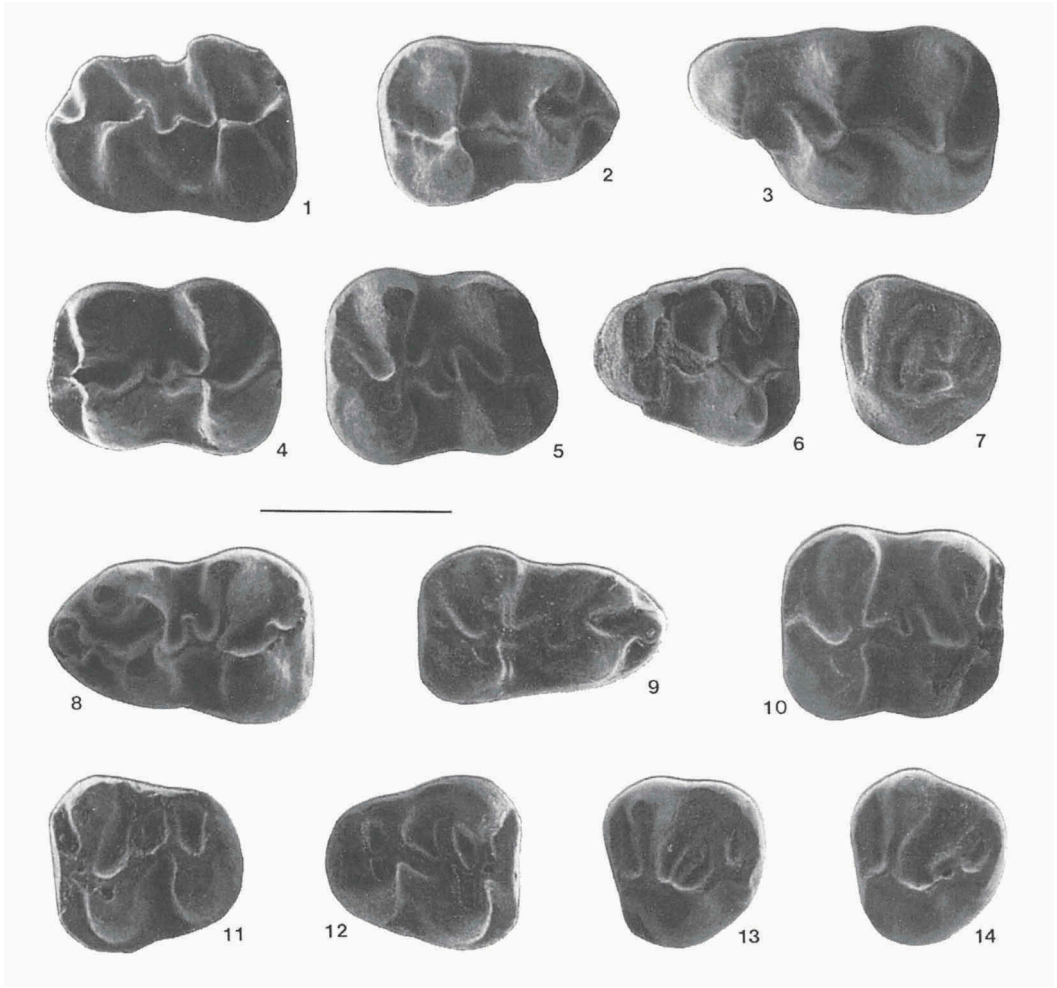

Plate 4

Atavocricetodon minusculus sp. nov. from Olalla 4A

Fig. 1. M_1 sin., OLA4 48, holotype.
Fig. 2. M_1 dext., OLA4 95.
Fig. 3. M^1 sin., OLA4 434.
Fig. 4. M_2 sin., OLA4 145.
Fig. 5. M_2 dext., OLA4 195.
Fig. 6. M_3 dext., OLA4 362.
Fig. 7. M^3 sin., OLA4 652.

Atavocricetodon minusculus sp. nov. from Montalbán 1D

Fig. 8. M_1 sin., MLB1D 10.
Fig. 9. M_1 dext., MLB1D 201.
Fig. 10. M_2 dext., MLB1D 484.
Fig. 11. M_3 sin., MLB1D 114.
Fig. 12. M_3 dext., MLB1D 567.
Fig. 13. M^3 sin., MLB1D 335.
Fig. 14. M^3 sin., MLB1D 337.

The scale represents 1 mm.

centrocone is absent, or present on the old entoloph. The metacone is absent. The posterosinus is closed.

Discussion — Peláez-Campomanes (1995) mentions that the metalophulid of the M_3 of *A. nanus* from Valdecollares is interrupted in 2 out of 18 specimens. This makes us think that, maybe, besides *A. nanus*, *A. minusculus* is present in that locality. One cannot be sure, however, because one of the larger M_3 of *A. nanoides* from OLA4A (OLA4 283, 11.5 x 10.2) also has an interrupted metalophulid.

Atavocricetodon nanus (Peláez-Campomanes, 1995)
Pl. 5, figs. 1-12.

Type-locality — Valdecollares (Cuenca, Spain).

Holotype — M_1 dext., VAL RQ065, Dept. of Paleontology, Universidad Complutense, Madrid.

Characterization of the material from Montalbán 1D — *Atavocricetodon* of medium size; M_1 with frequently incomplete anterolophulid (50%) and metalophulid (50%); ectolophid generally oblique or longitudinal (50%/50%); generally without ectomesolophid (70%); hypoconid hind arm frequently absent (60%); M_2 generally with mesolophid absent or short (85%); ectomesolophid generally absent (80 %); hypoconid hind arm generally absent (84%). M_3 frequently with ectomesolophid (90%). M^1 rarely with complete anterolophule. M^2 generally with high protocone-entoloph connection (88%); lingual border generally concave (83%). M^3 with poorly developed old entoloph (22% complete).

Material and measurements — See Table 1, Fig. 2.

Description — See Tables 4-9.

Comparison of *A. nanus* from MLB1D with *A. nanus* from Valdecollares:

M_1 — The metalophulid is less developed than in our other populations, but better than in Valdecollares. The protoconid hind arm is generally connected to the metaconid, like in Valdecollares. The labial posterolophid may be better developed.

M_2 — The mesolophid is more often present.

M_3 — The protoconid hind arm is longer.

M^1 — The mesoloph is longer. There is no entostyl.

M^2 — The mesoloph is longer, but this may be due to a difference in interpretation.

M^3 — Among our populations, *A. nanus* from MLB1D is the only one, that resembles *A. nanus* from Valdecollares in the degree of development of the old entoloph, the mesoloph and the centroloph.

Comparison of *A. nanus* from MLB1D with *A. atavus* from HB:

M_1 — On the anteroconid the cingulums are better developed; the anterolophulid is better developed; the metalophulid is less developed; the protoconid hind arm is lower and more frequently oblique; the sinusid and the mesosinusid are more frequently open; the ectolophid is more often oblique; the mesoconid and the mesolophid are better developed; the hypolophulid is more often oblique; the hypoconid

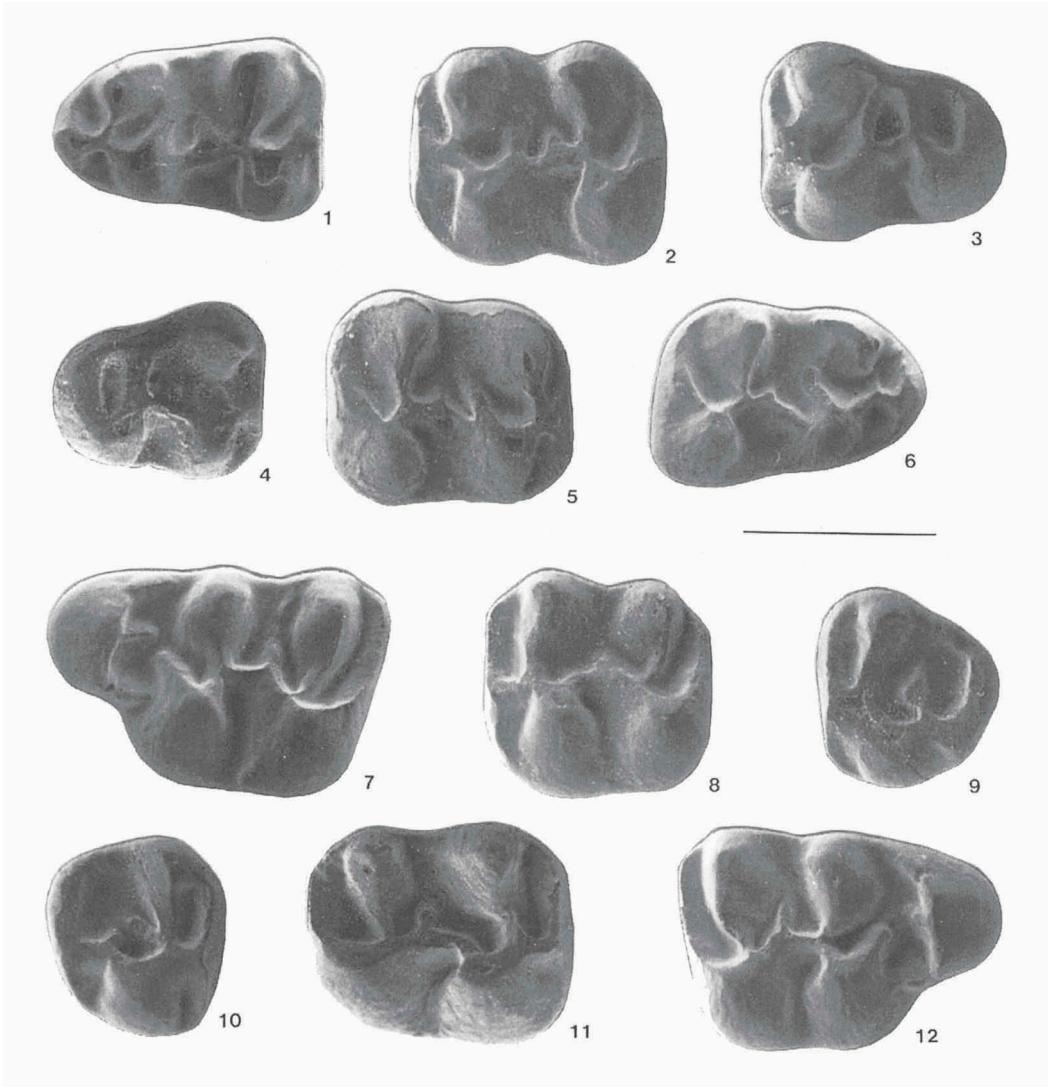

Plate 5

Atavocricetodon nanus (Peláez-Campomanes, 1995) from Montalbán 1D

Fig. 1. M_1 sin., MLB1D 268.
Fig. 2. M_2 sin., MLB1D 162.
Fig. 3. M_3 sin., MLB1D 115.
Fig. 4. M_3 dext., MLB1D 113.
Fig. 5. M_2 dext., MLB1D 170.
Fig. 6. M_1 dext., MLB1D 283.
Fig. 7. M^1 sin., MLB1D 40.
Fig. 8. M^2 sin., MLB1D 782.
Fig. 9. M^3 sin., MLB1D 99.
Fig. 10. M^3 dext., MLB1D 319.
Fig. 11. M^2 dext., MLB1D 829.
Fig. 12. M^1 dext., MLB1D 49.

The scale represents 1 mm.

hind arm is more frequently absent.

M_2 — The protoconid hind arm is more detached from the metaconid; the sinusid is more frequently closed; the mesosinusid is more frequently open; the ectolophid is on the average higher; the mesoconid is less developed; the mesolophid is on the average shorter; the hypolophulid is less frequently oblique.

M_3 — The labial anterolophid is much longer; the anterosinusid is frequently narrow; the protoconid hind arm is longer and more detached from the metaconid; the mesosinusid is more closed; the mesolophid is on the average shorter; the ectomesolophid is better developed; the entoconid is larger; the hypolophulid is less oblique; the posterosinusid is more often closed.

M^1 — The anterolophule is less frequently complete; there is hardly ever an anterior protolophule; the sinus and the mesosinus are more often open; there is often a connection between protocone and hypocone through the sinus; the metalophule is frequently transverse.

M^2 — There is less frequently a (trace of a) posterior protolophule; the sinus is more frequently open, and less frequently strongly proverse; the connection of the entoloph with the protocone is higher.

M^3 — The lingual anteroloph is less developed; the sinus is often smaller; the mesosinus is more frequently closed; the old entoloph is better developed; the centroloph is often absent or weak; the centrocone is more frequently present.

Comparison of *A. nanus* from MLB1D with *A. nanoides* from OLA4A: See under *A. nanoides*.

Comparison of *A. nanus* from MLB1D with *A. atavoides* from OLA4A: See under *A. atavoides*.

Atavocricetodon atavus (Misonne, 1957)

This species is, until now, only known from its type-locality Hoogbutsel. For a description see Freudenthal (1988). It is morphologically similar to the other *Atavocricetodon* species. It presents, however, different size relations. In the lower molars it overlaps the lower half of the size range of *A. atavoides* and *A. hugueneyae*, and the upper half of the size ranges of *A. nanus* and *A. nanoides*. In M^1 it hardly overlaps *A. atavoides* and *A. hugueneyae*, and almost completely overlaps *A. nanus* and *A. nanoides*. In the M^3 it almost completely overlaps the size range of *A. atavoides* and *A. hugueneyae*, and hardly that of *A. nanus* and *A. nanoides*.

This means that the lower teeth show the same length relations as the Spanish species, whereas in the upper dentition the M^1 is relatively shorter, and the M^3 relatively longer.

There are in Hoogbutsel, apart from *A. atavus*, a smaller and a larger species, and maybe the size range for *A. atavus* is incorrect, due to an erroneous determination of some specimens. But even this does not explain the different size relations, which separate *A. atavus* from the other *Atavocricetodon* species, including the material described by Dienemann (1987) from Möhren 13.

The description of *A. atavus* from Hoogbutsel, as represented in Tables 4-9, shows

some differences with the description by Freudenthal (1988). This is due to changes in the definitions of the character states I made after 1988. There is one detail, that is not represented in the tables of character states, and that may be distinctive for *A. atavus*: in the lower molars the metaconid and entoconid appear to be farther apart, and the mesosinusid wider, than in the Spanish *Atavocricetodon* material.

Analysis of character states

In Table 2 the derived states are listed of those features that gave a significant difference between at least two populations. The interpretation of what is the primitive state and what is the derived state, is based on the following arguments:
1. Within a dentition the M3 are the most advanced elements, and the M1 are the most conservative.
2. The condition found in populations of later age. Only Oligocene cricetids are used for comparison. The Miocene forms represent a completely different stock, and may show other tendencies.
3. The condition expected to be found in an original tritubercular tooth. The interpretations are listed and discussed hereafter. Every paragraph begins with the supposedly most derived state, even if that state is not realized in the studied material. The following states are supposed to be derived:

All dental elements:

Cingulum ridges are interpreted as added features, and therefore derived. This interpretation may turn out to be untrue, or at least too generalized. In younger populations cingulum ridges may be much better developed, or completely lacking. Probably both directions of development exist.

Lower dentition:

Anterolophulid complete (M_1). This is an additional element, not present in the hypothetical ancestor, fully developed in younger populations.

Metalophulid complete (M_1). The metalophulid is interpreted as a new connection between metaconid and protoconid, that replaces the old trigonid connection (protoconid hind arm). Fully developed in younger populations, better developed in M_2 and M_3 than in M_1.

Protoconid hind arm low or free. The old trigonid connection is reduced, or moved backwards and detached from the metaconid. Low or free in younger populations. Progressively lower and more detached from M_1 to M_3.

Mesolophid absent. The mesolophid is better developed in M_1 then in M_3; M_1 and M_2 are identical. But, the absence in M_3 should probably not be ascribed to the trend from M_1 to M_3, but to the reduced state of the posterior part of M_3. Therefore the interpretation is not certain. In younger populations the mesolophid may be better developed, or less developed; apparently both directions exist.

Mesoconid absent. Probably a disappearing character: absent or present in M_1, absent in M_2; generally absent in younger species.

Ectolophid longitudinal (M_1). The oblique ectolophid is usually lower, sometimes interrupted; in M_2 the ectolophid is higher and more longitudinal; some younger

species have an oblique ectolophid, others have a longitudinal one. The interpretation is uncertain.

Ectomesolophid better developed. This is an added element, less frequent in M_1, more frequent in M_2, and less frequent in M_3 due to the reduction of the posterior part of that tooth.

Hypoconid hind arm absent. Most frequent in M_1, less frequent in M_2, generally absent in M_3. The absence in M_3 cannot be ascribed to the M_1-M_3 trend, but is due to the reduced state of that tooth. In several younger species the hypoconid hind arm is present, but it is always smaller in M_2 than in M_1.

Anterosinusid smaller and metalophulid more forward (M_2 and M_3). The metalophulid moves forward, and reduces the anterosinusid; more expressed in M_3 than in M_2. In younger species the anterosinusid may disappear completely.

Hypolophulid more forward directed (M_2). The hypolophulid is supposed to move forward from an original, transverse, position. In M_1 it is more transverse than in M_2; it is most oblique in M_3, but this may be due to the reduction of that element. In younger species it may be more oblique.

Labial anterolophid longer (around the protoconid). More developed in M_3 than in M_2.

Shape of M_3. There are considerable differences, but a directional interpretation cannot be given. In some younger species the M_3 is very short, in others it is long.

Upper dentition:

Anterocone split (M^1). More frequent in younger species. Considered to be a progressive complication of an added structure.

Prelobe set-off (= lingual border between protocone and anterocone angular). The direction of this feature is not clear; both states (set-off and continuous) are present in younger species.

Anterolophule complete. The protocone fore arm gets detached from the paracone and moves forward towards the anterocone. Better developed in younger species.

Anterior protolophule absent. Related to the previous character (the shifting forward of the protocone fore arm) and to the next one (the shape of the sinus). The posterior protolophule of M^1 is homologous with the anterior protolophule of M^2; in the M^2 of Miocene cricetids a new posterior protolophule originates from the curving entoloph, but this situation is merely indicated in Oligocene cricetids.

Sinus. The development of the sinus is best analyzed in M^3: the protocone rotates and the entoloph curves sharply forward, causing the sinus to penetrate deeply into the center of the tooth; then a new connection arises between protocone and hypocone (neo-entoloph), and the old entoloph is progressively reduced. Together with the rotation of the protocone the protolophule shifts forward.

The same process is seen — less frequently and less developed — in M^2: often a deeply penetrating sinus, and occasionally traces of a neo-entoloph (here called pc-hc connection through the sinus). In M^1 this transformation is less advanced than in M^2, and the protolophule maintains a posterior position.

Lingual anteroloph better developed. It may partly separate the protocone from the lingual border. Its evolutionary direction is not clear.

Entoloph-protocone connection high (M^2). In younger species the connection is high.

Labial border convex (M^2). The typical situation in younger species.

Centroloph (= metalophule) and metacone absent. These structures disappear due to the general reduction of the M^3.

In Table 2 the five populations have been compared for those characters that gave a reliable difference between at least two populations. If a population has a more derived state for a character it scores two points; if it is less derived it scores 0, and if there is no difference both score 1 point. The last line of the table gives the sum of all scored points for each population.

A. atavus from Hoogbutsel has the lowest value (209), and might be considered the most archaic population. However, the table contains a mixture of important and less important, reliable and unreliable characters. Precisely in some 'good' characters HB scores higher than expected for the oldest population. Therefore I made a selection of characters that may be considered as more important than the rest. The results are presented in Table 3.

In Table 3 the archaic state of *A. atavus* from Hoogbutsel is confirmed by the low value of 79, and even accentuated in comparison with the other populations. Though the differences are not great, both populations from OLA4A score higher (114 and 110) than the two from MLB1D (92 and 105), which is opposed to their supposed stratigraphical sequence. It is not possible to draw any evolutionary relationships between these populations. Distribution of archaic and derived characters is mosaic, possibly due to a rapid diversification of these Cricetidae, in the period immediately after their first arrival in Europe.

Family Gliridae Muirhead, 1819

There is a discussion on whether the correct name of the family is Gliridae or Myoxidae. Pending a decision on case 2928 by the Commission of Zoological Nomenclature I prefer, for the moment, the family name Gliridae.

Genus *Glamys* Vianey-Liaud, 1989

Vianey-Liaud (1989) created the genus *Glamys* on the basis of skull characters observed in *Gliravus priscus* Stehlin & Schaub, 1951. Vianey-Liaud (1994) transferred a number of species, formerly attributed to the genus *Gliravus*, to the genus *Glamys*. Even if the skull characters are not conclusive, since we don't know their variability, the dental morphology and size of *G. priscus* may be good reasons to separate the species *priscus* from *Gliravus*. For *Gliravus devoogdi* and *Gliravus fordi*, whose skull characters are unknown, this seems less evident.

Glamys olallensis sp. nov.
Pl. 6, figs. 1-8.

Type-locality — Olalla 4A (Teruel, Spain).

Holotype — M_1 dext., OLA4A 817, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Derivatio nominis — Named after the type-locality.

Age — Late Eocene - Early Oligocene.

Diagnosis and differential diagnosis — Small size, smaller than *G. priscus* from La Débruge and the Isle of Wight (Bosma & de Bruijn, 1979) and *G. robiacensis* (see Hartenberger, 1971), larger than *Gliravus minor* (Bosma & de Bruijn, 1982). Morphology similar to *G. priscus*, but there is no trace of a posterior centroloph in the upper molars and the anteroloph is generally connected to the paracone. The anteroloph of P^4 is quite well developed. In the lower molars the mesoconid is often separated from the lingual border.

Distribution — Besides from its type-locality, *G. olallensis* is known from several unpublished localities in the same area, that are considered to be older than Olalla 4A (Freudenthal, in prep.).

Material and measurements (see also Figs. 3, 4)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
P_4	3	6.9	7.17	7.3	5.63	0.231	3	6.0	6.63	7.0	15.38	0.551
M_1	17	7.6	8.01	8.6	12.35	0.257	18	7.4	8.09	8.5	13.84	0.285
M_2	18	7.5	8.01	8.5	12.50	0.289	18	8.1	8.46	9.2	12.72	0.301
M_3	3	7.3	7.60	8.0	9.15	0.361	3	6.7	7.23	7.6	12.59	0.473
D^4	1	7.2	7.20	7.2	—	—	1	8.4	8.40	8.4	—	—
P^4	5	6.6	6.82	7.2	8.70	0.239	5	7.8	8.16	8.4	7.41	0.230
M^1	14	6.9	7.61	8.0	14.77	0.300	14	8.5	9.00	9.7	13.19	0.328
M^2	9	6.9	7.33	7.7	10.96	0.250	9	8.5	9.19	9.9	15.22	0.451
M^3	1	6.2	6.20	6.2	—	—	1	7.6	7.60	7.6	—	—

Description

P_4 — The anterolophid is interrupted. There are no extra crests. The metalophid is connected high to the metaconid. The centrolophid is absent. The mesoconid lies on the labial border (2) or more centrally (1). The mesolophid is absent, curved forward, or directed towards the metaconid.

M_1 — The anterolophid is not connected to the protoconid. There are no extra crests. The metalophid is free (1), connected to the base of the metaconid (7), or high to the metaconid (7). The centrolophid is absent (16) or short (1), not connected to the metaconid (16), or high connected (1). There is a mesostylid in one specimen. The mesoconid lies on the labial border (4) or more centrally (12). The mesolophid is short (1) or of medium length (14).

M_2 — The anterolophid is not connected to the protoconid. There is no extra crest in the anterior valley. The metalophid is free (1), connected to the base of the metaconid (12), or high to the metaconid (4). The centrolophid is absent. The mesoconid lies on the labial border (9) or more centrally (9). The mesolophid is of medium length (12), or longer and directed towards the metaconid (4), or towards the ento-

conid (1). There may be a small backward crest on the tip of the mesolophid. An extra crest in the posterior valley is absent (11), small (4), or of medium length (1).

M_3 — The anterolophid is not connected to the protoconid. There are no extra crests. The metalophid is free, connected to the base of the metaconid, or high to the metaconid. The centrolophid is absent. The mesostylid is absent (2) or present (1). The mesoconid lies on the labial border (2) or more centrally (1). The mesolophid is directed towards the entoconid (2), or connected to that cusp (1). Protoconid and hypoconid may be connected by an ectolophid.

D^4 — The labial border is round; the centroloph is very thick. For the rest it is similar to the P^4.

P^4 — The labial border is straight. The anteroloph is of medium length (1) or long (4), not connected to the protocone. There are no extra crests. The anterior centroloph is absent (1) or long (4), placed centrally in one case. The posterior centroloph is absent. The posteroloph is connected to the protocone in one case, separated in the others.

M^1 — The anteroloph is lingually free. There are no extra crests. The anterior centroloph is absent (1) or long (13); it is connected to the paracone (5), free (1), or placed centrally (7); in two of the latter cases it forms a mesostyl. The posterior centroloph is absent. The posteroloph is connected to the protocone in four cases.

M^2 — The anteroloph is lingually free. There are no extra crests. The anterior centroloph is long, connected to the paracone (4), free (1), or placed centrally (4); in two

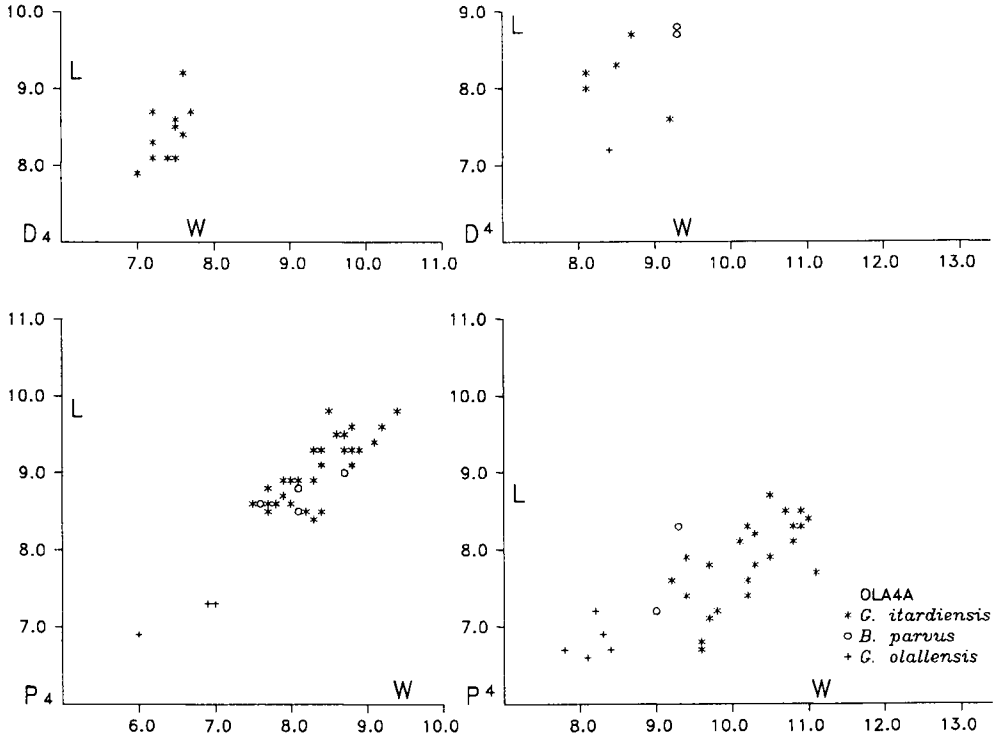

Fig. 3. Length/width diagrams of the deciduous molars and premolars of the Gliridae from Olalla 4A.

of the latter cases it forms a mesostyl. The posterior centroloph is absent. The posteroloph is connected to the protocone in four cases.

Gliravus itardiensis Vianey-Liaud, 1989
Pl. 6, figs. 9-18.

Type-locality — Itardies (Quercy, France).
Holotype — Skull fragment ITD 140.
Locality — Olalla 4A.
Characterization — Similar to *Gliravus micio*, but the extra crest between anterolophid and metalophid is absent. The mesolophid of the lower molars shows a tendency of being directed to the metaconid instead of towards the entoconid.

Remarks — I originally attributed this material to *Gliravus itardiensis* Vianey-Liaud, 1989. The author herself synonymized the species *itardiensis* in 1994 with *Peridyromys micio* Misonne, 1957, and transferred it to the genus *Bransatoglis*. I don't agree with that generic attribution, and prefer for the moment to place it in *Gliravus* (see discussion of *Bransatoglis*). The reasons for synonymizing *G. itardiensis* with *G. micio* were clearly explained (op. cit., p. 139-140), and the author stated that the taxon *itardiensis* might be 'reactivated', when more abundant material became available. I think the rich material from Olalla 4A (of which only a part is described in this paper) fulfills this condition.

Material and measurements (see also Figs. 3, 4)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
D_4	12	7.9	8.45	9.2	15.20	0.373	11	7.0	7.40	7.7	9.52	0.219
P_4	29	8.4	9.06	9.8	15.38	0.425	28	7.6	8.35	9.4	21.18	0.499
M_1	20	10.3	10.95	11.8	13.57	0.430	20	10.2	11.18	12.0	16.22	0.472
M_2	33	10.3	11.12	11.9	14.41	0.416	31	10.5	11.67	12.7	18.97	0.511
M_3	35	8.8	10.31	11.5	26.60	0.673	34	9.4	10.34	11.6	20.95	0.590
D^4	5	7.6	8.16	8.7	13.50	0.404	6	8.1	8.58	9.2	12.72	0.440
P^4	23	6.7	7.84	8.7	25.97	0.552	23	9.2	10.21	11.1	18.72	0.575
M^1	31	9.3	10.30	11.3	19.42	0.516	31	10.3	11.62	12.4	18.50	0.492
M^2	24	9.3	10.22	10.7	14.00	0.366	24	11.5	12.22	12.9	11.48	0.399
M^3	24	8.3	8.79	9.6	14.53	0.353	23	10.2	10.90	12.2	17.86	0.500

Description

D_4 —There is a high metaconid with an anterolophid that meets the protoconid (8), or ends before that cusp (3). The metalophid is connected to the metaconid (8), or ends free (4). The mesolophid is generally absent. The posterolophid is high, entoconid and hypoconid are usually well marked. There frequently are longitudinal structures in the talonid basin.

P_4 — The anterolophid is interrupted (6) or continuous (20). The metalophid is free (2), connected to the base of the metaconid (16), or higher to the metaconid (7).

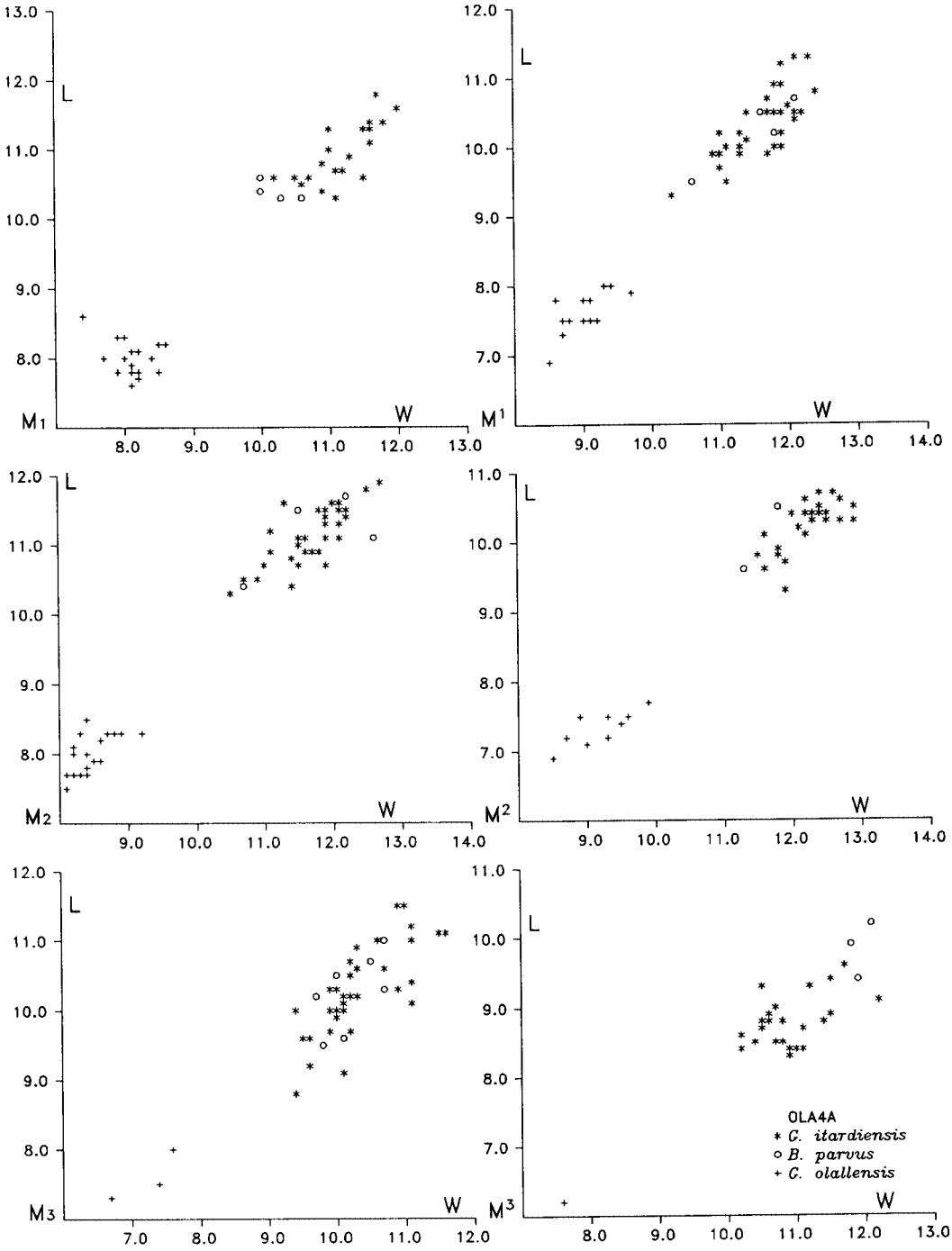

Fig. 4. Length/width diagrams of the molars of the Gliridae from Olalla 4A.

The centrolophid is absent (5), short (16), or of medium length (9); it is nearly always free from the metaconid. The mesolophid is directed to the metaconid (4), directed to the entoconid (15), connected to the entoconid (7), or connected to the lingual border of the tooth (4). There is an extra crest between mesolophid and posterolophid in 2 out of 29 specimens.

M_1 — The anterolophid is free from the protoconid. There is no extra crest in the anterior valley, except for one case. The metalophid ends free (3), it is connected to the base of the metaconid (11), or higher to the metaconid (4). The centrolophid is absent (5), short (1), of medium length (10), or long (2); it presents a low connection with the metaconid in two cases only. The mesolophid is of medium length (6), or longer; in the latter case it is directed towards the metaconid (6), connected to the metaconid (1), directed to the entoconid (2), connected to the entoconid (1), or long and straight, directed to the lingual border between metaconid and entoconid (4). The extra crest in the posterior valley is absent (2), very small (1), small (4), of medium length (3), or long (9).

M_2 — The anterolophid is free from the protoconid. There is no extra crest in the anterior valley, except for one case. The metalophid ends free (11), it is connected to the base of the metaconid (23), or higher to the metaconid (1). The centrolophid is absent (3), short (1), of medium length (18), or long (8); it is free from the metaconid (16), there is a low connection (11), or a high connection (3). The mesolophid is of medium length (4), or longer; in the latter case it is directed towards the metaconid (3), connected to the metaconid (1), directed to the entoconid (13), connected to the entoconid (10), or long and straight, directed to the lingual border between metaconid and entoconid (2). The extra crest in the posterior valley is absent (2), very small (1), of medium length (15), or long (14).

M_3 — The anterolophid is labially free (34), only in one case connected to the protoconid. Only in two cases there is a small extra crest in the anterior valley. The metalophid ends free (13), it is connected to the base of the metaconid (12), or higher to the metaconid (5). The centrolophid is absent (3), short (2), of medium length (22), or

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Plate 6

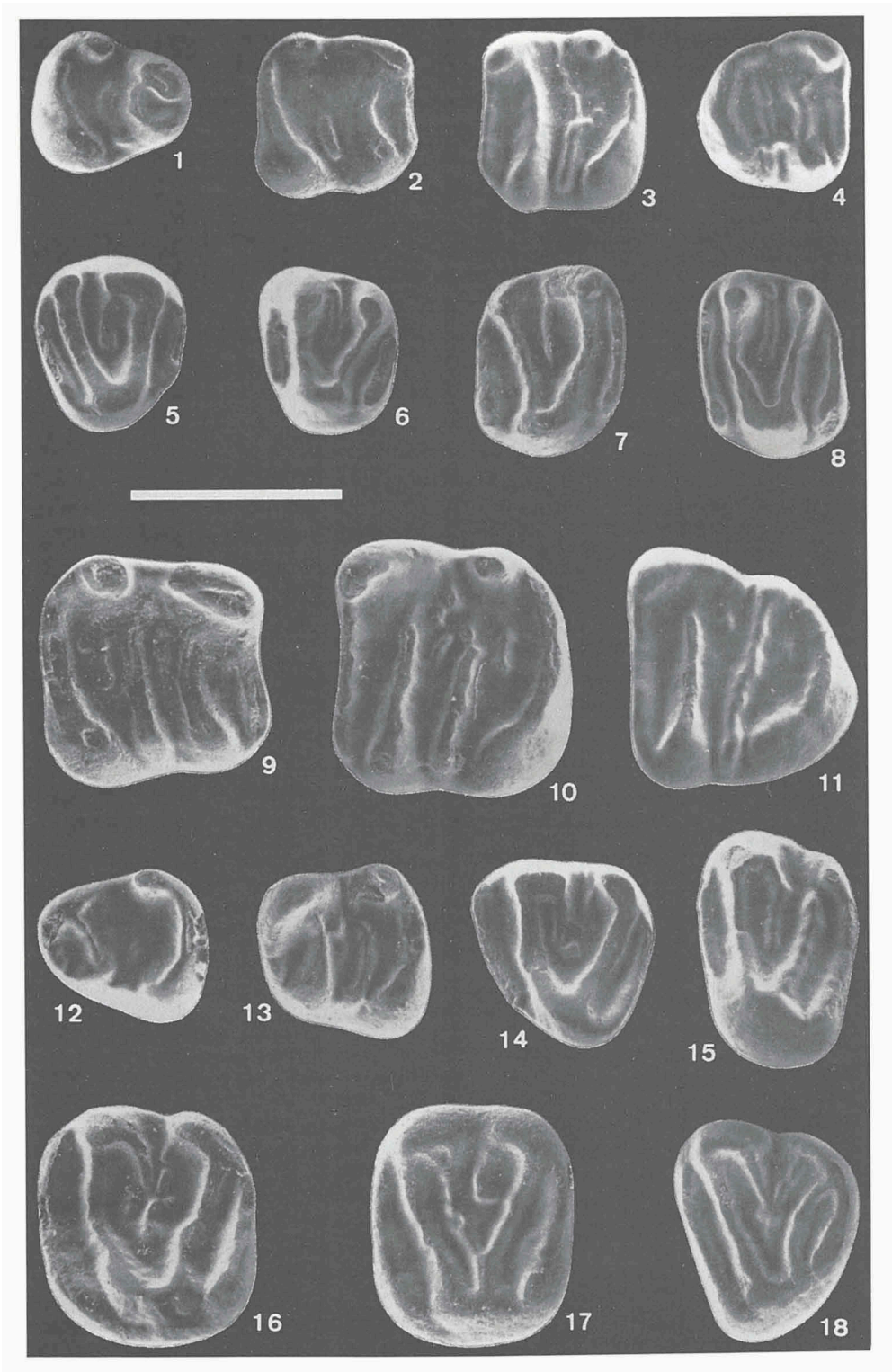
Glamys olallensis sp. nov. from Olalla 4A

Fig. 1. P_4 dext., OLA4A 803.
Fig. 2. M_1 dext., OLA4A 817, holotype.
Fig. 3. M_2 sin., OLA4A 823.
Fig. 4. M_3 dext., OLA4A 842.
Fig. 5. D^4 dext., OLA4A 848.
Fig. 6. P^4 sin., OLA4A 847.
Fig. 7. M^1 dext., OLA4A 862.
Fig. 8. M^2 sin., OLA4A 866.

Gliravus itardiensis from Olalla 4A

Fig. 9. M_1 dext., OLA4A 923.
Fig. 10. M_2 sin., OLA4A 937.
Fig. 11. M_3 sin., OLA4A 969.
Fig. 12. D_4 sin., OLA4A 877.
Fig. 13. P_4 sin., OLA4A 887.
Fig. 14. D^4 sin., OLA4A 1004.
Fig. 15. P^4 sin., OLA4A 1011.
Fig. 16. M^1 sin., OLA4A 1033.
Fig. 17. M^2 sin., OLA4A 1065.
Fig. 18. M^3 sin., OLA4A 1089.

The scale represents 1 mm.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long (4); it is free from the metaconid (8), low connected (13), or high connected (8). The mesolophid is directed towards the metaconid (1), directed towards the entoconid (3), or connected to the entoconid (31). An extra crest in the posterior valley is absent (2), very small (3), small (2), of medium length (12), or long (14).

D^4 — The anteroloph is short (1) or of medium length (5), and does not form a continuous entoloph. There are no extra crests. The anterior centroloph is of medium length (1) or long (5). The posterior centroloph is absent (3), short (2), or long (1). The centrolophs are not connected to each other. The posteroloph has a continuous connection with the protocone (4), or it is separated (2).

P^4 — The anteroloph is absent (1), short (4), of medium length (7), or long (11); it does not form a continuous entoloph. There are no extra crests. The anterior centroloph is always long. The posterior centroloph is absent (11), short (2), of medium length (5), or long (4). The centrolophs are rarely connected to each other. The posteroloph never has a continuous connection with the protocone.

M^1 — The anteroloph is lingually free (25), or it has a low connection with the protocone (3). There is no extra crest, neither in the anterior valley nor in the posterior valley. The anterior centroloph is nearly always long, and connected to the paracone. The posterior centroloph is frequently long, but on the average shorter than the anterior one, and the connection of the anterior centroloph with the paracone is much higher than the connection of the posterior centroloph with the metacone. There is a short extra crest inside the trigone (8), or no such crest (21); if present it is generally a ramification of the anterior centroloph. The centrolophs are not connected (9), connected midway (8), or connected at their lingual ends (12). The posteroloph has a continuous connection with the protocone (10), or it is separated (16).

M^2 — The anteroloph is lingually free (15), or it has a low connection with the protocone (6). There is no extra crest, neither in the anterior valley, nor in the posterior valley. The anterior centroloph is always long, and nearly always connected to the paracone. The posterior centroloph is generally long, but on the average shorter than the anterior one, and the connection of the anterior centroloph with the paracone is higher than the connection of the posterior centroloph with the metacone. In two cases the posterior centroloph is directed to the metacone, without reaching it, and in three cases it has a central position between paracone and metacone. There is a short extra crest inside the trigone (2), or no such crest (22). The centrolophs are not connected (6), connected midway (3), connected at their lingual ends (12), or there are two connections (2). The posteroloph has a continuous connection with the protocone (3), or it is separated (13).

M^3 — The anteroloph is lingually free (1), low connected to the protocone (2), or there is a high connection (13). There is an extra crest in the anterior valley in one case. The centrolophs are generally long, not connected (8), connected (11), or there are two connections (2). In many cases they are broken up into a complex pattern of little cusps and crests. Counting, as far as possible, the number of transverse crests inside the trigone, one finds specimens with two crests (11), and specimens with three crests (8). In five cases there is a mesostyl. The posteroloph has a continuous connection with the protocone.

Genus *Bransatoglis* Hugueney, 1967

Vianey-Liaud (1994) places the following species in the genus *Bransatoglis*:

Peridyromys micio Misonne, 1957
Gliravus itardiensis Vianey-Liaud, 1989
Bransatoglis concavidens Hugueney, 1967
Gliravus meridionalis Hartenberger, 1971
Paraglis fugax Hugueney, 1967
Bransatoglis cadeoti Bulot, 1978
Bransatoglis bahloi Bosma & de Bruijn, 1982
Oligodyromys planus Bahlo, 1975
Bransatoglis sjeni Ünay-Bayraktar, 1989
Bransatoglis misonnei Vianey-Liaud, 1994

This interpretation makes the genus *Bransatoglis* a heterogeneous group with very wide morphological and size ranges. It is based on supposed phylogenetic relationships, that, in my opinion, are far from sure.

In the Upper Eocene locality Aguatón 2 I have found a medium-sized *Bransatoglis* (about the size of *B. planus*), with a very advanced morphology, comparable with that of *B. concavidens*. In subsequent Upper Eocene and Lower Oligocene localities such well-developed *Bransatoglis* populations are frequently found, and they seem to form a homogeneous group, together with *B. concavidens*. Basically, what changes in this group is size, the species from Coderet being much larger than the one from Aguatón. I think the genus *Bransatoglis* should be restricted to this homogeneous group, and all other species should be removed from it.

Oligodyromys planus Bahlo, 1975 from Heimersheim may well belong to this group, and is therefore called *Bransatoglis planus* as proposed by Bosma & de Bruijn (1982).

The beds with *Bransatoglis bahloi* Bosma & de Bruijn, 1982 on the Isle of Wight are equal in age or younger than the locality of Aguatón, but the mentioned species has by far not yet achieved the morphological stage of the Aguatón species. I therefore remove the species *bahloi* from the genus *Bransatoglis*.

Also in Aguatón 2 I have found a very small glirid, that is identical or similar to *B. misonnei*. Such populations are very frequent in the Lower Oligocene, and appear to form a homogeneous group together with Late Oligocene *Microdyromys*.

The oldest occurrence of *Microdyromys* is now the one from the Upper Eocene of Aguatón. *Bransatoglis misonnei* Vianey-Liaud, 1994 should — in my opinion — be placed in *Microdyromys*, and that genus is constantly present from the Late Eocene until in the Miocene.

Gliravus meridionalis Hartenberger, 1971 and *Peridyromys micio* Misonne, 1957 have no apparent similarities with *Bransatoglis*, and the genus *Bransatoglis* should probably be restricted to the following species:

B. concavidens Hugueney, 1967
B. fugax (Hugueney, 1967)
B. planus (Bahlo, 1975)
B. cadeoti Bulot, 1978
B. sjeni Ünay-Bayraktar, 1989 ?
B. parvus sp. nov.
B. sp. nov. from Aguatón 2

Bransatoglis parvus sp. nov.
Pl. 7, figs. 1-11.

Type-locality — Olalla 4A (Teruel, Spain).

Holotype — M_2 sin., OLA4A 1127, kept in the Departamento de Ciencias de la Tierra, University of Zaragoza.

Derivatio nominis — Latin parvus = small.

Age — Late Eocene -Early Oligocene.

Diagnosis — Molars with thick crests. Lower molars generally with seven crests, upper molars with two centrolophs, generally an accessory crest in the first valley, sometimes an accessory crest inside the trigone.

Differential diagnosis — Smaller than all known species of *Bransatoglis*.

Material and measurements (see also Figs. 3, 4)

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
P_4	4	8.5	8.73	9.0	5.71	0.222	4	7.6	8.13	8.7	13.50	0.450
M_1	4	10.3	10.40	10.6	2.87	0.141	4	10.0	10.23	10.6	5.83	0.287
M_2	4	10.4	11.18	11.7	11.76	0.574	5	10.7	11.66	12.6	16.31	0.750
M_3	8	9.5	10.34	11.0	14.63	0.558	7	9.7	10.21	10.7	9.80	0.418
D^4	2	8.7	8.75	8.8	1.14	0.071	2	9.3	9.30	9.3	—	—
P^4	2	7.2	7.75	8.3	14.19	0.778	2	9.0	9.15	9.3	3.28	0.212
M^1	4	9.5	10.23	10.7	11.88	0.525	4	10.6	11.53	12.1	13.22	0.650
M^2	2	9.6	10.05	10.5	8.96	0.636	2	11.3	11.55	11.8	4.33	0.354
M^3	3	9.4	9.83	10.2	8.16	0.404	3	11.8	11.93	12.1	2.51	0.153

Description

P_4 — Accessory crests are absent in two specimens, present in one. The anterolophid is connected to protoconid and metaconid. The metalophid is connected to the metaconid, the centrolophid is connected or isolated. The mesolophid is connected to the entoconid (4) or slightly interrupted (1).

M_1 — The anterolophid is not connected to the protoconid. The anterior extra crest is small or large. The metalophid is connected to the metaconid; the centrolophid is long, never isolated; it is connected to the metaconid (4), or lingually free (1), and it is connected to the protoconid (3), or labially free (2). The mesolophid is connected to the entoconid (2), interrupted near the entoconid (2), or interrupted midway; the interrupted mesolophid may form a longitudinal connection with the centrolophid and/or with the posterior extra crest. The posterior extra crest is strongly developed, but never connected to hypoconid or entoconid.

M_2 — The anterolophid is not connected to the protoconid. The anterior extra crest is small or large. The metalophid is connected to the metaconid (2), or ends at its base (2); the centrolophid is long, connected to the metaconid (3), or lingually free (1); it is not connected to the protoconid or to the metalophid at its labial end. The

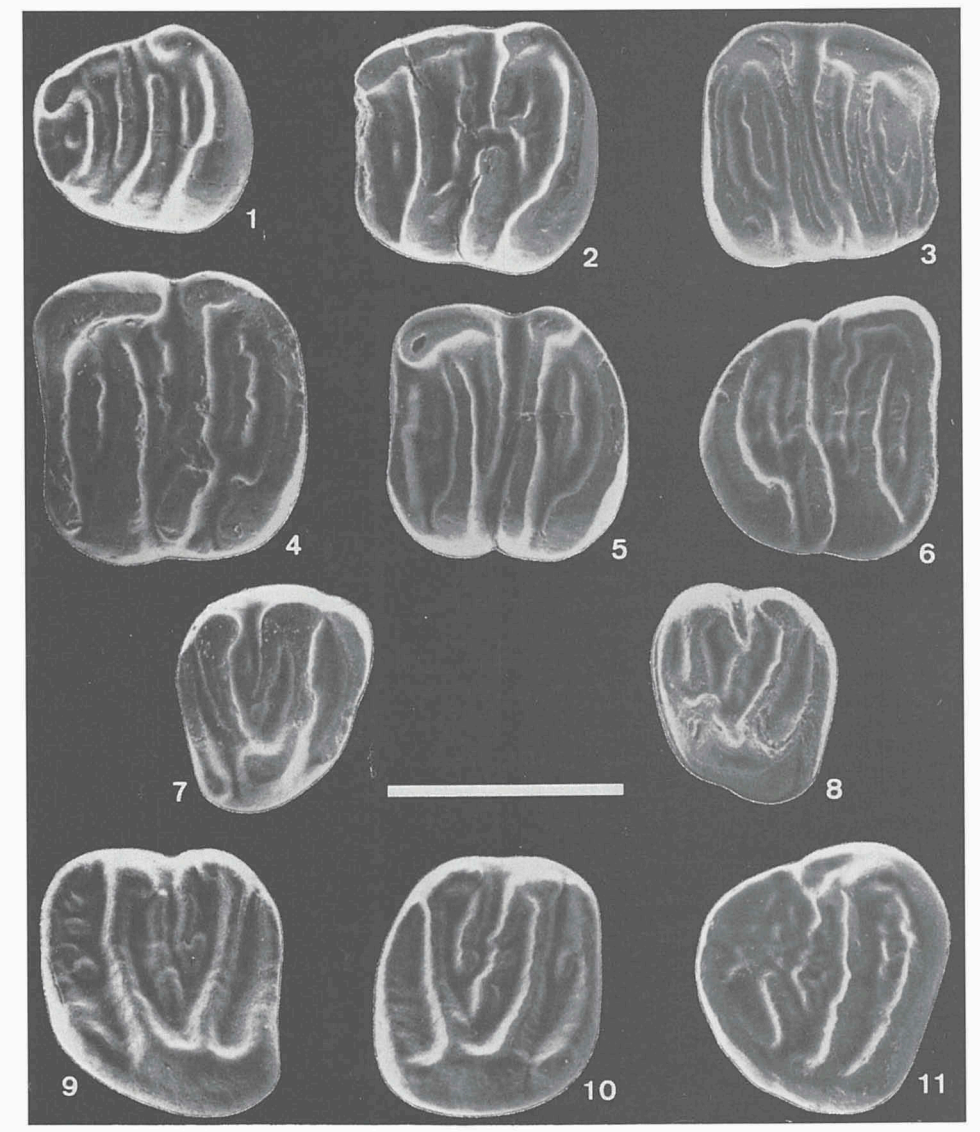

Plate 7

Bransatoglis parvus from Olalla 4A

Fig. 1. P_4 sin., OLA4A 1111.
Fig. 2. M_1 sin., OLA4A 1121.
Fig. 3. M_1 dext., OLA4A 1123.
Fig. 4. M_2 sin., RGM 418 103.
Fig. 5. M_2 sin., OLA4A 1127, holotype.
Fig. 6. M_3 dext., OLA4A 1132.
Fig. 7. D^4 dext., OLA4A 1009.
Fig. 8. P^4 sin., OLA4A 1135.
Fig. 9. M^1 sin., OLA4A 1141.
Fig. 10. M^2 dext., OLA4A 1142.
Fig. 11. M^3 dext., OLA4A 1144.

The scale represents 1 mm.

mesolophid is connected to the entoconid; in one case it is interrupted near the mesoconid. The posterior extra crest is strongly developed, isolated.

M_3 — The anterolophid is connected to the protoconid (2) or not connected (4). The anterior extra crest is absent (2), small (1), or large (3). The metalophid is connected to the metaconid (7) or not connected (2); the centrolophid is of medium length or long, connected to the metaconid, and in one case connected to the mesoconid. The mesolophid is connected to the entoconid in eight out of nine specimens. The posterior extra crest is strongly developed, isolated.

D^4 — Rounded teeth with long anteroloph, two centrolophs, and a posteroloph that is isolated from protocone and metacone in one case, and connected to these cusps in the other one.

P^4 — Rounded tooth with a short anteroloph, that is connected to the protocone; there are two centrolophs, that unite into a long central crest; the protoloph is interrupted near the protocone; the posteroloph is connected to protocone and metacone.

M^1 — The anteroloph is isolated from the protocone, or connected to it. There is an anterior extra crest between anteroloph and protoloph, which may be very weak or fairly strong, or consisting of a series of small cusps. There are two long centrolophs, that may unite in the center of the tooth;.they are connected to the paracone and the metacone respectively. In two specimens there are no extra crests inside the trigone, in the other two specimens there are two such crests. The posteroloph is connected to the protocone (3), or not connected (1).

M^2 — The anteroloph is isolated from the protocone, or connected to it. There is a weak extra crest between anteroloph and protoloph in two out of three specimens. There are two long centrolophs, that may unite in the center of the tooth; they are connected to the paracone and the metacone respectively. In one specimen there is an extra crest inside the trigone. The posteroloph is connected to the protocone, or not connected.

M^3 — The anteroloph is isolated from the protocone, or connected to it. There is an anterior extra crest between anteroloph and protoloph, which may be one little cusp, or consisting of a series of small cusps. There are two long centrolophs, that unite in the center of the tooth, where they form an intricate pattern of ramified little crests. The paracone shows a tendency to split off a mesostyl, which bears the anterior centroloph. The posteroloph is connected to the protocone (3).

Discussion — The morphological variability of the lower molars appears to be rather great: some specimens have well-developed straight and complete crests, in other ones the crests are somewhat more irregular, sometimes interrupted, and there are some longitudinal structures. One might think, that we are dealing with two different species, but comparison with younger *Bransatoglis* populations from several levels at Montalbán made it clear, that this is not the case. In the younger populations the same differences exist, but the specimens with irregular crests are considerably less frequent, and the fully achieved *Bransatoglis* morphology with well-developed straight crests is dominant.

Biostratigraphy

The faunal list of Olalla 4A is composed of the following taxons:

Blainvillimys langei Vianey-Liaud, 1972
Pseudoltinomys gaillardi Lavocat, 1951
Elfomys sp.
Sciuromys cayluxi Schlosser, 1884
Palaeosciurus aff. *goti* Vianey-Liaud, 1974
Oligopetes lophulus Heissig, 1979
Eomys aff. *fahlbuschi* Ünay-Bayraktar, 1989
Atavocricetodon atavoides sp. nov.
Atavocricetodon nanoides sp. nov.
Atavocricetodon minusculus sp. nov.
Glamys olallensis sp. nov.
Gliravus itardiensis Vianey-Liaud, 1989
Bransatoglis parvus sp. nov.

Remark — Alvarez Sierra et al. (1987) mention *Steneofiber* from Olalla 4. This is probably due to an error, since I did not find one single specimen of this taxon among the thousands of specimens from this locality.

In the following we will compare the fauna of Olalla 4A, with the fauna from several levels of Montalbán. Olalla and Montalbán are some 30 km apart, and correlation in the field is impossible.

The presence of Cricetidae makes it clear that Olalla 4A is younger than the 'Grande Coupure', the absence of *Pseudocricetodon* makes it older than Montalbán.

Atavocricetodon species show a mosaic distribution of archaic and derived characters, and do not serve — for the moment — for a decision of the relative age of Olalla 4A and Montalbán 1D.

Blainvillimys langei Vianey-Liaud, 1972 has less advanced enamel differentiation than *B. gregarius* from Montalbán, which confirms the older age.

Pseudoltinomys gaillardi Lavocat, 1951: the maximum height of unworn $M_{1,2}$ is 20.0. In Montalbán 3C (lower than MLB1D) this is 22.0, and in MLB10 (higher than MLB1D) it is 22.8. In a level lower than OLA4A I found a maximum of 18.0 for a population provisionally attributed to *Pseudoltinomys cuvieri* (Pomel, 1852). These populations may represent an evolutionary lineage. The OLA4A material appears to have the morphology of *Pseudoltinomys gaillardi*, but maybe it is less hypsodont. On the whole the Spanish specimens seem to be less hypsodont than the French ones with equivalent dental morphology. If this is not due to a different way of measuring, it may mean that we are dealing with different lineages, and that large distance correlation on the basis of *Pseudoltinomys* may be hazardous.

Sciuromys cayluxi Schlosser, 1884: this species, represented by a few specimens only, is also found in various levels of Montalbán, both older and younger than the classical site MLB1D. It does not give additional information on the position of OLA4A.

Elfomys sp. is represented by three damaged specimens, that are considerably smaller than the corresponding elements of *Pseudoltinomys gaillardi*. The scarcity of

Elfomys in comparison with MLB1D may have a biostratigraphic significance.

For the Sciuridae, *Palaeosciurus* aff. *goti* Vianey-Liaud, 1974 and *Oligopetes lophulus* Heissig, 1979, see Cuenca Bescós & Canudo (1992).

The only thing that can be said about the Eomyidae is, that they are more frequent in MLB1D than in OLA4A.

Glamys olallensis sp. nov. does not permit any correlation. *Glamys priscus* is present in older levels; it is replaced by *Glamys olallensis* in OLA4A, and reappears in MLB1D.

Gliravus itardiensis Vianey-Liaud, 1989: a *Gliravus* species of similar size and morphology is found in MLB1D; it is somewhat smaller, and there are quite a number of morphological differences. I provisionally attribute it to *G. tenuis* Bahlo, 1975. Nothing can be said about the relationships between these two populations.

Bransatoglis parvus sp. nov.: also in this case there is a similar, but not identical, population in MLB1D. Relationships are unclear, the more so, since both populations are poor in specimens. There are quite rich populations in various levels of Montalbán, both older and younger than MLB1D, that will be studied in a forthcoming publication.

Concludingly we may say, that the Cricetidae fix quite reliably the age limits of the Olalla fauna, and that some of the other faunal components confirm this. The time span between the 'Grande Coupure' and Montalbán may be considerable, but a more detailed specification is for the moment impossible.

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Tables

Table 1. Measurements of *Atavocricetodon* species.
*+ = A. atavus, * = A. atavoides, & = A. hugueneyae, @ = A. nanoides, # = A. nanus, - = A. minusculus.*

	Length						Width					
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ
M_1												
HB +	21	14.3	15.70	16.8	16.08	0.589	22	9.7	10.49	11.5	16.98	0.419
OLA4A *	32	15.7	16.66	18.2	14.75	0.639	30	10.4	11.19	12.4	17.54	0.457
MLB1D &	8	15.7	16.16	16.9	7.36	0.393	10	10.2	10.90	11.4	11.11	0.377
OLA4A @	47	13.4	14.38	15.6	15.17	0.545	49	8.6	9.59	10.6	20.83	0.440
MLB1D #	28	13.5	14.57	15.4	13.15	0.520	31	8.9	9.83	11.0	21.11	0.557
OLA4A -	6	12.5	12.85	13.2	5.45	0.295	7	8.2	8.54	8.9	8.19	0.237
MLB1D -	2	12.7	12.95	13.2	3.86	0.354	2	8.3	8.75	9.2	10.29	0.636
M_2												
HB +	38	12.7	13.85	14.9	15.94	0.489	38	10.2	11.47	12.7	21.83	0.561
OLA4A *	35	14.3	14.96	16.0	11.22	0.455	35	11.1	12.28	13.2	17.28	0.523
MLB1D &	9	14.4	14.87	15.6	8.00	0.390	9	11.5	12.14	12.7	9.92	0.433
OLA4A @	70	11.6	12.88	13.8	17.32	0.502	68	9.9	10.70	12.1	20.00	0.489
MLB1D #	42	12.6	13.26	13.9	9.81	0.387	43	10.2	11.02	12.2	17.86	0.478
OLA4A -	3	11.5	11.73	11.9	3.42	0.208	3	9.0	9.33	9.6	6.45	0.305
MLB1D -	2	11.8	11.90	12.0	1.68	0.141	2	9.9	10.20	10.5	5.88	0.424
M_3												
HB +	15	11.5	12.83	14.0	19.61	0.722	14	9.8	10.65	11.3	14.22	0.454
OLA4A *	24	12.5	13.66	15.0	18.18	0.737	26	10.7	11.44	12.2	13.10	0.435
MLB1D &	10	12.8	13.21	14.1	9.67	0.387	10	10.6	11.08	11.8	10.71	0.329
OLA4A @	75	10.3	11.32	12.5	19.30	0.509	79	8.8	9.76	10.8	20.41	0.429
MLB1D #	44	10.5	11.42	12.4	16.59	0.455	44	8.8	9.89	10.8	20.41	0.475
OLA4A -	6	9.7	10.28	10.6	8.87	0.319	6	8.7	9.13	9.6	9.84	0.301
MLB1D -	2	10.2	10.25	10.3	0.98	0.071	2	8.9	9.00	9.1	2.22	0.141
M^1												
HB +	27	16.5	18.03	19.0	14.08	0.616	34	10.8	11.71	12.7	16.17	0.485
OLA4A *	16	18.5	19.72	21.1	13.13	0.836	18	11.8	12.82	13.8	15.63	0.488
MLB1D &	6	18.6	19.25	20.0	7.25	0.539	16	12.1	13.08	14.0	14.56	0.553
OLA4A @	40	15.6	17.27	18.4	16.47	0.725	47	10.6	11.32	12.3	14.85	0.460
MLB1D #	18	16.1	17.26	18.3	12.79	0.663	30	10.6	11.68	12.4	15.65	0.430
OLA4A -	1	15.4	15.40	15.4	—	—	1	10.1	10.10	10.1	—	—
MLB1D -	1	15.1	15.10	15.1	—	—	1	10.6	10.60	10.6	—	—
M^2												
HB +	29	12.8	13.47	14.5	12.45	0.471	29	11.5	12.22	12.9	11.48	0.420
OLA4A *	38	13.8	14.58	15.5	11.60	0.461	38	12.2	13.33	14.6	17.91	0.567
MLB1D&	14	13.6	14.34	15.7	14.33	0.613	15	12.1	13.27	14.3	16.67	0.643
OLA4A@	77	11.2	12.25	13.4	17.89	0.555	77	10.1	11.50	12.8	23.58	0.539
MLB1D #	48	11.5	12.60	13.6	16.73	0.528	49	10.8	11.82	13.2	20.00	0.560
M^3												
HB +	12	9.6	10.44	11.3	16.27	0.494	13	9.9	10.87	12.2	20.81	0.571
OLA4A *	43	10.1	10.81	11.7	14.68	0.473	43	10.5	11.54	12.5	17.39	0.509
MLB1D &	20	9.8	10.41	11.2	13.33	0.410	20	11.1	11.47	12.1	8.62	0.272
OLA4A @	87	8.0	9.14	10.1	23.20	0.479	89	9.1	9.94	10.9	18.00	0.361
MLB1D #	35	8.4	9.04	10.2	19.35	0.382	34	9.2	9.96	10.8	16.00	0.457
OLA4A -	2	7.9	8.10	8.3	4.94	0.283	2	8.5	8.60	8.7	2.33	0.141
MLB1D -	2	8.1	8.10	8.1	—	—	2	9.2	9.40	9.6	4.26	0.283

Table 2. Comparison of discriminating characters.

	HB *atavus*	OLA4 *atavoides*	MLB1D *hugueneyae*	OLA4 *nanoides*	MLB1D *nanus*
M_1 acd less lingual cingulum	8	1	1	4	6
M_1 anterolophulid more complete	0	7	3	7	3
M_1 ectolophid more longitudinal	6	5	1	6	2
M_1 ectomesolophid better	4	7	1	6	2
M_1 hcd hindarm less	3	0	6	5	6
M_1 mesoconid less	7	5	3	2	3
M_1 mesolophid less	8	1	3	4	4
M_1 mesosinusid more closed	4	4	8	4	0
M_1 metalophulid better	5	6	5	4	0
M_1 pcd hindarm lower/free	0	7	2	6	5
M_1 sinusid more closed	5	6	5	4	0
M_2 anterosinusid smaller	4	2	2	6	6
M_2 ectolophid higher	1	5	4	5	5
M_2 ectomesolophid better	3	6	2	6	3
M_2 hcd hind arm less	4	0	3	7	6
M_2 hypolophulid more oblique	5	6	1	6	2
M_2 mesoconid less	1	6	8	1	4
M_2 mesolophid less	3	2	5	3	7
M_2 mesosinusid more closed	6	7	1	5	1
M_2 metalophulid to acd	4	3	4	4	5
M_2 pcd hind arm lower/free	1	8	1	6	4
M_2 sinusid more closed	1	5	4	5	5
M_3 anterosinusid smaller	3	3	4	3	7
M_3 ectomesolophid better	1	8	4	3	4
M_3 entoconid smaller	7	1	6	1	5
M_3 hypolophulid more oblique	5	5	3	6	1
M_3 lab. anterolophid longer	0	4	5	4	7
M_3 mesolophid less	0	5	5	5	5
M_3 mesosinusid more closed	0	5	5	5	5
M_3 pcd hind arm lower/free	0	7	3	7	3
M_3 posterosinusid more closed	0	5	5	5	5
M_3 shape more trapezoidal	4	5	6	0	5
M_3 sinusid more closed	3	4	6	3	4
M^1 anterior protolophule less	1	6	1	6	6
M^1 anterocone more split	6	2	4	2	6
M^1 anterolophule more complete	8	3	1	4	4
M^1 mesoloph less	3	3	4	6	4
M^1 mesosinus more closed	5	5	5	3	2
M^1 metalophule more posterior	4	0	5	4	7
M^1 pc-hc connection better	2	2	8	2	6
M^1 prelobe more set-off	2	7	5	5	1
M^1 sinus more closed	3	8	6	3	0
M^1 sinus more proverse	5	7	2	3	3
M^2 entoloph-pc connection higher	0	2	8	4	6
M^2 labial border more convex	1	6	7	5	1
M^2 lingual anteroloph better	4	7	5	2	2
M^2 mesosinus more closed	4	3	8	2	3
M^2 pc-hc connection better	5	5	5	1	4

M^2 posterior protolophule more	7	6	2	2	3
M^2 sinus more closed	4	7	6	2	1
M^2 sinus more proverse	5	5	5	5	0
M^2 sinus more subdivided	5	6	3	2	4
M^3 centroloph less	3	3	3	3	8
M^3 lingual anteroloph better	7	4	3	5	1
M^3 mesoloph less	7	0	3	3	7
M^3 mesosinus more closed	0	5	5	5	5
M^3 metacone less	4	5	2	5	4
M^3 old entoloph less	8	1	2	3	6
total	209	259	233	235	224

Table 3. Comparison of selected characters.

	HB *atavus*	OLA4 *atavoides*	MLB1D *hugueneyae*	OLA4 *nanoides*	MLB1D *nanus*
M_1 anterolophulid more complete	0	7	3	7	3
M_1 metalophulid better	5	6	5	4	0
M_1 pcd hind arm lower/free	0	7	2	6	5
M_2 anterosinusid smaller	4	2	2	6	6
M_2 ectolophid higher	1	5	4	5	5
M_2 hypolophulid more oblique	5	6	1	6	2
M_2 pcd hind arm lower/free	1	8	1	6	4
M_3 anterosinusid smaller	3	3	4	3	7
M_3 entoconid smaller	7	1	6	1	5
M_3 hypolophulid more oblique	5	5	3	6	1
M_3 mesosinusid more closed	0	5	5	5	5
M_3 pcd hind arm lower/free	0	7	3	7	3
M_3 posterosinusid more closed	0	5	5	5	5
M^1 anterior protolophule less	1	6	1	6	6
M^1 anterocone more split	6	2	4	2	6
M^1 anterolophule more complete	8	3	1	4	4
M^1 pc-hc connection better	2	2	8	2	6
M^1 sinus more proverse	5	7	2	3	3
M^2 entoloph-pc connection higher	0	2	8	4	6
M^2 labial border more convex	1	6	7	5	1
M^2 pc-hc connection better	5	5	5	1	4
M^2 sinus more proverse	5	5	5	5	0
M^3 centroloph less	3	3	3	3	8
M^3 metacone less	4	5	2	5	4
M^3 old entoloph less	8	1	2	3	6
total	79	114	92	110	105

Table 4. Character states of M_1.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 anteroconid	21		32		9		48		30	
2 small	10	47.6	0	0.0	1	11.1	1	2.1	2	6.7
3 broad	11	52.4	31	96.9	8	88.9	36	75.0	15	50.0
4 labial cingulum	0	0.0	1	3.1	0	0.0	11	22.9	13	43.3
2 prelobe	22		33		9		50		31	
2 short	1	4.5	5	15.2	1	11.1	7	14.0	6	19.4
3 long	21	95.5	28	84.8	8	88.9	43	86.0	25	80.6
3 anterolophulid	22		32		9		49		31	
2 absent	3	13.6	0	0.0	0	0.0	1	2.0	1	3.2
3 interrupted	5	22.7	1	3.1	0	0.0	1	2.0	1	3.2
4 low	8	36.4	4	12.5	4	44.4	11	22.4	14	45.2
5 complete	6	27.3	27	84.4	5	55.6	36	73.5	15	48.4
4 anterosinusid	21		33		9		49		29	
2 narrow	3	14.3	7	21.2	2	22.2	11	22.4	12	41.4
3 wide	18	85.7	26	78.8	7	77.8	38	77.6	17	58.6
5 metalophulid	22		33		10		51		33	
2 absent	3	13.6	2	6.1	1	10.0	5	9.8	11	33.3
3 anterior interrupted	5	22.7	1	3.0	1	10.0	5	9.8	5	15.2
4 anterior complete	14	63.6	30	90.9	8	80.0	38	74.5	16	48.5
5 to anteroconid	0	0.0	0	0.0	0	0.0	3	5.9	1	3.0
6 pcd hind arm	23		33		12		52		35	
3 short free	0	0.0	0	0.0	1	8.3	3	5.8	1	2.9
4 trans to mcd low	4	17.4	9	27.3	4	33.3	23	44.2	11	31.4
5 trans to mcd high	18	78.3	9	27.3	6	50.0	7	13.5	10	28.6
6 long free	0	0.0	9	27.3	0	0.0	12	23.1	2	5.7
7 bent to mcd low	1	4.3	3	9.1	1	8.3	6	11.5	8	22.9
8 bent to mcd high	0	0.0	3	9.1	0	0.0	1	1.9	3	8.6
7 sinusid	23		31		11		52		34	
2 open	2	8.7	3	9.7	4	36.4	3	5.8	16	47.1
3 half closed	6	26.1	3	9.7	1	9.1	8	15.4	8	23.5
4 closed	8	34.8	24	77.4	6	54.5	31	59.6	8	23.5
5 ectostylid	7	30.4	1	3.2	0	0.0	10	19.2	2	5.9
8 sinusid	23		33		11		50		34	
2 forward	0	0.0	0	0.0	0	0.0	0	0.0	1	2.9
3 narrow transverse	2	8.7	0	0.0	0	0.0	0	0.0	2	5.9
4 broad transverse	9	39.1	18	54.5	6	54.5	30	60.0	17	50.0
5 narrow backwards	0	0.0	0	0.0	1	9.1	0	0.0	1	2.9
6 broad backwards	12	52.2	15	45.5	4	36.4	20	40.0	13	38.2

Table 4. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
9 mesosinusid	22		33		12		49		34	
2 open	0	0.0	0	0.0	0	0.0	4	8.2	13	38.2
3 closed	3	13.6	1	3.0	1	8.3	0	0.0	2	5.9
4 mcd ridge open	12	54.5	25	75.8	4	33.3	37	75.5	10	29.4
5 mcd ridge closed	6	27.3	5	15.2	7	58.3	6	12.2	9	26.5
6 mesostylid	1	4.5	2	6.1	0	0.0	2	4.1	0	0.0
10 ectolophid	24		34		12		52		34	
2 longitudinal	20	83.3	28	82.4	5	41.7	39	75.0	15	44.1
3 oblique	4	16.7	5	14.7	7	58.3	12	23.1	17	50.0
5 interrupted	0	0.0	1	2.9	0	0.0	1	1.9	2	5.9
11 mesoconid	22		32		11		51		34	
2 absent	13	59.1	17	53.1	4	36.4	8	15.7	6	17.6
3 weak	7	31.8	11	34.4	4	36.4	25	49.0	15	44.1
4 strong	2	9.1	4	12.5	3	27.3	18	35.3	13	38.2
12 mesolophid	23		33		12		51		36	
2 absent	11	47.8	0	0.0	2	16.7	2	3.9	1	2.8
3 short	4	17.4	6	18.2	3	25.0	20	39.2	16	44.4
4 medium	8	34.8	22	66.7	5	41.7	23	45.1	15	41.7
5 long	0	0.0	4	12.1	2	16.7	6	11.8	4	11.1
6 border	0	0.0	1	3.0	0	0.0	0	0.0	0	0.0
13 ectomesolophid	22		33		11		51		36	
2 absent	12	54.5	11	33.3	9	81.8	21	41.2	25	69.4
3 weak	6	27.3	11	33.3	1	9.1	17	33.3	8	22.2
4 strong	4	18.2	11	33.3	1	9.1	13	25.5	3	8.3
14 hypolophulid	21		33		12		51		34	
2 anterior oblique	0	0.0	1	3.0	2	16.7	4	7.8	8	23.5
3 anterior transverse	20	95.2	32	97.0	10	83.3	47	92.2	25	73.5
4 transverse	1	4.8	0	0.0	0	0.0	0	0.0	1	2.9
15 hypoconid branch	22		33		11		49		35	
2 absent	5	22.7	1	3.0	5	45.5	12	24.5	21	60.0
3 short	7	31.8	3	9.1	2	18.2	8	16.3	3	8.6
4 long	9	40.9	24	72.7	4	36.4	24	49.0	3	8.6
5 long connected	1	4.5	5	15.2	0	0.0	5	10.2	8	22.9
16 posterosinusid	21		33		11		48		34	
2 open	5	23.8	2	6.1	0	0.0	3	6.3	5	14.7
3 closed	16	76.2	31	93.9	11	100.0	45	93.8	29	85.3
17 lab. posterolophid	20		29		11		45		27	
2 absent	5	25.0	5	17.2	2	18.2	8	17.8	6	22.2
3 small	8	40.0	15	51.7	6	54.5	19	42.2	9	33.3
4 strong	7	35.0	9	31.0	3	27.3	18	40.0	12	44.4

Table 5. Character states of M_2.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 anteroconid	30		35		8		54		40	
2 absent	15	50.0	18	51.4	2	25.0	29	53.7	9	22.5
3 small	13	43.3	14	40.0	5	62.5	25	46.3	22	55.0
4 large	2	6.7	3	8.6	1	12.5	0	0.0	9	22.5
2 ling. anterolophid	35		36		9		69		43	
2 absent	2	5.7	0	0.0	0	0.0	0	0.0	0	0.0
3 short	1	2.9	2	5.6	0	0.0	5	7.2	1	2.3
4 long	32	91.4	34	94.4	9	100.0	64	92.8	42	97.7
3 lab. anterolophid	34		35		9		67		44	
2 short	5	14.7	1	2.9	0	0.0	10	14.9	0	0.0
3 to pcd	29	85.3	31	88.6	8	88.9	55	82.1	41	93.2
4 around pcd	0	0.0	3	8.6	1	11.1	2	3.0	3	6.8
4 anterolophulid	23		34		8		54		42	
5 complete	23	100.0	34	100.0	8	100.0	54	100.0	42	100.0
5 anterosinusid	35		36		9		69		40	
2 absent	1	2.9	0	0.0	0	0.0	0	0.0	1	2.5
3 small	2	5.7	0	0.0	0	0.0	9	13.0	8	20.0
4 large	32	91.4	36	100.0	9	100.0	60	87.0	31	77.5
6 metalophulid	35		37		8		72		41	
3 anterior interrupted	0	0.0	0	0.0	0	0.0	0	0.0	1	2.4
4 to anteroconid	2	5.7	2	5.4	0	0.0	3	4.2	10	24.4
5 to anterolophulid	31	88.6	35	94.6	7	87.5	69	95.8	30	73.2
6 to protoconid	2	5.7	0	0.0	1	12.5	0	0.0	0	0.0
7 pcd hind arm	35		37		9		73		43	
2 absent	0	0.0	0	0.0	1	11.1	4	5.5	0	0.0
3 short free	5	14.3	2	5.4	1	11.1	27	37.0	7	16.3
4 trans to mcd low	15	42.9	7	18.9	5	55.6	15	20.5	13	30.2
5 trans to mcd high	3	8.6	0	0.0	1	11.1	0	0.0	0	0.0
6 long free	4	11.4	23	62.2	1	11.1	22	30.1	14	32.6
7 bent to mcd low	8	22.9	4	10.8	0	0.0	5	6.8	8	18.6
8 bent to mcd high	0	0.0	1	2.7	0	0.0	0	0.0	1	2.3
8 sinusid	34		34		8		68		40	
2 open	17	50.0	7	20.6	3	37.5	24	35.3	13	32.5
3 half closed	10	29.4	6	17.6	0	0.0	15	22.1	7	17.5
4 closed	6	17.6	20	58.8	5	62.5	27	39.7	20	50.0
5 ectostylid	1	2.9	1	2.9	0	0.0	2	2.9	0	0.0
9 sinusid	34		37		9		73		43	
3 narrow transverse	5	14.7	12	32.4	5	55.6	29	39.7	21	48.8
4 broad transverse	17	50.0	5	13.5	1	11.1	20	27.4	8	18.6
5 narrow backwards	7	20.6	11	29.7	3	33.3	13	17.8	13	30.2
6 broad backwards	5	14.7	9	24.3	0	0.0	11	15.1	1	2.3

Table 5. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
10 mesosinusid	36		36		9		68		43	
2 open	13	36.1	15	41.7	7	77.8	40	58.8	41	95.3
3 closed	1	2.8	1	2.8	0	0.0	0	0.0	0	0.0
4 mcd ridge open	20	55.6	12	33.3	1	11.1	28	41.2	2	4.7
5 mcd ridge closed	2	5.6	8	22.2	1	11.1	0	0.0	0	0.0
11 ectolophid	24		22		6		40		33	
2 high	6	25.0	10	45.5	2	33.3	19	47.5	15	45.5
3 low	18	75.0	12	54.5	3	50.0	20	50.0	15	45.5
4 interrupted	0	0.0	0	0.0	1	16.7	1	2.5	3	9.1
12 mesoconid	35		36		8		67		40	
2 absent	19	54.3	30	83.3	8	100.0	39	58.2	35	87.5
3 weak	12	34.3	5	13.9	0	0.0	26	38.8	3	7.5
4 strong	4	11.4	1	2.8	0	0.0	2	3.0	2	5.0
13 mesolophid	36		37		9		74		43	
2 absent	2	5.6	0	0.0	3	33.3	11	14.9	4	9.3
3 short	12	33.3	6	16.2	4	44.4	27	36.5	33	76.7
4 medium	20	55.6	26	70.3	2	22.2	27	36.5	6	14.0
5 long	2	5.6	5	13.5	0	0.0	9	12.2	0	0.0
14 ectomesolophid	36		37		9		74		42	
2 absent	31	86.1	16	43.2	9	100.0	42	56.8	33	78.6
3 weak	4	11.1	15	40.5	0	0.0	25	33.8	8	19.0
4 strong	1	2.8	6	16.2	0	0.0	7	9.5	1	2.4
15 hypolophulid	36		36		9		70		42	
2 anterior oblique	29	80.6	27	75.0	2	22.2	44	62.9	19	45.2
3 anterior transverse	7	19.4	9	25.0	6	66.7	25	35.7	23	54.8
4 transverse	0	0.0	0	0.0	1	11.1	1	1.4	0	0.0
16 hypoconid branch	35		35		9		68		43	
2 absent	28	80.0	17	48.6	6	66.7	64	94.1	36	83.7
3 short	4	11.4	7	20.0	3	33.3	1	1.5	4	9.3
4 long	3	8.6	11	31.4	0	0.0	3	4.4	3	7.0
17 posterosinusid	33		35		8		71		41	
2 open	13	39.4	1	2.9	0	0.0	3	4.2	3	7.3
3 closed	20	60.6	34	97.1	8	100.0	68	95.8	38	92.7
18 lab. posterolophid	34		35		8		65		42	
2 absent	23	67.6	22	62.9	6	75.0	37	56.9	22	52.4
3 small	9	26.5	9	25.7	2	25.0	23	35.4	19	45.2
4 strong	2	5.9	4	11.4	0	0.0	5	7.7	1	2.4
19 greatest width	34		34		9		65		42	
2 anterior	0	0.0	4	11.8	0	0.0	7	10.8	2	4.8
3 equal	8	23.5	6	17.6	8	88.9	11	16.9	28	66.7
4 posterior	26	76.5	24	70.6	1	11.1	47	72.3	12	28.6

Table 6. Character states of M_3.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 anteroconid	10		27		10		60		38	
2 absent	5	50.0	10	37.0	3	30.0	14	23.3	18	47.4
3 small	5	50.0	17	63.0	5	50.0	46	76.7	18	47.4
4 large	0	0.0	0	0.0	2	20.0	0	0.0	2	5.3
2 ling. anterolophid	15		27		10		77		41	
2 absent	0	0.0	0	0.0	0	0.0	1	1.3	0	0.0
3 short	0	0.0	0	0.0	2	20.0	2	2.6	7	17.1
4 long	15	100.0	27	100.0	8	80.0	74	96.1	34	82.9
3 lab. anterolophid	14		27		10		79		43	
2 short	1	7.1	0	0.0	1	10.0	10	12.7	2	4.7
3 to pcd	13	92.9	23	85.2	7	70.0	63	79.7	26	60.5
4 around pcd	0	0.0	4	14.8	2	20.0	6	7.6	15	34.9
4 anterolophulid	12		27		10		70		38	
2 absent	0	0.0	0	0.0	0	0.0	0	0.0	1	2.6
3 interrupted	0	0.0	1	3.7	0	0.0	0	0.0	4	10.5
4 short	1	8.3	0	0.0	0	0.0	0	0.0	6	15.8
5 long	11	91.7	26	96.3	10	100.0	70	100.0	26	68.4
6 double	0	0.0	0	0.0	0	0.0	0	0.0	1	2.6
5 anterosinusid	14		27		10		78		40	
2 absent	0	0.0	0	0.0	0	0.0	1	1.3	2	5.0
3 narrow	0	0.0	0	0.0	2	20.0	2	2.6	10	25.0
4 wide	14	100.0	27	100.0	8	80.0	75	96.2	28	70.0
6 metalophulid	13		27		10		74		37	
2 absent	0	0.0	0	0.0	1	10.0	0	0.0	2	5.4
3 anterior interrupted	2	15.4	0	0.0	0	0.0	1	1.4	1	2.7
4 to anteroconid	2	15.4	1	3.7	1	10.0	3	4.1	9	24.3
5 to anterolophulid	9	69.2	26	96.3	7	70.0	67	90.5	22	59.5
6 to protoconid	0	0.0	0	0.0	1	10.0	3	4.1	2	5.4
7 double	0	0.0	0	0.0	0	0.0	0	0.0	1	2.7
7 pcd hind arm	15		27		10		80		43	
3 short free	0	0.0	3	11.1	4	40.0	6	7.5	4	9.3
4 trans to mcd low	2	13.3	0	0.0	2	20.0	0	0.0	0	0.0
5 trans to mcd high	1	6.7	0	0.0	0	0.0	0	0.0	1	2.3
6 long free	7	46.7	17	63.0	1	10.0	61	76.3	8	18.6
7 bent to mcd low	5	33.3	2	7.4	1	10.0	6	7.5	14	32.6
8 bent to mcd high	0	0.0	0	0.0	0	0.0	1	1.3	1	2.3
9 long to border	0	0.0	5	18.5	2	20.0	6	7.5	15	34.9
8 sinusid	13		26		9		78		43	
2 open	7	53.8	10	38.5	2	22.2	44	56.4	17	39.5
3 half closed	2	15.4	3	11.5	0	0.0	13	16.7	9	20.9
4 closed	4	30.8	13	50.0	7	77.8	21	26.9	15	34.9
5 ectostylid	0	0.0	0	0.0	0	0.0	0	0.0	2	4.7

Table 6. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
9 sinusid	14		26		10		75		42	
3 narrow transverse	2	14.3	1	3.8	4	40.0	5	6.7	13	31.0
4 broad transverse	1	7.1	9	34.6	2	20.0	33	44.0	23	54.8
5 narrow backwards	4	28.6	4	15.4	2	20.0	3	4.0	3	7.1
6 broad backwards	7	50.0	12	46.2	2	20.0	34	45.3	3	7.1
10 mesosinusid	14		27		10		80		42	
2 open	3	21.4	0	0.0	0	0.0	2	2.5	1	2.4
3 closed	11	78.6	27	100.0	10	100.0	78	97.5	41	97.6
11 mesolophid	13		27		10		80		42	
2 absent	5	38.5	26	96.3	10	100.0	75	93.8	38	90.5
3 short	3	23.1	1	3.7	0	0.0	4	5.0	3	7.1
4 medium	4	30.8	0	0.0	0	0.0	1	1.3	0	0.0
5 long	1	7.7	0	0.0	0	0.0	0	0.0	1	2.4
12 ectomesolophid	13		26		10		80		41	
2 absent	12	92.3	14	53.8	10	100.0	63	78.8	36	87.8
3 weak	1	7.7	11	42.3	0	0.0	15	18.8	5	12.2
4 strong	0	0.0	1	3.8	0	0.0	2	2.5	0	0.0
13 entoconid	13		26		9		58		37	
2 absent	3	23.1	0	0.0	3	33.3	0	0.0	9	24.3
3 small	9	69.2	13	50.0	5	55.6	37	63.8	20	54.1
4 large	1	7.7	13	50.0	1	11.1	21	36.2	8	21.6
14 hypolophulid	12		27		10		71		41	
2 anterior oblique	8	66.7	22	81.5	3	30.0	52	73.2	7	17.1
3 anterior transverse	4	33.3	5	18.5	7	70.0	19	26.8	33	80.5
4 transverse	0	0.0	0	0.0	0	0.0	0	0.0	1	2.4
15 hypoconid branch	11		24		9		67		39	
2 absent	10	90.9	24	100.0	8	88.9	67	100.0	39	100.0
3 short	1	9.1	0	0.0	1	11.1	0	0.0	0	0.0
16 posterosinusid	11		23		10		69		40	
2 open	1	9.1	0	0.0	0	0.0	3	4.3	1	2.5
3 half closed	8	72.7	9	39.1	5	50.0	25	36.2	4	10.0
4 closed	2	18.2	14	60.9	5	50.0	41	59.4	35	87.5
17 shape	14		24		10		75		43	
2 short triangle	0	0.0	0	0.0	0	0.0	1	1.3	6	14.0
3 long triangle	7	50.0	9	37.5	2	20.0	71	94.7	13	30.2
4 trapezoid	7	50.0	15	62.5	8	80.0	3	4.0	24	55.8

Table 7. Character states of M^1.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 anterocone	27		15		6		42		20	
2 simple	24	88.9	15	100.0	5	83.3	42	100.0	15	75.0
3 half-split	3	11.1	0	0.0	1	16.7	0	0.0	3	15.0
4 bifid	0	0.0	0	0.0	0	0.0	0	0.0	2	10.0
2 prelobe	31		17		11		44		28	
2 narrow set-off	0	0.0	1	5.9	1	9.1	5	11.4	1	3.6
4 broad set-off	18	58.1	14	82.4	7	63.6	30	68.2	12	42.9
5 broad continuous	13	41.9	2	11.8	3	27.3	9	20.5	15	53.6
3 anterolophule	30		17		10		45		29	
2 absent	2	6.7	1	5.9	0	0.0	3	6.7	2	6.9
3 ac-spur	4	13.3	1	5.9	1	10.0	3	6.7	4	13.8
4 pc-spur	0	0.0	3	17.6	1	10.0	7	15.6	4	13.8
5 ac + pc spurs	12	40.0	11	64.7	7	70.0	30	66.7	14	48.3
6 complete	9	30.0	1	5.9	0	0.0	2	4.4	3	10.3
7 double	3	10.0	0	0.0	1	10.0	0	0.0	2	6.9
4 anterolophule	33		18		13		52		36	
2 irrelevant	7	21.2	2	11.1	1	7.7	6	11.5	6	16.7
3 longitudinal	4	12.1	0	0.0	1	7.7	1	1.9	2	5.6
4 oblique	22	66.7	16	88.9	11	84.6	45	86.5	28	77.8
5 ling. anteroloph	31		18		13		48		34	
2 incomplete	4	12.9	0	0.0	0	0.0	0	0.0	0	0.0
3 complete	23	74.2	18	100.0	8	61.5	42	87.5	25	73.5
4 protostyl	4	12.9	0	0.0	5	38.5	6	12.5	9	26.5
6 protocone platform	32		18		15		49		33	
2 absent	8	25.0	3	16.7	4	26.7	14	28.6	13	39.4
3 small	7	21.9	8	44.4	2	13.3	18	36.7	11	33.3
4 large	5	15.6	2	11.1	4	26.7	9	18.4	8	24.2
5 crest	12	37.5	5	27.8	5	33.3	8	16.3	1	3.0
7 anterosinus	27		17		12		42		28	
2 open	4	14.8	0	0.0	3	25.0	3	7.1	8	28.6
3 closed	23	85.2	17	100.0	9	75.0	39	92.9	19	67.9
4 anterostyl	0	0.0	0	0.0	0	0.0	0	0.0	1	3.6
8 protolophule	33		18		15		52		35	
3 anterior	2	6.1	0	0.0	0	0.0	1	1.9	0	0.0
4 anterior plus	1	3.0	0	0.0	0	0.0	0	0.0	0	0.0
5 transverse	2	6.1	0	0.0	0	0.0	0	0.0	1	2.9
6 double	5	15.2	1	5.6	4	26.7	4	7.7	1	2.9
7 posterior plus	9	27.3	0	0.0	3	20.0	5	9.6	0	0.0
8 posterior interrupted	1	3.0	0	0.0	0	0.0	0	0.0	0	0.0
9 posterior	13	39.4	17	94.4	8	53.3	42	80.8	33	94.3

Table 7. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
9 sinus	31		17		15		52		34	
2 open	13	41.9	3	17.6	4	26.7	26	50.0	27	79.4
3 half closed	10	32.3	5	29.4	6	40.0	9	17.3	7	20.6
4 closed	6	19.4	9	52.9	5	33.3	13	25.0	0	0.0
5 entostyl	2	6.5	0	0.0	0	0.0	4	7.7	0	0.0
10 sinus	33		18		14		50		34	
2 strong forward	12	36.4	8	44.4	2	14.3	14	28.0	4	11.8
3 forward	13	39.4	9	50.0	10	71.4	33	66.0	19	55.9
4 subdivided	3	9.1	0	0.0	1	7.1	0	0.0	0	0.0
5 transverse	5	15.2	1	5.6	1	7.1	3	6.0	11	32.4
11 pc-hc connection	32		18		14		51		36	
2 absent	32	100.0	18	100.0	7	50.0	51	100.0	29	80.6
3 weak	0	0.0	0	0.0	2	14.3	0	0.0	5	13.9
4 interrupted	0	0.0	0	0.0	5	35.7	0	0.0	2	5.6
12 mesosinus	29		17		14		47		31	
2 open	17	58.6	8	47.1	8	57.1	35	74.5	23	74.2
3 closed	10	34.5	9	52.9	5	35.7	10	21.3	8	25.8
4 mesostyl	2	6.9	0	0.0	1	7.1	2	4.3	0	0.0
13 mesoloph	32		18		15		53		35	
2 absent	1	3.1	0	0.0	0	0.0	7	13.2	3	8.6
3 short	10	31.3	10	55.6	6	40.0	22	41.5	10	28.6
4 medium	19	59.4	7	38.9	7	46.7	22	41.5	20	57.1
5 long	2	6.3	1	5.6	1	6.7	2	3.8	1	2.9
6 border	0	0.0	0	0.0	1	6.7	0	0.0	1	2.9
14 entomesoloph	33		18		15		51		35	
2 absent	30	90.9	18	100.0	15	100.0	51	100.0	35	100.0
3 short	3	9.1	0	0.0	0	0.0	0	0.0	0	0.0
15 metalophule	32		13		13		43		29	
2 anterior	28	87.5	13	100.0	7	53.8	32	74.4	15	51.7
3 anterior interrupted	0	0.0	0	0.0	0	0.0	1	2.3	1	3.4
4 anterior plus	4	12.5	0	0.0	0	0.0	0	0.0	0	0.0
5 transverse	0	0.0	0	0.0	5	38.5	10	23.3	11	37.9
7 posterior plus	0	0.0	0	0.0	1	7.7	0	0.0	0	0.0
8 posterior	0	0.0	0	0.0	0	0.0	0	0.0	1	3.4
11 to posteroloph	0	0.0	0	0.0	0	0.0	0	0.0	1	3.4
16 posterosinus	33		17		13		48		27	
2 large open	14	42.4	1	5.9	3	23.1	5	10.4	0	0.0
3 large closed	19	57.6	16	94.1	10	76.9	43	89.6	26	96.3
5 small closed	0	0.0	0	0.0	0	0.0	0	0.0	1	3.7
17 labial border	29		17		13		41		24	
2 concave	2	6.9	0	0.0	0	0.0	0	0.0	0	0.0
3 straight	2	6.9	1	5.9	0	0.0	2	4.9	1	4.2
4 convex	25	86.2	16	94.1	13	100.0	39	95.1	23	95.8

Table 8. Character states of M^2.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 ling. anteroloph	31		35		15		71		51	
2 absent	0	0.0	0	0.0	0	0.0	2	2.8	0	0.0
3 weak	11	35.5	4	11.4	4	26.7	32	45.1	26	51.0
4 strong	20	64.5	22	62.9	6	40.0	35	49.3	22	43.1
5 around pc	0	0.0	9	25.7	5	33.3	2	2.8	3	5.9
2 protolophule	32		34		15		72		54	
3 anterior	12	37.5	13	38.2	8	53.3	47	65.3	36	66.7
4 anterior plus	18	56.3	20	58.8	4	26.7	19	26.4	9	16.7
5 transverse	0	0.0	0	0.0	1	6.7	0	0.0	0	0.0
6 double	2	6.3	0	0.0	2	13.3	5	6.9	6	11.1
7 posterior plus	0	0.0	1	2.9	0	0.0	1	1.4	3	5.6
3 sinus	32		38		15		71		53	
2 open	12	37.5	11	28.9	4	26.7	42	59.2	38	71.7
3 half closed	8	25.0	5	13.2	1	6.7	9	12.7	9	17.0
4 closed	8	25.0	22	57.9	8	53.3	18	25.4	6	11.3
5 entostyl	4	12.5	0	0.0	2	13.3	2	2.8	0	0.0
4 sinus	33		36		15		74		52	
2 strong forward	18	54.5	18	50.0	9	60.0	43	58.1	16	30.8
3 forward	7	21.2	13	36.1	5	33.3	31	41.9	33	63.5
4 subdivided	5	15.2	5	13.9	0	0.0	0	0.0	1	1.9
5 transverse	3	9.1	0	0.0	1	6.7	0	0.0	2	3.8
5 mesosinus	30		38		15		74		52	
2 open	18	60.0	25	65.8	5	33.3	64	86.5	35	67.3
3 closed	12	40.0	11	28.9	10	66.7	10	13.5	16	30.8
4 mesostyl	0	0.0	2	5.3	0	0.0	0	0.0	1	1.9
6 mesoloph	32		38		15		75		53	
2 absent	0	0.0	1	2.6	1	6.7	2	2.7	1	1.9
3 short	6	18.8	9	23.7	3	20.0	33	44.0	13	24.5
4 medium	20	62.5	25	65.8	10	66.7	39	52.0	37	69.8
5 long	6	18.8	2	5.3	1	6.7	1	1.3	2	3.8
6 border	0	0.0	1	2.6	0	0.0	0	0.0	0	0.0
7 entoloph-pc conn.	24		17		10		30		34	
2 high	2	8.3	5	29.4	8	80.0	16	53.3	30	88.2
3 low	21	87.5	12	70.6	2	20.0	14	46.7	4	11.8
4 interrupted	1	4.2	0	0.0	0	0.0	0	0.0	0	0.0
8 pc-hc connection	31		37		15		73		53	
2 absent	23	74.2	26	70.3	8	53.3	70	95.9	43	81.1
3 weak	1	3.2	2	5.4	5	33.3	1	1.4	1	1.9
4 interrupted	4	12.9	6	16.2	1	6.7	0	0.0	5	9.4
5 low	2	6.5	1	2.7	1	6.7	2	2.7	4	7.5
6 complete	1	3.2	2	5.4	0	0.0	0	0.0	0	0.0

Table 8. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
9 metalophule	31		36		14		75		50	
3 anterior	28	90.3	36	100.0	13	92.9	74	98.7	44	88.0
5 transverse	3	9.7	0	0.0	1	7.1	1	1.3	3	6.0
7 posterior plus	0	0.0	0	0.0	0	0.0	0	0.0	1	2.0
10 absent	0	0.0	0	0.0	0	0.0	0	0.0	1	2.0
12 curved backward	0	0.0	0	0.0	0	0.0	0	0.0	1	2.0
10 posterosinus	27		37		15		76		46	
2 large open	6	22.2	13	35.1	1	6.7	15	19.7	2	4.3
3 large closed	21	77.8	24	64.9	14	93.3	61	80.3	44	95.7
11 shape	29		37		15		74		51	
2 subrectangular	16	55.2	14	37.8	3	20.0	18	24.3	4	7.8
3 trapezoid	13	44.8	23	62.2	12	80.0	56	75.7	47	92.2
12 labial border	30		38		15		74		46	
2 straight or convex	1	3.3	19	50.0	10	66.7	26	35.1	8	17.4
3 concave	29	96.7	19	50.0	5	33.3	48	64.9	38	82.6

Table 9. Character states of M^3.

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
1 ling. anteroloph	13		42		18		82		34	
2 absent	0	0.0	4	9.5	3	16.7	10	12.2	2	5.9
3 weak	4	30.8	19	45.2	9	50.0	29	35.4	22	64.7
4 strong	8	61.5	12	28.6	6	33.3	40	48.8	10	29.4
5 around pc	1	7.7	7	16.7	0	0.0	3	3.7	0	0.0
2 protolophule	13		41		18		75		36	
3 to anterocone	3	23.1	7	17.1	2	11.1	21	28.0	9	25.0
4 to anterolophule	10	76.9	34	82.9	15	83.3	54	72.0	26	72.2
6 double	0	0.0	0	0.0	1	5.6	0	0.0	1	2.8
3 sinus	13		43		18		80		34	
2 absent	0	0.0	2	4.7	1	5.6	1	1.3	1	2.9
3 very small	0	0.0	8	18.6	8	44.4	25	31.3	9	26.5
4 small	13	100.0	30	69.8	9	50.0	53	66.3	24	70.6
5 deep	0	0.0	3	7.0	0	0.0	1	1.3	0	0.0
4 neo-entoloph	11		37		18		83		35	
2 absent	0	0.0	0	0.0	0	0.0	1	1.2	0	0.0
3 interrupted	0	0.0	1	2.7	0	0.0	0	0.0	0	0.0
4 low	0	0.0	2	5.4	1	5.6	0	0.0	0	0.0
5 high	11	100.0	34	91.9	17	94.4	82	98.8	35	100.0
5 mesosinus	11		43		18		87		35	
2 open	4	36.4	6	14.0	2	11.1	7	8.0	2	5.7
3 closed	7	63.6	37	86.0	16	88.9	80	92.0	33	94.3
6 mesoloph	13		42		18		85		36	
2 absent	10	76.9	4	9.5	6	33.3	27	31.8	22	61.1
3 short	2	15.4	17	40.5	4	22.2	26	30.6	10	27.8
4 medium	1	7.7	10	23.8	7	38.9	28	32.9	3	8.3
5 long	0	0.0	9	21.4	0	0.0	4	4.7	1	2.8
6 border	0	0.0	2	4.8	1	5.6	0	0.0	0	0.0
7 old entoloph	13		43		18		83		36	
2 absent	9	69.2	8	18.6	3	16.7	18	21.7	19	52.8
3 short spur	2	15.4	2	4.7	1	5.6	8	9.6	6	16.7
4 curved spur	1	7.7	1	2.3	3	16.7	4	4.8	1	2.8
5 long spur	1	7.7	7	16.3	3	16.7	18	21.7	2	5.6
6 complete	0	0.0	25	58.1	8	44.4	35	42.2	8	22.2

Table 9. (continued).

	HB *atavus*		OLA4A *atavoides*		MLB1D *hugueneyae*		OLA4A *nanoides*		MLB1D *nanus*	
	N	%	N	%	N	%	N	%	N	%
8 axioloph	12		43		18		85		36	
2 absent	1	8.3	10	23.3	7	38.9	25	29.4	10	27.8
3 anterior spur	4	33.3	0	0.0	0	0.0	0	0.0	1	2.8
4 post. spur short	0	0.0	4	9.3	1	5.6	14	16.5	11	30.6
5 post. spur long	5	41.7	3	7.0	2	11.1	11	12.9	3	8.3
6 two spurs	0	0.0	0	0.0	0	0.0	0	0.0	1	2.8
7 complete	2	16.7	1	2.3	0	0.0	0	0.0	2	5.6
8 = old entoloph	0	0.0	25	58.1	8	44.4	35	41.2	8	22.2
9 centroloph	12		43		18		86		36	
2 absent	0	0.0	0	0.0	1	5.6	1	1.2	7	19.4
3 weak	0	0.0	0	0.0	2	11.1	1	1.2	3	8.3
4 strong	3	25.0	32	74.4	10	55.6	57	66.3	16	44.4
5 = metalophule	9	75.0	11	25.6	5	27.8	27	31.4	10	27.8
10 centrocone	12		40		18		83		35	
2 absent	10	83.3	31	77.5	11	61.1	65	78.3	18	51.4
3 present	0	0.0	0	0.0	4	22.2	6	7.2	14	40.0
4 isolated	1	8.3	4	10.0	0	0.0	4	4.8	1	2.9
5 on old entoloph	1	8.3	5	12.5	3	16.7	8	9.6	2	5.7
11 metacone	10		42		19		79		33	
2 absent	8	80.0	36	85.7	13	68.4	69	87.3	25	75.8
3 present	2	20.0	6	14.3	6	31.6	10	12.7	8	24.2
12 posterosinus	11		41		18		72		36	
2 open	0	0.0	5	12.2	1	5.6	9	12.5	1	2.8
3 closed	11	100.0	36	87.8	17	94.4	63	87.5	35	97.2

Appendix: Description of character states

M1 inf.

1: anteroconid
- 2 small: anteroconid is called small, when there are no descending cingulum ridges, or when such ridges are set off from the cusp.
- 3 broad: descending cingulum ridges are continuous with the anteroconid.
- 4 labial cingulum: the lingual wall of the anteroconid is round, the labial wall bears a continuous cingulum.

2: prelobe
- 2 short: the distance from protoconid to the anterior border of the tooth is smaller than the antero-posterior length of the protoconid.
- 3 long: the distance is clearly greater than the length of the protoconid.

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

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

5: metalophulid
- 2 absent: no anterior metalophulid; the anterolabial wall of the metaconid is smooth and round.
- 3 anterior interrupted: either from the metaconid, or from the anterolophulid, or from both, a spur indicates the anterior metalophulid.
- 4 anterior complete: the anterior metalophulid is complete.
- 5 to anteroconid: complete, and connnected to the anteroconid.

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

7: sinusid
- 2 open: not a trace of a cingulum ridge.
- 3 half closed: an interrupted cingulum ridge, no ectostylid.
- 4 closed: a generally low cingulum ridge is present.
- 5 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

8: sinusid
- 2 forward: the anterior or the posterior border of the sinus is directed forward.
- 3 narrow transverse: the length is less than 1/4 of the molar length; the posterior limit is transverse.
- 4 broad transverse: the length is about 1/4 of the molar length or more; the posterior limit is transverse.
- 5 narrow backwards: the length is less than 1/4 of the molar length; the posterior limit is curved backwards.
- 6 broad backwards: the length is about 1/4 of the molar length or more; the posterior limit is curved backwards.

9: mesosinusid
- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low cingulum ridge is present.
- 4 mcd ridge open: a ridge descends from the metaconid, and does not reach the entoconid.
- 5 mcd ridge closed: the ridge from the metaconid meets the entoconid.
- 6 mesostylid: a (small) distinct cusp.

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

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

12: mesolophid
- 2 absent: no trace of a mesolophid.
- 3 short: length less than 1/3 of the width of the mesosinusid.
- 4 medium: length between 1/3 and half.
- 5 long: more than half the width of the mesosinusid.
- 6 border: reaching the border of the molar.

13: ectomesolophid
- 2 absent: no trace of a labial sput on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid.

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

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

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

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

M2 inf.

1: anteroconid
- 2 absent: no trace of a cusp.
- 3 small: the anterolophid is swollen at the junction with the anterolophulid.
- 4 large: a distinct cusp, that is higher than the anterolophid.

2: lingual anterolophid
- 2 absent: the anterolingual wall of the tooth is formed by the metaconid.
- 3 short: the lingual anterolophid occupies less than half of the lingual part of the anterior border.
- 4 long: it reaches the metaconid at the anterolingual corner of the tooth.

3: labial anterolophid
- 2 short: it does not reach the protoconid.
- 3 to protoconid: it reaches the protoconid base.
- 4 around protoconid: it separates the protoconid from the labial border, at least partly.

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

5: anterosinusid
- 2 absent: no valley between anterolophid and metaconid.
- 3 small: the valley is shorter than half the distance between anteroconid and anterolingual corner of the tooth, or narrower than the enamel thickness.
- 4 large: the valley separates the metaconid from the anterior border almost completely.

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

7: protoconid hind arm (posterior branch of the protoconid)
- 2 absent: the posterior corner of the protoconid continues smoothly into the ectolophid.
- 3 short free: not longer than the width of the valley between protoconid and metaconid, not connected to the metaconid.
- 4 trans to mcd low: transversely connected to the metaconid at less than half its height.
- 5 trans to mcd high: transversal and at least half as high as the metaconid.

- 6 long free: oblique backwards, surpassing the width of the valley between protoconid and metaconid.
- 7 bent to mcd low: directed obliquely backward, and then curved and connected to the metaconid at less than half its height.
- 8 bent to mcd high: idem, but higher than half the height of the metaconid. In some cases the connection seems to be composed of a protoconid branch and a crest descending from the metaconid.

8: sinusid
- 2 open: not a trace of a cingulum ridge.
- 3 half closed: an interrupted cingulum ridge, no ectostylid.
- 4 closed: a generally low cingulum ridge is present.
- 5 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

9: sinusid
- 2 forward: the anterior or the posterior border of the sinus is directed forward.
- 3 narrow transverse: the length is less than 1/3 of the molar length; the posterior limit is transverse.
- 4 broad transverse: the length is about 1/3 of the molar length or more; the posterior limit is transverse.
- 5 narrow backwards: the length is less than 1/4 of the molar length; the posterior limit is curved backwards.
- 6 broad backwards: the length is about 1/4 of the molar length or more; the posterior limit is curved backwards.

10: mesosinusid
- 2 open: not a trace of a cingulum ridge.
- 3 closed: a generally low cingulum ridge is present.
- 4 mcd ridge open: a ridge descends from the metaconid, and does not reach the entoconid.
- 5 mcd ridge closed: the ridge from the metaconid meets the entoconid.
- 6 mesostylid: a (small) distinct cusp.

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

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

13: mesolophid
- 2 absent: not a trace of a mesolophid.
- 3 short: length less than 1/3 of the width of the mesosinusid
- 4 medium: length between 1/3 and half.
- 5 long: more than half the width of the mesosinusid.
- 6 border: reaching the border of the molar.

14: ectomesolophid
- 2 absent: no trace of a labial spur on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid.

15: hypolophulid
- 2 anterior oblique: oblique and placed in front of the hypoconid.

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

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

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

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

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

M3 inf.

1: anteroconid
- 2 absent: no trace of a cusp.
- 3 small: the anterolophid is swollen at the junction with the anterolophulid.
- 4 large: a distinct cusp, that is higher than the anterolophid.

2: lingual anterolophid
- 2 absent: the anterolingual wall of the tooth is formed by the metaconid.
- 3 short: the lingual anterolophid occupies less than half of the lingual part of the anterior border.
- 4 long: it reaches the metaconid at the anterolingual corner of the tooth.

3: labial anterolophid
- 2 short: it does not reach the protoconid.
- 3 to protoconid: it reaches the protoconid base.
- 4 around protoconid: it separates the protoconid from the labial border, at least partly.

4: anterolophulid
- 2 absent: there is no connection between protoconid and anteroconid.
- 3 interrupted: the crest is interrupted, either between protoconid and metalophulid, or between metalophulid and anteroconid.
- 4 short: the crest is not longer than the width of the metalophulid.
- 5 long: the crest is longer than the width of the metalophulid.
- 6 double: there is a second crest, more lingual, between metalophulid and anterolophulid.

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

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

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

8: sinusid
- 2 open: not a trace of a cingulum ridge.
- 3 half closed: an interrupted cingulum ridge, no ectostylid.
- 4 closed: a generally low cingulum ridge is present.
- 5 ectostylid: a (small) ectostylid is present instead of a cingulum ridge, or on the cingulum ridge.

9: sinusid
- 2 forward: pointing obliquely forward.
- 3 narrow transverse: there is no longitudinal part in the protoconid-hypoconid connection; the posterior limit is transverse.
- 4 broad transverse: the connection between protoconid and hypoconid is — at least partly — a longitudinal crest; the posterior limit is transverse.
- 5 narrow backwards: there is no longitudinal part in the protoconid-hypoconid connection; the posterior limit is curved backwards.
- 6 broad backwards: the connection between protoconid and hypoconid is — at least partly — a longitudinal crest; the posterior limit is curved backwards.

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

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

12: ectomesolophid
- 2 absent: no trace of a labial spur on the ectolophid.
- 3 weak: some crest is visible on the labial wall of the ectolophid.
- 4 strong: the crest continues into the horizontal part of the sinusid.

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

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

15: hypoconid branch
- 2 absent
- 3 short: not longer than two times the enamel thickness.
- 4 long: longer, but not connected to the entoconid.
- 5 long connected: connected to the base of the entoconid.

16: posterosinusid
- 2 open: the posterolophid does not meet the entoconid.
- 3 half closed: the posterolophid is low, before reaching the entoconid.
- 4 closed: the posterolophid meets the entoconid.

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

M1 sup.

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

2: prelobe
- 2 narrow set-off: half as wide (or less) than the tooth width; the lingual border between anterocone and protocone is angular.
- 3 narrow continuous: half as wide (or less) than the tooth width; the lingual border between anterocone and protocone is smooth.
- 4 broad set-off: more than half as wide as the tooth width; the lingual border between anterocone and protocone is angular.
- 5 broad continuous: more than half as wide as the tooth width; the lingual border between anterocone and protocone is smooth.

3: anterolophule
- 2 absent: the protocone fore arm is reduced, or completely fused to the paracone, no ac-spur.
- 3 ac-spur: there is a backward spur on the anterocone.
- 4 pc-spur: there is a forward spur on the protocone, with at least a tendency to be separated from the paracone.
- 5 ac + pc spurs: there are spurs on anterocone and protocone, but no continuous central crest.
- 6 complete: a complete crest between the anterolabial corner of the protocone and the (labial part of the) anterocone.
- 7 double: two posterior crests on the anterocone, either complete or incomplete.

4: anterolophule
- 2 irrelevant: protocone fore arm absent or connected to paracone.
- 3 longitudinal: from the anterolabial corner of the protocone, longitudinally forward.
- 4 oblique: from the anterolabial corner of the protocone, obliquely towards the labial part of the anterocone.

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

6: protocone platform
- 2 absent: no flat surface in front of the protocone.
- 3 present: a flat surface in front of the protocone, lingually of the cingulum, either small or large.
- 4 crest: a crest on this platform, that may partly surround the protocone.

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

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

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

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

11: pc-hc connection
- 2 absent: not a trace of a connection through the sinus.
- 3 weak: a vague crest crosses the sinus from the posterior wall of the protocone to the hypocone.
- 4 interrupted: the crest is clearly visible, but not complete.
- 5 complete: the crest connects protocone and hypocone.

12: mesosinus
- 2 open: cingulum absent or interrupted.

- 3 closed: cingulum complete.
- 4 mesostyl: cingulum complete or incomplete, there is a mesostyl cusp.

13: mesoloph
- 2 absent: no mesoloph.
- 3 short: shorter than 1/3 the distance between entoloph and labial border.
- 4 medium: between 1/3 and half this distance.
- 5 long: longer than half the distance between entoloph and labial border.
- 6 border: reaching the labial border.

14: entomesoloph
- 2 absent: no entomesoloph.
- 3 short: some trace of an entomesoloph present.
- 4 long: the entomesoloph is more than a mere trace.

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

16: posterosinus
- 2 large open
- 3 large closed
- 4 small open
- 5 small closed

large: wider than the thickness of the posteroloph.
small: narrower than the thickness of the posteroloph.
open: the posteroloph does not meet the metacone.
closed: the posteroloph meets the metacone.

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

M2 sup.

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

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

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

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

5: mesosinus
- 2 open: cingulum absent or interrupted.
- 3 closed: cingulum complete.
- 4 mesostyl: cingulum complete or incomplete, there is a mesostyl cusp.

6: mesoloph
- 2 absent: no mesoloph.
- 3 short: shorter than 1/3 the distance between entoloph and labial border.
- 4 medium: between 1/3 and half this distance.
- 5 long: longer than half the distance between entoloph and labial border.
- 6 border: reaching the labial border.

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

8: pc-hc connection
- 2 absent: no trace of a connection through the sinus.
- 3 weak: a vague connection between protocone and entoloph or hypocone, through the sinus.
- 4 interrupted: there is a backward spur on the posterior wall of the protocone.
- 5 low: the connection is complete and lower than the entoloph.
- 6 complete: the connection is complete and almost as high as the entoloph.

9: metalophule
- 2 anterior: either oblique, transverse, or curved towards the anterior tip of the hypocone, or towards the entoloph.
- 3 anterior interrupted: idem, but interrupted.
- 4 anterior plus: anterior plus a trace of a posterior connection.

- 5 transverse: towards the centre of the hypocone.
- 6 double: both an anterior and a posterior connection.
- 7 posterior plus: posterior plus a trace of an anterior connection.
- 8 posterior: towards the posterior tip of the hypocone.
- 9 posterior interrupted: towards the posterior tip of the hypocone, interrupted.
- 10 absent: no connection.
- 11 to posteroloph: towards the posterior branch of the hypocone.
- 12 curved backward: longitudinal towards the posteroloph.

10: posterosinus
- 2 large open
- 3 large closed
- 4 small open
- 5 small closed

large: wider than the thickness of the posteroloph.
small: narrower than the thickness of the posteroloph.
open: the posteroloph does not meet the metacone.
closed: the posteroloph meets the metacone.

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

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

M3 sup.

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

2: protolophule
- 2 absent: no connection between protocone and paracone.
- 3 to anterocone: connected to the anterior border.
- 4 to anterolophule: connected to the crest between anterocone and protocone.
- 5 transverse: paracone connected to the centre of the protocone.
- 6 double: anterior and posterior connection complete.

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

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

- 5 high: continuous connection as high as protocone and hypocone.

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

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

7: old entoloph
- 2 absent: no crest parting from the labial wall of the protocone.
- 3 short spur: spur on the labial wall of the protocone.
- 4 curved spur: spur bent backwards to form a posterior axioloph.
- 5 long spur: extends transversally beyond the position of the axioloph.
- 6 complete: curved crest between the labial wall of the protocone and hypocone or neo-entoloph.

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

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

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

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

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