Upper Oligocene micromammals from Pareja, Loranca Basin, prov. of Guadalajara, Spain

R. Daams, M. Freudenthal, J.I. Lacomba & M.A. Alvarez

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Eight rodent species from the Upper Oligocene of Pareja are described. The Theridomyidae are represented by *Issiodoromys minor* and *Archaeomys (A.) gervaisi* and the Eomyidae by *Eomys* cf. *molassicus*. Four cricetid species are described: *Heterocricetodon landroveri* sp. nov., *Eucricetodon margaritae* sp. nov., *Eucricetodon* cf. *atavus*, and *Eucricetodon* sp. One new glirid species, *Gliravus caracensis*, is recognized. The fauna of Pareja is considered to be somewhat older than that of Carrascosa del Campo, and considerably younger than that of Montalbán.

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Introduction

In the framework of the project 'Geological Evolution of the Tertiary Basin of Loranca: Biostratigraphy, Sedimentology and Basin Analysis', financed by the CICYT, No. PB

85/0022, a systematic prospection and exploration of the continental sediments is being carried out. Of the numerous Upper Oligocene and Miocene fossil-bearing localities present in the basin, the microfauna of Pareja is dealt with in this paper. A biostratigraphical subdivision of the central part of the basin was published by Díaz Molina & López Martínez (1979), Daams et al. (1986), and Alvarez et al. (1987).

The northern part of the basin, where the locality of Pareja is situated, still lacks sedimentological and regional geological studies. The fossil-bearing bed is a beige and green marl intercalated between coarse sandstones, which form part of the Lower Detrital Formation as defined by Díaz & López (1979). The beds have an approximately N-S strike and dip steeply to the west. They form part of the western flank of the N-S directed anticline of Pareja. The core of this anticline consists of massive gypsum beds of probably Late Cretaceous to Early Tertiary age (see Geological Map 1:50 000, no. 537, Auñon). The locality is situated in a road-cut on the western side of the road from Pareja to Alcocer (Fig. 1). C. 2050 kg of sediment were processed, which yielded some 800 dental remains of rodents.

The theridomorph and glirid teeth were measured with a Nikon monocular digital measuring microscope. The cricetid specimens were measured with the Leitz Ortholux measuring equipment described by Freudenthal, 1966. The nomenclature of parts of the Theridomyidae cheek teeth is after Vianey-Liaud (1979), that of the Gliridae after Daams (1981), that of the Cricetidae after Mein & Freudenthal (1971) and Freudenthal & Daams (1988), and that of the Eomyidae after Alvarez (in Alvarez et al., 1987).

The specimens are stored at the Museo Nacional de Ciencias Naturales, Madrid.

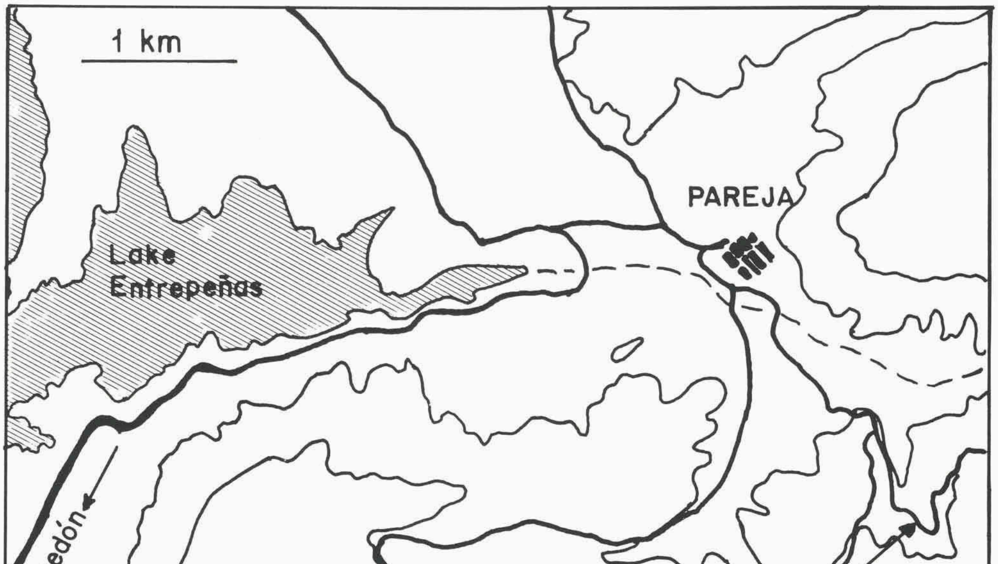


Fig. 1. Detail of the topographic map 1:50 000, no. 537, Auñon, Province of Guadalajara, with indication of the locality of Pareja.

Systematic descriptions

THERIDOMYIDAE ALSTON, 1876
ISSIODOROMYINAE LAVOCAT, 1951
Issiodoromys Croizet, 1845

Issiodoromys minor Bravard, in Gervais, 1848
Pl. 1, figs. 1-4; Pl. 2, figs. 1-4.

Material and measurements

	Length				Width				Height			
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.
D^4	4	22.3	23.8	25.6	4	15.5	16.6	17.8	–	–	–	–
P^4	10	16.6	18.0	19.4	10	16.0	17.8	19.5	4	23.4	23.6	23.8
$M^{1,2}$	33	16.2	18.0	20.2	30	15.0	19.0	23.0	7	26.1	27.9	29.1
M^3	13	14.1	16.0	17.7	11	15.4	17.9	20.6	3	22.6	23.2	24.0
D_4	3	25.8	26.0	26.6	5	12.9	13.3	14.1	–	–	–	–
P_4	16	19.0	21.0	23.3	16	14.8	16.3	18.5	6	17.5	18.2	19.0
$M_{1,2}$	49	16.1	19.8	22.9	49	14.8	17.9	20.8	7	20.9	23.3	24.6
M_3	9	17.2	19.6	21.8	10	15.0	16.0	19.0	2	24.6	24.7	24.9

Description

D^4 – Four synclines are present. The anteroloph is isolated in 2 specimens; it is connected to the protocone by a narrow and low ridge in the other 2 teeth. The longitudinal ridge is low. There is a tendency towards the formation of a labial wall. The mesoloph is long and oblique, and reaches the labial border. The metalophule is oblique, and may be interrupted. The posteroloph does not reach the metacone.

P^4 –The anteroloph is very short and syncline I is open. The connection between the protoloph and the protocone is narrower and lower than the other main ridges. The longitudinal ridge, the connection between mesoloph and pseudohypocone, and the metalophule-posteroloph junction are low. The posteroloph joins the metacone, thus reducing syncline IV to a small island.

$M^{1,2}$ – Five main ridges and 4 synclines are present. With progressive wear syncline IV is the first one to disappear, immediately followed by syncline I. Just before the latter wear stage, the occclusal surface reaches the longitudinal ridge. Syncline II is the deepest valley. The anteroloph-paracone connection is the lowest one, although syncline I is still closed at the anterior side.

M^3 – Syncline IV is not present and syncline III is open at the posterior wall in fresh specimens. The occlusal surface reaches the longitudinal ridge when synclines I and III are still distinct as small islands. With further wear only syncline II persists as a small circular island. In little worn specimens the posteroloph is short; the metalophule may be very short and join the pseudohypocone, thus subdividing syncline III.

D_4 – The metalophid is isolated in 1 specimen, although it has anterior prolongations toward the labial and lingual branches of the anterolophid. In the other complete specimen the metalophid joins the labial branch of the anterolophid by means of a narrow and low ridge. The mesolophid is isolated in 4 specimens, and in 1 case it joins the labial border by means of a weak connection. The synclinids III and IV are open, whereas synclinid II is closed by the lingual wall.

P_4 – The metalophid is small in 10 specimens, and absent in 6. The posterolophid-entoconid connection is lower than the rest of the lingual wall in fresh specimens. In much worn specimens synclinid III is reduced to a small island by the presence of a continuous lingual wall.

$M_{1,2}$ – A shallow anterior furrow is present in 30 out of 50 specimens. In fresh teeth synclinid II is reduced to an island and the metalophid-metaconid connection is as high as the rest of the lingual wall. In the posterior lobe the entoconid-posterolophid connection is lower than the rest of the lingual wall, although this feature disappears with progressive wear. When there is a metalophid, it is small. In an advanced wear stage synclinid II disappears, followed by synclinid IV. In a later wear stage, synclinid III is reduced to a small island by the formation of a continuous labial wall.

M_3 – The vertical anterior furrow is present in 3 out of 10 specimens. The metalophid is very small or absent. In 1 specimen a double metalophid is present; one is a longitudinal ridge between anterolophid and mesolophid, and the other one curves 90° backwards and is situated between anterolophid and protoconid. The latter structure may correspond to a tiny, rudimentary synclinid I (the anterosinusid). In this specimen the height of the entoconid-posterolophid connection is the same as that of the lingual wall, but in the other specimens this connection is lower. In 1 specimen without metalophid, there is a subtransverse connection, delimiting a small island.

Discussion – *Issiodoromys minor* from Pareja is larger than the same species from Belgarric (Vianey-Liaud, 1976), and its morphology and hypsodonty appear to be more evolved. It most resembles *I. minor* from Rigal-Jouet. The absence of cement in the sinus(id)s sets the species from Pareja apart from *I. pauffiensis* Vianey-Liaud, 1976 from Mas de Pauffié.

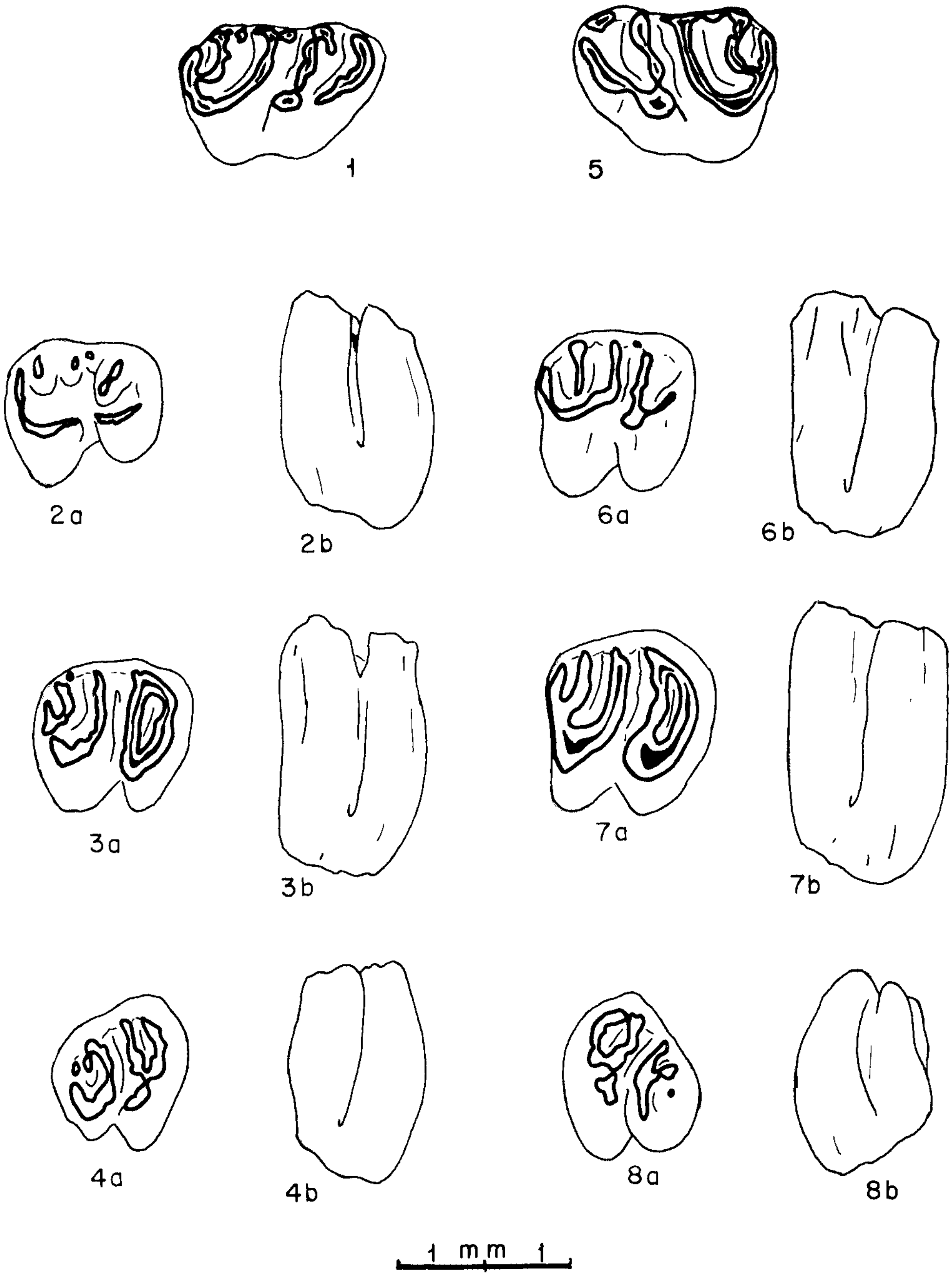
A comparison between *I. minor* from Pareja and the same species from Carrascosa (Lacomba & Morales, 1987), reveals that size and hypsodonty are only slightly larger in Carrascosa. Morphologically some slight differences may be observed, which may point at a slightly older age of the species from Pareja, without reaching the evolutionary stage of *I.* aff. *minor* of the
Heimersheim level (see Vianey-Liaud & Schmidt-Kittler, 1987). These slight differences are the following:
In the D^4 from Carrascosa the anteroloph is separated from the protocone in 17 out of 19 specimens, whereas in Pareja this occurs in 2 out of 4.
In the P^4 from Carrascosa the ridges are longer and more continuous, and the labial wall is better developed.
In the upper cheek teeth of Carrascosa the sinus is narrower and the crown height is slightly larger than in Pareja.
In the lower cheek teeth of Carrascosa the sinusids are narrower than in Pareja.

THERIDOMYINAE ALSTON, 1876
Archaeomys Laizer & Parieu, 1839

Archaeomys (Archaeomys) gervaisi Thaler, 1966
Pl. 3, figs. 1-10.

Material and measurements

Plate 1



Issiodoromys minor Bravard, in Gervais, 1848
from Pareja
Fig. 1. D^4 dext., PAJ 35.
Fig. 2a. P^4 dext., PAJ 89; 2b. lingual view.
Fig. 3a. M^{1,2} dext., PAJ 92; 3b. lingual view.
Fig. 4a. M^3 dext., PAJ 140; 4b. lingual view.

Issiodoromys minor Bravard, in Gervais, 1848
from Carrascosa
Fig. 5. D^4 sin., CAS 384.
Fig. 6a. P^4 dext., CAS 457; 6b. lingual view.
Fig. 7a. M^{1,2} dext., CAS 425; 7b. lingual view.
Fig. 8a. M^3 sin., CAS 453; 8b. lingual view.

	Length				Width				Height			
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.
D^4	2	28.5	29.8	31.1	2	21.5	22.0	22.6	–	–	–	–
P^4	2	24.4	24.4	24.4	2	17.8	19.6	21.5	1	–	28.6	–
$M^{1,2}$	17	16.3	19.7	21.8	17	19.2	22.2	27.7	1	–	31.9	–
M^3	2	24.0	24.9	25.9	2	22.2	23.1	24.0	1	–	17.8	–
D_4	3	33.7	33.7	33.7	5	15.9	17.6	19.2	–	–	–	–
P_4	8	27.7	29.3	31.1	9	17.4	18.5	21.5	3	23.4	24.7	26.3
$M_{1,2}$	20	15.9	22.1	24.8	21	17.4	20.5	22.9	1	–	21.9	–
M_3	6	15.2	18.2	20.3	6	17.0	18.0	19.6	1	–	20.0	–

Description

D^4 – Five synclines are present. In one considerably worn specimen a badly developed longitudinal ridge is present. The anticline, situated in front of the anteroloph, joins this ridge labially. The protoloph joins the middle part of the anteroloph below the occlusal surface. Syncline IV is the first one to disappear with progressive wear.

P^4 – There are 4 synclines, of which synclines I and IV are already isolated in fresh specimens. In fresh specimens the longitudinal ridge is narrower and lower than the main ridges. Syncline IV is the first one to disappear with progressive wear, followed by the isolation of the labial portion of syncline II.

$M^{1,2}$ – Synclines I and IV are already isolated in fresh specimens, and they disappear rapidly with progressive wear. Moderately worn specimens have three main ridges.

M^3 – Syncline I is the first one to disappear with progressive wear, followed by syncline IV. In fresh specimens syncline IV may be incompletely isolated, and it may be open towards the labial side.

D_4 – The ridges are oblique at the labial border and transverse at the lingual one, with the exception of the short anterolophid. At the lingual border the ridges and cusps are isolated from one another. The lingual end of the anterolophid is wider than the rest of this ridge. A low and narrow ridge is present between the interior wall of the anterolophid and the central anterior part of the metalophid. This way a small island is formed in the anterior part of synclinid I. Synclinid II and the sinusid-synclinid III complex form continuous valleys from the lingual to the labial tooth border. The entoconid is conneted to the central part of the posterolophid by means of a robust ridge.

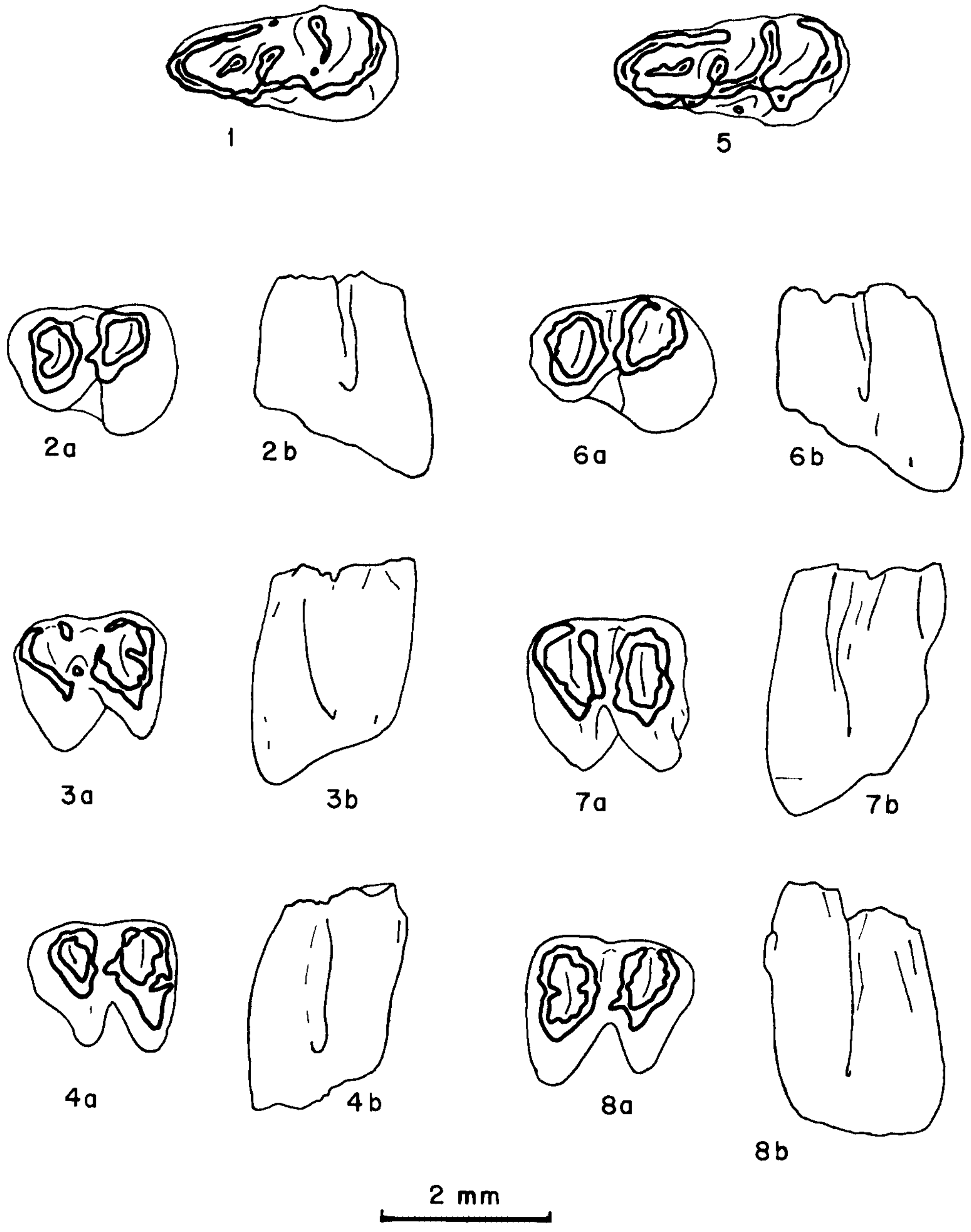
P_4 – In fresh specimens the anterolophid is separated from the protoconid, but with little wear these two units join at the occlusal surface. Synclinid II is lingually deep and open, so that metaconid and metalophid are separated. The sinusid and synclinid III form a continuous valley. Synclinid IV is lingually open in fresh or little worn specimens, but it is the first valley to be closed with progressive wear.

$M_{1,2}$ – In fresh specimens synclinids II, III and IV are distinct. With progressive wear synclinid IV disappears, and afterwards the anterior end of synclinid II becomes isolated. In a following wear stage, a labial wall is present which closes synclinids II and III.

M_3 – The dental pattern is similar to that of $M_{1,2}$, although synclinid IV is shallower in this element.

Discussion – The main diagnostic feature to distinguish *Archaeomys (A.) gervaisi* from *A. (A.) gracilis* (Schlosser, 1884) is the lingually open synclinid II of P_4 in the former

Plate 2



Issiodoromys minor Bravard, in Gervais, 1848 from Pareja
Fig. 1. D_4 sin., PAJ 4.
Fig. 2a. P_4 sin., PAJ 9; 2b. labial view.
Fig. 3a. $M_{1,2}$ dext., PAJ 63; 3b. labial view.
Fig. 4a. M_3 dext., PAJ 74; 4b. lingual view.

Issiodoromys minor Bravard, in Gervais, 1848 from Carrascosa
Fig. 5. D_4 sin., CAS 290.
Fig. 6a. P_4 sin., CAS 303; 6b. lingual view.
Fig. 7a. $M_{1,2}$ dext., CAS 313; 7b. lingual view.
Fig. 8a. M_3 sin., CAS 368; 8b. lingual view.

species. In the latter one this synclinid is closed. Our assemblage from Pareja has the synclinid II of P_4 lingually open, and is therefore assigned to *A. (A.) gervaisi.*

Vianey-Liaud (1979) distinguishes two evolutionary lineages in the subgenus *Archaeomys*, one is that of *A. gracilis* and the other lineage is that of *A. gervaisi-laurillardi.* The latter lineage would be characterized by a trend toward increase of hypsodonty. According to the same author *A. gervaisi* has less hypsodont teeth than the earliest representatives of *A. gracilis.*

The size of *A. gervaisi* from Pareja is similar to that of *A. gracilis* from Carrascosa (Lacomba & Morales, 1987), Belgarric and Rigal-Jouet (Vianey-Liaud, 1979). Probably the size of the Spanish species is slightly smaller than that of the French material, although the comparison is hazardous due to the lack of uniform criteria for taking measurements of hypsodont teeth.

Although *A. gracilis* is poorly represented in Carrascosa, some differences with respect to *A. gervaisi* from Pareja may be observed:

In the D_4 from Carrascosa there is an axial connection subdividing synclinid II into two. This feature is absent in Pareja.

In the P_4 from Carrascosa synclinid II is lingually closed, whilst it is open in Pareja.

The $M_{1,2}$ from Carrascosa are slightly more hypsodont than those from Pareja. In Carrascosa the ridges have a steeper antero- posterior inclination.

The P^4 is the only element of the upper cheek teeth present in the Carrascosa collection. In Lacomba & Morales (1987) fig. 12 is supposed to represent an $M^{1,2}$, but in reality it is a very worn $M_{1,2}$. The hypsodonty and inclination of the ridges is similar in both species, but the synclines I and IV appear to be more reduced in Carrascosa than in Pareja. This difference does not correspond with the differences observed by Vianey-Liaud (1979) in Rigal-Jouet and Belgarric.

GLIRIDAE THOMAS, 1897
GLIRAVINAE DE BRUIJN, 1967
Gliravus de Bruijn, 1967

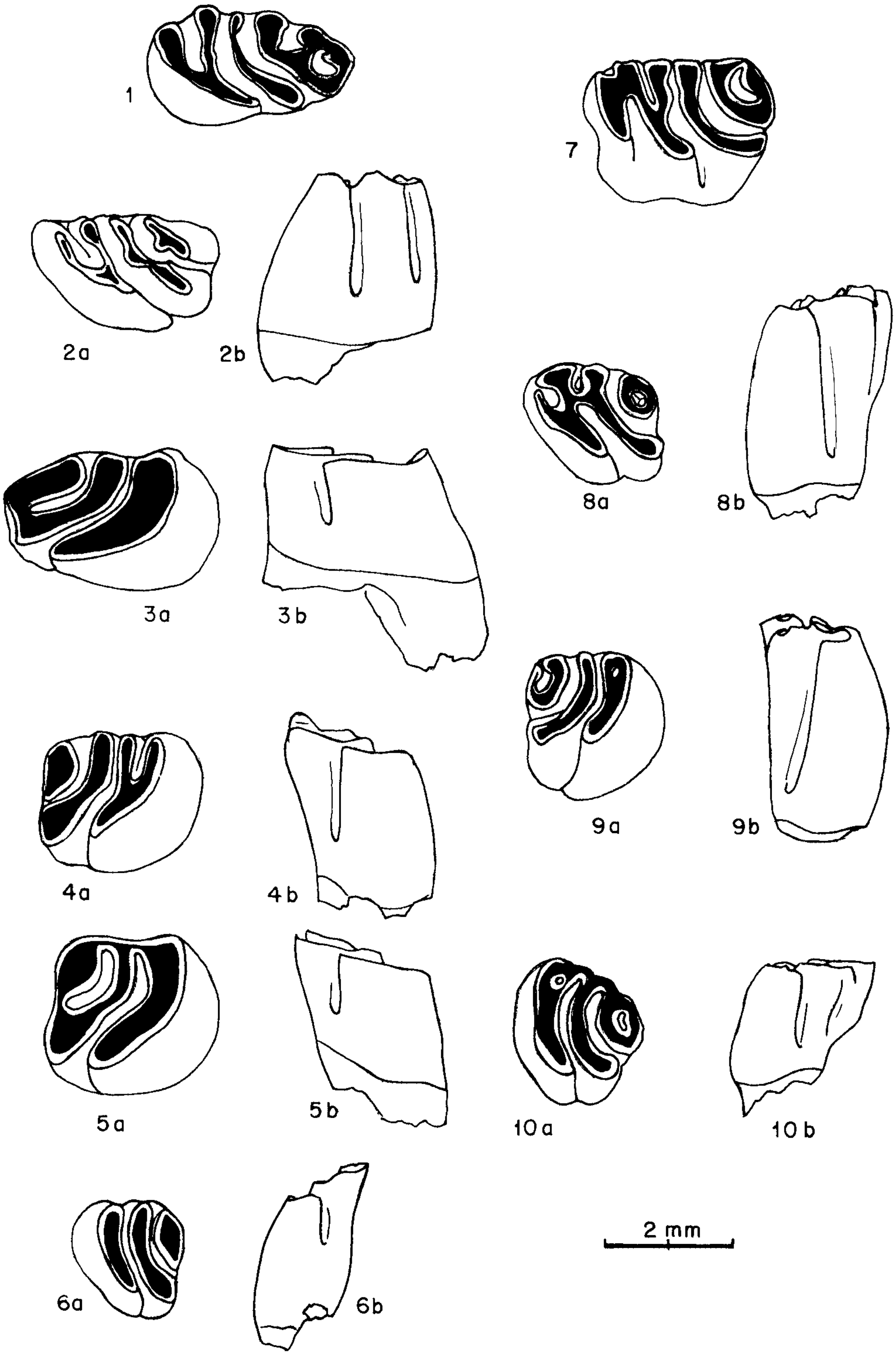
Gliravus caracensis sp. nov.
Pl. 4, figs. 1-15.

Holotype — M^2 dext., PAJ 554, Pl. 4, fig. 8.
Type-locality — Pareja.
Age — Late Oligocene.
Derivatio nominis — Caracensis is the ancient Latin adjective of Guadalajara.

Plate 3

Archaeomys (A.) gervaisi Thaler, 1966 from Pareja
Fig. 1. D_4 dext., PAJ 191.
Fig. 2a. P_4 dext., PAJ 288; 2b. labial view.
Fig. 3a. P_4 sin., PAJ 197; 3b. labial view.
Fig. 4a. $M_{1,2}$ sin., PAJ 208; 4b. labial view.
Fig. 5a. $M_{1,2}$ sin., PAJ 230; 5b. labial view.
Fig. 6a. M_3 dext., PAJ 233; 6b. labial view.
Fig. 7. D^4 sin., PAJ 160.
Fig. 8a. P^4 sin., PAJ 163; 8b. lingual view.
Fig. 9a. $M^{1,2}$ dext., PAJ 183; 9b. lingual view.
Fig. 10a. M^3 sin., PAJ 187; 10b. lingual view.

Plate 3



Diagnosis – Small to medium-sized *Gliravus*, of which the upper cheek teeth show a tendency to form a continuous lingual wall by the junction of anteroloph and posteroloph. The upper molars have only one centroloph, and the lower molars lack extra ridges.

Differential diagnosis – *Gliravus caracensis* sp. nov. is compared to other species from the Oligocene. It differs from *G. alvarezae* Lacomba & Morales, 1987 from Carrascosa by its slightly smaller size and by the incomplete lingual cingulum in P^4 and $M^{1,2}$ formed by the anteroloph and the posteroloph.

G. caracensis differs from *G. tenuis* Bahlo, 1975 from Heimersheim by its simpler dental pattern and by the tendency to form a continuous ridge lingually of the protocone.

G. caracensis differs from *G. bruijni* Hugueney, 1967 from Coderet by its much smaller size, by the metalophid-metaconid connection in $M_{1,2}$, by the tendency to form a continuous ridge lingually of the protocone, and by the presence of only 1 centroloph in $M^{1,2}$.

G. caracensis differs from *G. priscus* Stehlin & Schaub, 1951 from the Upper Eocene and Lower Oligocene by its much larger size and by the lingual wall formed by anteroloph and posteroloph of $M^{1,2}$.

G. caracensis differs from *G. meridionalis* Hartenberger, 1971 from the Upper Eocene and Lower Oligocene by its simpler dental pattern, and by the lingual wall formed by anteroloph and posteroloph in $M^{1,2}$.

Material and measurements

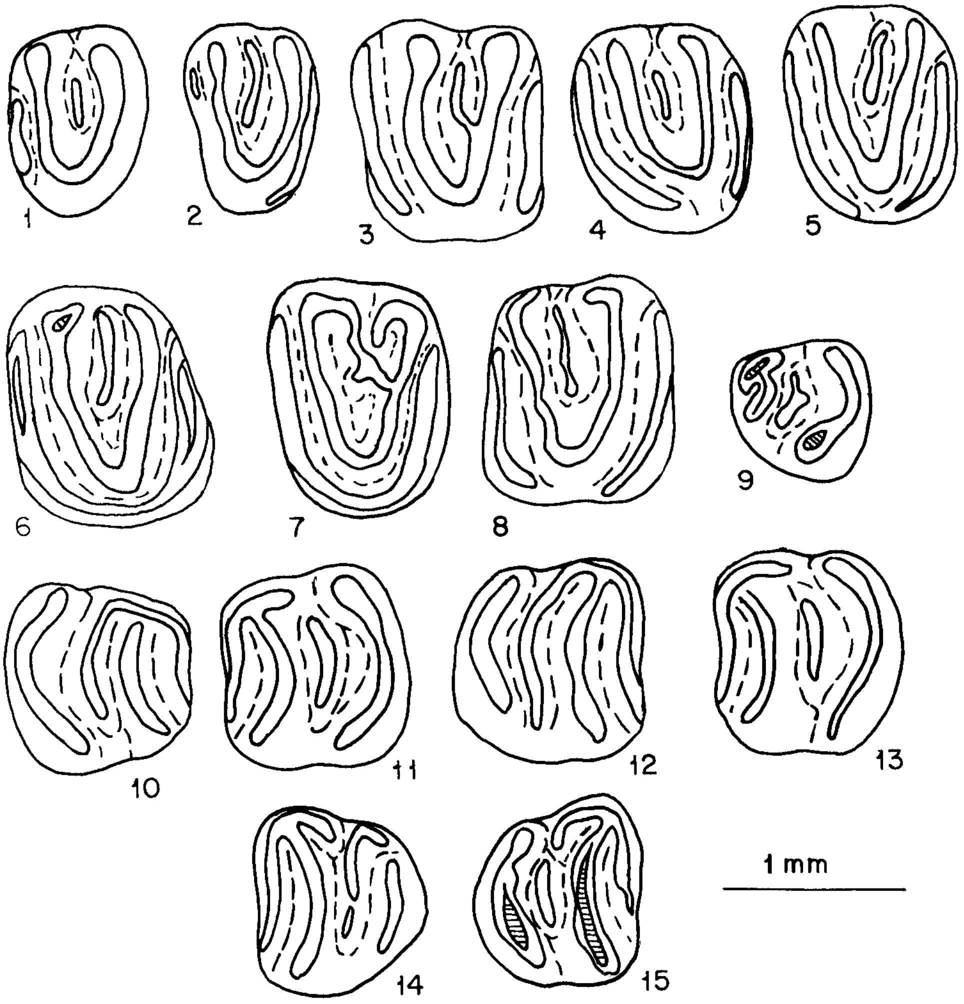
	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
P^4	5	6.0	6.9	7.5	5	9.2	9.9	10.8
$M^{1,2}$	58	8.2	9.2	10.2	58	9.8	11.2	12.7
P_4	1	–	7.3	–	1	–	6.9	–
M_1	21	9.1	9.5	9.9	20	9.2	9.9	11.0
M_2	21	9.0	9.5	10.3	22	9.3	10.6	11.6
M_3	9	8.4	8.8	9.0	10	8.9	9.5	10.1

Description

P^4 – Wide and very short teeth. The anteroloph is absent, or it is indicated by a very low and narrow ridge near the labial border. The centrally situated protocone is high. Protoloph and metaloph form a sharp V-pattern. A medium-sized centroloph is present in 5 specimens. This centroloph is connected to the metacone in 3 cases, it is an isolated central ridge in 2, and in 1 specimen the centroloph is short and connected to the paracone. The posteroloph is a low, isolated, relatively long ridge.

$M^{1,2}$ – The anteroloph is separated from both paracone and protocone. This ridge descends toward the lingual border, where it continues to meet the lingual end of the posteroloph at the basis of the protocone in 8 out of 61 specimens. This configuration separates the centrally situated protocone from the lingual tooth border. In 27 specimens the anteroloph and posteroloph do not meet at their lingual ends, and the protocone is situated toward the labial part of the tooth. In 26 specimens the lingual ends of anteroloph and posteroloph terminate separately at the lingual border and the protocone is situated at the lingual border. The paracone is higher than the metacone. Protoloph and metaloph form a sharp V-pattern. A centroloph is present, it is

Plate 4



Gliravus caracensis sp. nov.
Fig. 1. P^4 dext., PAJ 509.
Fig. 2. P^4 sin., PAJ 507.
Fig. 3. $M^{1,2}$ sin., PAJ 527.
Fig. 4. $M^{1,2}$ sin., PAJ 535.
Fig. 5. $M^{1,2}$ sin., PAJ 526.
Fig. 6. $M^{1,2}$ sin., PAJ 531.
Fig. 7. $M^{1,2}$ sin., PAJ 541.
Fig. 8. $M^{1,2}$ dext., PAJ 554, holotype.
Fig. 9. P_4 sin., PAJ 457.
Fig. 10. M_1 dext., PAJ 458.
Fig. 11. M_1 sin., PAJ 466.
Fig. 12. M_2 dext., PAJ 494.
Fig. 13. M_2 sin., PAJ 486.
Fig. 14. M_3 sin., PAJ 520.
Fig. 15. M_3 dext., PAJ 513.

connected to the base of the metacone in 18 specimens, and it is isolated in 40. In 1 specimen it joins the base of the paracone. The posteroloph is labially isolated.

P_4 – This tooth has a very reduced dental pattern. The anterior portion consists of a small, irregularly shaped, composite ridge. The posterior part is formed by the posterolophid.

M_1 – The anterolophid descends from the metaconid and ends freely at the base of the anterior tooth border. The metalophid is connected to the top of the metaconid or somewhat lower. The centrolophid is very short and it extends along the lingual border. The mesolophid is generally an isolated ridge; it does not reach the labial border, with the exception of 1 case. In 2 specimens its thin lingual end meets the base of the centrolophid. The well-developed posterolophid is an isolated ridge. Extra ridges are absent. This element has three roots.

M_2 – The dental pattern corresponds more or less to that of M_1, although the mesolophid tends to be somewhat longer; in 13 out of 23 specimens the lingual end is connected to the centrolophid, and the low labial end appears to be nearer to the tooth border.

M_3 – It has basically the same pattern as M_1 and M_2, although the mesolophid joins the entoconid in 5 out of 9 specimens. In 1 specimen its labial end reaches the tooth border.

Discussion – *Gliravus caracensis* sp. nov. from Pareja differs from *G. alvarezae* Lacomba & Morales, 1987 from Carrascosa by its slightly smaller size, and by the incomplete lingual cingulum in P^4, $M^{1,2}$, formed by the junction of anteroloph and posteroloph. In all other dental features these two species resemble each other. They are considered to be closely related, *G. caracensis* being the ancestor of *G. alvarezae.*

G. caracensis from Pareja is difficult to compare with *G. major* Stehlin & Schaub, 1951, because of the scarcity of material of the latter species. Our species seems to be somewhat smaller. According to Stehlin & Schaub the M^3 of *G. major* is characterized by the lingual wall formed by the junction of anteroloph and posteroloph, but unfortunately in our material the M^3 is absent. The teeth, referred to as *G. major* by Vollmayr (1966), agree morphologically with our material, but they are of larger size. *G.* aff. *major* from the Quercy localities Mas de Got, Mège and Pech-Crabit (Vianey-Liaud, 1969) does not resemble *G. major* as figured by Stehlin & Schaub. The Quercy material has a more complicated dental pattern and the upper molars lack the tendency to form a lingual wall, made up by anteroloph and posteroloph.

Agustí et al. (1985) described several teeth from Gandesa (Ebro Basin) as *G.* aff. *bruijni.* The $M^{1,2}$ dext. shows a continuous lingual wall formed by anteroloph and posteroloph, it has only 1 centroloph and the lower molars agree well with those of *G. caracensis* and *G. alvarezae.* This small assemblage should be assigned to *G.* cf. *alvarezae.*

EOMYIDAE DEPERET & DOUXAMI, 1902

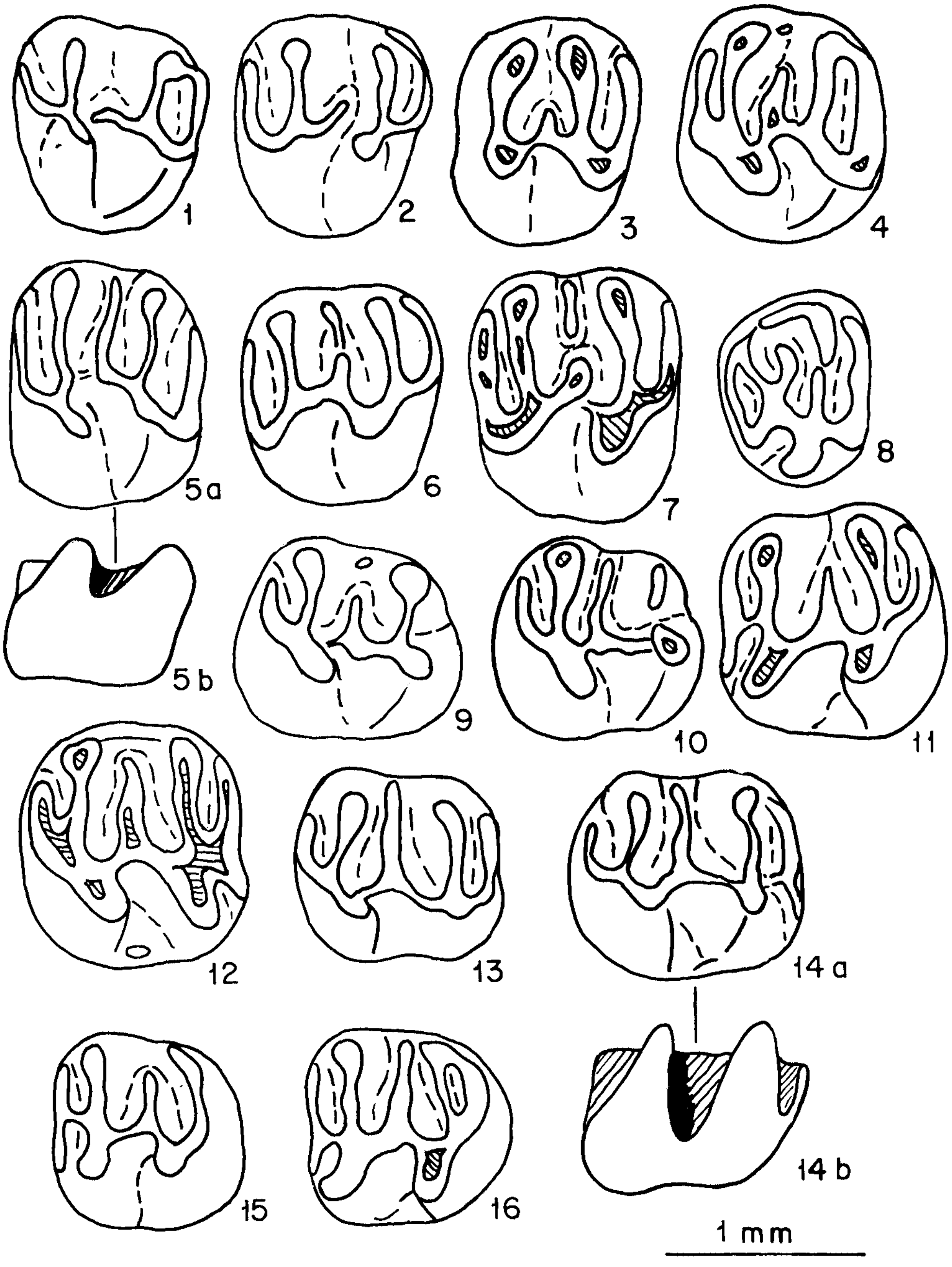
Eomys Schlosser, 1884

Eomys cf. *molassicus* Engesser, 1987
Pl. 5, figs. 1-16.

Material and measurements

	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
D^4	6	8.1	8.8	9.3	6	9.0	9.9	10.5
P^4	7	8.7	9.4	10.2	7	10.0	10.5	11.2
$M^{1,2}$	13	8.8	9.3	9.7	11	10.1	11.5	12.5
M^3	3	6.7	7.1	7.4	3	8.6	9.1	9.4
P_4	5	10.0	10.4	10.8	5	8.9	9.2	9.5
$M_{1,2}$	15	8.8	10.2	12.0	14	8.9	10.1	11.2
M_3	7	8.5	9.2	9.7	7	8.6	9.2	9.6

Plate 5



Eomys cf. *molassicus* Engesser, 1987
Fig. 1. D^4 sin., PAJ 401.
Fig. 2. D^4 dext., PAJ 406.
Fig. 3. P^4 sin., PAJ 413.
Fig. 4. $M1,^2$ sin., PAJ 414.
Fig. 5a. M^2 sin., PAJ 418;
Fig. 5b. idem, lingual,view.
Fig. 6. M^1 dext., PAJ 419.
Fig. 7. M^2 dext., PAJ 422.
Fig. 8. M^3 dext., PAJ 427.
Fig. 9. P_4 dext., PAJ 431.
Fig. 10. P_4 dext., PAJ 432.
Fig. 11. $M_{1,2}$ sin., PAJ 435.
Fig. 12. M_2 dext., PAJ 449.
Fig. 13. M_1 dext., PAJ 443.
Fig. 14a. M_1 dext., PAJ. 445;
Fig. 14b. idem, labial view.
Fig. 15. M_3 sin., PAJ 452.
Fig. 16. M_3 sin., PAJ 453.

Description

D^4 – The anteroloph is low and narrow. It ends freely at the labial tooth border, and its lingual end is connected to the protoloph. The anteroloph sticks so close to the paracone that there is no place for an anterosinus, with the exception of 1 specimen. The protoloph is transverse. The sinus and mesosinus form a continuous valley in 3 specimens. In the other 3 a low, narrow and oblique longitudinal ridge is present between the labial side of the protocone and the short mesoloph. The sinus points obliquely forward. Two specimens have a mesostyl. The metaloph is more or less transverse. The labial end of the posteroloph is connected to the base of the metacone, thus closing the posterosinus.

P^4 – The anteroloph is absent. The protoloph is more or less transverse. The sinus is transverse or it points slightly forward. The longitudinal ridge runs from the postero-labial side of the protocone obliquely into the mesosinus, where it curves to meet the antero-labial side of the hypocone. The mesoloph is absent in 1 specimen, it is short in 4, of medium length in 1, and long without reaching the labial tooth border in another. The metaloph is transverse. The posteroloph is connected to the base of the metacone.

$M^{1,2}$ – The well-developed anteroloph encloses the anterosinus. The protoloph is tranverse. The longitudinal ridge is like the one in P^4. The mesoloph is short in 6 specimens, of medium length in 4, and long, reaching the labial tooth border in 2. The sinus points obliquely forward. The anterior part of the longitudinal ridge is low and narow in 2 specimens. Labially the posterosinus is either open or slightly barred.

M3 – The anteroloph is long and well-developed, and it is labially connected to the base of the paracone. The protoloph is transverse. The sinus is lingually open, and it points obliquely forward. The longitudinal ridge makes an angle of c. 45° with the longitudinal axis of the tooth. The mesoloph is of medium length. The mesosinus is labially closed. The metaloph points obliquely forward. The posteroloph closes the posterosinus.

P_4 – A very small anteroconid is present on the antero- lingual slope of the protoconid in 4 out of 5 specimens. The metalophid is present in 3 specimens. In the other 2 protoconid and metaconid are separated by a longitudinal furrow. The longitudinal ridge is almost straight. The sinusid is wide and more or less transverse. The mesolophid is of medium length in 2, and long, reaching the lingual tooth border, in 2 specimens. The hypolophid is more or less transverse. In 1 specimen it is connected to the hypoconid, and the posterolophid forms a small and low ridge at the posterior wall of the tooth. In 3 other specimens posterolophid and hypoconid form one unit, and the hypolophid joins this unit midway. Lingually the posterolophid ends freely.

$M_{1,2}$ – M_2 is wider than long, M_1 is generally longer than wide. The anteroloph is well developed. Labially it ends freely, and lingually it may be connected to the base of the metaconid. The anterolophid is connected to the middle of the protoconid-metaconid unit in 8 specimens, and to the antero-lingual side of the protoconid in 4. The metalophid points slightly forward in 4 specimens, it is transverse in 6, and it points slightly backward in 2. The well-developed longitudinal ridge is complete. The sinusid is transverse or it points slightly backward. The mesolophid is short in 2 specimens, of medium length in 9, and long, reaching the lingual tooth border in 4. The hypolophid points obliquely backward, and it joins the posterolophid, which ends freely at the posterior wall of the entoconid, without reaching the lingual border. Two specimens have a small ectostylid in the sinusid. Three roots are present.

M_3 – The anterolophid is well developed and morphologically like the ones in $M_{1,2}$. It joins the protoconid-metaconid unit midway. The metalophid is transverse in 3 specimens, and it points obliquely forward in 3 others. The mesolophid is of medium length in 3 specimens, and long, reaching the lingual tooth border in 3 others. The sinusid points slightly backward. In 1 out of 5 specimens a distinct posterolophid is present, enclosing the posterosinusid, the other 4 specimens lack this ridge completely.

Discussion — The genus *Eomys* may be subdivided into a group of species of relatively large size on the one hand, and one of relatively small size on the other.

The first group consists of the following species, with their respective type-localities:
E. huerzeleri Engesser, 1982, Rickenbach.
E. gigas Comte & Vianey-Liaud, 1987, Pech-du-Fraysse.
E. quercyi Comte & Vianey-Liaud, 1987, Pech-du-Fraysse.

The group of relatively small-sized species consists of:
E. molassicus Engesser, 1987, Oensingen.
E. ebnatensis Engesser, 1987, Ebnat-Kappel.
E. zitteli Schlosser, 1884, Mouillac.
E. minor Comte & Vianey-Liaud, 1987, Belgarric.
E. antiquus (Aymard, 1853).

E. cf. *molassicus* from Pareja is of relatively small size and will therefore only be compared with the species of the latter group.

E. molassicus is known by a few teeth from its type-locality and from Schwendibach. The size of our species from Pareja agrees well with that of the Swiss material, but there are some slight morphological differences:
In the P_4 from Pareja the metaconid is separated from the protoconid in 2 out of 4 specimens. In the Swiss material these two cusps are united.
In Pareja M_1 is longer than wide, and M_2 is wider than long. In the Swiss material M_1 is almost as long as wide, and M_2 wider than long (Engesser, 1987, p. 949), but the length/width scatterdiagrams of M_1 and M_2 (Engesser, 1987, fig. 7, p. 956) show that on the average both M_1 and M_2 of *E. molassicus* are longer than wide.
In Pareja the lengths of the mesolophids of $M_{1,2}$ vary from short (2), to medium (9), and long (4). In the Swiss material the length of these ridges varies from medium to long in the 6 available specimens.
In Pareja the posterosinusid is slightly smaller in M_2 than in M_1, but it is still well-developed. In the Swiss material the posterosinusid of M_2 seems to be more reduced.
The M_3 are very much alike with the exception of 1 specimen from Pareja in which the posterosinusid is well developed.
The only known P^4 of *E. molassicus* from Switzerland has a long mesoloph. In Pareja the mesoloph is absent in 1 specimen, it is short in 4, of medium length in 1, and long in 1.
The only M^1 of the Swiss material has a mesoloph of medium length, and the only M^2 has a long one. In Pareja the mesolophs of $M^{1,2}$ are short in 6, of medium length in 4, and long in 2 specimens.
Resuming it may be said that some slight differences are present, which may turn out to fall within the intraspecific variation, when larger collections of the Swiss material become available. Therefore our material is described as *E.* cf. *molassicus*.

E. cf. *molassicus* from Pareja differs from *E. ebnatensis* from the Upper Oligocene of Switzerland by its distinctly smaller size, by its larger posterosinusid of M_1 and M_2, by the better developed anterosinus of $M^{1,2,3}$, and by its more brachyodont teeth.

E. cf. *molassicus* from Pareja differs from *E. minor* from Belgarric by its considerably larger size and by the presence of mesolophids and well-developed posterolophids.

E. cf. *molassicus* from Pareja differs from *E. zitteli* from Gaimersheim (see Fahlbusch, 1970) by its slightly smaller size, by the anterolophid being connected to the metaconid-protoconid unit in all specimens and by the generally shorter mesoloph of $M^{1,2}$.

No direct comparison with *E. antiquus* could be made. According to Engesser (1987) *E. molassicus* has larger teeth, it has a better developed anterolophid and longer mesolophids in the lower molars, and the posterosinusid of M_2 is less reduced.

Engesser (1987) suggests that *E. molassicus* is the ancestor of *E. ebnatensis*, and that the evolutionary trend would be toward more hypsodont molars. The size and morphological features of our species from Pareja would point to a close relationship with the above mentioned lineage. Unfortunately the poor material of *E. molassicus* from its type-locality Oensingen does not allow a more detailed comparison.

CRICETIDAE ROCHEBRUNE, 1883

Four species of Cricetidae have been found in Pareja. Three of these are attributed to the genus *Eucricetodon*, one is placed in the genus *Heterocricetodon*. Although the total material of 295 specimens is quite a good collection the material is not sufficient to solve all the problems.

First of all a considerable number of specimens show signs of corrosion, probably caused by the gastric acid of some carnivorous mammal or bird. Such specimens cannot be measured reliably and have to be discarded from the measurement tables and scatter diagrams. This would not be too much of a problem if it were possible to determine beyond doubt whether a specimen has preserved its original dimensions. In the Pareja material this is not always possible, and either choice, accepting a specimen or rejecting it, may influence the statistical results in an unwanted way, if the decision taken is incorrect. There is no way to avoid this bias.

Secondly, the 4 species are not equally represented. The most frequent species is represented by 20-30 specimens per element, which is quite good; the second one is known from c. 10 specimens per element, which is quite poor already; the third one is known by less than 5 specimens per element, and of the fourth one only an M_1 and an M^1 were found. In cases where the various species differ strongly this need not be too much of a problem, but among Oligocene cricetids this presents serious difficulties. Populations with abundant material of Oligocene Cricetidae have been described from the uppermost Oligocene, much too young for a direct comparison with Pareja, or they come from fissure fillings that may contain chronologically heterogeneous faunas. The lack of knowledge on the variability of Oligocene Cricetidae obliged us to separate from the total collection those specimens that could be distinguished more or less easily, and leave the rest in one single species (*Heterocricetodon landroveri* sp. nov.), that risks to be a waste-basket. Inspection of the length/width diagrams shows a discontinuous scattering of the dimensions of the M_1, M_3, and M^1 of this species, that might mean that in reality two species are present among this material. It has not been possible to separate these groups morphologically.

Methodology – In the description of the teeth authors use terms like 'short, long, weak, well-developed', etc. without defining exactly what their meaning is in each specific case. One of us (M.F.) is working on a computerized system for standardization of such descriptive terms. Since this system is not yet available we feel a need to explain the value of at least one of the descriptive terms: the length of mesoloph(id)s.

Mesoloph(id)s may be absent, short, of medium length, or long. The value of these terms is:

Absent: no trace of a mesoloph(id) present.

Short: less than one third of the distance between ectolophid (entoloph) and the lingual (labial) border of the tooth.
Medium: between one third and half this distance.
Long: more than half this distance.

PSEUDOCRICETODONTINAE ENGESSER, 1987
Heterocricetodon Schaub, 1925

Heterocricetodon landroveri sp. nov.
Pl. 6, figs. 1-11.

Holotype — M^1 sin., PAJ 583, Pl. 6, fig. 1.
Type-locality — Pareja.
Age — Late Oligocene.
Derivatio nominis — In honour of our Landrovers, that fortunately did not break down the day we collected the sample at Pareja.

Diagnosis — The dental pattern, especially of the upper molars, is characterized by the lophodont structure, the crests being more important than the cusps. Posterior branch of the protoconid least developed in M_1 and best developed in M_3. In M_1 2 or even 3 mesolophids are frequently present. M_3 frequently with an accessory crest in the posterosinusid. In M^1 there is a crest from the anterocone to the paracone. The anterior branch of the protocone ends freely, not farther forward than the anterior base of the paracone. In M^2 the lingual anteroloph may separate the protocone from the lingual border of the tooth, and continue beyond the sinus to the hypocone.

Differential diagnosis — Smaller than all species attributed to *Heterocricetodon*, larger than all species attributed to *Pseudocricetodon*, except *E. incertus*. It differs from *H. hausi* Engesser, 1987 by the total absence of a connection between the anterocone and the anterior branch of the protocone. For a comparison with *H. incertus* see the discussion after the description.

Material and measurements

	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
M^1	15	19.5	21.39	22.8	23	12.5	14.06	15.4
M^2	29	14.0	15.66	17.1	25	13.9	15.31	16.5
M^3	22	11.0	12.48	14.0	23	11.5	13.11	14.3
M_1	31	16.4	18.64	20.0	33	10.7	12.12	13.4
M_2	31	15.5	16.65	17.8	32	13.0	13.91	15.3
M_3	23	14.0	15.51	17.5	24	11.8	13.12	14.0

Description

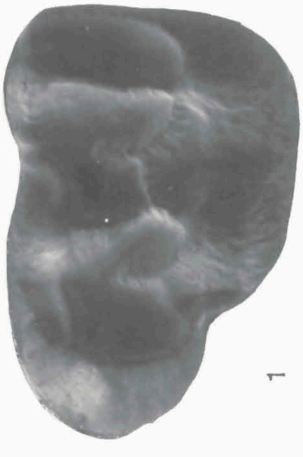
M^1 — The general impression of the upper molars is, that crests dominate over cusps. The labial border of the tooth is straight or concave, sometimes convex. The prelobe of M^1 is rather broad (more than half the width of the molar), and the lingual border makes an angle in front of the protocone. The anterocone is a not very well-marked cusp in the labial part of the anteroloph. In 1 specimen a second, low cusp is found in the lingual part of the anteroloph. The labial anteroloph descends as a weak crest towards the paracone. One specimen has an anterostyl. The lingual anteroloph is better developed, connected to the protocone (8), forming a protostyl in front of the protocone (7), bending towards the labial border in front of the protocone (2), or leaving the protosinus partly open (1). There is a backward crest from the anterocone towards the paracone, which is complete in 9 specimens and interrupted in 8, only in 2 specimens this crest fails. In 1 case the crest is double, and in another case even triple. The anterior branch of the protocone ends free (24), or it is connected to the base of the paracone (2). It never continues farther forward than the base of the paracone; there is not the slightest indication of a connection with the anteroloph/anterocone. The entoloph runs from the middle of the protocone in a labial direction, and then bends sharply backwards towards the hypocone. The protolophule is transverse or points obliquely backwards, towards the bend of the entoloph. Only in 2 specimens it is connected to the protocone in front of the entoloph. In 2 specimens the protolophule is absent, and in 2 it is interrupted. The sinus is curved forward, open (9), blocked by a small cingulum ridge (2), or by a more or less well-developed entostyl (10). The paracone bears no posterior spur (6), there is a spur along the border of the molar (11), or this spur begins more labially, and bends towards the labial border (4); it is not in contact with the mesoloph or mesostyl. The mesoloph is long, ending in a mesostyl (5), long without a mesostyl (6), of medium length (13), or short (1); in 10 specimens there is an isolated mesostyl. In 2 specimens there is a trace of a connection between mesoloph and metalophule. The metalophule is straight, connected to the hypocone, or to the entoloph just in front of the hypocone. The posteroloph is straight, and very much parallel to the metalophule. The posterosinus is long and straight, labially open.

M^2 – The posterior part of the tooth is narrower than the anterior part, due to the reduction of both hypocone and metacone (in comparison with M^1). The labial anteroloph is low, but it may gain height at its labial end; it may or may not close the long and narrow anterosinus. The protosinus is closed by the lingual anteroloph, which may end at the anterior base of the protocone (7), or continue farther along the protocone (11). In 5 of these 11 specimens it continues all the way backwards to the anterior wall of the hypocone. The protolophule is anterior, connected to the crest between protocone and anteroloph. The posterior protolophule is complete (8), long and interrupted (11), short and interrupted (6), or absent (2). Ectoloph and sinus are as in M^1. Generally there is a spur along the labial border, descending from the paracone, that leaves the mesosinus open. The mesoloph is long, ending in a mesostyl (4), just long (10), of medium length (16), or short (1); in 2 specimens there is an isolated mesostyl. In 8 specimens there is a trace of a connection between mesoloph and metalophule. In 1 specimen there are 2 mesolophs. Metalophule, posteroloph, and posterosinus are like in M^1. In 1 specimen there is a longitudinal connection between metalophule and posteroloph.

M^3 – This element is difficult to interpret and to describe. Separation of the M^3 of *H. landroveri* and *E. margaritae* is difficult, and we are not sure that all determinations are correct. For a general discussion on the M^3 of cricetids see Freudenthal & Daams (1988) and Fig. 2.

Plate 6

Heterocricetodon landroveri sp. nov.
Fig. 1. M^1 sin., PAJ 583, holotype.
Fig. 2. M^1 dext., PAJ 622.
Fig. 3. M^2 sin., PAJ 635.
Fig. 4. M^2 dext., PAJ 650.
Fig. 5. M^3 sin., PAJ 681.
Fig. 6. M^3 sin., PAJ 682.
Fig. 7. M_1 sin., PAJ 731.
Fig. 8. M_1 dext., PAJ 756.
Fig. 9. M_2 dext., PAJ 818.
Fig. 10. M_3 sin., PAJ 845.
Fig. 11. M_3 dext., PAJ 866.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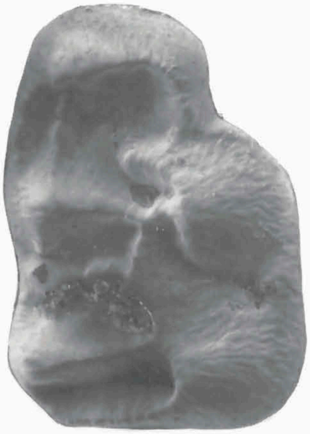
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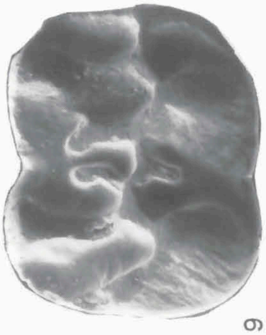
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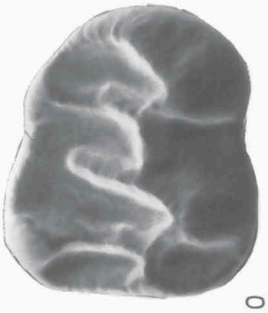
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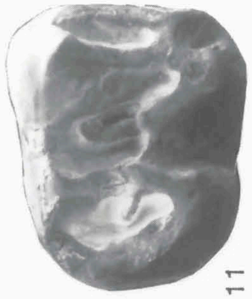
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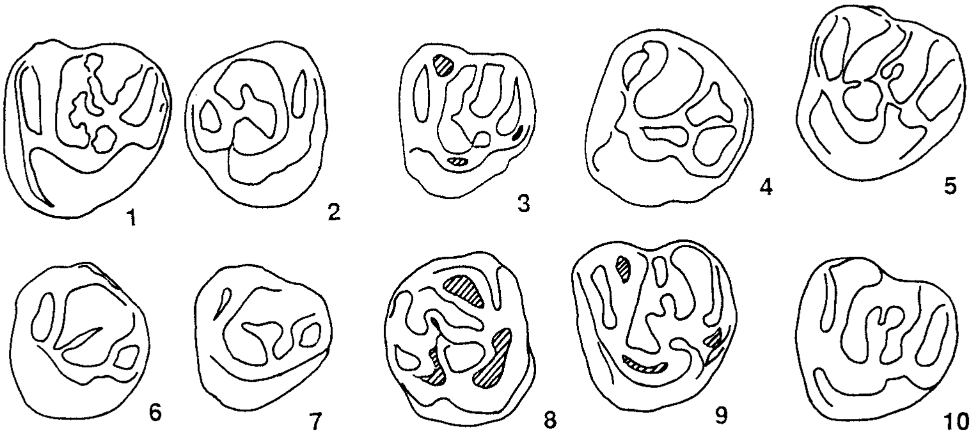


Fig. 2. Morphotypes of M^3.
Heterocricetodon landroveri
1: PAJ 681; 2: PAJ 709; 3: PAJ 682; 4: PAJ 694; 5: PAJ 686; 6: PAJ 679; 7: PAJ 695.
Eucricetodon margaritae.
8: PAJ 699; 9: PAJ 678; 10: PAJ 676.

Our material attributed to *H. landroveri* contains 3 small specimens with a very simple dental pattern: protocone, paracone, hypocone, and metalophule. In 2 of these a free-ending axioloph starts from the meeting-point of protocone and paracone; in the other one there is no axioloph, but there is a transverse crest from the hind part of the protocone towards the centrocone, which is supposed to be the anterior part of the ancient entoloph. Maybe these specimens belong to *E.* aff. *atavus.*

In 15 out of 18 specimens the neo-entoloph is closed, only in 3 specimens the sinus is curved and deep. The axioloph is complete (6), or interrupted (9); the interrupted axioloph generally is a forward spur on the centrocone. In 7 specimens the ancient entoloph is complete or almost complete, forming an almost complete circle between the posterior corner of the protocone and the anterior corner of the hypocone. Together with the neo-entoloph it encloses a funnel. The mesoloph is generally long. The metalophule has a variable position. In the specimens without axioloph it tends to be more transverse, in the ones with axioloph it is oblique to almost longitudinal.

M_1 – The outline of the molar is rather elongated, rarely short. The anteroconid is a small simple cusp with descending cingulum ridges. The lingual ridge normally reaches the metaconid, but the connection with the metaconid is not continuous because the anterior wall of this cusp is almost vertical. The lingual ridge may reach the protoconid or end before this cusp. The anterior metalophulid is absent (8), interrupted (7), or complete (4). The posterior metalophulid is formed by the posterior branch of the protoconid, that is always in contact with the metaconid at half height, and nearly always ascends as a tiny structure up to the top of the metaconid.

The sinusid is broad, more or less rectangular, and not blocked by a cingulum ridge. The mesosinusid is partly blocked by a long crest descending from the metaconid along the border of the molar. The ectolophid has a low connection with the posterior wall of the protoconid; it is longitudinal or slightly oblique. Although mesolophids and ectomesolophids are well developed, the ectolophid is not inflated, and there is no mesoconid. There is 1 mesolophid (6), 2 mesolophids (10), or 3 mesolophids (2). The extra mesolophid may originate directly from the ectolophid, or it presents itself as a ramification of the mesolophid. The posterior mesolophid in some cases tends to get into contact with the entoconid. The ectomesolophid is absent (6), or present (16); in one specimen there are two ectomesolophids. The posterior branch of the hypoconid is absent (17), or present (4). In two specimens there is crest-like structure on the posterior wall of the entoconid, that is not in contact with the posterolophid. The posterolophid closes the posterosinusid at a low level.

M_2 – The outline of many specimens is characterized by the fact that the anterior part of the tooth is narrower than the posterior half. There is no anteroconid at the meeting-point of anterolophid and anterolophulid. The lingual anterolophid is long and closes the well-developed anterosinusid. The labial anterolophid is shorter, descends more steeply, and leaves the protosinusid open. The protosinusid often is somewhat curved backwards, due to the rotation of the protoconid. The anterolophulid is long. The anterior metalophulid meets the anterolophulid halfway between protoconid and anterolophid. The posterior branch of the protoconid is well developed, and ends free in the mesosinusid (22), or it is in contact with the base of the metaconid (10), or it is short and ending free (2). In one specimen the end of this crest is ramified. In 4 specimens a crest-like structure on the hind wall of the metaconid indicates a remnant of the connection with the posterior branch of the protoconid. The sinusid is nearly always open. The mesosinusid may be blocked by the ridge descending from the metaconid, or it remains open. In several cases the descending ridge ends abruptly in front of the entoconid, leaving a deep and narrow channel at the exit of the mesosinusid. The mesolophid is absent (4), short (5), of medium length (25), or long (3). In several cases it has lost contact with the ectolophid. The ectomesolophid is absent (6), or present (28). The posterosinusid is like that of M_1. In 3 specimens there is a trace of a posterior hypolophulid.

M_3 – The posterior part of the tooth is not very much reduced; it doesn't have the triangular outline that is common in many cricetids. The anterior part of the tooth (anterolophid, anterosinusid, and protosinusid) is like that of M_2. The metalophulid is connected to the anterolophulid somewhat farther forward than it is in M_2. In 3 specimens it is connected to the meeting-point of anterolophid and anterolophulid, in 1 specimen there is no metalophulid. The posterior branch of the protoconid is long, ending free in the mesosinusid, with respect to the size of the molar even better developed than in M_2. In 2 specimens it is bifurcated; in 7 specimen a remnant of the posterior metalophulid is indicated on the hind wall of the metaconid. The sinusid is open, the mesosinusid blocked by a cingulum ridge. Besides the posterior branch of the protoconid a mesolophid is present in 1 specimen only. The ectomesolophid is absent (9), or present (18). In 7 out of 24 specimens an accessory crest is present in the posterosinusid; it may be interpreted as a remnant of a posterior hypolophulid. In a few specimens a cingulum ridge is present at the base of the posterior wall of the tooth.

Discussion – The rather lophodont dental pattern of *H. landroveri* places this taxon in the vicinity of *Pseudocricetodon* Thaler, 1966, *Heterocricetodon* Schaub, 1925, and *Eucricetodon incertus* (Schlosser, 1884). Hugueney (1980) placed *E. incertus* in the genus *Pseudocricetodon*. Dienemann (1987) prefers to leave it in *Eucricetodon*. Freudenthal (1989) states that - on the basis of dental features - there exists no workable diagnosis for the genus *Pseudocricetodon*; cranial features prove the value of this genus (Parent, 1983), but species of which only teeth are known cannot be distinguished from *Eucricetodon* beyond doubt. Neither exists a good diagnosis for *Heterocricetodon*. In our opinion Engesser (1987) was right when he placed the abovementioned taxons in a close concept, though it is a pity that he could not give a better definition for the genera *Pseudocricetodon* and *Heterocricetodon*. Accepting Engesser's Pseudocricetodontinae as a group of relatively lophodont Oligocene cricetids, it is evident that *E. incertus* belongs to this subfamily too. Probably it is a heterogeneous group, but it is useful at our present state of knowledge.

Within the subfamily Pseudocricetodontinae *Pseudocricetodon* comprises species of small size, and *Heterocricetodon* species of large size. *Eucricetodon incertus* is of intermediate size, but closer to *Heterocricetodon*. Therefore we think, it best be placed in that genus, though we are well aware of the fact that this is only a provisional solution.

Our new species *H. landroveri* is quite close to the *Heterocricetodon incertus* described by Dienemann (1987) from Ehrenstein 7, both in size and morphology. Our species is somewhat larger: the mean values agree more or less with the maxima found by Dienemann in Ehrenstein 7, and our minima coincide with the mean values of the Ehrenstein population.

Morphologically there are agreements: in M^1 the backward crest on the anterocone and the free anterior branch of the protocone that remains in a backward position; in M^2 the lingual anteroloph that continues around the protocone and reaches the hypocone. Among the differences are the complex mesoloph(id) structures in our material, the more complex M^3, more frequent ectomesolophids, and the better developed posterior protolophule in M^2.

The complex mesoloph(id) structures are very characteristic of *H. landroveri*, and they are found in various species of *Pseudocricetodon* and in *H. hausi* as well.

Lacomba & Morales (1987) and Lacomba (in press) describe *Pseudocricetodon incertus* from Carrascosa del Campo (Loranca Basin, Spain). Comparison of this material with ours has shown that the two populations resemble each other highly, and that the Carrascosa material may be attributed to *H. landroveri*. There are a few differences, e.g. the less-developed mesolophids in the Carrascosa material. A greater difference, the meaning of which cannot be assessed at present, is the fact that among 10 specimens of M^3 from Carrascosa, 7 have a morphotype that we didn't find in *H. landroveri* from Pareja. They lack the ancient entoloph and the axioloph, and have a well-developed centroloph; 5 of these 7 are quite similar to the specimens from Pareja that we placed in *E. margaritae*.

EUCRICETODONTINAE MEIN & FREUDENTHAL, 1971

Eucricetodon Thaler, 1966

Eucricetodon margaritae sp. nov.

Pl. 7, figs. 1-7.

Holotype — M^1 sin., PAJ 595, Pl. 7, fig. 1.
Type-locality — Pareja.
Age — Late Oligocene.
Derivatio nominis — In honour of Dr Margarita Díaz, Madrid.

Diagnosis — Cusps very massive, valleys narrow. Anterocone of M^1 subdivided. M_1 very short in relation to the length of M^1. Metalophulid in M_1 double and symmetric. Mesoloph(id)s thick, wedge-shaped, rather long.

Differential diagnosis — *E. margaritae* sp. nov. differs from *E. huerzeleri* Vianey-Liaud, 1972 by its considerably smaller size. It differs from the *E. aquitanicus-infralactorensis* group by its smaller size and its well-developed posterosinus in M^1 and M^2.

It differs from all other *Eucricetodon* species by its split anterocone.

Material and measurements

	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
M^1	6	22.3	23.32	23.9	6	14.8	15.15	15.5
M^2	9	15.6	16.76	17.7	9	15.1	15.73	16.6
M^3	10	12.1	13.21	14.3	10	13.1	13.91	14.5
M_1	8	17.8	18.78	20.3	11	10.9	12.35	13.3
M_2	10	16.3	16.96	18.2	10	12.7	14.04	14.9
M_3	11	13.8	14.86	16.7	11	11.4	12.49	13.7

Description

M^1 – The labial border of the tooth is straight or convex. The border between prelobe and protocone doesn't make a sharp angle. The anterocone consists of two cusps, separated by a not too deep furrow in the anterior wall. The labial anteroloph closes the anterosinus incompletely. The lingual anteroloph is better developed, and reaches the protocone; in 2 out of 8 specimens it bears a lingual spur, just in front of the protocone. The labial anterocone cusp bears a free-ending backward spur in 6 out of 8 specimens. The anterior branch of the protocone is well developed and nearly always draws near to the posterior spur of the anterocone. The protolophule is directed slightly backwards. The entoloph is a slight curve, or a straight line between protocone and hypocone, the sinus is transverse or curved forward, not closed by a cingulum. The mesosinus is open; there may be some crest- or cusp-like cingulum structure at the antero-labial base of the metacone. The mesoloph is thick, either long (1), of medium length (7), or short (1). The metalophule is directed slightly forward, connected to the entoloph (7), or to the hypocone (1). The posterosinus is not closed.

M^2 – The anterosinus is closed. The protosinus is either moderately developed (3), or almost disappeared (6). The metalophule is anterior (5), anterior with a trace of a posterior connection (2), or posterior with a trace of an anterior connection (1); in 1 specimen the entoloph continues forward beyond the protocone, and is connected to the anterior protolophule. Mesosinus and sinus are open; the sinus is narrow and more curved than in M^1. The mesoloph is long (2), or of medium length (8). The metalophule is slightly directed forward, connected to the entoloph just in front of the hypocone. The posterosinus is open or closed.

M^3 – As explained before we have not been able to separate unquestionably the M^3 of *H. landroveri* and *E. margaritae*. Ten specimens are attributed to *E. margaritae*. They are characterized by a nearly always closed neo-entoloph, and a well-developed centroloph on the posterior corner of the protocone. This centroloph is interpreted as the anterior part of the ancient entoloph, and it may bear a mesoloph, or some trace of an anterior connection towards the protolophule. Only 1 specimen has a complete axioloph; in 2 specimens the curved entoloph is still complete.

M_1 – Anterosinusid and protosinusid are blocked by cingulum ridges, or they remain open. The anterolophulid is short and complete. In 1 specimen there is an antero-labial spur on the anterior wall of the protoconid. The anterior metalophulid is always present. The posterior branch of the protoconid is connected to the metaconid in 7 specimens, forming a posterior metalophulid that is almost as well-developed as the anterior one; the 2 metalophulids form a symmetric pair. In 3 specimens the posterior branch remains free from the metaconid, and in 2 of these it is connected to the mesolophid, forming a funnel. The ectolophid is oblique, and may be provided with a mesoconid. The sinusid is either transverse or curved backwards, open or blocked by a cingulum ridge. The mesosinusid may be blocked by a cingulum ridge descending from the metaconid, or it remains open; in 1 specimen there is a mesostylid. The mesolophid is well-developed, thick, and of medium length or long. In 2 specimens there is a small ectomesolophid. The hypolophulid is transverse, connected to the ectolophid. There is a short and thick spur on the posterolophid, that does not reach the entoconid (4), or a swelling of the posterolophid (4), or no such structure (2). The posterosinusid is closed by the posterolophid.

M_2 — The lingual anterolophid closes the anterosinusid, the protosinusid remains open. The metalophulid is connected to the middle of the anterolophid, where a small cusp may exist (anteroconid). There is a trace of a posterior metalophulid on the posterior wall of the metaconid in 2 specimens; in 2 others there is a short free posterior branch of the protoconid (besides the mesolophid). The sinusid is open, or less frequently closed by a low ridge. The mesosinusid is open; in 2 specimens there is a tiny mesostylid. The mesolophid is thick, long or of medium length. One specimen has a short posterior hypolophulid, another one has a slightly swollen posterolophid. Hypolophulid, posterolophid, and posterosinusid are like those in M_1.

M_3 — The outline of the tooth is much more triangular than in the M_3 of *H. landroveri*, making separation of the two species rather easy. Anterosinusid and protosinusid are closed by the anterolophids. The metalophulid is connected to the anteroconid (7), or to the anterolophulid, a slightly more backward position than in M_2. The mesolophid is of medium length (4), short (5), or absent (2); its shape makes one think, that it is the posterior branch of the protoconid, and not the mesolophid; comparison with M_2 shows, however, that it best be called a mesolophid; furthermore, in 1 specimen there is a very small posterior branch in front of the mesolophid. The sinusid is open or slightly barred. Mesosinusid and posterosinusid are closed by an almost continuous wall. However, the entoconid remains somewhat isolated by an incision of the labial wall between entoconid and metaconid, and sometimes also by an incision behind the entoconid.

Discussion — The morphology of this species resembles that of *E. huerzeleri*, but the dimensions of our new species are much smaller.

According to Comte (1985) some specimens of *E. huberi* from Rigal-Jouet have a split anterocone (his 'morphotype *huerzeleri*'). We think it is possible that the material from Rigal-Jouet represents a mixture of two species, the larger one of which might be close to *E. margaritae.*

Among the material of *E. dubius* from Vivel del Río (Hugueney et al., 1987) some specimens have a slightly split anterocone. We have been able to notice this feature thanks to the kindness of M. Hugueney, who showed us the material. She also expressed her doubt about the specific attribution of some of the larger specimens (personal communication). Maybe a species close to *E. margaritae* is present among the abundant material of *E. dubius* from Vivel del Río.

Plate 7

Eucricetodon margaritae sp. nov.
Fig. 1. M^1 sin., PAJ 595, holotype.
Fig. 2. M^2 sin., PAJ 637.
Fig. 3. M^3 sin., PAJ 676.
Fig. 4. M_1 sin., PAJ 727.
Fig. 5. M_1 dext., PAJ 754.
Fig. 6. M_2 sin., PAJ 785.
Fig. 7. M_3 sin., PAJ 835.

Eucricetodon sp.
Fig. 8. M^1 dext., PAJ 619.
Fig. 9. M_1 sin., PAJ 743.


1

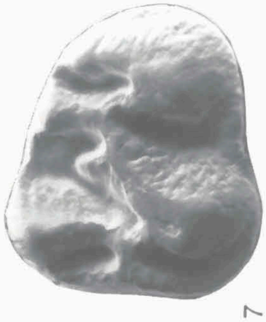

2


3


4


5


6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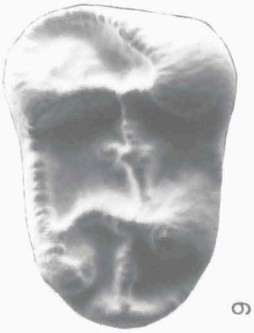
8


9

Eucricetodon aff. *atavus* Misonne, 1957

Material and measurements

	Length n	min.	mean	max.	Width n	min.	mean	max.
M^1	1	–	18.6	–	1	–	12.2	–
M^2	3	13.8	13.93	14.1	3	13.4	13.53	13.7
M^3	1	–	10.3	–	1	–	11.3	–
M$_1$	4	16.2	16.92	17.3	4	10.0	10.60	10.9

Description – Unfortunately the material is poorly preserved and a full description is not possible.

M^1 – The anterocone is broad, possibly slightly bifid. The anterosinus is open, the protosinus is closed by the cingulum ridge descending from the anterocone; in 1 specimen this cingulum ridge is interrupted halfway betweenn th anterocone and the protocone. There is a posterior spur on the anterocone. The anterior branch of the protocone ends free (2), or it is connected to the base of the paracone (1). The sinus is curved, not blocked. The mesoloph is of medium length.

M^2 – The protolophule is anterior (1), or anterior with a trace of a posterior connection (2). The mesoloph is of medium length. In 1 specimen the lingual anteroloph continues beyond the protocone towards the hypocone. The sinus is curved.

M^3 – The protolophule is short, connected to the middle of the labial anteroloph. The tooth is very much reduced; in the posterior part only a hypocone, metalophule, and a small centrocone are present.

M$_1$ – Simple dental pattern. The anterolophulid is long and complete; there is no anterior metalophulid. The posterior branch of the protoconid is connected to the metaconid. The mesolophid is absent or short. The sinusid is a wide rectangle. In 1 out of 6 specimens there is a trace of a posterior hypolophulid.

Discussion – These are the smallest cricetid specimens from Pareja. They differ from *H. landroveri* by their simple dental pattern. They may belong to *E. atavus*, but the material is too poor, and to badly preserved, to be certain.

Eucricetodon sp.
Pl. 7, figs. 8-9.

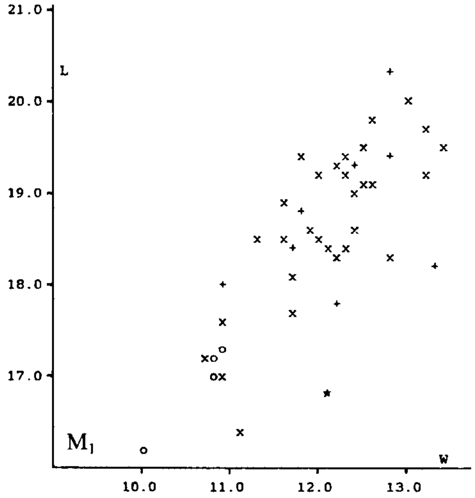
Material and measurements

1 M$_1$: 16.8 x 12.10; 1 M^1: 19.4 x 14.0

Description

M^1 – The prelobe is broad and doesn't form a sharp angle with the lingual border. Anterosinus and protosinus are blocked. The anterior branch of the protocone touches the base of the paracone, and continues to the anterocone. The protolophule is transverse, connected to the protocone. The entoloph is somewhat interrupted near the protocone. The sinus is open and strongly curved. The mesoloph is medium-sized, and there is a mesostyl. The posterosinus is open.

Fig. 3. Length/width diagrams of the Cricetidae from Pareja. x: *Heterocricetodon landroveri* sp. nov.; +: *Eucricetodon margaritae* sp. nov.; o: *Eucricetodon* aff. *atavus*; *: *Eucricetodon* sp.


21.0
20.0
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L
M_1
W
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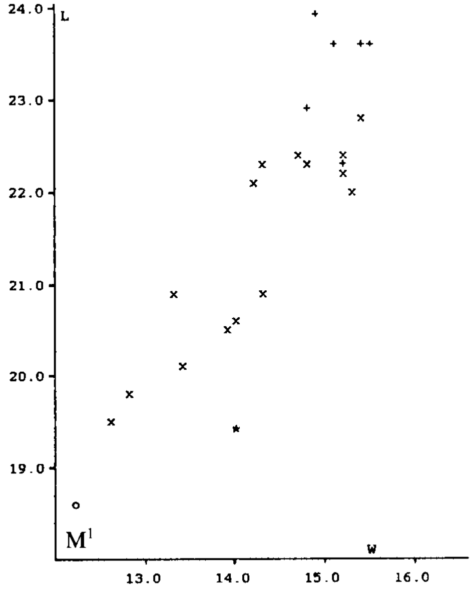
24.0
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M^1
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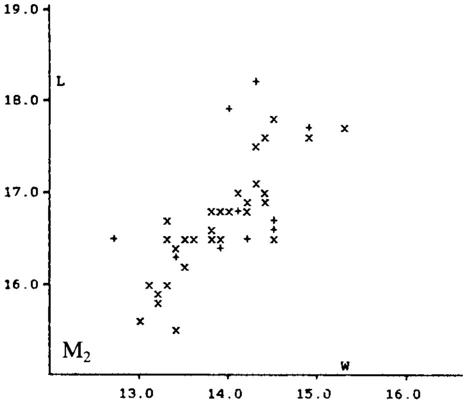
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L
M_2
W
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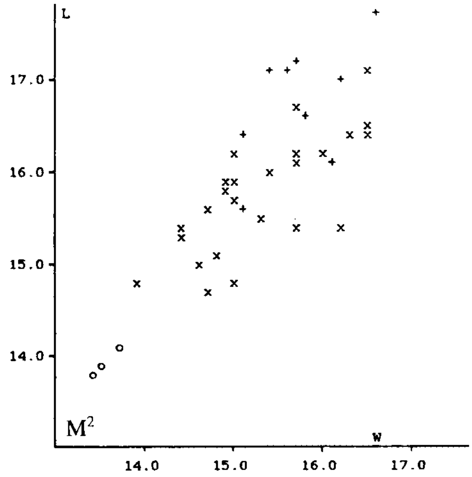
17.0
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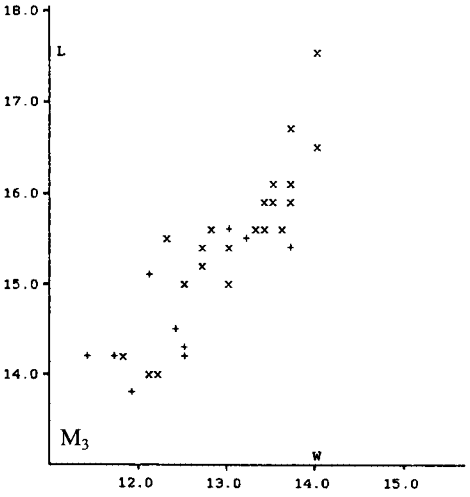
18.0
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L
M_3
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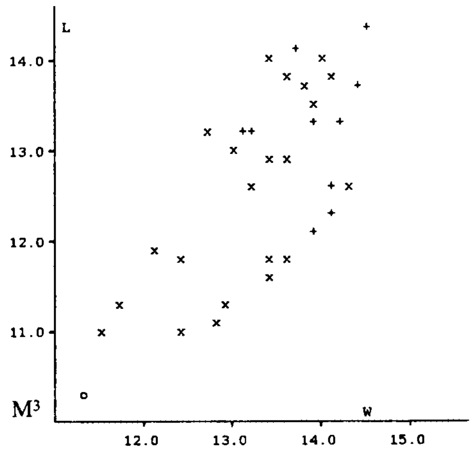
14.0
13.0
12.0
11.0
L
M^3
W
12.0
13.0
14.0
15.0

M_1 – The prelobe is very short, due to the blunt anterior wall of the anteroconid, and to the very advanced position of the metaconid. There is no lingually descending ridge on the anteroconid. Labially there is one, which leaves the protosinusid open. The metalophulid is posterior. The sinus is wide and transverse. The mesosinusid is wide, and blocked by the extremely long cingulum ridge descending from the metaconid. The mesolophid is short, and there is a small ectomesolophid. There is no posterior hypolophulid. The posterosinusid is wide and open.

Discussion – These two specimens differ from the rest of the cricetid material by their great width in relation to the length. If they are not aberrant specimens, they probably belong to an unknown species.

Conclusions

Hitherto, efforts of European mammalian paleontologists to establish a sound and detailed bio- and chronostratigraphic framework, were focused on the Neogene. The first attempt to make a subdivision of the Paleogene has been made by Thaler (1966), but it was not generally accepted. The first one to establish a continental stage in the Paleogene was Bosma (1974). Though this Upper Eocene stage (the Headonian) has a well-exposed type-section, with various superposed fossiliferous levels, it has hardly been considered as a chronostratigraphic unit and specialists on Paleogene faunas have generally preferred to use reference levels and mammal units as established at the Munich Symposium (Fahlbusch, 1976), and the MP zones created at the Mainz Symposium (Schmidt-Kittler, 1987, pp. 15-19).

However, we reject the artificial framework of the MP zones for a number of reasons. First of all, the MP units cannot be considered to be stratigraphic terms since they do not comply with the rules of stratigraphic nomenclature.

Secondly, many localities used as reference levels for the MP zones are fissure fillings, mainly from the Quercy, that lack any stratigraphic context. Even worse, our own research and studies by Mayo (1987a, 1987b), and Engesser & Mayo (1987) have shown that many fissure fillings from the Quercy may contain mixtures of faunas from various biozones.

For that matter the evolutionary lineages supposed by Vianey-Liaud (1976, 1979) and Vianey-Liaud & Schmidt-Kittler (1987) should be treated with the greatest care.

Research on the biostratigraphy and chronostratigraphy of the Spanish Paleogene is still in a preliminary stage, and for the moment, for the correlation of the locality of Pareja, we depend on the supposed *Issiodoromys minor-terminus* lineage. If this lineage is correct the fauna of Pareja might be somewhat older than that of Carrascosa because of the slightly more primitive evolutionary stage of *I. minor.*

Because of the abundance of *Issiodoromys minor* (26 %) of the rodent fauna) we think that relatively dry conditions prevailed. *Archaeomys (A.) gervaisi* (15 %), *Gliravus caracensis* (17 %), and *Eucricetodon margaritae* (9 %) corroborate this assumption. *Eomys* cf. *molassicus*, as a dweller of humid biotopes, only constitutes 4 % of the rodent fauna.

References

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

Alvarez, M.A., 1987. Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior español. – Scripta Geol., 86: 1-207, 33 pls.

Alvarez, M.A., R. Daams, J.I. Lacomba, N. López Martínez & M.A. Sacristán, 1987. Succession of micromammal faunas in the Oligocene of Spain. – Münchner Geowiss. Abh., A, 10: 43-48.

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

Bosma, A.A., 1974. Rodent biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. – Utrecht Micropal. Bull., 1: 1-128, 7 pls.

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

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

Comte, B., & M. Vianey-Liaud, 1987. Nouveaux Eomyidae du Palèogéne d'Europe occidentale. – C.R. Acad. Sci. Paris, 304, 2, 15: 951-955.

Daams, R., 1981. The dental pattern of the dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. – Utrecht Micropal. Bull., Spec. Publ. 3: 1-115, 5 pls.

Daams, R., J.I. Lacomba & N. López Martínez, 1986. Nuevas faunas de micromamíferos del Terciario Continental de la Depresión Intermedia (Provincia de Cuenca, España Centro-Oriental). – Estudios Geol., 42: 181-196.

Díaz Molina, M., & N. López Martínez, 1979. El Terciario continental de la Depresión Intermedia (Cuenca). Bioestratigrafía y Paleogeografía. – Estudios Geol., 35: 149-167.

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

Engesser, B., 1982. Le plus grand représentant du genre *Eomys* (Rodentia, Mammalia) de l'Oligocène de l'Europe: *Eomys huerzeleri* nov. sp. – Géobios 15, 2: 261-266.

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

Engesser, B., & N.A. Mayo, 1987. A biozonation of the Lower Freshwater Molasse (Oligocene and Agenian) of Switzerland and Savoy on the basis of fossil mammals. – Münchner Geowiss. Abh., A, 10: 67-84.

Fahlbusch, V., 1970. Populationsverschiebungen bei tertiären Nagetieren, eine Studie an oligozänen und miozänen Eomyidae Europas. – Abh. Bayer. Akad. Wiss., Math.-naturw. Kl., N.F., 145: 1-136, 11 pls.

Fahlbusch, V., 1976. Report on the International Symposium on mammalian stratigraphy of the European Tertiary. – Newsl. Stratigr., 5, 2-3: 160-167.

Freudenthal, M., 1966. On the mammalian fauna of the *Hipparion*- beds in the Calatayud-Teruel Basin (prov. Zaragoza, Spain). Part 1. The genera *Cricetodon* and *Ruscinomys* (Rodentia). – Proc. Kon. Ned. Akad. Wetensch., B, 69, 2: 296-316, 2 pls.

Freudenthal, M., 1989. Redescription of *Eucricetodon atavus* (Misonne, 1957) (Rodentia) from Hoogbutsel (Belgium). – Bull. Kon. Belg. Inst. Natuurw., Aardwetensch., 58 (in press).

Freudenthal, M., & R. Daams, 1988. Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon, Fahlbuschia, Pseudofahlbuschia* nov. gen., and *Renzimys*. – Scripta Geol., Spec. Issue 1: 133-252, 16 pls.

Hugueney, M., 1969. Les rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Bransat (Allier). – Doc. Lab. Ge'ol. Fac. Sci. Lyon, 34: 1-227, 5 pls.

Hugueney, M., 1980. La faune de mammifères de l'Oligocène moyen de Saint-Menoux (Allier). – Rev. Sci. Bourbonnais, 1980: 57-72.

Hugueney, M., R. Adrover, E. Moissenet & N. Schmidt-Kittler, 1987. Les Mammifères de Vivel del Ri'o (prov. de Teruel, Espagne; Oligocène supérieur): un riche gisement stratifié en comparaison ave des faunes karstiques. – Münchner Geowiss. Abh., A, 10: 117-130, 1 pl.

Lacomba, J.I., & J. Morales, 1987. Los mamíferos del Oligoceno superior de Carrascosa del Campo (Prov. Cuenca, España). – Münchner Geowiss. Abh., A, 10: 289-299, 2 pls.

Mayo, N.A., 1987a. The development of the Theridomyidae in the Oligocene Molasse of Switzerland and Savoy. – Münchner Geowiss. Abh., A, 10: 159-168.

Mayo, N.A., 1987b. Die Verschiedenaltrigkeit der fossilen Säugetierfaunen aus den Karstspalten des Quercy. – Eclog. Geol. Helv., 80, 3: 1087-1104.

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

Parent, J.P., 1983. Anatomie et valeur systématique de l'oreille moyenne des rongeurs actuels et fossiles. – Mammalia, 47, 1: 93-122.

Schlosser, M., 1884. Die Nager des europäischen Tertiärs. – Palaeontographica, 31: 19-162,pl. 5-12.

Schmidt-Kittler, N. (ed.), 1987. International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene - Mainz, Febr. 18th - 21st, 1987. – Münchner Geowiss. Abh., A, 10: 1-312.

Stehlin, H.G., & S. Schaub, 1951. Die Trigonodontie der simplicidentaten Nager. – Schweiz. Pal. Abh., 67: 1-385.

Thaler, L., 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. – Mém. Mus. Natl. Hist. Nat., C, 17: 1-295, 27 pls.

Vianey-Liaud, M., 1969. Rongeurs de l'Oligocène moyen provenant de nouvelles fouilles dans les Phosphorites du Quercy. – Palaeovertebrata, 2, 5: 209-239.

Vianey-Liaud, M., 1972. L'évolution du genre *Theridomys* a' l'Oligocène moyen. Interêt biostratigraphique. – Bull. Mus. Natl. Hist. Nat., Paris, 3, 98, Sci. Terre, 18: 295-372, 4 pls.

Vianey-Liaud, M., 1976. Les Issiodoromyinae (Rodentia, Theridomyidae) de l'Eocène supérieur à l'Oligocène supérieur en Europe occidentale. – Palaeovertebrata, 7, 1-2: 1-115.

Vianey-Liaud, M., 1979. Evolution des rongeurs a' l'Oligocène en Europe occidentale. – Palaeontographica, A, 166, 4-6: 136-236.

Vianey-Liaud, M., & N. Schmidt-Kittler, 1987. Biostratigraphie de l'Oligocène d'Europe: importance des lignées-guides de rongeurs Theridomyidae, et particulièrement des *Issiodoromys*. – Münchner Geowiss. Abh., A, 10: 211-216.

Vollmayr, T., 1966. Oberoligozäne Gliridae (Rodentia, Mammalia) aus der süddeutschen Faltenmolasse. – Mitt. Bay. Staatssamml. Pal. Hist. Geol., 6: 65-107, 3 pls.