

NEW GLIRIDAE AND CRICETIDAE FROM THE MIDDLE AND UPPER MIOCENE OF THE DUERO BASIN, SPAIN*

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SUMMARY.— In this paper a new genus (*Myolidus*, Gliridae) and four new species (*Ramys perezii*, *Peridyromys rex*, Gliridae; *Megacricetodon lopezae*, *Megacricetodon freudenthali*, Cricetidae), are described from the upper Aragonian and lower Vallesian of the Torremormojón and Ampudia sections. These sections contain six and three superposed localities respectively.

RESUMEN.— Se describe por primera vez un género (*Myolidus*, Gliridae) y cuatro especies (*Ramys perezii*, *Peridyromys rex*, Gliridae; *Megacricetodon lopezae*, *Megacricetodon freudenthali*, Cricetidae). Estos taxones se distribuyen en el Aragoniense superior y el Vallesiense inferior de las secuencias de Torremormojón y Ampudia, que contienen seis y tres yacimientos superpuestos respectivamente.

INTRODUCTION

The Duero Basin is located in the northwestern part of the Iberian Peninsula. Two sections have been studied in this basin, containing four assemblage zones (ÁLVAREZ-SIERRA & GARCÍA-MORENO, 1985) that are correlated with the units defined in other Spanish basins, as Calatayud-Daroca (DAAMS & FREUDENTHAL, 1981) and the Vallés-Penedés (AGUSTÍ, 1981), on the basis of shared taxa.

HERNÁNDEZ-PACHECO (1915) and ROYO GÓMEZ (1922) studied for the first time the continental fauna of the Duero Basin (large mammals and shells, respectively). Other studies on large mammals in this zone are by DANTIN (1912), HERNÁNDEZ-PACHECO (1914, 1930), CRUSAFONT & VILLALTA (1951, 1954),

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BERGONIOUX & CROUZEL (1958), CRUSAFONT & TRUYOLS (1960) and MAZO (1977). LÓPEZ-MARTÍNEZ & SANCHÍZ (1982) studied for the first time the small mammal faunas and proposed a preliminary biostratigraphy. ÁLVAREZ-SIERRA (1983) and GARCÍA-MORENO (1983) studied respectively the Vallesian and upper Aragonian of the Torremormojón section and mentioned the presence of five new taxa.

The collections described here are stored in the Department of Paleontology of the Complutense University of Madrid.

The cheek teeth have been measured partly with a Leith Orthoplan Microscope with measuring clocks and partly with a wild Microscope with a measuring objective.

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SYSTEMATICS

Order Rodentia, BODWICH, 1821.

Family Gliridae, THOMAS, 1897.

Genus *Peridyromys* STEHLIN & SCHAUB, 1951.

Diagnosis: STEHLIN & SCHAUB, 1951.

Type species: *Peridyromys murinus* (POMEL, 1853).

Other species belonging to this genus:

P. prosper THALER, 1966.

P. brailloni (THALER, 1966).

P. aquatilis de BRUIJN & MOLTZER, 1974.

P. jaejeri AGUILAR, 1974.

Peridyromys rex GARCÍA-MORENO *nov. sp.*

Pl. 4, fig. 1-10

Holotype: M¹ sin., TM6bRG1. Coll. Universidad Complutense de Madrid (Pl. 4, fig. 1).

Type locality: Torremormojón 6b (TM6b), province of Palencia, Duero Basin, Spain.

Type level: *M. aff. crusafonti* assemblage zone (GARCÍA-MORENO, 1983).

Age: Upper Aragonian (continental middle Miocene).

Derivatio nominis: from the latin rex = king, due to its huge size.

Diagnosis: Big sized *Peridyromys*, of which M¹ are longer than 1.41 mm. and wider than 1.85 mm. Rectangular outlined molars, concave occlusal surface, seven or eight ridges in the upper molars and seven to nine ridges in the lower ones. There is no endoloph. The anterolophid and the metalophid may be connected at the protoconid of the M₁ and M₂.

Differential diagnosis: *Peridyromys rex* differs from the other species belonging to the genus by its larger size and by the higher frequency of morphotypes with anterolophid and metalophid connected at the protoconid of the M₁ and M₂. It differs from *P. aquatilis* by the absence of an endoloph in the M³.

It differs from the species belonging to the genus *Miodyromys* by its V-shaped trigone, by having no tendency to form an ectolophid in the M₁ and M₂, by the design of the ridges, more regular, and by its lower ratio Length P⁴/length M¹.

P. rex differs from the simple dental pattern species belonging to the genus *Pseudodryomys* (*P. simplicidens*, *P. robustus*), by its more complex dental pattern, especially in the lower molars and in the M³. It differs from the rest of the species belonging to *Pseudodryomys* by the absence of morphotypes in which the anterior centrolophid is longer than the posterior one in the M³.

It differs from the species belonging to the genus *Myomimus* by its more complex dental pattern in the lower molars, by its higher frequency of morphotypes of the M₁ and M₂ with the metalophid reaching the metaconid, by the existence of morphotypes of the M₁ and M₂ with the anterolophid connected to the metalophid at the protoconid, by its lower length P⁴/length M¹ ratio and by the outline of the M¹, always rectangular.

MATERIAL AND MEASUREMENTS

Localities	Elem.	L			N	W		
		min.	mean.	max.		min.	mean.	max.
TM6b	D ⁴	0.85	0.90	0.95	2	1.19	1.19	1.19
	P ⁴	—	1.09	—	1	—	1.42	—
	M ¹	1.42	1.44	1.47	2	1.86	1.90	1.95
	M ³	1.22	1.35	1.42	3	1.64	1.70	1.76
	P ₄	0.97	0.98	1.00	2	0.85	0.90	0.95
	M ₁	—	1.66	—	1	—	1.66	—
	M ₂	—	1.61	—	1	—	1.76	—
	M ₃	—	1.57	—	1	—	1.61	—
TM6a	M ₁	—	1.61	—	1	—	1.66	—

DESCRIPTION

Material corresponding to Torremormojón 6b (TM6b):

D⁴. They have a triangular outline, and a concave occlusal surface. They show four main ridges and two centrolophs. The anteroloph is reduced. An extra ridge between the protoloph and the anterior centroloph may be present. The anterior centroloph is always longer than the posterior one. The protoloph and the metaloph are connected by their lingual ends, forming a Y.

P⁴. It has an elliptical outline, and the occlusal surface is somewhat concave. It shows four main ridges and a posterior centroloph.

M¹. They have a rectangular outline and a concave occlusal surface. The protocone is high. The ridges have a regular design. There are four main ridges and two centrlophs, and an extra ridge between the protoloph and the anterior centroloph. There is a molar with a tubercle between the metaloph and the posteroloph. In one of the cases, the centrolophs are connected to the protoloph and the metaloph at the paracone and the metacone, and their lingual edges are in contact. The other molar shows an isolated posterior centroloph. There is not an endoloph, being the anteroloph and the protoloph well separated. The metaloph may be connected or separated from the posteroloph at the metacone indistinctly. The anteroloph is not connected to the protoloph in the paracone.

M³. They have a trapezium shaped outline. The paracone is high. They show four main ridges and two centrolophs, and one or two extra ridges, which lie

between the protoloph and the anterior centroloph and between the posterior centroloph and the metaloph. The centrolophs are connected to the protoloph and the metaloph at the paracone and the metacone in two out of three cases. The anterior centroloph is longer than the posterior one in two molars. There is no endoloph. The anteroloph and the posteroloph may be connected or separated from the protoloph and the metaloph in the paracone and metacone indistinctly.

P₄. They have a triangular outline. The mesolophid and posterolophid are well distinguishable, but the rest of the elements of the occlusal surface are not developed. The anterior part is very reduced.

M₁. It has a rectangular outline. The posterior part is wider than the anterior one. There are four main ridges and a centrolophid. It shows four extra ridges, one between the metalophid and the centrolophid, another one between the mesolophid and the centrolophid and the last two between the mesolophid and the posterolophid. The centrolophid is divided into several segments, is 1/4 the molar width long and is connected to the anterolophid both by its lingual and labial edges.

M₂. It has a square shaped outline. There are four main ridges and a centrolophid. It shows two extra ridges, being one between the metalophid and the centrolophid and the other one between the mesolophid and the posterolophid. The centrolophid is connected to the anterolophid by its lingual edge, and is 3/4 the molar width long. The metalophid reaches the anterolophid by its lingual edge, but both ridges are separated from each other by their labial edges. This molar is two-rooted.

M₃. It has a triangular outline. There are four main ridges and a centrolophid. It shows three extra ridges; one of them lies between the anterolophid and the metalophid and the other two are between the mesolophid and the posterolophid. The centrolophid is connected to the anterolophid by its lingual edge.

Material corresponding to Torremormojón 6a (TM6a):

M₁. It has a rectangular outline. There are four main ridges and a centrolophid. There are three extra ridges, one of them between the metalophid and the centrolophid, another one between the centrolophid and the mesolophid, and the last one between the mesolophid and the posterolophid. The centrolophid is connected to the anterolophid by its lingual edge. The metalophid reaches the anterolophid both by its lingual and labial edges.

DISCUSSION

The material of Torremormojón 6a and Torremormojón 6b is morphologically and biometrically homogeneous, and it is characterized by its large size and a rather simple dental pattern. This is the largest glirid ever attributed to *Peridyromys*.

The inclusion of this species in a particular genus has been based on morphological characters. Genera as *Glirulus* and *Microdyromys* are far from *P. rex*, having and endoloph in the upper molars, as a major difference.

The simpler species of *Pseudodryomys* (*P. simplicidens*, *P. robustus*), are distinguishable from *P. rex* by its lower number of extra ridges in the upper and lower molars. *Pseudodryomys ibericus*, as the other *Pseudodryomys* almost always shows and endoloph in the M³, which is not known in *P. rex*.

Myomimus differs from *P. rex* by its simpler dental pattern, the higher frequency of morphotypes of the M¹ and M² with square shaped outline, the wider valleys and the contacts between ridges (see differential diagnosis, p. 147). Moreover, most of the M₁ and M₂ of *Myomimus* are three-rooted. The only M₂ of *P. rex* in which the number of roots could be observed, is two-rooted.

The closer genera to this new glirid are *Miodyromys* and *Peridyromys*. It is a diagnostical character of *Miodyromys* to show a U-shaped trigone. *P. rex* has a V-shaped trigone. Moreover, species as *M. aegercii* are far from *P. rex*, with a more complex dental pattern, especially in the upper molars.

The genus *Peridyromys* agrees in its diagnosis with *P. rex*. *P. murinus* is morphologically close to *P. rex*, being difficult to distinguish both species except for biometrical differences.

Genus *Ramys* GARCÍA-MORENO & LÓPEZ MARTÍNEZ, in press.

Type species: *Ramys multicrestatus* (DE BRUIJN, 1966).

Other species attributed to the genus: *Ramys perezii* nov. sp.

Ramys perezii ÁLVAREZ-SIERRA nov. sp.

Pl. 1, 2 and 3; figs. 1-6, 11-14

Synonymy: "*Peridyromys*" aff. *multicrestatus* in LÓPEZ & SANCHÍZ, 1982.

Holotype: M¹⁻² dex., cat. nr. AMP 9-77 (Pl. 2, fig. 1) stored in the collections of the Universidad Complutense of Madrid.

Type locality: Ampudia 9 (AMP 9), Prov. Palencia, Duero Basin, Spain.

Type level: *Cricetulodon hartenbergeri* assemblage zone (lower Vallesian, upper Miocene), ÁLVAREZ-SIERRA et al. 1985.

Derivatio Nominis: *perezi* - after Dr. A. Pérez González of the Instituto Geológico y Minero de España (I.G.M.E.) because of his interest in the biostratigraphy of continental basins, and because of the coordination of the geological studies of the Duero Basin.

Diagnosis: Medium-sized dormouse with concave occlusal surface. The valleys between the ridges are narrow. The $M^{1,2}$ have one to four accessory ridges, and the anterior centroloph is longer than the posterior one. The $M_{1,2}$ are three-rooted and have three or four extra ridges. An accessory ridge between the centrolophid and the mesolophid is situated in 50-70% of $M_{1,2}$. The centrolophid is long, but in the M_3 this ridge is shorter than in the $M_{1,2}$.

Differential diagnosis: *Ramys perezi* n. sp. differs from *Ramys multicrestatus* (DE BRUIJN, 1966) by the following features:

- a) Its larger size.
- b) The low frequency of $M^{1,2}$ with endoloph (one out of 32 specimens only).
- c) The extra ridge between the centrolophid and mesolophid in $M_{1,2}$ is more frequently present in *R. perezi*.
- d) In the lower molars the anterolophid is always labially isolated, and the mesolophid is always lingually connected to the posterolophid.

Ramys perezi differs from *Miodyromys hamadryas* (MAYOR, 1899) and *Miodyromys biradiculus* MAYR, 1979 by:

- a) Its larger size.
- b) Its more complicated dental pattern of the upper molars.
- c) The presence of the posterior extra ridge in all P_4 's.

R. perezi differs from *M. hamadryas* also by the longer centrolophid of the $M_{1,2}$.

Moreover, *R. perezi* differs from *M. biradiculus* by the three-rooted lower molars and the more complicated M^3 .

Ramys perezi differs from *Miodyromys aegercii* BAUDELLOT, 1972 from the German localities Schönenberg and Sandelszhausen (MAYR, 1979) by:

- a) The labially and lingually isolated anteroloph of P^4 .
- b) The posterior centroloph being always connected to the metacone in $M^{1,2}$.
- c) In one $M^{1,2}$ of *R. perezi* an accessory ridge is present outside the trigone.
- d) In the $M^{1,2}$ of *R. perezi* the posteroloph is, or is not, connected to the metacone, whereas in *M. aegercii* this ridge is always isolated.
- e) The metalophid and centrolophid of P_4 are better developed.
- f) The centrolophid of $M_{1,2}$ is longer and the anterolophid is labially isolated in all specimens.

MATERIAL AND MEASUREMENTS

		L			N	W			N ⁺
		min.	mean.	max.		min.	mean.	max.	
AMP9	D ⁴	0.73	0.76	0.79	9/10	0.92	0.96	1.03	19
	P ⁴	0.79	0.89	1.02	15/13	1.05	1.20	1.33	16
	M ¹	1.16	1.28	1.42	6	1.35	1.51	1.65	
	M ²	1.23	1.26	1.31	5/7	1.47	1.52	1.58	32
	M ^{1,2}	1.18	1.28	1.41	7/3	1.53	1.54	1.57	
	M ³	1.00	1.08	1.15	12/11	1.34	1.39	1.43	14
	D ₄	0.81	0.84	0.86	15	0.71	0.77	0.87	15
	P ₄	0.94	1.04	1.20	11	0.95	1.03	1.11	15
	M ₁	1.23	1.36	1.52	9	1.24	1.36	1.46	9
	M ₂	1.25	1.34	1.47	10	1.32	1.40	1.49	12
	M ₃	1.05	1.21	1.29	12/11	1.05	1.25	1.36	15
TM 3	M ₁	—	1.30	—	1	—	1.32	—	2
TM 4	D ⁴	—	0.81	—	1	—	1.01	—	1
	P ⁴	0.84	0.93	0.99	7/6	1.10	1.19	1.36	8
	M ^{1,2}	1.25	1.31	1.39	4/3	1.56	1.59	1.62	4
	M ³	—	1.11	—	1	—	1.29	—	2
	D ₄	0.83	0.91	1.02	3	0.72	0.79	0.88	3
	P ₄	0.95	1.04	1.14	8	0.90	1.02	1.10	8
	M ₁	1.34	1.39	1.44	2	1.30	1.31	1.32	2
	M ₂	1.31	1.36	1.42	4/3	1.28	1.30	1.33	4
TM 5	M ₃	1.16	1.21	1.29	7	1.13	1.21	1.28	10
	D ⁴	0.75	0.75	0.76	2	0.95	0.97	1.00	2
	M ¹	1.28	1.28	1.29	2	1.43	1.54	1.66	2
	M ²	1.28	1.35	1.42	4	1.42	1.54	1.66	4
	M ³	1.00	1.14	1.28	5	1.14	1.38	1.61	5
	D ₄	0.57	0.61	0.66	2	0.61	0.63	0.66	2
	P ₄	—	0.95	—	1	—	1.04	—	1
	M ₂	1.33	1.39	1.42	4	1.42	1.55	1.66	4
	M ₃	—	1.28	—	1	—	1.38	—	1

N⁺) Total number of studied specimens.

DESCRIPTION

Material corresponding to *Ampudia* 9 (AMP 9).

General features of the upper dentition: The occlusal surface is concave and the valleys are narrow. Generally the accessory ridges are lower and narrower than the main ridges.

D⁴. Triangular circumference. Two morphotypes are present:

a) This type is of relatively large size. The four main ridges and two centrolophs are present. The short anteroloph is connected to the protoloph, with the exception of one specimen, and to the anterior centroloph at the paracone, but at the lingual border it ends freely. The protoloph and the metaloph meet at the protocone. The posterior centroloph is connected to the metaloph at the metacone, and it is shorter than the anterior centroloph. In two specimens the posteroloph is an isolated ridge both lingually and labially, but in the other specimen the posteroloph is connected to the protocone. A small extra ridge is present between the posterior centroloph and the metaloph.

b) This type is smaller than the above described one and it has a simpler dental pattern. The four main ridges and one centroloph are present. The anteroloph is ill-developed, and consists of a cusp in most specimens. In 4 cases it reaches the middle half of the tooth, and in 5 specimens it is labially connected to the protoloph. Lingually the anteroloph ends freely in all specimens. The proto- and metaloph meet at the protocone. The only centroloph present is the posterior one, or it has a central position. The posteroloph ends generally freely at the labial border, with the exception of one specimen, and lingually it reaches the protocone in two cases only.

P⁴. Two types are present; a relatively small one and a relatively large one. The dental pattern is similar, however. It has an oval circumference. The four main ridges and one centroloph are present. In fresh, or little worn specimens, the anteroloph is an isolated ridge. The posterior centroloph is generally connected to the metacone. In one specimen only it represents a central cusp. In six specimens the posteroloph is connected to the metacone, and lingually this ridge is connected to the protocone, with one exception.

M^{1,2}. The M¹ and M² could not be distinguished from one another in all specimens. Generally the M² is narrower posteriorly than anteriorly. M¹ and M² are described together as a consequence. The four main ridges and two centrolophs are present. The anteroloph reaches the paracone in 4 specimens, and in 12 it is separated from this cusp. Lingually the anteroloph ends closely to the protocone, but it reaches this cusp in one specimen only, thus forming an endoloph. The anterior centroloph is always longer than the posterior one. The anterior

centroloph is connected to the paracone in 22 specimens, and in the other 10 specimens this ridge is separated from the paracone by a furrow. The posterior centroloph is connected to the metacone. The posteroloph reaches the metacone in 7 cases, and in 10 specimens it is isolated labially.

The position of the extra ridges enabled us to distinguish four morphotypes. These are as follows:

- a) One extra ridge is present, which is situated between the protoloph and the anterior centroloph. Two specimens have this morphology.
- b) The same extra ridge as described above, is present, and a cusp between the two centrolophs. This morphology has been found in two specimens as well.
- c) Two accessory ridges are present; one between the protoloph and the anterior centroloph, and another smaller one between the posterior centroloph and the metaloph. Two specimens are of this type.
- d) This is the most complicated type. The extra ridge between the protoloph and the anterior centroloph is present, and between the two centrolophs, cusps or small extra ridges are situated. Moreover, a small accessory ridge, sometimes cusplike, is situated between the posterior centroloph and the metaloph. One of the 19 specimens of this type presents various small cusps distributed over the occlusal surface.

In two specimens the anterior extra ridge is connected to the posterior centroloph. (Pl. 2, fig. 2). In one specimen the two centrolophs and the anterior extra ridge meet in the central valley. (Pl. 2, fig. 3). One specimen shows a slight ornamentation on the lingual border.

M³. The occlusal surface is less concave than that of the M^{1,2}. The dental pattern consists of the four main ridges, the two centrolophs and various accessory ridges. In 11 out of 15 specimens an endoloph is present. In three specimens, the anteroloph and posteroloph do not reach the paracone and metacone respectively. In the central part of the tooth one to five extra ridges are present. Generally one well-developed extra ridge is situated centrally, although this ridge may be confused with a centroloph. The other accessory ridges are of varying length, width and height. In some specimens a small extra ridge is present between the anteroloph and the protoloph.

D₄. It has a rounded circumference. The anterior part is reduced. When recognizable, the anterolophid is a semicircular, well-developed ridge. In one specimen the anterolophid meets the posterolophid labially. The meta- and centrolophid are isolated ridges, and these ridges can be observed in two specimens only. Generally, the central part of the D₄ presents a chaotic pattern. The mesolophid meets the posterolophid lingually, with two exceptions. An extra ridge is present in the posterior valley.

P₄. The P₄ is larger than the D₄. The anterior part is slightly reduced. The four main ridges and the centrolophid are present. The anterolophid is a semicircular, well-developed ridge. Labially this ridge is connected to the metalophid with the exception of two specimens. Generally the anterolophid is connected to the metaconid. The mesolophid and posterolophid are well-developed ridges, which meet lingually in all specimens, and labially in three specimens only. In two specimens a cusp is present between the anterolophid and the metalophid, and in one specimen an accessory ridge is situated at the same place. A well-developed extra ridge is present in the posterior valley.

M₁. The valleys are narrow. The four main ridges and the centrolophid are present. The anterolophid is lingually connected to the centrolophid, and when the tooth is little worn, the anterolophid ends freely labially. In two out of nine specimens the metalophid is connected to the metaconid. The large centrolophid is connected to the mesolophid at the labial border in one specimen only. The mesolophid meets the posterolophid at the lingual border of the molar. All main ridges, with the exception of the anterolophid, have anteriorly pointing labial ends. In all specimens at least three accessory ridges are present: a small one between the anterolophid and the metalophid, a small one between the metalophid and the centrolophid, and a large one between the mesolophid and the posterolophid. Six specimens present an extra ridge between the centrolophid and the mesolophid. One molar has an accessory ridge behind the posterolophid. The extra ridges are smaller than the main ridges, with the exception of the well-developed ridge in the posterior valley.

M₂. Basically the M₂ is similar to the M₁. In 7 out of 12 specimens an extra ridge is present between the centrolophid and the mesolophid.

M₃. The anterolophid does not reach the labial border, and the labial ends of the other main ridges curve around towards the anterior side of the tooth. Basically the M₃ resembles the M₁ and M₂. The centrolophid is slightly shorter and the morphology is more simple, however. All specimens have two accessory ridges at least; a well-developed one between the anterolophid and the metalophid, and a large one in the posterior valley. Only three specimens show a small extra ridge between the metalophid and the centrolophid.

Material corresponding to Torremormojón 4 and 3 (TM 4 and TM 3).

On the whole, *Ramys perezii* from TM 4 and TM 3, presents the same dental pattern as in AMP 9. Therefore, we restrict our description to some peculiarities of these assemblages.

D⁴. The only specimen present, is from TM 4, and it is relatively large. A small extra ridge is present between the protoloph and the centroloph.

P⁴. In three out of eight specimens the posteroloph is connected to the protocone. The posteroloph does not reach the metacone. In four specimens a small cusp is present between the protoloph and the posterior centroloph.

M^{1,2}. The antero- and posteroloph are isolated from the paracone and metacone, respectively.

M³. An endoloph is absent in the two M³ found in TM 4.

D₄. The anterolophid is lingually connected to the centrolophid, and labially it meets the metalophid. A small extra ridge is present between the centrolophid and the mesolophid, which is connected to the latter ridge.

P₄. There is no extra ridge between the anterolophid and the metalophid. In some specimens a small accessory cusp is present.

M₁. In one specimen the centrolophid meets the mesolophid labially, thus closing the central valley.

M₃. In two specimens an extra ridge is present between the centrolophid and the mesolophid.

Material corresponding to Torremormojón 5 (TM 5).

The material from TM 5 is similar to that of AMP 9, although some features should be mentioned. These are the smaller size of the D₄ and the larger width of the M³ in TM 5. Furthermore, the only M₃ found, presents 4 extra ridges, whereas in AMP 9 this element has three accessory ridges only.

DISCUSSION

Ramys perezii has various features in common with *R. multicrostus* (DE BRUIJN, 1966) from the lower Vallesian of Pedregueras 2A. Some of these are the three-rooted lower molars, the complexity of the dental pattern of the upper molars and the length of the centrolophid. On the other hand differences are present as well. These are the larger size of *R. perezii*, and the lower frequency of specimens with endolophs. Generally the lower molars of *R. perezii* have a more complicated dental pattern, as the most common morphotype of *R. multicrostus* has two accessory ridges only (GARCÍA-MORENO & LÓPEZ MARTÍNEZ, in press). Moreover the extra ridge between the centrolophid and the mesolophid is more frequent in *R. perezii*.

The small differences that present the assemblages from TM 3, TM 4 and TM 5 with respect to AMP 9, are attributed to intraspecific variation.

R. perezii from AMP 9 has a P⁴ which differentiates in two size groups. In TM 4 only one size group is present, which is intermediate between those of AMP 9. Similar size differences within one assemblage have been mentioned by DAAMS (1981) in *Dryomys nitedula* Pallas, 1778 from Ulu Dag (Turkey) and in *Microdyromys* DE BRUIJN, 1966 from Anwil. We therefore consider these differences to be intraspecific.

Miodyromys aegercii BAUDELLOT, 1972 from the middle Miocene German localities of Schöenberg and Sandelszhausen (MAYR, 1979) has various features in common with *R. perezii*. These are the three-rooted lower molars and the similar complicated pattern of upper and lower molars. Differences between these two species, are:

- a) The oval shaped P⁴ of *R. perezii*.
- b) the labially and lingually isolated anteroloph of P⁴ of *R. perezii*.
- c) the always isolated, both labially and lingually, anteroloph of M^{1,2} of *M. aegercii*.
- d) Extra ridge outside the trigone, are absent in *M. aegercii*.
- e) the always labially isolated posteroloph of M^{1,2} of *M. aegercii*.
- f) the better developed metalophid and centrolophid of P₄ of *R. perezii*.
- g) the longer centrolophid of M_{1,2} of *R. perezii*.
- h) the labially isolated anterolophid of M_{1,2} of *R. perezii*.

Genus *Myolidus* ÁLVAREZ-SIERRA *nov. gen.*

Derivatio Nominis: *Myo* - Greek for mouse, and *Olid* -after Valladolid.

Type Species: *Myolidus sinuosus nov. gen. nov. sp.*

Diagnosis: Medium-sized Gliridae with concave occlusal surface, and a very complicated dental pattern. The valleys and ridges are narrow. The ridges are not straight, but are more or less undulating. In the upper molars the ridges are generally at right angles with the longitudinal axis of the tooth. An endoloph is present, and the anterior centroloph is longer than the posterior one. The number of extra ridges varies between 2 and 6. The M₁ has an endolophid. The long centrolophid is labially connected to the mesolophid in the majority of the M_{1,2}. Six accessory ridges are present in the M_{1,2}.

Differential diagnosis: *Myolidus* differs from other genera with complicated dental pattern by the strongly undulating ridges and by the main and extra ridges being of more or less the same height and width.

Myolidus differs from *Microdyromys* DE BRUIJN 1966, *Dryomys* PALLAS 1778 and *Branssatoglis* HUGUENEY 1967 by:

- a) the presence of an endolophid in the M_1 .
- b) the high frequency of a labial connection between the centrolophid and the mesolophid in $M_{1,2}$.
- c) the more complicated dental pattern.
- d) the smaller size of *Microdyromys* and *Dryomys*.
- a) the lingual ornamentation of the upper molars.
- b) the transverse ridges at right angles to the longitudinal axis of the tooth.
- c) the presence of an endolophid in M_1 .
- d) the labial connection between the centrolophid and the mesolophid in $M_{1,2}$.

Myolidus differs from *Glirulus* THOMAS, 1906 by:

- a) its more complicated dental pattern.
- b) the labial connection between the centrolophid and the mesolophid of $M_{1,2}$.

Myolidus differs from *Paraglrulus* ENGESSER, 1972 by:

- a) the presence of an endolophid in M_1 .
- b) the labial connection between the centrolophid and the mesolophid.
- c) the anterior centroloph never reaching the endoloph.

Myolidus differs from *Ebromys* CUENCA, 1985 by:

- a) the ornamentation on the lingual border of the upper molars.
- b) the presence of an endoloph.
- c) its narrower valleys.
- d) its less complicated P_4 .
- e) the presence of labial connections between the ridges of the upper molars.

Myolidus differs from Gliridae X in ENGESSER, 1972 by:

- a) the lingual ornamentation of the upper molars.
- b) the presence of an endolophid in M^1 .
- c) the labial connection between the centrolophid and mesolophid of $M_{1,2}$.

Myolidus sinuosus ÁLVAREZ-SIERRA *nov. sp.*

Pl. 1 and 3; fig. 7-8, 1-10

Derivatio Nominis: *sinuosus* -because of the undulating ridges.

Holotype: M_2 dext. (AMP 3-33), Pl. 3, fig. 3, stored in the collections of the Universidad Complutense of Madrid.

Type Locality: Ampudia 3 (AMP 3), prov. of Palencia, duero Basin, Spain.

Type Level: *Progonomys hispanicus* assemblage zone, ÁLVAREZ-SIERRA et. al. 1985, upper Vallesian, upper Miocene.

Diagnosis and differential diagnosis: see genus.

Synonymy: Gliridae nov. cf. *Glirulus* in LÓPEZ & SANCHÍZ, 1982.

MATERIAL AND MEASUREMENTS

		L			N	W			N ⁺
		min.	mean.	max.		min.	mean.	max.	
AMP 3	P ⁴	—	0.91	—	1	—	1.14	—	2
	M ²	—	1.28	—	1	—	1.51	—	2
	M ³	—	1.04	—	1/2	1.39	1.41	1.42	2
	P ₄	—	1.02	—	1/2	0.99	1.01	1.02	2
	M ₁	—	1.37	—	1	—	1.35	—	1
	M ₂	1.25	1.31	1.42	3/2	1.29	1.35	1.42	4
	M ₃	—	1.15	—	2	1.16	1.20	1.25	2
AMP 3A	D ⁴	—	0.79	—	1	—	0.93	—	1
	M ³	—	1.06	—	1	—	1.40	—	1
	P ₄	—	1.07	—	1	—	1.02	—	1
	M ₂	—	1.42	—	1	—	1.42	—	1
TM 1A	P ⁴	—	0.91	—	1/0	—	—	—	1
TM 1	P ⁴	0.82	0.85	0.88	2/3	1.01	1.08	1.15	3
	M ^{1,2}	—	—	—	0/1	—	1.50	—	1
	M ³	—	1.00	—	1	—	1.38	—	2
	P ₄	—	0.81	—	1	—	0.88	—	1
	M ₁	1.18	1.23	1.29	4/2	1.26	1.28	1.29	4
	M ₂	—	1.12	—	1	—	1.21	—	1
	M ₃	0.88	0.94	1.00	2	0.89	0.94	0.99	2

N⁺) total number of studied specimens.

DESCRIPTION

Material corresponding to Ampudia 3 (AMP3):

Upper dentition: The occlusal surface is concave. The lingual border shows ornamentation. The valleys and undulating ridges are narrow. Generally the main ridges are of the same width as the accessory ridges. The anteroloph and posteroloph do not reach the paracone and metacone, respectively. An endoloph is present.

P⁴. The four main ridges and the two centrolophs are present. The anterior centroloph is shorter than the posterior one, and it is not connected to the paracone. In one of the specimens two small cusps are present; one between the posterior centroloph and the metaloph, and one between the metaloph and the posteroloph.

M^{1,2}. The four main ridges and the two centrolophs are present. The anterior centroloph is longer than the posterior one, although in some specimens these two ridges meet in the central valley to form a composite ridge. The anterior and posterior centroloph are connected to the paracone and metacone respectively. Three long extra ridges are present; one between the anteroloph and the protoloph, which is connected to the paracone, one between the centrolophs nearly reaching the endoloph, and one between the metaloph and the posteroloph. Three smaller extra ridges are present in the following positions; between the protoloph and the anterior centroloph, between the central extra ridge and the posterior centroloph, and between the posterior centroloph and the metaloph.

M³. The four main ridges and various extra ridges are present. The two centrolophs meet in the central valley. The anterior centroloph is connected to the paracone. The posterior centroloph is isolated from the metacone. Four accessory ridges of variable size and position are present. A long extra ridge is always present between the anteroloph and the protoloph. Small accessory cusps are present at various places of the occlusal surface.

Lower dentition; The occlusal surface is concave. The valleys and undulating ridges are narrow. Generally the main ridges and extra ridges are of the same width. Complicated dental pattern.

P₄. A rounded circumference. The four main ridges and the centrolophid are present. In one specimen the anterolophid and posterolophid meet both lingually and labially to form a circular ridge. The other specimen is too worn to observe this character. One of the specimens has three accessory ridges: one between the metalophid and centrolophid, one between the centrolophid and the mesolophid, and one in the posterior valley.

M₁. The four main ridges and the centrolophid are present. The anterolophid does not reach the labial border. The metalophid and posterolophid curve forward at the labial border. The centrolophid and mesolophid meet at the labial border, thus closing the central valley. An endolophid is present. The centrolophid and mesolophid reach the endolophid, but the metalophid is separated from the endolophid. Six accessory ridges are present; one between the anterolophid and metalophid, one between the metalophid and the centrolophid meeting lingually the metalophid, one between the centrolophid and the mesolophid, and three in the posterior valley, of which the central one is the largest.

M₂. The four main ridges and the centrolophid are present. The anterolophid does not reach the labial border, but the centrolophid does. One out of four specimens has an endolophid. Lingually the anterolophid meets the centrolophid, and the mesolophid the posterolophid. In three specimens the long centrolophid meets the mesolophid near the labial border. Lingually the metalophid ends freely. Six extra ridges are present, which are situated as in the M₁. Small accessory cusps are present as well. The extra ridges may be interrupted.

M₃. An endolophid is absent. At the lingual border the anterolophid meets the centrolophid, and the mesolophid the posterolophid. The metalophid is separated from the metaconid. The centrolophid meets the mesolophid at the labial border. A long extra ridge is present between the anterolophid and the metalophid. A small extra ridge is present between the metalophid and the centrolophid, which is lingually connected to the metalophid in one specimen. Another small extra ridge is situated between the centrolophid and the mesolophid, and a long accessory ridge is present between the mesolophid and posterolophid. One of the specimens has an accessory cusp in the lingual part of the posterior valley.

Material corresponding to Ampudia 3A (AMP3A):

D⁴. The circumference of the occlusal surface is triangular. The four main ridges and the two centrolophs are present. The valleys are narrow. The anteroloph is an isolated ridge. The metaloph does not reach the protocone. The anterior centroloph and the posterior one are connected to the paracone and metacone respectively. Two extra ridges are present; one between the protoloph and the anterior centroloph, and one between the metaloph and the posteroloph.

P⁴. The dental pattern of this element agrees rather well with that of the type locality. Some slight differences have been observed, however. In one of the specimens the anterior centroloph is longer than the posterior one, and an extra ridge is present between the protoloph and the anterior centroloph.

M^{1,2}. The posterior centroloph is labially isolated, and only two extra ridges are present. Furthermore the dental pattern agrees with that of the type locality.

M³. Five extra ridges are present. The remaining dental pattern is similar to that of the type locality.

P₄. An endolophid is present. The anterolophid and posterolophid reach the endolophid, the other ridges do not. A longitudinal ridge extends from the metalophid towards the posterior extra ridge, without reaching it, however. A small extra ridge is present between the anterolophid and the metalophid.

M₂. This element agrees with the M₂ of the type locality.

Material corresponding to Torremormojón 1 and 1A (TM1 and TM1A):

Generally the material from these localities agrees well with that of the type locality Ampudia 3. Therefore, only the deviating features are mentioned.

P⁴. One specimen shows a posterior centroloph which is longer than the anterior one. In the other specimens the anterior centroloph is longer than the posterior one. One specimen has an extra ridge between the protoloph and the anterior centroloph.

M^{1,2}. Only two accessory ridges are present. One is present between the protoloph and the anterior centroloph, and the other one between anteroloph and the protoloph.

P₄. The anterolophid, metalophid, centrolophid and mesolophid meet at the labial border.

M₁. The anterolophid is centrally interrupted.

M₂. In the only M₂ present, the anterolophid is connected to the metalophid at the labial border. The posterior extra ridge is labially connected to the posterolophid.

M₃. The anterolophid and metalophid meet labially, but lingually the metalophid is isolated. The centrolophid is not connected to the mesolophid at the labial border. The mesolophid meets the posterolophid labially.

DISCUSSION

Myolidus sinuosus nov. gen. n. sp. has been found in four localities of late Miocene age in the Duero Basin in the province of Palencia: Ampudia 3 (type locality), Ampudia 3A, Torremormojón 1 and Torremormojón 1A.

Some slight differences have been observed between the assemblages of Ampudia on one hand, and those of Torremormojón on the other. First of all the

P₄ and lower molars from TM 1 and 1A are somewhat smaller. Furthermore, the only M^{1,2} present in TM 1 has only, two accessory ridges, contrasting with the six extra ridges present in the type material. Other slight differences are present as well, but in general we consider all mentioned deviations to fall within the intra-specific variation.

In the differential diagnosis it is demonstrated that *Myolidus* is characterized by a set of features that separates it well from other dormouse genera. Most characteristic features are the undulating ridges, the ornamentation of the endoloph, the parallel running ridges at right angles with the longitudinal axis of the tooth, the presence of an endolophid and the labial connection between the centrolophid and the mesolophid in the M₁ and M₂.

The phylogenetic relations of the majority of the Gliridae are still unknown. Some authors (VAN DE WEERD, 1976; MAYR, 1979; AGUSTI, 1981; DAAMS, 1981 and 1985) have described lineages of various dormouse species, but phylogenetic relationships between genera have never been clearly demonstrated. GARCÍA-MORENO & LÓPEZ-MARTÍNEZ (in press) compare *Ramys multicrestatus* from Pedregueras 2A with twelve other Gliridae species from 5 genera. Their numerical taxonomical study shows that the observed groups are characterized by a combination of features, and not by the exclusion of features. Therefore it seems hazardous to attach great importance to one specific character.

The possible phylogenetic relations of the new dormice from this paper, remain obscure so far. We suggest the necessity of a revision of the diagnostic features of the subfamilies of the Gliridae in order to establish more phylogenetically related groups than those existing today.

Family Cricetidae STEHLIN & SCHAUB, 1951.

Subfamily Cricetodontinae STEHLIN & SCHAUB, 1951.

Genus *Megacricetodon* FAHLBUSCH, 1964.

Type species: *Megacricetodon gregarius* (SCHAUB, 1925).

Other species belonging to the genus:

M. minor (LARTET, 1851).

M. bourgeoisi (SCHAUB, 1925).

M. gregarius (SCHAUB, 1925).

M. ibericus (SCHAUB, 1944).

M. collongensis (MEIN, 1958).

M. primitivus (FREUDENTHAL, 1963).

M. crusafonti (FREUDENTHAL, 1963).

M. bavaricus FAHLBUSCH, 1964.

M. similis FAHLBUSCH, 1964.

M. minutus DAXNER, 1967.

M. debruijni FREUDENTHAL, 1968.

M. gersii AGUILAR, 1980.

M. germanicus AGUILAR, 1980.

Megacricetodon lopezae, GARCÍA-MORENO *nov. sp.*

Pl. 5, fig. 1-12

Synonymies: *M. similis* FAHLBUSCH, 1964 in FREUDENTHAL, 1968. *M. aff. crusafonti* GARCÍA-MORENO, 1983.

Holotype: Fragmentary dextral mandible, with M_1 and M_2 . SIM2RH1 (Pl. 5, fig. 1).

Type locality: Simancas 2 (SIM2), province of Valladolid, Duero Basin, Spain.

Type level: *Megacricetodon lopezae* assemblage zone (ÁLVAREZ-SIERRA et al. 1985).

Age: Late Aragonian (continental middle Miocene).

Derivatio nominis: Dedicated to Professor Dr. Nieves López Martínez, Universidad Complutense de Madrid, Spain.

Diagnosis: *Megacricetodon* larger than *M. minor* and smaller than *M. crusafonti*. The anteroconid is simple in 50% of the molars, it divided into two cusps in 25% of the cases, and it is slightly split in 25% of the cases.

The anterocone is divided in 70% of the specimens, being slightly split in the rest of the cases. The mesolophid is frequently absent, but a short mesolophid may be present. There is often a short mesoloph, but in some cases it may be long or it may be absent. In the M^2 , the internal valley is frequently directed forwards, and rarely it may be transverse. The posterolophid is always long. In the M^1 , there is often a short posteroloph, but long and absent posterolophs may appear with a significative frequency. In the M^2 the posteroloph is long.

Differential diagnosis: *M. lopezae* differs from *M. crusafonti-ibericus* also present in Simancas 2 by its smaller size (Fig. 1), and by the higher frequency of primitive morphotypes in the upper and lower molars; *M. similis* has the same size as *M. lopezae*, but the former often shows a simple anteroconid, and frequently shows a posterior spur of the paracone on the M^1 and M^2 , currently connected to the mesoloph, which is long in most of the cases. *M. lopezae* does not share this morphology.

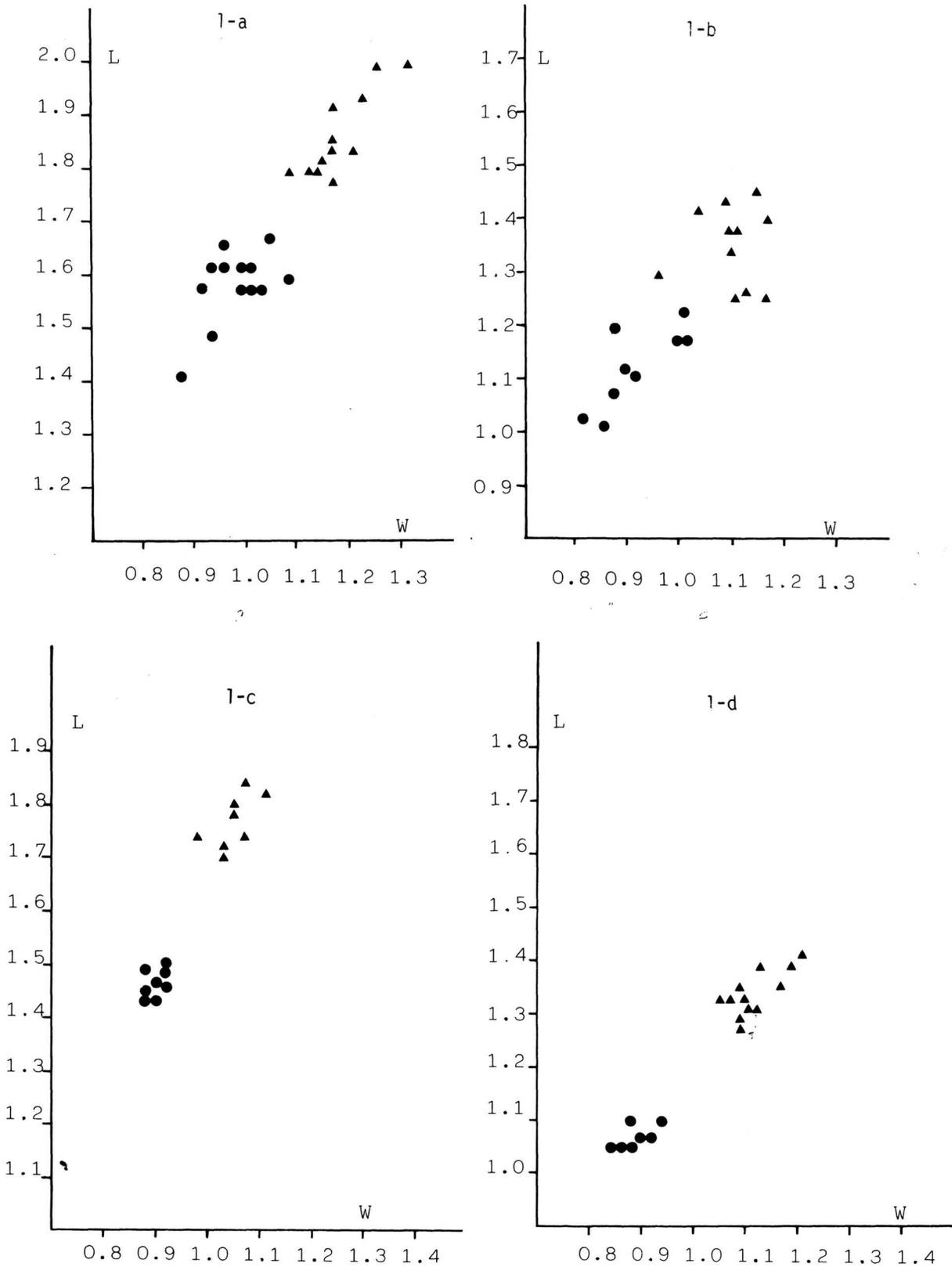


Figure 1. Scatter diagrams of *M. Lopezae* (●) and *M. crusafonti-ibericus* (▲) of Simancas 2. a: M^1 , b: M^2 , c: M_1 , d: M_2 .

MATERIAL AND MEASUREMENTS

Locality	Elem.	L			N	W		
		min.	mean.	max.		min.	mean.	max.
	M ₁	1.43	1.46	1.50	8	0.88	0.89	0.92
	M ₂	1.05	1.07	1.11	8	0.86	0.89	0.92
SIM2	M ₃	0.70	0.77	0.84	7	0.84	0.97	1.03
	M ¹	1.39	1.56	1.66	13	0.88	0.98	1.09
	M ²	1.00	1.11	1.22	9	0.82	0.92	1.02
	M ³	0.58	0.65	0.72	3/2	0.76	0.77	0.78

DESCRIPTION

M₁. In four cases, the anteroconid is simple, in two cases it is slightly split with a short anterior furrow and in the other two cases, the anteroconid is divided with a long anterior furrow. There may be a ridge in the anterior part of the molar. In five cases, there is not a mesolophid. In other three specimens, the mesolophid is short. The metalophulid and the hipolophulid are directed backwards in four cases; in three molars they are perpendicularly connected to the longitudinal ridge, and in one specimen they are directed forwards. In five molars, the external valley is transverse, and in three cases the external valley is directed forwards. In one specimen, the metalophulid is connected to the anterolophulid. In seven molars, the metalophulid is connected to the anterior edge of the protoconid. In six cases, the hipolophulid is connected to the anterior edge of the hipoconid. In the rest of the molars, the hipolophulid is connected to the ectolophid.

M₂. The metalophulid is connected to the anterolophid in one case. In six molars, there is a lingual anterolophid which is well separated from the metalophulid by a wide valley. The metalophulid is always directed forwards, and it is always connected to the ridge which joins the protoconid and the anterolophid. In four molars, there is no mesolophid; in three cases, there is a short mesolophid. Six specimens show a transverse external valley, and in the last one the external valley is directed backwards.

M₃. It is rather difficult to distinguish the M₃ of *M. lopezae* from the ones of *M. crusafonti-ibericus*, which appears associated in Simancas 2, although the bigger specimens should belong to *M. crusafonti-ibericus* and the smaller ones to *M. lopezae*.

There is always a long anterolophid in the anterior part of the molar. In two cases, there is not a mesolophid, and in other two there is a short one. The entoconid is very small. In two molars, the metalophulid is connected to the anterior edge of the protoconid; in one case, the metalophulid is connected to the protoconid itself, and in the last molar, the metalophulid is interrupted, separated from the protoconid by a narrow valley.

M¹. In nine molars, the anterocone is divided and there is a long furrow in the anterior part of this cusp. In four cases, the ridge is short. There may appear a ridge in the anterior edge of the molar. The protolophule is always simple; it is directed backwards in eight cases and it is transverse in the other five. In ten specimens, the protolophule is connected to the posterior edge of the procone; in three molars, it is connected to the ectoloph. The metalophule is always directed backwards. In ten molars, the metalophule is connected to the posterior edge or the hipoconid. In three cases, it is connected to the posteroloph. There is not a mesoloph in four molars. In six specimens there is a short mesoloph, and in the last three, the mesoloph is long. In seven cases the internal valley is transverse, being in the rest of the molars directed forwards. The posteroloph is long in two cases, short in nine, and absent in the last two cases.

M². The internal valley is directed forwards in seven molars, and it is transverse in two. In one of the molars with transverse internal valley, the protolophule is double. The rest are simple. Six of the latter cases show the protolophule directed forwards and in the last two, the protolophule is transverse to the longitudinal ridge. In three specimens there is not a mesoloph; four cases have a short one and the last two show a long mesoloph. The posteroloph is always long.

M³. In one of the molars, the protolophule is connected to a thickening of the anterolophid. In a different specimen, the protolophule is connected immediately after the anterolophid. In the third molar, this character is not observable. In one of the cases there is a ridge which starts in the protolophule and points back longitudinally, towards a small cusp in the centre of the molar, and in that point, the ridge is divided in two; one of the branches goes towards the labial edge of the molar and the other one towards the hipocone. In the other two molars there is a similar morphology, but it lacks the ridge which starts in the protolophule. The central valley is very small.

DISCUSSION

M. crusafonti-ibericus coexists with *M. lopezae* in Simancas 2, and both species are easily distinguishable due to a wide discontinuity in the size of this population

of *Megacricetodon* (fig. 1). There is also a discontinuity in the distribution of some morphotypes, as the internal valley of the M² (fig. 2a) and the anteroconid (fig. 2b). In the M² of *M. lopezae* there is an internal valley directed forwards in a 77% of the M², while in *M. crusafonti-ibericus* of Simancas 2 this morphotype is unknown. It is also significative the larger frequency of simple anteroconids in *M. lopezae* (50%), than in *M. crusafonti-ibericus* of Simancas 2 (25%).

In the latter *Megacricetodon* the morphotype of split anteroconid predominates (75%). Such a morphotype is represented in *M. lopezae* just by a 25%.

Comparing the size of *M. lopezae* with populations of *M. crusafonti* from outside the Duero Basin, like the ones of Daroca Basin (FREUDENTHAL, 1968), we found a certain overlapping of the scattered points, but *M. lopezae* is always around the lower limits of size of *M. crusafonti*. Comparison of the size of *M. lopezae* with other contemporary populations of *M. crusafonti-ibericus* of the Duero Basin -Torrelobatón 1, Otero 2 (upper Aragonian), García Moreno, in prep.- always permits to distinguish easily both species.

FREUDENTHAL & CUENCA (1984) have proposed a «variation coefficient» (V') which is used to estimate the degree of heterogeneity of a sample: its application to the cricetids permits to decide if a sample contains more than one species. This coefficient depends on the range (R = difference between the maximum and the minimum of length or width), and the middle point (M = arithmetic mean of the maximum and minimum), according to the following ratio:

$$V' = \frac{100 R}{M}$$

The value of V' has been determined for the M¹ and M₁ of *Megacricetodon* of Simancas 2, since referring to measuring errors, «It seems that M¹ and M₁ are the least variable teeth of cricetids (...)», FREUDENTHAL & CUENCA, 1984, p. 8. Values of V' obtained for the population of *Megacricetodon* of Simancas 2, and compared with the ones of the 140 populations analyzed by FREUDENTHAL & CUENCA, confirm the existence in Simancas 2 of two species of *Megacricetodon*.

Phylogenetic relationships of *M. lopezae* will be discussed together with *M. freudenthali* (p. 173).

Megacricetodon freudenthali GARCÍA-MORENO nov. sp.

Pl. 6, fig. 1-13

Synonymys: *Megacricetodon minor-debruijani* ÁLVAREZ-SIERRA, 1983.

Megacricetodon minor-debruijani ÁLVAREZ-SIERRA & GARCÍA-MORENO, 1985.

Holotype: M¹ sin. AMP9RH15 (Pl. 6, fig. 1).

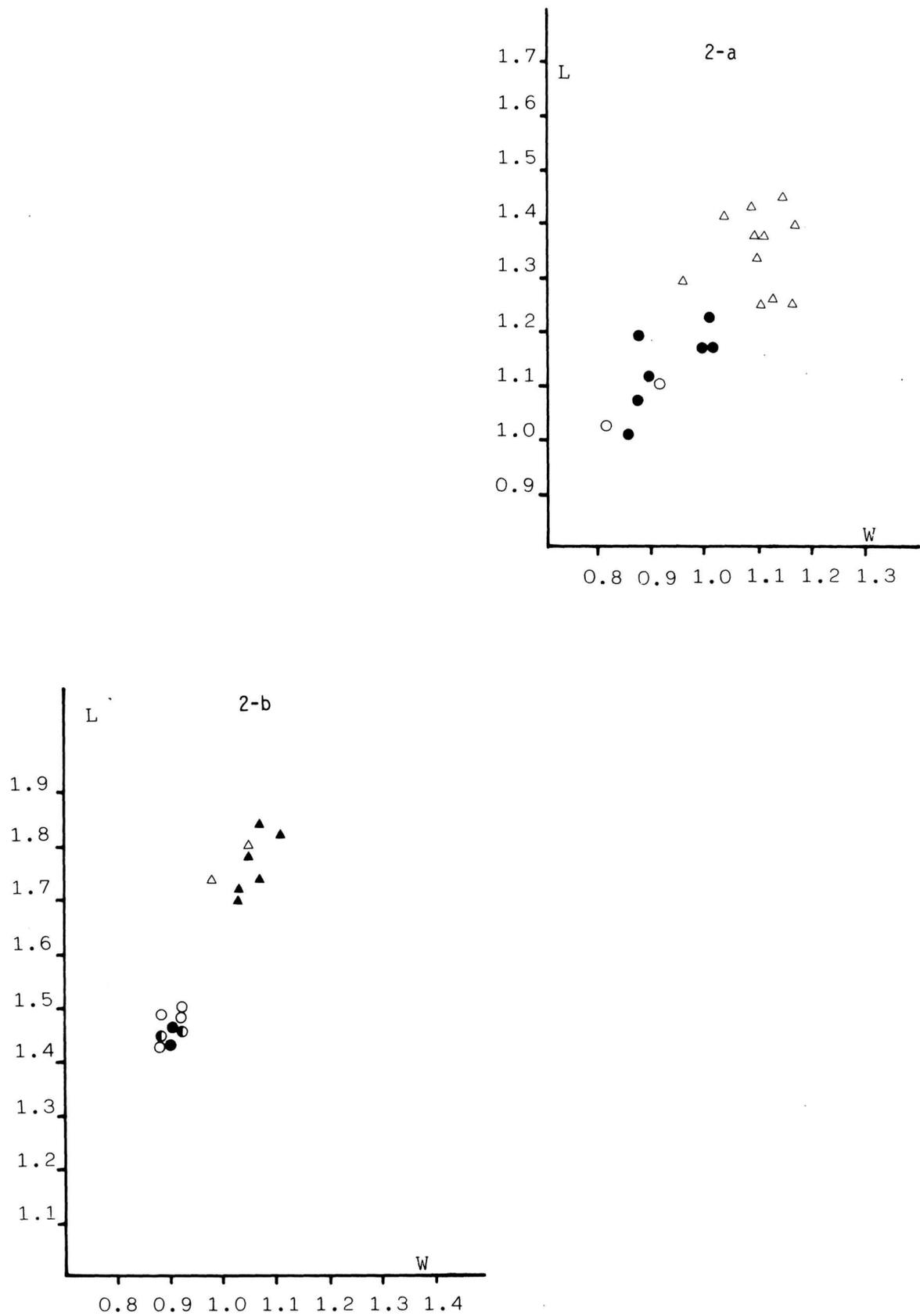


Figura 2. a- Distribution of the morphotypes of the internal valley of the M^2-0 : transverse, •: directed forwards. b-distribution of the morphotypes of the anteroconid of the M_1-0 : simple, ◯ :slightly split, ● split.
 ◯-: *M. Lopezae*
 Δ-: *M. crusafonti-ibericus*.

Type locality: Ampudia 9 (AMP9), province of Palencia, Spain.

Type level: *Cricetulodon hartenbergeri* assemblage zone (ÁLVAREZ-SIERRA et al. 1985).

Age: Lower Vallesian (continental upper Miocene).

Derivatio nominis: Dedicated to Dr. M. Freudenthal, Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands.

Diagnosis: Small sized *Megacricetodon*. The anteroconid is simple. The M_1 and M_2 almost always have an mesolophid, which often is long. The anterocone is simple or bilobulated, and the anterior furrow is very slight or absent. The M^1 and M^2 almost always have a mesoloph. The external valley in the M^2 is generally directed forwards. In the M^1 and M_1 the posteroloph ('id) is always long, as well as in the M^2 .

Differential diagnosis: *M. freudenthali* differs from *M. debuijni* by its simple anteroconids. It differs from *M. minor* by its higher frequency of primitive morphotypes, especially the frequency of simple anterocones and the frequency of long mesolophs ('ids) and posterolophs ('ids). The rest of the known species of *Megacricetodon* with simple anteroconids have a morphology still more simple than *M. freudenthali*.

MATERIAL AND MEASUREMENTS

Localities	Elem.	L			N	W		
		min.	mean.	max.		min.	mean.	max.
AMP9	M_1	1.25	1.33	1.37	5	0.76	0.79	0.84
	M_2	1.00	1.03	1.09	6	0.76	0.80	0.84
	M_3	0.88	0.94	1.00	3	0.74	0.75	0.78
	M^1	1.34	1.34	1.34	4	0.81	0.86	0.91
	M^2	0.96	1.06	1.13	4	0.88	0.90	0.92
TM ₃	M_1	—	1.14	—	1	—	0.73	—
	M_2	—	1.04	—	1	—	0.81	—
	M^1	1.33	1.36	1.39	2	0.91	0.92	0.94
TM ₄	M^1	1.33	1.36	1.39	4	0.85	0.91	0.98
	M^2	—	1.06	—	1	—	0.93	—

DESCRIPTION

Material corresponding to *Ampudia* 9 (AMP9):

M_1 . The anteroconid is always simple. Two molars have two ridges which start in the anteroconid; the labial one reaches the posterior part of the protoconid. The lingual one is smaller. In other two specimens, there is only the labial ridge. The last molar, does not show these ridges, but in this specimen the anterolophid bifurcates in its middle part; the lingual branch reaches the anteroconid, but the labial branch keep separated from the anteroconid by a narrow valley. There is a molar in which the anteroconid is isolated, because of the reduction of the anterolophid, which does not reach it. In two cases there is a short mesolophid; in the last three molars, there is a long mesolophid. The external valley is transverse in three molars. In the last two it is directed forwards. The metalophulid and the hipolophulid are transverse. The metalophulid is connected to the anterior edge of the protoconid in four cases, and it is connected to the anterolophid in one specimen. The hipolophulid is connected to the anterior edge of the hipoconid in four molars; in the last one it is connected to the endoloph. There is a molar in which a ridge starts from the metalophulid and has a longitudinal direction. In another case, there is a small ridge in a simetrical position respect to the mesolophid. There is always a long posterolophid, separated from the entoconid by a wide valley.

M_2 . In one specimen, the metalophulid is connected to the anterolophid. In another one, it is connected at the protoconid. The third molar does not have an anterolophid. There is one case in which the metalophulid is connected to the anterior part of the protoconid. In the last two molars this connection is not observable. The anteroloph is double in two out of six specimens. In one molar there is a small ridge which starts in the metalophulid. There is a long mesolophid in three molars and a short one in other three cases. The internal valley is transverse in four molars and it is directed backwards in the last two molars. The hipolophulid is transverse and it is always connected at the anterior edge of the hipoconid. The posterolophid is long in four cases and it is short in two. There is a posterior spur of the metaconid in one case.

M_3 . Two out of three molars show anterolophid. The metalophulid is connected at the anterior part of the protoconid. There is a posterior spur of the metaconid in one case. In two molars, mesolophid and posterolophid are connected and enclose the entoconid. In the last molar, the mesolophid is hardly observable. The internal valley is directed bakwards.

M^1 . The anterocone is simple or bilobulated. There is not an anterior furrow of the anterocone, or the furrow is very slight (the anterocone fastly becomes simple

when worn). In one molar, the anterocone is simple. In two cases, the anterocone lobes are simetric. In the third one, there is a lobe bigger than the other one. In this molar, there is a ridge which starts in the labial lobe (the bigger one), pointing backwards. The protolophule is simple and transverse, and it is connected in two molars at the posterior part of the protoconid and in the other two cases at the ectoloph. The mesoloph is always long. The metalophule points backwards in two cases and it is transverse in the other two. The internal valley is always directed forwards. The posteroloph is always long.

M². There is always an anteroloph, which is double in two cases. The protoloph is connected at the posterior part of the protocone in two molars, and in the other two cases this ridge is connected somewhat before. In three molars there are a long mesoloph. In the last one the mesoloph is short. The internal valley is directed forwards in three molars and it is transverse in one case. The metalophule is transverse and it is connected to the hipocone in two cases, while in the other two molars, the connection appears in the anterior edge of this cusp. The posteroloph is always long.

Material corresponding to Torremormojón 3 (TM3):

Differences between the population of Torremormojón 3 and the type population are: the M₁ does not have a mesolophid. The metalophulid points forwards. In the M₂, the hipolophulid is directed forwards. In the M¹ there is not a mesoloph, and the internal valley is transverse.

Material corresponding to Torremormojón 4 (TM4):

Differences between the population of Torremormojón 4 and the type population are: in the M² the mesoloph is very short.

DISCUSSION

Similarities between *M. minor*, *M. debruijni* and *M. freudenthali* are mainly biometrical. Morphological differences are remarkable and in short they are:

Anterocone: FREUDENTHAL (1968) describes, in the type locality of *M. debruijni*, only morphotypes with split anterocone. Upper Aragonian *M. minor* populations in Almazán Basin (SESÉ, 1980) and Calatayud-Daroca Basin (FREUDENTHAL, 1963), always show split anterocones with a deep anterior furrow. In contrast, *M. freudenthali* never has a completely split anterocone; there are not a deep anterior furrow, and the bilobulation of the anterocone is so slight that when the anterocone is somewhat worn it fastly becomes a simple cusp.

Anteroconid: *M. freudenthali* always shows a simple anteroconid. *M. minor*

populations of Nombrevilla (FREUDENTHAL, 1963), Manchones 1 (FREUDENTHAL, 1963) and the *M. minor-debruijini* of Escobosa de Calatañazor (SESÉ, 1980), may show morphotypes of bilobulated anteroconid, although they always make a small number. *M. debruijini* populations of Pedregueras 2A, Pedregueras 2C (FREUDENTHAL, 1968) and Carrilanga 1 (DAAMS pers. com.) typically show split anteroconids in wide percentages.

Mesolophid in the M_1 : percentages of long mesolophids in Pedregueras 2A, Pedregueras 2C and Carrilanga 1 are respectively 6.5%, 0% and 18% (DAAMS, pers. com.) while this morphotype appears in *M. freudenthali* in 50% of the cases. *M. minor* populations of Nombrevilla and Escobosa never show long mesolophids. Nevertheless, the percentages of this morphotype in Manchones 1 and Ampudia 9 are similar.

Mesolophid in the M_2 : *M. freudenthali* has a higher frequency of long mesolophids than *M. debruijini*. The former one has a 42% of long mesolophids, while in Pedregueras 2A, Pedregueras 2C and Carrilanga 1, percentages are 13%, 2% and 30% respectively (DAAMS, pers. com.). On the other hand, the percentages of absent mesolophids in pedregueras 2A, Pedregueras 2C and Carrilanga 1 are 52%, 10% and 33% respectively (DAAMS, pers. com.), while in *M. freudenthali* is 0% (the seven M_2 of Ampudia 9 have a mesolophid). Something similar happens with Nombrevilla and Escobosa *M. minor* populations, where percentage of long mesolophids are 22% and 0%, and percentages of absent mesolophids are 22% and 100% respectively (DAAMS, pers. com.). In Manchones 1, only five M_2 are known. Three have a long mesolophid and the other two do not show this ridge (DAAMS, pers. com.).

Morphological differences between *M. freudenthali* and *M. minor-M. debruijini* are enough to separate both taxa at first sight. Although perhaps some populations which appear in our analysis may not be documented enough to permit establishing undoubtful discontinuities in the distribution of some characters, it is very significant that every difference between *M. freudenthali* and the other two *Megacricetodon* species always point to characterize the morphology of the former cricetid as plesiomorphic in respect to the one of *M. minor* and *M. debruijini*. From this point of view, it seems that the phylogenetical relationship between these three *Megacricetodon* could be clear. However, a complete analysis presents an interesting phylogenetical problem which will be dealt with later.

PHYLOGENETIC RELATIONSHIPS

The coexistence of *M. lopezae* and *M. crusafonti-ibericus* in Simancas 2 (fig. 3) probably means that both taxa are not related in an ancestor-descendant way. On

the other hand, it is as difficult to suppose that *M. lopezae* belongs to the *M. crusafonti-M. ibericus* lineage as to think that the former belongs to the *M. minor-M. debruijni* lineage. This lineage is present in the Duero Basin in older, contemporaneous and more modern localities than Simancas 2. Moreover, *M. lopezae* coexists with *M. minor* in Torremormojón 6b (fig. 3). *M. Lopezae* cannot be an ancestor of *M. freudenthali* because the latter one shows a more simple morphology than *M. lopezae* being associated with more modern faunas (*Cricetulodon* assemblages; lower Vallesian). Therefore, at least three lineages of *Megacricetodon* are recognizable in the Aragonian of the Duero Basin. *M. lopezae* should be a representative of an independent lineage, contemporaneous of the large sized *M. crusafonti-M. ibericus* and of the small sized *M. minor-M. debruijni*.

All the characters which differentiate *M. freudenthali* from *M. minor* are plesiomorphic in the former one. Both are of the same size, and ignoring their stratigraphical positions they could be phylogenetically related. In fact, *M. freudenthali* could agree with an hypothetic ancestor of *M. minor* (see comparison between *M. freudenthali* and *M. minor*, p. 172). Nevertheless, *M. freudenthali* occurs in more modern levels than *M. minor*, in *Cricetulodon* and *Progonomys* assemblages (lower Vallesian), with no other representative of the genus *Megacricetodon*.

Assemblages of *M. minor-M. debruijni* occur in the Duero Basin in the older localities Torrelobaton 1 and Otero 2 (GARCÍA MORENO, in. prep.), in association with *M. ibericus* (upper Aragonian and lower Vallesian). Therefore, the stratigraphic position of *M. freudenthali* and *M. minor-M. debruijni* in the Duero Basin implies that *M. freudenthali* is not an ancestor of *M. minor*. Neither it can be a descendant, because of its simple dental pattern. It is neither possible, to relate *M. freudenthali* with the *M. crusafonti-M. ibericus* lineage, because both taxa are morphologically and biometrically very different. Therefore, it is only possible to guess that *M. freudenthali* is an immigrant which represents a new evolutive lineage, with a great morphological primitivism during the lower vallesian. That is to say, there are four recognizable evolutive lineages of *Megacricetodon* in the upper Aragonian and lower Vallesian of the Duero Basin.

It is a striking fact that the discovery of *M. freudenthali* as the representative of a new line is based on its inversed stratigraphic position in respect to *M. minor*, its theoretical descendant. If the discovery of *M. freudenthali* were an isolated datum, the biostratigraphic position of Ampudia 9 could be considered to be lower than the duerian localities with *M. minor*. This a frequent kind of error when studying isolated localities and it illustrates once more the needing of using always sequences which contain several stratigraphically superposed localities. The type locality of *M. freudenthali* is included in a sequence which contains three micromammal localities (ÁLVAREZ-SIERRA & GARCÍA-MORENO, 1985).

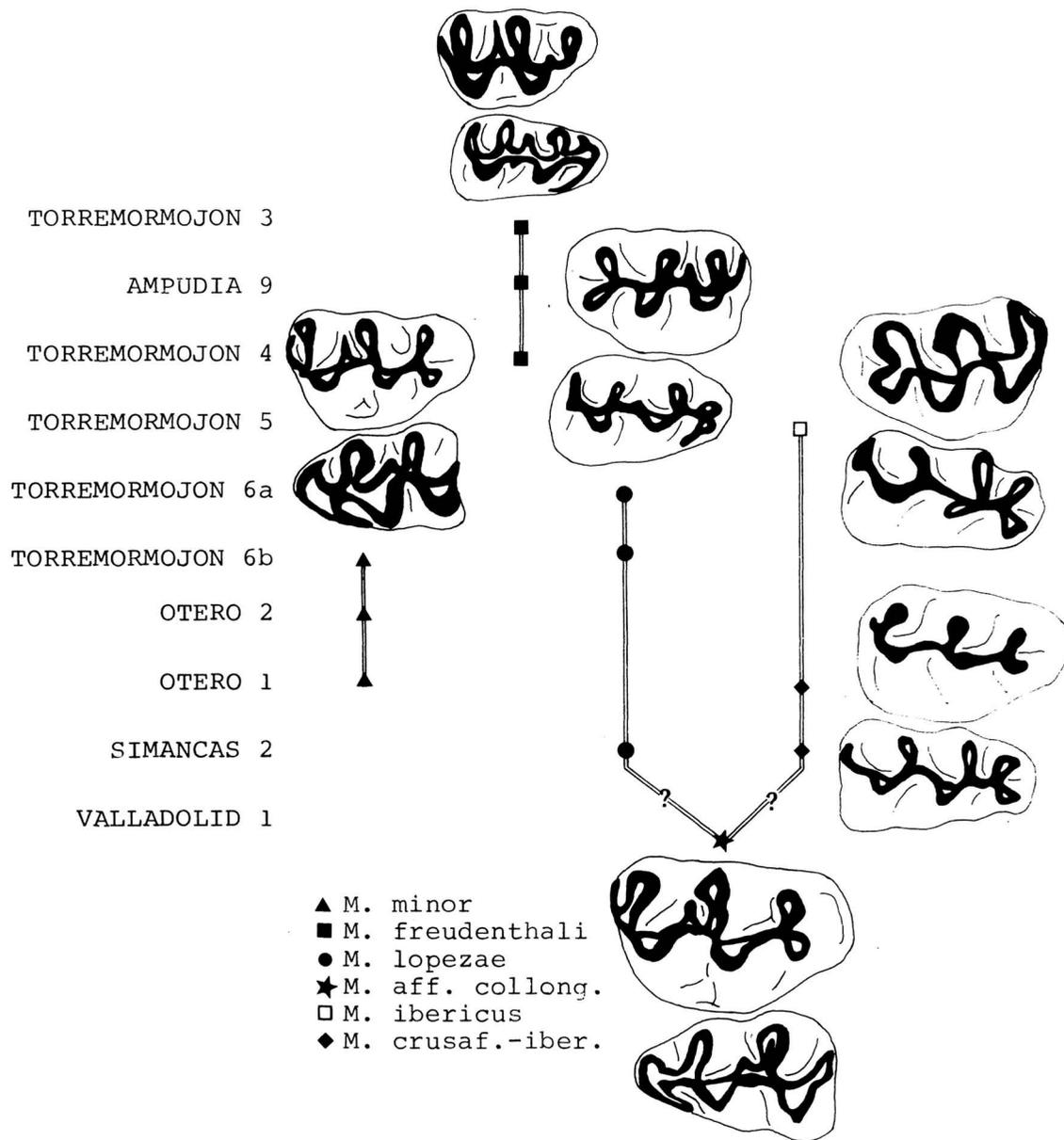


Figure 3. Chart showing the phylogenetic relationships of the duerian species of *Megacricetodon*. Localities have been arranged following the stratigraphic sequence.

REFERENTES

- AGUSTÍ, J. (1981). Roedores Miomorfos del Neógeno de Cataluña. *Thesis*. Universidad de Barcelona. 293 p.
- ÁLVAREZ-SIERRA, M. A. (1983). Paleontología y Bioestratigrafía del Mioceno superior del sector central de la Cuenca del Duero. Estudio de los Micromamíferos de la serie de Torremormojón (Palencia). *Masters dissertation*. U. Compl. Madrid.
- ÁLVAREZ-SIERRA, M. A., GARCÍA-MORENO, E. & LÓPEZ-MARTÍNEZ, N. (1985). Biostratigraphy and paleoecological reconstruction of middle-upper Miocene micromammal successions in northern Spain. *VIII RCMNS Congress*. Budapest.
- BERGONIOUX, F. & CROUCEL, F. (1958). Les mastodontes de l'Espagne. *Est. geol.* 14, pp. 223-263.
- CRUSAFONT, M. & TRUYOLS, J. (1960). El Mioceno de las cuencas de Castilla y de la Cordillera Ibérica. *Not. Com. Inst. Geolog. y Min.* 60, pp. 127-140.
- CRUSAFONT, M. & VILLALTA, J. F. (1957). Los nuevos mamíferos del Neógeno de España. *Not. y Com. Inst. Geol. y Min. España* n.º 22 pp. 3-25.
- CRUSAFONT, M. & VILLALTA, J. F. (1954). Ensayo de síntesis sobre el Mioceno de la Meseta Castellana. *Bol. R. Soc. Española Hist. Nat.* Vol. Hom. H. Pacheco. pp. 215-227.
- DAAMS, R. (1981). The dental pattern of the dormice *Dryomys*, *Myomimus* *Microdryomys* and *Peridyromys*. *Utrecht Micropal. Bull. Spec. Publ.* 3. 115 p.
- DAAMS, R. (in press). Glirinae (Gliridae, Rodentia, Mammalia) from the Aragonian type area and adjacent areas (Prov. of Zaragoza and Teruel, Spain). *Scripta Geologica*.
- DAAMS, R. & FREUDENTHAL, M. (1981). Aragonian: The stage concept versus Neogene mammal zones. *Scripta Geologica*, 62 pp. 1-17.
- DATIN, J. (1912). Noticias del descubrimiento de *Mastodon* y otros mamíferos en el Cerro del Cristo del Otero (Palencia). *Bol. R. Soc. Esp. Hist. Nat.* 12, pp. 78-84.
- ENGESSER, B. (1972). Die Obermiozäne Säugetierfauna von Anwil (Baselland). *Tät. Naturf. Ges. Baselland*. Band. 28. 363 p.
- FREUDENTHAL, M. (1963). Entwicklungsstufen der miozänen Cricetodontinae (Mammalia, Rodentia) Mittelspaniens und ihre stratigraphische Bedeutung. *Beaufortia*, 119 (10): 55-157.
- FREUDENTHAL, M. (1968). ON the mammalian fauna of the *Hipparion* beds in the Calatayud-Teruel Basin (Prov. Zaragoza, Spain). The genus *Megacricetodon* (Rodentia). *Proc. 57-72 Konin. Ned. Akad. Wetensch. Series B.* 71, N. 1, pp. 57-72.
- FREUDENTHAL, M. & CUENCA, G. (1984). Size variation of fossil rodent populations. *Scripta Geologica*, 76. pp. 1-28.
- GARCÍA-MORENO, E. (1983). Paleontología y Bioestratigrafía del Mioceno medio del sector Central de la Cuenca del Duero. Estudio de los micromamíferos de la serie de Torremormojón (Palencia). *Masters dissertation*. U. Compl. Madrid.
- GARCÍA-MORENO, E. & N. LÓPEZ MARTÍNEZ (in press). *Ramys*, a new genus of gliridae (Rodentia, Mammalia) from the lower Vallesian of Spain. *Scripta Geologica*.

- HERNÁNDEZ-PACHECO, E. (1915). Geología y Paleontología del Mioceno de Palencia. *Junta Ampl. Est. e Inv. Cient.*, 5.
- HERNÁNDEZ-PACHECO, E. (1930). Fisiografía, Geología y Paleontología del territorio de Valladolid. *Mem. Com. de invest. Paleont. y Prehist.* 37, pp. 38-95.
- LÓPEZ, N. & B. SÁNCHEZ (1982). Los primeros microvertebrados de la Cuenca del Duero: Listas faunísticas preliminares e implicaciones bioestratigráficas y paleofisiográficas. *1.ª reunión sobre la Geología de la Cuenca del Duero. IGME parte 1.ª* p. 341-353.
- MAYR, H. (1979). Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. Dissertation. München. 380 p.
- MAZO, A. V. (1977). Revisión de los Mastodontes de España. *Doctoral Thesis*. U. Comp. Madrid.
- ROYO GÓMEZ, J. (1922). El Mioceno continental ibérico y su fauna malacológica. *Mem. de la Com. de Invest. Paleont. y Prehist.* 30, pp. 1-230.
- SESÉ BENITO, C. (1977). Los cricétidos (Rodentia, Mammalia) de las fisuras del Mioceno medio de Escobosa de Calatañazor (Soria, España). *Trab. Neog. Cuat.* 8, pp. 127-180. C.S.I.C.
- WEERD; A. VAN DE (1976). Rodent faunas of the Mio-Pliocene continental sediments of the Teruel Alfambra región, Spain. *Utrecht Micropal. Bull. Spec. Publ.* 2. 185 p.

PLATE 1

Ramys perezii ÁLVAREZ-SIERRA n. sp.

- Figure 1. P⁴ dex. TM4-6
2. M² sin. TM4-8
3. M₃ dex. TM4-23
4. P₄ dex. TM4-14
5. M₁ dex. TM4-19
6. M₃ sin. TM4-31

Myolidus sinuosus ÁLVAREZ-SIERRA n. gen. n. sp.

- Figure 7. M³ dex. TM1-52
8. M₁ dex. TM1-60

Megacricetodon freudenthali GARCÍA-MORENO n. sp.

- Figure 9. M₁ dex. TM3-7
10. M¹ sin. TM4-34
11. M¹ sin. TM3-2

All figures x 28

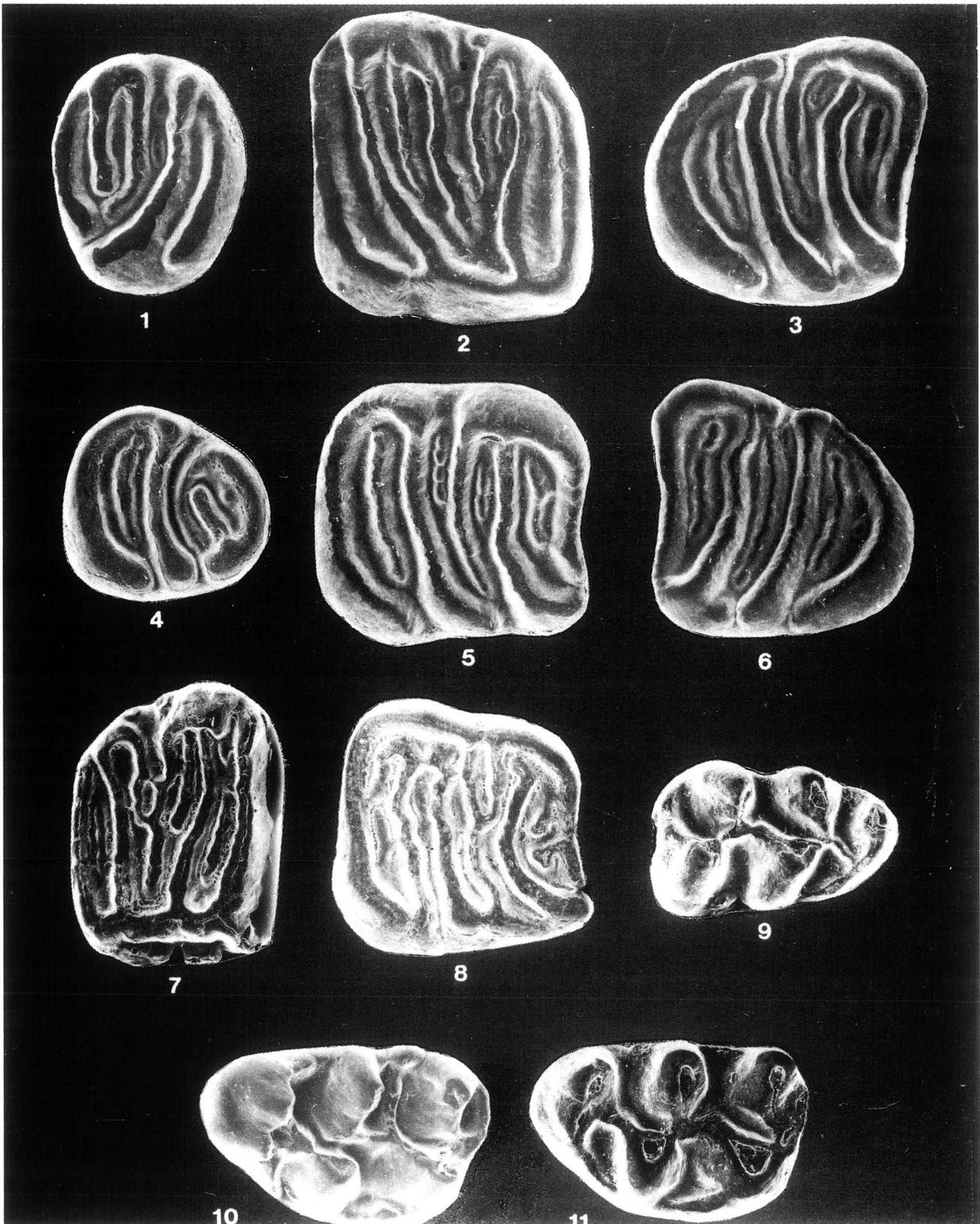
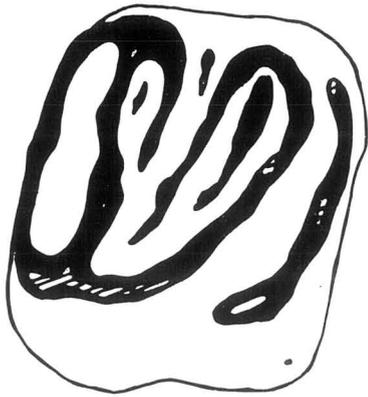


PLATE 2

Ramys perezii ÁLVAREZ-SIERRA n. sp.

- Figure 1. M^{1-2} dex. AMP9-77. Holotype.
2. M^{1-2} dex. AMP9-79
3. M^{1-2} dex. AMP9-84
4. M^3 sin. AMP9-95
5. M^3 sin. AMP9-98
6. P_4 sin. AMP9-114
7. D_4 sin. AMP9-100
8. M_1 dex. AMP9-123
9. M_1 dex. AMP9-122
10. M_2 dex. AMP9-125
11. M_3 dex. AMP9-146
12. M_3 dex. AMP9-142

All figures x 27



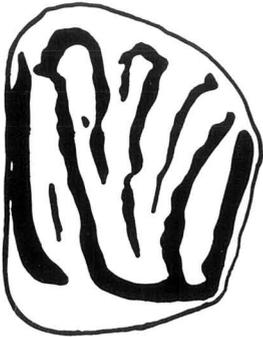
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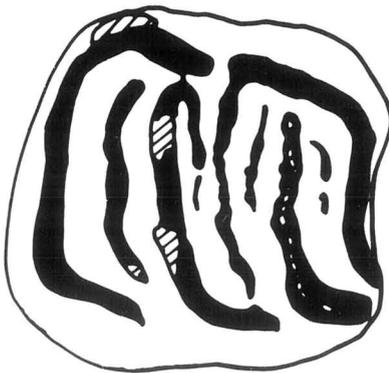
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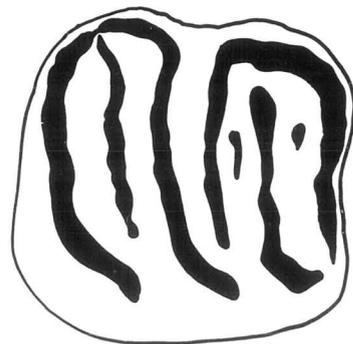
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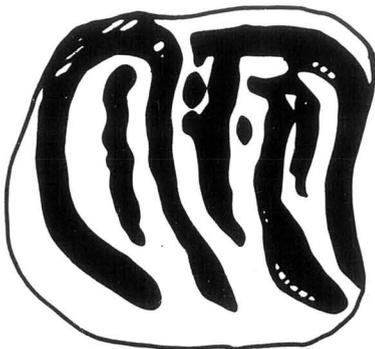
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10



11



12

PLATE 3

Myolidus sinuosus ÁLVAREZ-SIERRA n. gen. n. sp.

- Figure 1. D⁴ dex. AMP3A-1
2. P⁴ sin. AMP3-16
3. M¹⁻² dex. AMP3-33. Holotype.
4. M³ sin. AMP3-20
5. D₄ dex. AMP3-24
6. M₁ dex. AMP3-32
7. M₂ sin. AMP3-27
8. M₂ dex. AMPE3A-6
9. M₃ sin. AMP3-30
10. P₄ sin. AMP3A-5

Ramys perezii ÁLVAREZ SIERRA n. sp.

- Figure 11. D⁴ sin. AMP9-56
12. D⁴ dex. AMP9-61
13. P⁴ sin. AMP9-67
14. P⁴ dex. AMP9-73

All figures x 27

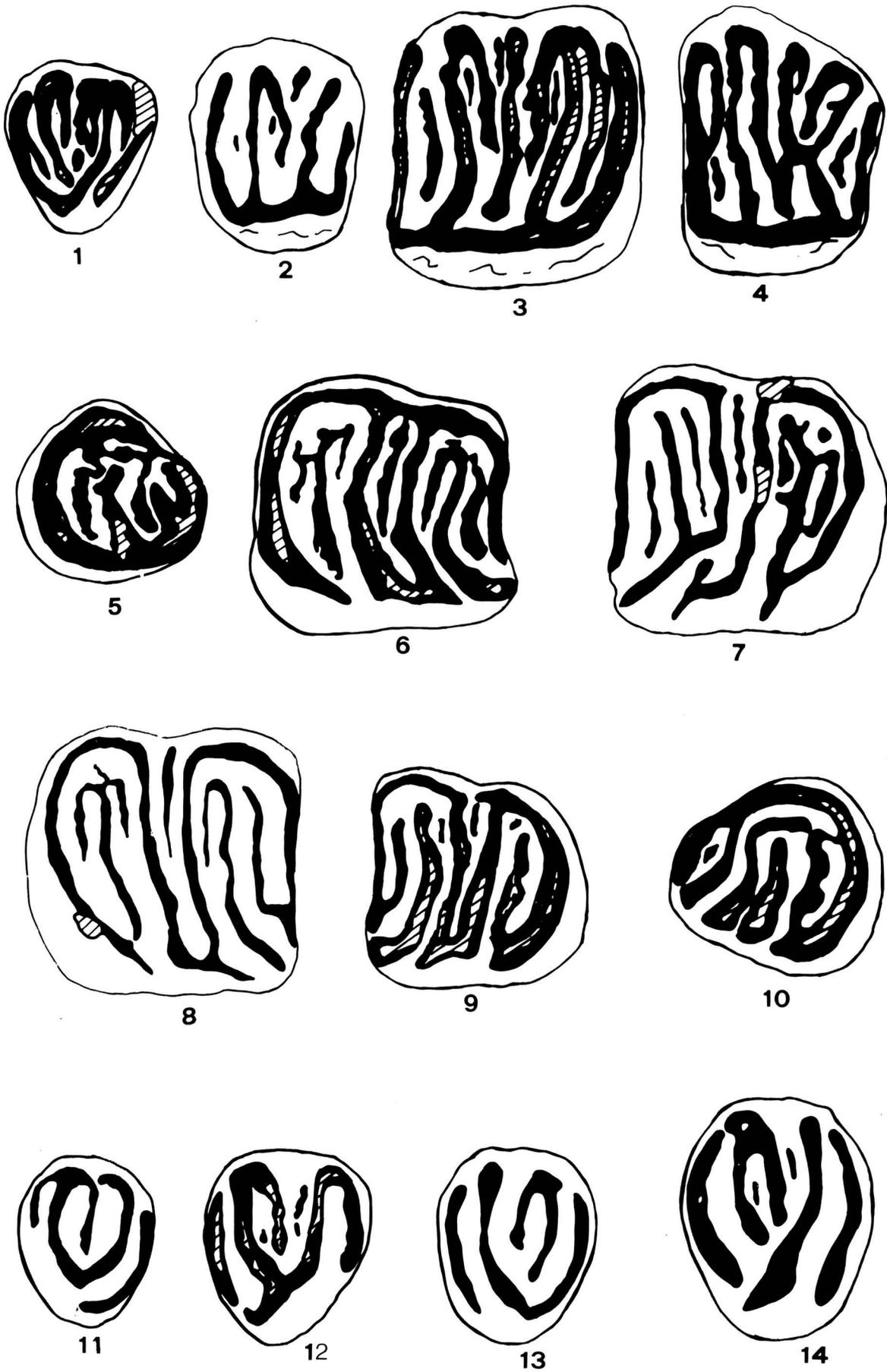


PLATE 4

Peridyromys rex GARCÍA-MORENO *nov. sp.*

- Figure 1. M¹ dex. TM6bRG1. Holotype.
2. P⁴ dex. TM6bRG3
3. M¹ sin. TM6bRG4
4. M³ dex. TM6bRG5
5. D⁴ dex. TM6bRG2
6. M³ dex. TM6bRG6
7. M₂ dex. TM6bRG9
8. P₄ dex. TM6bRG7
9. M₃ sin. TM6bRG10
10. M₁ sin. TM6bRG8

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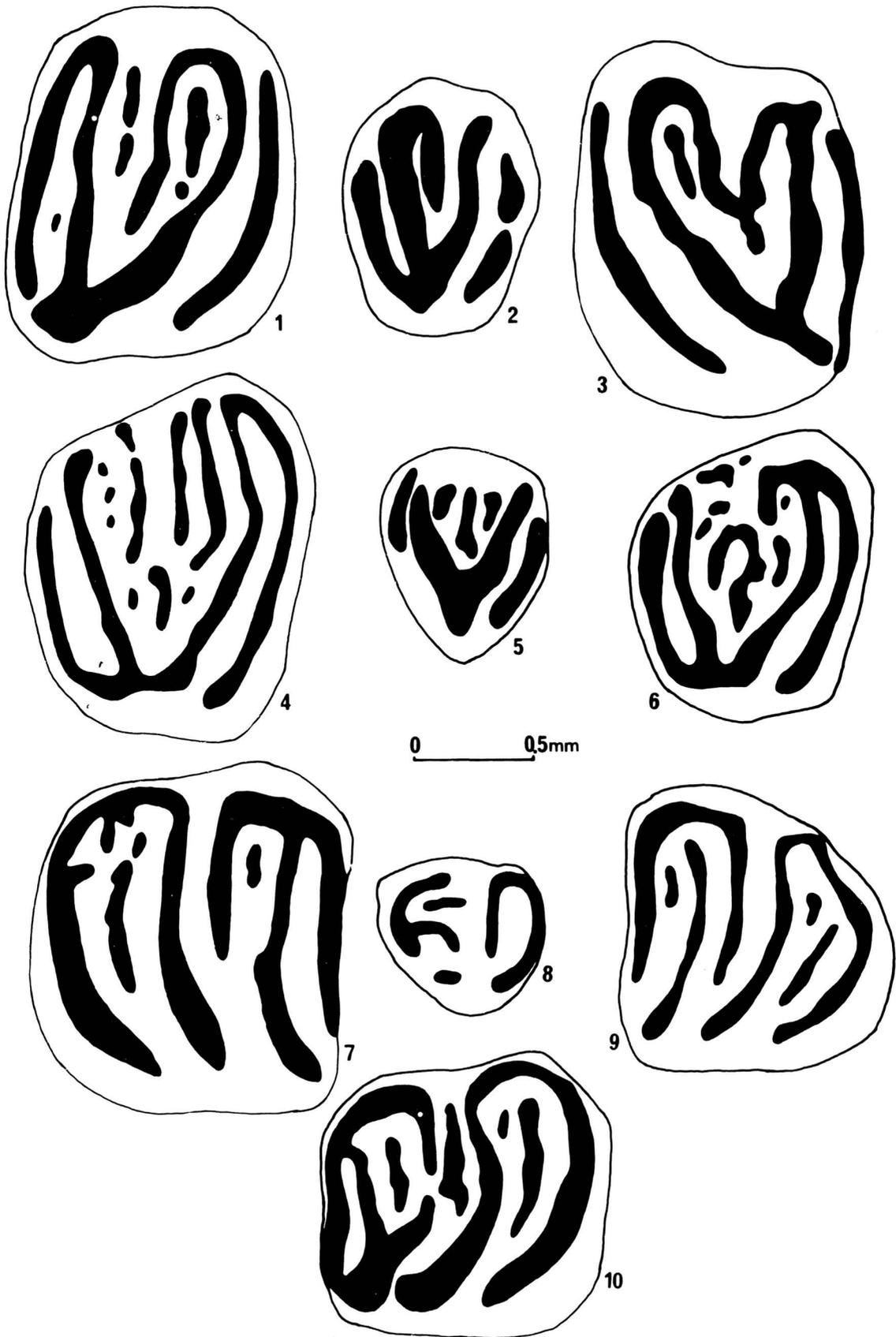


PLATE 5

Megacricetodon lopezae GARCÍA-MORENO *nov. sp.*

Figure 1. M_1 - M_2 dex. SIM2RH1. Holotype.

2. M sin. SIM2RH2
3. M^1 dex. SIM2RH3
4. M^1 sin. SIM2RH4
5. M^1 sin. SIM2RH5
6. M_1 sin. SIM2RH8
7. M_1 dex. SIM2RH9
8. M^2 sin. SIM2RH6
9. M_2 sin. SIM2RH10
10. M dex. SIM2RH7
11. M_2 sin. SIM2RH11
12. M_2 dex. SIM2RH12

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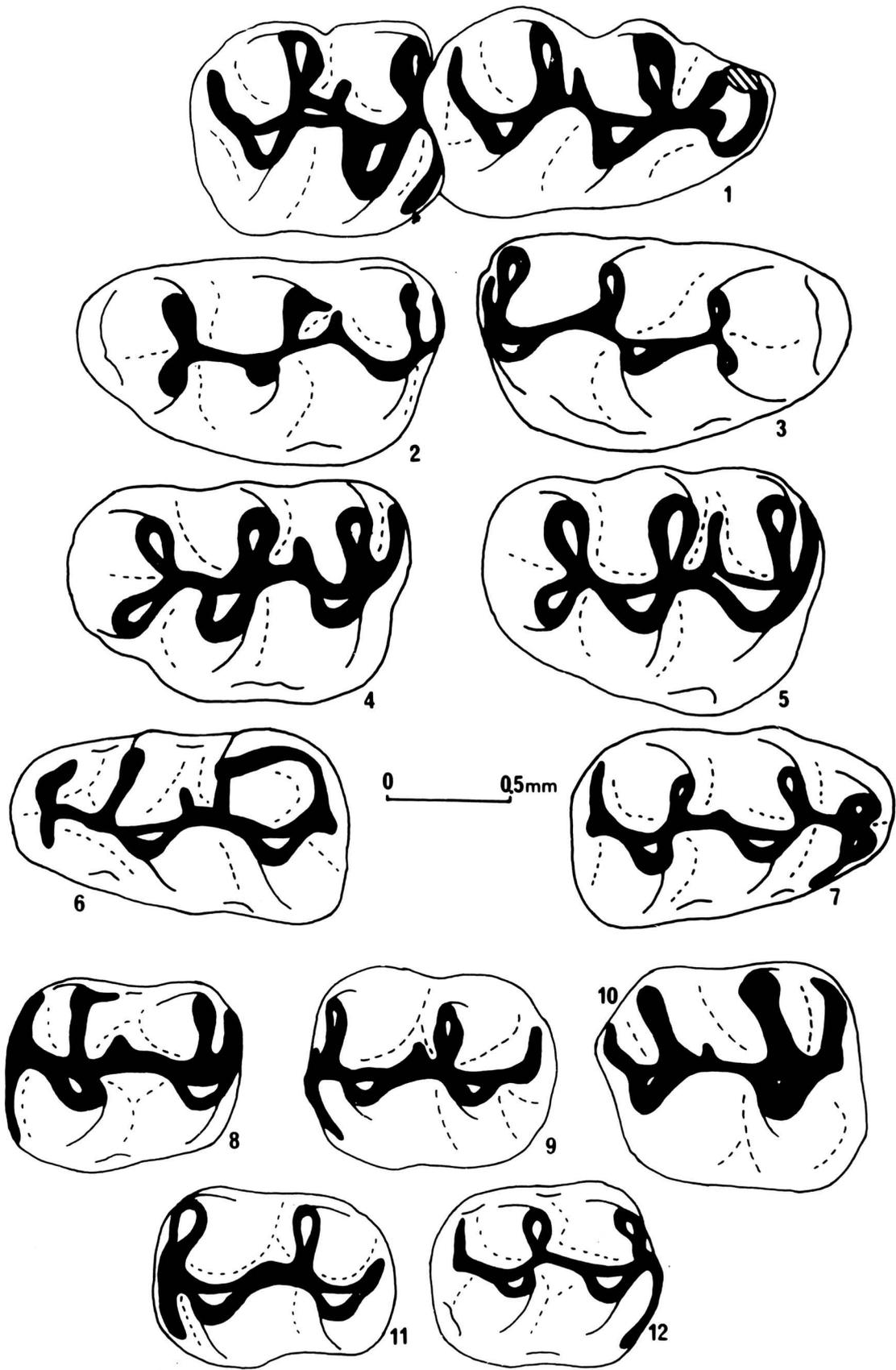


PLATE 6

Megacricetodon freudenthali GARCÍA-MORENO *nov. sp.*

- Figure 1. M¹ dex. AMP9RH15, Holotype.
2. M¹ sin. AMP9RH1
3. M¹ dex. AMP9RH2
4. M₁ dex. AMP9RH7
5. M₁ dex. AMP9RH8
6. M₁ sin. AMP9RH9
7. M² sin. AMP9RH3
8. M² sin. AMP9RH4
9. M² sin. AMP9RH5
10. M² sin. AMP9RH6
11. M₂ dex. AMP9RH10
12. M₂ dex. AMP9RH11
13. M₂ sin. AMP9RH12

Coll. Dpmnt. of Paleontology. UCM.

