The Middle Aragonian (Middle Miocene) Micromammals from La Retama (Intermediate Depression, Tagus Basin) Province of Cuenca, Spain

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ABSTRACT

The micromammal fauna from the Middle Miocene (Middle Aragonian) of La Retama, eastern central Spain, is described. It is a relatively poor rodent fauna composed by ten species only, associated to a highly diverse bat fauna, which includes five genera. The insectivores are represented by two species. This fossil assemblage has been correlated to zone Db (MN 5). The palaeoenvironmental reconstruction based on micromammals indicates open and dry conditions for this locality.

Key words: Rodents, Insectivores, Bats, Systematic, Biochronology, Paleoecology.

RESUMEN

Se describen los micromamíferos del Mioceno medio (Aragoniense medio) de La Retama, sector centro-oriental español. La fauna de roedores es relativamente pobre y está compuesta únicamente por diez especies. Sin embargo, cabe destacar la elevada diversidad de los quirópteros, representados por cinco géneros. Se describe también dos taxa de insectívoros. Esta asociación fósil ha sido correlacionada con la zona Db (MN5). La reconstrucción paleoambiental de La Retama inferida a partir de la fauna de micromamíferos corresponde a un ambiente abierto y seco.

Palabras clave: Roedores, Insectívoros, Murciélagos, Sistemática, Biocronología, Paleoecología.

Introduction

The locality of La Retama is located in the Intermediate Depression (Tagus Basin). It was discovered in 1988 by palaeontologists from the National Natural History Museum of Madrid and it was excavated as a macromammal site during the summers of 1988, 1989 and 1992 (Morales *et al*., 1993).

The fossiliferous locality is situated in a crop field next to Loranca del Campo (Province of Cuenca) and very near to fossil localities from the Early Miocene, local Zone Z, (Díaz-Molina y López-Martínez, 1979; Daams *et al*., 1986 and 1996; Ginsburg *et al*., 1987; Alcalá *et al*., 1990 and 1992; Cerdeño, 1992a; Álvarez Sierra *et al*., 1994; De Miguel *et al*., 1996; Morales *et al*., 1999). Part of the mammal

fauna of La Retama has been previously studied by diverse authors, among them: Morales (1989), Daams (1991), Cerdeño (1992b; 1996), Morales *et al*. (1999). These studies indicated a Middle Aragonian age (Middle Miocene) for this locality. Morales *et al*. (1993) carried out both taphonomical and sedimentological studies and provided a discussion about "*Hispanotherium* faunas".

The fossiliferous level consists of silt-marls with carbonate concretions and vegetal remains. Morales *et al*. (1993) considered these sediments as deltaic facies from a small fan delta. They noticed the fossil remains are well preserved. Neither the bones nor the teeth analysed showed any signs of major transport. Only in a few cases some signs of corrosion by humic acids were observed.

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In this article we discuss the entire rodent, insectivore and bat fauna from La Retama. The micromammal material studied comes from sediments collected during the macrovertebrate excavations during the summers of 1988 and 1989. Some 1.200 kg of sediment from La Retama were screened. The teeth were measured using a Nikon monocular digital measuring microscope, measurements are given in mm. The nomenclature of the cheek teeth for the Cricetidae is after Freudenthal *et al.* (1994), for the Sciuridae after Cuenca Bescós (1988), for the Gliridae after Daams (1981), for the Insectivora after van den Hoek Ostende (2003) and for the Chiroptera after Sigé (1968). The specimens are stored at the National Museum of Science of Madrid (MNCN).

Systematic Palaeontology

Rodentia Bowdich,1821
Sciuridae Fischer von Waldheim, 1817
Heteroxerus Stehlin y Schaub, 1951
Heteroxerus rubricati Crusafont, Villalta y Truyols, 1955
(Plate 1, Figures 1-10)
Material and measurements: Table 1

Description

D4: The outline of this element is triangular because the anteroloph forms a well-developed anterior lobe. The labial end of this crest is wide although a parastyle is not differentiated. A rather large anteroconule is present in 50% of the specimens. The protoloph is thin and is the longest crest. The paracone is well developed. A small mesostyle is present in 12 out 50 specimens. There is always a well-developed metaconule adjacent to the metacone. Thus, the metaloph is formed by these two structures only, with no crest connecting them. The metaloph is normally connected to the short posteroloph, but in 9 specimens an additional connection to the protocone is present. In one specimen the metaloph is connected to the hypocone. The hypocone is smaller and situated more lingually than the protocone.

P4: The general pattern of the P4 is rather robust. Its anterior wall is generally concave. The anteroloph is lower than the other crests. It shows an anteroconule of variable development in several specimens. The four main cusps are of similar development. A metaconule is present in all specimens. The metaloph is generally connected to the posteroloph. In 5% of the specimens there is a connection between the metaloph and the protoloph. The posteroloph is generally small; in a few specimens it is absent.

M1-2: The four main cusps are well developed. The protocone is generally the largest cusp and remaining three, hypocone, metacone and paracone, show a similar development. The metaconule is always present and can be as large as the metacone, especially in the M1. The long and straight anteroloph may include on its labial end a more or less developed anteroconule. A small mesostyle is present in 15% of the material. The metaloph is generally connected to the posteroloph, although in about 10% of the specimens both structures are unconnected. In a few specimens (5%) a double connection between the metaloph and the posteroloph is present. This feature, however, is difficult to observe in worn specimens, and therefore it is possible that some specimens with this double connection have been misinterpreted as single connection.

M3: The outline of this element is from triangular to circular. There are two main cusps, the protocone

Table 1.— **Measurements of *Heteroxerus rubricati***

H. rubricati	Length					Width			
	Min.	Mean	Max.	s.d.	N	Min.	Mean	Max.	s.d.
D4	1.11	1.24	1.37	0.052	36/39	1.10	1.28	1.41	0.079
P4	1.08	1.21	1.33	0.056	96/95	1.21	1.47	1.75	0.086
M1-2	1.14	1.29	1.44	0.058	187/188	1.39	1.63	1.94	0.102
M3	1.08	1.26	1.46	0.072	98/98	1.16	1.38	1.61	0.085
d4	1.05	1.12	1.20	0.045	42/41	0.78	0.89	0.99	0.052
p4	1.03	1.18	1.33	0.063	100/100	0.97	1.13	1.31	0.068
m1	1.26	1.41	1.55	0.062	110/110	1.16	1.41	1.62	0.093
m2	1.30	1.46	1.66	0.066	129/128	1.25	1.48	1.69	0.077
m3	1.20	1.45	1.64	0.090	98/98	1.20	1.36	1.53	0.079

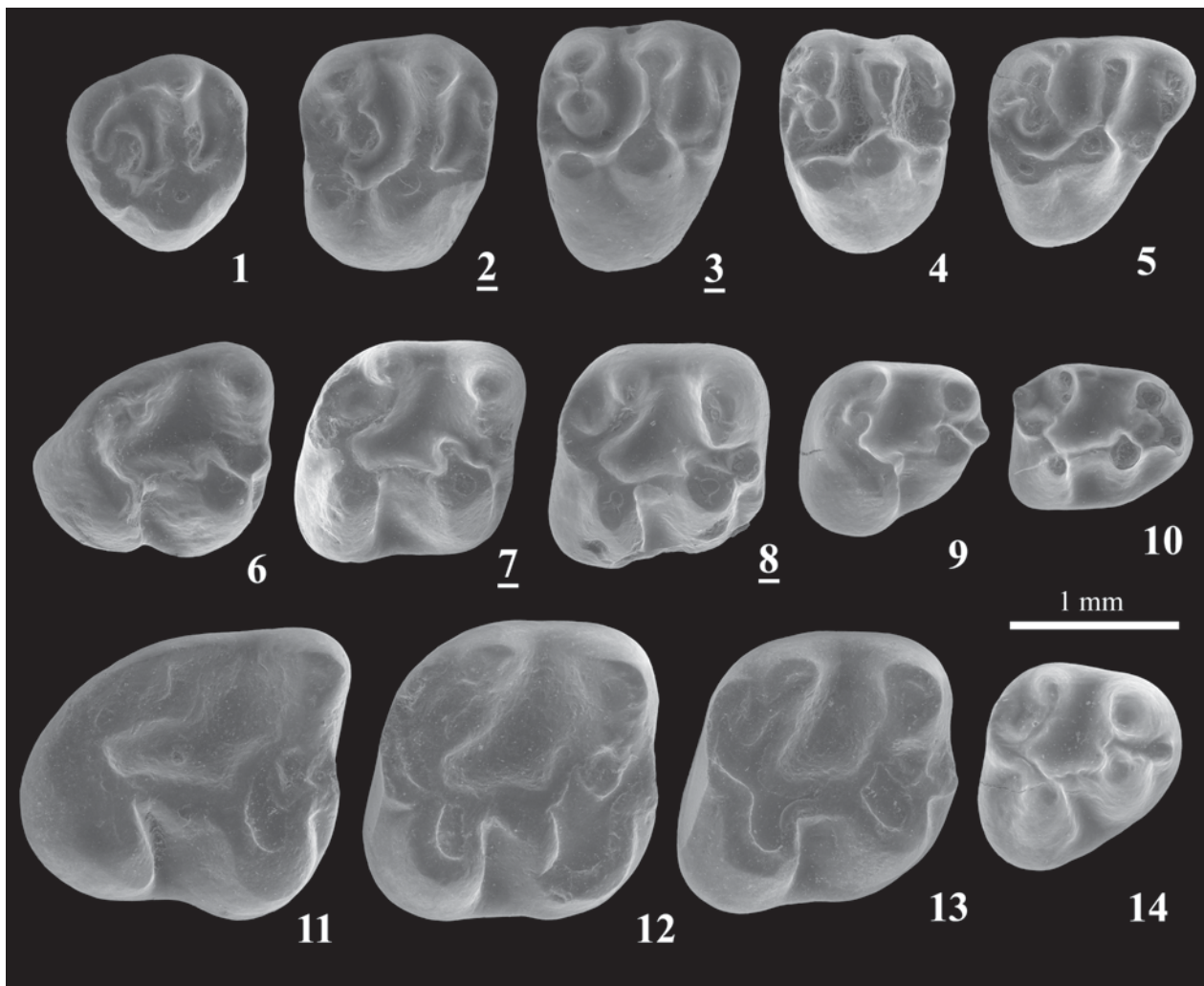N = number of specimens; s. d. = Standard deviation.

Plate 1.—Figures 1-10 *Heteroxerus rubricati* Crusafont, Villalta y Truyols, 1955; 1. M3 right, (REM- 2109); 2. M1-2 left, (REM- 1842), reversed; 3. M1-2 left, (REM- 1807) reversed; 4. P4 right, (REM- 2393); 5. D4 right, (REM- 2464); 6. m3 right, (REM- 1865); 7. m2 left, (REM- 1921), reversed; 8. m1 left, (REM- 1649), reversed; 9. p4 right, (REM- 2213); 10. d4 right, (REM- 2305); Figures 11-17 *Heteroxerus grivensis* (Forsyth Major, 1893); 11. m3 right, (REM- 2000); 12. m2 right, (REM- 1731); 13. m1 right, (REM- 1712); 14. p4 right, (REM- 2209).

and paracone, connected by the protoloph. Generally the protoloph is wider in its middle part, corresponding with a small protoconule. Hypocone and metacone are included in the posteroloph, which runs from the protocone to the paracone. These two cusps have a variable development, from small to indistinguishable. There is always a metaconule in the middle of the central basin. It is generally isolated although in several specimens (30%) it is connected to the posteroloph and in another specimens (10%) it forms part of the metaloph.

d4: The four main cusps are well developed although the entoconid is slightly smaller than the other three. Two conulids, the anteroconid and the hypoconulid, are also well developed. The anteroconid is situated in front of the protoconid and paraconid and in a lower position. It is either isolated or connected to the protoconid (19/45), but it never occurs connected to the metaconid. The metaconid and the protoconid are connected by a metalophid in 18 out of 45 specimens. The entolophid runs between the hypoconulid and the entoconid. The posterolophid is very small.

p4: The p4 shows a morphology very similar to the d4. The main differences are that the p4 is more robust than the d4, the anteroconid is smaller (in few

specimens even absent), and the metaconid and protoconid are very close each other, resulting in the anterior part being narrower than the posterior one.

m1-2: All the analyzed specimens show a more or less developed anterior cingulum, being strong in 55% of the specimens. The anteroconid is also present in all specimens. This structure is connected to the protoconid and metaconid in most of the material, although it can be connected only to the metaconid or, more rarely, only to the protoconid. The posterior arm of the protoconid ends generally free in the central basin, although in 20% of the material this structure is connected to the metaconid forming a metalophid. The ectolophid is complete in all specimens. The entolophid is always well developed. The hypoconulid is of similar size as the entoconid. The posterolophid is generally reduced, the reduction being stronger in the m1 than in the m2.

m3: The outline is triangular with the anterior part much wider than the posterior one. The anterior cingulum is present in 85 out of 95 specimens, being strong in 19, medium in 45 and small in 21 specimens. The anteroconid is present in all specimens. This structure is connected to the protoconid and metaconid in most of the material, although it can be connected only to the metaconid. The posterior arm of the protoconid ends generally free in the central basin; only in one specimen this structure is connected to the metaconid, forming a metalophid. The ectolophid is complete in all specimens. The entolophid is generally present although it is poorly developed in most of the material. The posteroloph is a thick short crest that includes a more or less developed hypoconulid.

Heteroxerus grivensis (Forsyth Major, 1893)
(Plate 1, Figures 11-14)
Material and measurements: Table 2

Description

P3: The only specimen found shows a simple morphology with a main cusp and a small cingulum that runs from the lingual side towards the posterior part. It has a low position compared to the main cusp. It is assigned to *Heteroxerus grivensis* because the fragment of the maxilla shows partially the alveoli of the P4 and the size of them is too large to belong to *H. rubricati*, the other recorded species.

D4: Three D4 have been identified. The outline of this element is triangular as the anteroloph forms a

Table 2.—**Measurements of *Heteroxerus grivensis***

	Length				Width		
H. grivensis	Min.	Mean	Max.	N	Min.	Mean	Max.
P3		0.54		1/1		0.56	
D4		1.44		1/3	1.44	1.45	1.46
P4		1.45		1/1		1.63	
M1-2	1.55	1.60	1.64	2/0			
M3		1.59		1/1		1.77	
m1		1.79		1/1		1.78	
m2		1.81		1/1		1.92	
m3	1.81	1.91	2.01	2/2	1.65	1.76	1.87

N = number of specimens; s. d. = Standard deviation.

well-developed anterior lobe. The labial end of this crest is wide, but a parastyle is not differentiated. A rather large anteroconule is present in one of the specimens, this cusp being small in the other two. The protoloph is thin and is the longest crest. The paracone is well developed. There is always a well-developed metaconule adjacent to the metacone, therefore the metaloph is formed by these two structures only, with no crest connecting both of them. The metaloph is connected to the short posteroloph and in one specimen there is another low connection with the protocone. The hypocone is smaller and is situated more lingually than the protocone.

P4: The pattern of the only P4 is rather robust. Its anterior wall is concave. The anteroloph is lower than the other crests. The anteroconule is small. The four main cusps are of similar development. There is a strong metaconule. The metaloph is connected to the posteroloph. The posteroloph is absent.

M1-2: The four main cusps are well developed. The protocone is generally the largest cusp and the other three —hypocone, metacone and paracone— show a similar development. The metaconule is always present and can be as large as the metacone, especially in the M1. The long and straight anteroloph includes on its labial end a well-developed anteroconule. The metaloph is connected to the posteroloph in three of the specimens and isolated in a fourth specimen. The posteroloph is small, especially in the M2.

m1-2: The two specimens show an anterior cingulum of medium development. The anteroconid is present in both specimens. This structure is connected to the protoconid and metaconid. The posterior arm of the protoconid is connected to the metaconid forming a metalophid. The ectolophid is complete in all specimens. The entolophid is well developed.

The hypoconulid is of similar size as the entoconid. The posterolophid is reduced, the reduction being stronger in the m1 than in the m2.

m3: There are two specimens. The outline is triangular with the anterior part slightly wider than the posterior one. A medium anterior cingulum is present in both specimens. The anteroconid is small. This structure is connected to the protoconid and metaconid. The posterior arm of the protoconid ends free in the central basin in one specimen and is connected to the metaconid forming a metalophid in the other. The ectolophid is complete in all specimens. The entolophid is present, although poorly developed. The posteroloph is a thick short crest.

Remarks on *Heteroxerus*

The m1 and m2 are generally distinguishable by the outline. The m1 are trapezoidal with the anterior part narrower than the posterior part, while the m2 are more square, with the anterior and posterior parts of similar width. However, the strong overlap in their pattern makes difficult to assign several intermediate forms to one or the other dental element. Therefore, it is possible that some of the specimens could be misidentified. The same problem, but even more accentuated, happens with the M1 and M2. Therefore, in this case, we have preferred to present together their descriptions and measurements.

The *Heteroxerus* material from La Retama has been assigned to two different species. Most of the material belongs to the small species, *H. rubricati*, while a smaller number of specimens have been identified as belonging to *H. grivensis*. The size and morphology of this scarce material fits perfectly with the material described by Cuenca Bescós (1988) from the type area of the Aragonian. The material described here as *H. rubricati* shows a general morphology that agrees with the material described by Cuenca Bescós (1988), but it is of significant smaller size. Cuenca Bescós (1988) includes in her study the material of *H. rubricati* from Córcoles, a locality that is situated in the Intermediate Depression near La Retama. She showed that this material has the smallest size among all the studied populations. The material from La Retama is even smaller than that from Córcoles. Despite this difference in size, we prefer to assign this material to *H. rubricati*, due to the absence of morphological differences with other assemblages included in this species.

Gliridae Muirhead, 1819
Armantomys de Bruijn, 1966
Armantomys aragonensis DE BRUIJN, 1966
(Plate 2, Figures 1-8)
Material and measurements: Table 3

Description

P4: It has a subtriangular outline and a very simple dental pattern. The anteroloph varies from a short ridge to a very small cusp, and it is absent in 13 out of 39 specimens. The protoloph and metaloph are oblique ridges, especially in specimens without an anteroloph. The posteroloph is low and narrow.

M1-2: The anteroloph is well developed and is an isolated ridge. The protoloph runs diagonally, being almost straight in the M1, while in the M2 it has a stronger inflexion at the medial part. The metaloph is the shortest ridge. The metaloph is lingually isolated in 27 out of 35 M1 and in 41 out of 58 M2. The lingual part of the metaloph is connected to the posteroloph in 8 out of 35 M1 and 17 out of 58 M2. The metaloph is connected labially to the postero-

Table 3. **Measurements of *Armantomys aragonensis***

A. aragonensis	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
P4	1.02	1.12	1.26	0.073	34/32	1.35	1.60	1.79	0.100
M1	1.58	1.77	1.96	0.105	32/26	1.89	2.14	2.38	0.125
M2	1.37	1.56	1.68	0.075	61/55	1.82	2.11	2.32	0.097
M3	1.05	1.20	1.42	0.071	45/43	1.58	1.73	1.95	0.097
p4	0.95	1.11	1.30	0.096	12	0.92	1.07	1.15	0.070
m1	1.64	1.79	1.93	0.079	31/29	1.60	1.77	1.94	0.085
m2	1.53	1.72	1.93	0.086	53/47	1.72	1.92	2.12	0.082
m3	1.36	1.52	1.70	0.084	45/40	1.46	1.67	1.87	0.093

N = number of specimens; s. d. = Standard deviation.

loph in one M1 and in two M2. In 2 M1 and 2 M2 the metaloph shows a small anterior spur. The posteroloph is usually separated from the protocone by a narrow furrow in the M1 as well as in the M2.

M3: It has more variable morphology than the M1 and M2. The outline of the occlusal surface is trapezoidal. The anteroloph is an isolated ridge in 46 out of 50 specimens and is labially connected to the protoloph in 4 out of 50 specimens. In 27 out of 50 specimens the protoloph is divided, with the labial part forming an isolated small ridge, and the lingual part joining the metaloph. The protoloph is not divided in 23 out of 50 specimens, in which 19 have an isolated metaloph. In 2 specimens the metaloph connects to the protoloph and both form an "Y". In another 2 specimens the metaloph is lingually connected to the posteroloph.

p4: The p4 has a very simple dental pattern consisting of three cusp-like ridges. These ridges are isolated in 17 out of 31 specimens. The anterior elongated cusp joins the labial part of the mesolophid in 8 out of 31 specimens, and the labial part of posterolophid in 5 out of 31. In one specimen the anterior cusp is connected to both the mesolophid and posterolophid.

m1-2: The anterolophid and metalophid are lingually connected forming a continuous curve. In unworn m1 and m2, the labial ends of the anterolophid and metalophid are frequently separated by a furrow. The mesolophid is lingually isolated from posterolophid in 22 out of 35 m1 and in 44 out 51 m2.

m3: The anterior part has the same morphology as described for m1 and m2. The configuration of the posterior part is more variable. Mesolophid and posterolophid are always disconnected lingually. The most common morphology (46 out of 50 specimens) consists of the mesolophid and posterolophid connected labially, forming an "Y", and the posterior valley reduced. The connection between mesolophid and posterolophid occurs near the lingual border and the posterior valley is more reduced in 25 out of 50 specimens, while in 21 out of 50 specimens this connection is situated near the labial border. In 4 out of 50 specimens the mesolophid and posterolophid are isolated ridges and the posterior valley is not reduced in extension.

Remarks

The *Armantomys* material from La Retama was included in Daams' (1991) study on hypsodont Gli-

ridae from Spain. The frequency of the different morphotypes in the upper molars and m3 of *A. aragonensis* was shown in that paper. In the present article we describe again this material, only with small variations in the number of specimens and performing a more complete description of all the elements.

As Daams (1991) and García Paredes (2006) pointed out, the *Armantomys aragonensis* molars from different localities fluctuate in size considerably. The size difference among the premolars, however, is less conspicuous. Nevertheless, the material described here fits in the ranges of size and morphology of *A. aragonensis* described by García Paredes (2006) from the type area of the Aragonian (Calatayud-Montalbán Basin).

Armantomys aragonensis makes its first appearance in the Early Ramblian, being quite abundant in the micromammal assemblages (Daams, 1991). In the Late Ramblian and Aragonian it has a regular but scarce record (Daams, 1991; García Paredes, 2006). However, *A. aragonensis* is relatively abundant among the Gliridae material from La Retama. Since *Armantomys aragonensis* is supposed to be an open country and dry conditions inhabitant (Daams y van der Meulen, 1984), its abundance may indicate the predominance of such ecological conditions in the area.

Armantomys jasperi Daams, 1991
Material and measurements: M1 (- x 1.66); M3 (0.94 x 1.37)

Description

M1: The anteroloph and protoloph are well developed and isolated ridges. The metaloph and the posteroloph are connected lingually.

M3: The protoloph is divided and the labial part forms an isolated small ridge. The metaloph is connected with the lingual part of the protoloph.

Remarks

Armantomys jasperi is included in the lineage of consecutive species *Armantomys bijmai – A. daamsi – A. parsani – A. jasperi* proposed by Daams (1991).

It has a simple dental pattern consisting in four moderately hypsodont ridges with winding borders. Beside these morphological features, this species can be distinguished from *A. aragonensis* by its

Table 4.—**Measurements of *Pseudodryomys ibericus***

P. ibericus	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
P4		0.89			1		1.14		
M1	1.25	1.28	1.31	0.042	2/1		1.46		
M2		1.18			1		1.39		
M3		0.93			1		1.25		
m2		1.38			1				
m3		1.14			1				

N = number of specimens; s. d. = Standard deviation.

smaller size. *Armantomys jasperi* has a regular but quite scarce record (Daams, 1991; García Paredes, 2006). The material from La Retama is among the most modern records for this species.

Pseudodryomys de Bruijn, 1966
Pseudodryomys ibericus de Bruijn, 1966
(Plate 2, Figures 9-10)
Material and measurements: Table 4

Description

P4: The only specimen has 5 ridges and its outline is oval. The anteroloph and the posteroloph are isolated ridges. The trigon, including protoloph and metaloph, has a "Y" shape. There is a posterior centroloph labially connected to the metaloph.

M1: The anterolabial part of 2 out of 3 specimens is broken. The posterior centroloph is longer than the anterior one and it is connected lingually to the metaloph in all M1. The posteroloph is isolated.

M2: There is only one M2. The posterior centroloph is longer than the anterior one. The lingual border of the posterior centroloph does not join the metaloph. The anterior centroloph and the posterior one join the protoloph and metaloph respectively at the labial border of the occlusal surface.

M3: The unique specimen has a trapezoidal outline and the posterior part is narrower than the anterior one. The anteroloph is isolated lingually, its labial border is very near to the labial border of the protoloph, but is not connected to it. The trigon does not form a "Y" as in the M1 and M2, because the protoloph and metaloph are connected near the lingual border of the occlusal surface. This specimen has 2 centrolophs, the anterior being larger the posterior one. The anterior centroloph and the posterior one join the protoloph and metaloph at the

labial border of the occlusal surface. The posterior wall of the posterior centroloph is slightly winding.

m2: The only specimen has four main ridges, a centrolophid which runs perpendicular to the lingual border into the central valley, and a extra ridge situated in the posterior valley. The anterolophid, metalophid and centrolophid are connected in the anterior corner of the lingual border. The labial part of the centrolophid joins the metalophid roughly halfway the total width of the occlusal surface. The mesolophid and posterolophid are connected lingually.

m3: The two m3 show similar pattern to the m2 described before, although there are several differences. The posterior part is rounded and narrower than the anterior one. The extra ridge of the posterior valley is small. In one specimen the metalophid is isolated lingually. The mesolophid and posterolophid are not connected lingually.

Remarks

The presence of *Pseudodryomys ibericus* in La Retama was previously mentioned in Morales *et al*. (1999), but this material had not been described. Despite the scarcity of the material from La Retama, it fits in the measurements and morphology ranges of *P. ibericus* described by de Bruijn (1966) in its type locality, Ateca 1 (Calatayud-Montalbán Basin), as well as in the ranges of the material from the type area of the Aragonian (Calatayud-Montalbán Basin) extensively studied by García Paredes (2006).

In general, *Pseudodryomys ibericus* is a common and abundant species in the Lower and Middle Miocene of Spain. However, this species is rare among the Gliridae material from La Retama. In the type area of the Aragonian (Calatayud-Montalbán Basin), *P. ibericus* becomes less frequent after zone Db (García Paredes, 2006).
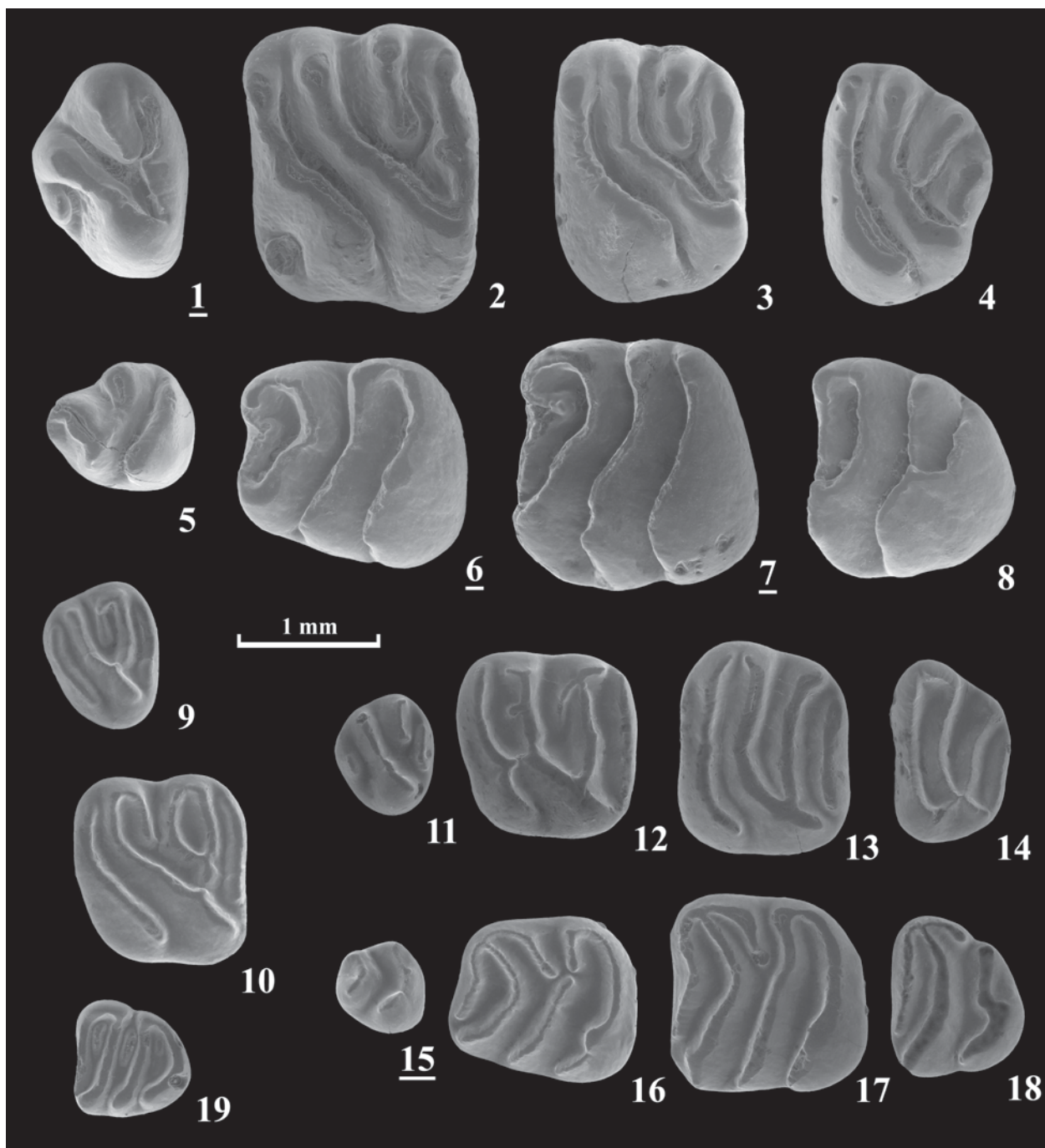
Plate 2.—Figures 1-8 *Armantomys aragonensis* de Bruijn, 1966; 1. P4 right, (REM-621), reversed; 2. M1 left, (REM-650); 3. M2 left, (REM-683); 4. M3 left, (REM-763); 5. p4 left, (REM-791); 6. m1 right, (REM-841), reversed; 7. m2 right,(REM-887) reversed; 8. m3 left, (REM-916); Figures 9-10 *Pseudodryomys ibericus* de Bruijn, 1966; 9. P4 left, (REM-1590); 10. M1 left, (REM-1591); Figures 11-18 *Pseudodryomys simplicidens* de Bruijn, 1966; 11. P4 left, (REM-1010); 12. M1 left, (REM-1066); 13. M2 left, (REM-1150); 14. M3 left, (REM-1230); 15. p4 right, (REM-1320), reversed; 16. m1 left, (REM-1421); 17. m2 left, (REM-1464); 18. m3 left, (REM-1527); Figure 19 *Microdyromys koenigswaldi* de Bruijn, 1966; 19. m3 left (REM-978).

Table 5.—**Measurements of *Pseudodryomys simplicidens***

P. simplicidens	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
P4	0.71	0.81	0.94	0.050	48/51	0.81	0.96	1.11	0.061
M1	1.23	1.35	1.54	0.060	67/50	1.43	1.52	1.65	0.051
M2	1.16	1.25	1.38	0.043	86/66	1.48	1.60	1.76	0.055
M3	0.76	0.89	1.00	0.050	77/69	1.10	1.26	1.44	0.066
p4	0.61	0.68	0.76	0.042	26/25	0.58	0.73	0.85	0.058
m1	1.27	1.39	1.51	0.052	72/69	1.16	1.32	1.50	0.065
m2	1.27	1.37	1.48	0.057	64/63	1.32	1.46	1.59	0.053
m3	0.78	0.99	1.13	0.062	76/70	1.05	1.19	1.33	0.060

N = number of specimens; s. d. = Standard deviation.

Pseudodryomys simplicidens de Bruijn, 1966
(Plate 2, Figures 11-18)
Material and measurements: Table 5

Description

P4: The occlusal surface is slightly concave and it has an oval or subtriangular outline. The dental pattern is very simple. Most specimens (50 out of 53) have the four main ridges. The anteroloph is absent in 2 and the metaloph in one out of 53 specimens. The anteroloph varies from a short ridge to a small cusp and it is situated in the middle part of the anterior border. The protoloph is divided in 22 out of 53 specimens. The metaloph is a short cusp-like ridge. It is absent in one out of 53 specimens. The lingual border of the metaloph joins the protoloph in 21 out of 53 specimens, and in 18 out of 53 it joins the posteroloph. The metaloph is an isolated ridge in 14 out 53 specimens. The posteroloph is short, but longer than the anteroloph.

M1: The occlusal surface is concave and it has a square outline. The anteroloph is well developed and its labial and lingual part end free in all the specimens. It shows a medial connection with the protoloph in 23 out of 70 specimens. Protoloph and metaloph are connected forming a composite "Y" shape. There is a short posterior centroloph connected to the labial part of the metaloph in 2 out of 70 specimens. In most specimens the posteroloph is isolated, it is labially connected to the metaloph in 7 out of 57 specimens and it is lingually connected to the protoloph in 7 out of 65 specimens.

M2: It has a concave occlusal surface and its outline is more rectangular than in the M1. The lingual part of the anteroloph ends free in all specimens, but its labial part joins the labial part of the protoloph in 19 out of 85 specimens. The anteroloph shows a medial connection with the protoloph in 23 out of 101 specimens. As in the M1, the protoloph and the metaloph are connected forming a composite "Y" shape in all specimens. There is an anterior centroloph in one out of 101 specimens, and 2 out of 101 specimens has a short posterior centroloph connected to the labial part of the metaloph. The posteroloph is connected lingually to the protoloph in 57 out of 77 specimens and it is only labially connected to the metaloph in 26 out of 78 specimens.

M3: It has a concave occlusal surface and a trapezoidal outline. The anteroloph is labially connected to the protoloph in 74 out of 79 specimens. Its lingual border joins the protoloph in 68 out of 76 specimens. The anteroloph shows a medial connection with the protoloph only in one out of 79 specimens. In most specimens, the protoloph and metaloph are connected near the lingual border of the occlusal surface, so the trigon does not form a "Y" as in the M1 and M2. There is a short posterior centroloph connected to the labial part of the metaloph in 12 out of 79 specimens. The posteroloph is connected lingually to the protoloph in 56 out of 77 specimens and it joins labially the metaloph only in 9 out of 77 specimens.

p4: The outline of the occlusal surface is oval. The p4 pattern is so reduced that the main ridges are difficult to determine. The anterior part is occupied by a sharp bend ridge, which is isolated in all specimens. The mesolophid is a very small cusp-like ridge. It is isolated in 9 out of 28 specimens. In 19 out of 28 specimens the mesolophid is connected to the posterolophid forming the posterior border of

the tooth. Sometimes the mesolophid and posterolophid cannot be distinguished in the unique posterior ridge.

m1: The occlusal surface is slightly concave. The anterolophid is quite a short ridge and its labial part ends free in all specimens. The metalophid has a strong inflexion in its middle part forming a sharp angle. The anterolophid, metalophid and centrolophid are connected in the anterior corner of the lingual border in 67 out of 71 specimens. The centrolophid is isolated in 4 out of 71 specimens, and its labial end joins the mesolophid in 2 out of 71 specimens. In the central valley, 8 out of 71 specimens has a small extra cusp-like ridge near the lingual border. The mesolophid is a relatively diagonal ridge and is divided in 6 out of 71 specimens. The mesolophid and posterolophid are connected lingually in 58 out of 74 specimens. In 2 specimens out of 71 there is a small cusp-like ridge in the posterior valley.

m2: The anterolophid is usually longer than in the m1 and its labial part does not join with the metalophid. The anterolophid, metalophid and centrolophid are connected in the anterior corner of the lingual border in 64 out of 69 specimens. The lingual end of the metalophid is isolated and does not reach the lingual border of the occlusal surface in 2 out of 69 specimens. The centrolophid is isolated in 2 out of 69 specimens, and its labial part joins the mesolophid in 2 out of 69 specimens. There is only one m2 without a centrolophid. Two out of 69 specimens have a small extra cusp-like ridge near the lingual border in the central valley. The mesolophid is less diagonal than in the m1, and is divided in 2 out of 69 specimens. The mesolophid and posterolophid are connected lingually in 49 out of 64 specimens.

m3: The outline of the m3 forms a half-ellipse. The anterior part has a similar morphology as described in the m2. The anterolophid, metalophid and centrolophid are connected in the anterior corner of the lingual border in 53 out of 61 specimens. The lingual end of the metalophid is isolated and reaches the lingual border of the occlusal surface in all but one of the 69 specimens. The centrolophid is isolated in 5 out of 61 specimens, and it is absent in 2 out of 61 specimens. The posterior part of the m3 is rounded, narrow and reduced. The labial part of the mesolophid is reduced and joins the posterolophid in all specimens, so the posterior valley is always reduced. In 34 out of 65 specimens this connection occurs near the

lingual border and the posterior valley is very short. In those specimens, the posterolophid can be divided, its lingual part being isolated. The mesolophid and posterolophid form together a composite posterior ridge in 24 out of 65 specimens, in which case the posterior valley disappears completely. In 7 out of 65 specimens the connection between mesolophid and posterolophid occurs near the labial border, thus giving place to a less reduced posterior valley.

Remarks

The presence of *Pseudodryomys simplicidens* in La Retama was previously mentioned by Morales *et al.* (1999) but this quite abundant material remainded undescribed up to now. *Pseudodryomys simplicidens* from La Retama fits perfectly in the ranges of measurements and morphology of *P. simplicidens* described by de Bruijn (1966) in its type locality, Valdemoros 3B (Calatayud-Montalbán Basin).

Pseudodryomys simplicidens from the type area of the Aragonian (Calatayud-Montalbán Basin) has been extensively studied and discussed by García Paredes (2006), showing trends toward size increase of the molars, simplification of the p4 and simplification of the posterior part in the m3. The morphology and size of material from La Retama is similar to the one from localities of biozone Db in the type area of the Aragonian.

Microdyromys de Bruijn, 1966
Microdyromys koenigswaldi de Bruijn, 1966
(Plate 2, Figure 19)
Material and measurements: m3 (0.91 x 0.91)

Description

Microdyromys koenigswaldi is represented in La Retama by a single m3. This specimen has 7 ridges: the 4 main ones, the centrolophid and 2 small extra ridges, one of which is situated in the anterior valley and the other one in the posterior valley. The anterolophid and the metalophid are connected lingually. The centrolophid is isolated and does not reach the lingual border of the occlusal surface. Mesolophid and posterolophid are connected lingually.

Table 6.—**Measurements of *Democricetodon decipiens***

D. decipiens	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
M1	1.69	1.80	1.87	0.076	8	1.16	1.21	1.27	0.036
M2	1.24	1.35	1.48	0.077	9/8	1.16	1.22	1.30	0.052
M3	0.91	1.00	1.17	0.096	7	0.95	1.02	1.12	0.067
m1	1.58	1.65	1.77	0.070	6/7	1.00	1.09	1.21	0.064
m2	1.29	1.41	1.49	0.069	9	1.08	1.17	1.28	0.063
m3	1.21	1.27	1.33	0.049	4	0.94	1.03	1.13	0.078

N = number of specimens; s.d. = Standard deviation.

Remarks

This material from La Retama was assigned by Morales *et al*. (1999) to *M. legidensis*. In our opinion, the morphology and size of this material is closer to the measurements and morphology found in *M. koenigswaldi* from the type locality, Valdemoros 3B, described by de Bruijn (1966), Daams (1981) and García Paredes (2006), and from several other localities from zone D, than to the material from the Calatayud-Daroca area assigned to *M. legidensis*, and is therefore referred to the first species.

Cricetidae Fischer von Waldheim, 1817
Democricetodon Fahlbusch, 1964
Democricetodon decipiens Freudenthal and Daams, 1988
(Plate 3, Figures 1-11)
Material and measurements: Table 6

Description

M1: The anterocone is simple in all ten specimens; the protolophule is always posterior; the metalophule is posterior in seven out of nine, and absent in the remaining two; the mesoloph is absent in four specimens, short in four and medium in two. There is no paracone spur.

M2: The protolophule is double anterior in one out of eight specimens, double posterior in three, and double symmetrical in three; branches of the double lophules may be very low; the metalophule is absent in two out of nine specimens, single anterior in four, single posterior in two; the mesoloph is short in all nine specimens.

M3: There are six specimens. The outline is triangular. The protocone has a mid-lingual position, while the small hypocone (if present) has a more labial position at the posterior side. The protolophule connects to the anterior arm of the protocone. The region behind the protocone and the paracone is highly variable.

m1: In two out of six specimens the lingual anterosinusid is open, closed in one, while in the other three the feature could not be evaluated; the metalophulid is short and anteriorly directed in five specimens and not observable in another one. The mesolophid is absent in two specimens, short in two, and not observable in another two.

m2: The lingual anterosinusid is poorly developed in three specimens, absent in three, and not observable in four specimens; the mesolophid is observable in eight specimens, in five it is absent and in three it is short; a metaconid ridge has not been observed in the six suitable specimens.

m3: There are three specimens, which have a somewhat elongated triangular outline. The lingual anterosinusid is very poorly developed, the entoconid is absent and the sinusid is deep.

Remarks

Van der Meulen *et al*. (2003) gave a revision of *Democricetodon* from the Aragonian sections in the type area, and their work is used as a frame of reference for the *Democricetodon* from La Retama. We are aware of the opinions expressed by Freudenthal (2006) on both the 2003 revision and the multidisciplinary study of Daams *et al*. (1999a) on the litho-, magneto- and biostratigraphy of the Aragonian sections in the type area. The current paper, however, is not the place to comment on these views.

Democricetodon decipiens is considered as a member of the *D. hispanicus – D. lacombai* lineage, because of the exclusive presence of the single proto-
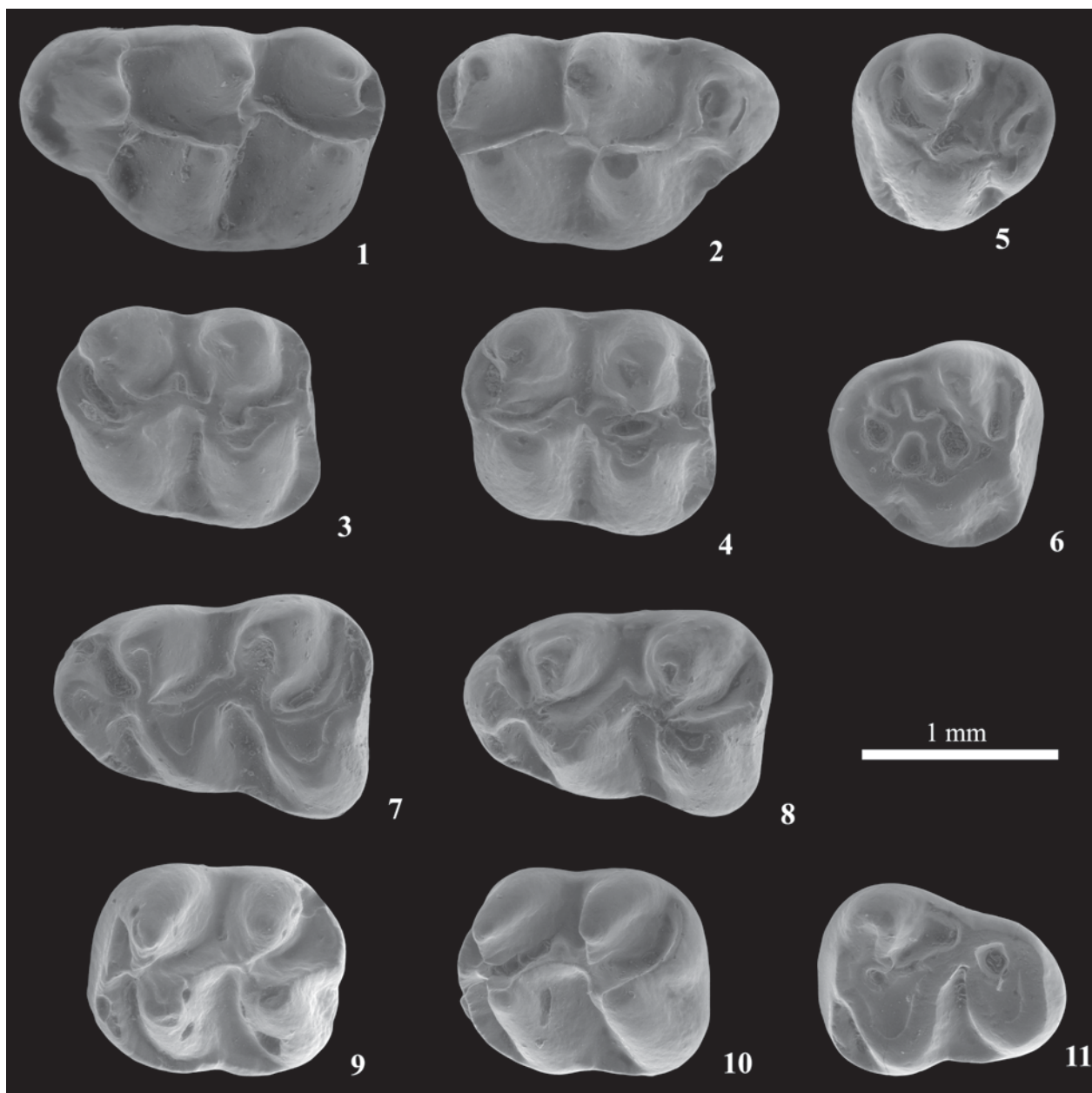
Plate 3.—Figures 1-11 *Democricetodon decipiens* (Freudenthal and Daams, 1988); 1. M1 left, (REM- 473); 2. M1 right, (REM- 477); 3. M2 right, (REM- 481); 4. M2 right, (REM- 483); 5. M3 left, (REM- 490); 6. M3 right, (REM- 489); 7. m1 left, (REM- 498); 8. m1 left, (REM- 497); 9. m2 left, (REM- 502); 10. m2 right, (REM- 507); 11. m3 left, (REM- 514).

lophule of M1 in combination with single metalophules in M2. Although our material of *Democricetodon* from La Retama is scarce, the observed frequencies are not compatible with those of the *D. franconicus – D. crusafonti* lineage, in which the protolophu-

les of M1 and the metalophules of M2 are commonly double (van der Meulen *et al,*, 2003). In size, the studied material agrees best with *D. decipiens* from Buñol and the younger populations of the species in the Aragonian sections of the Villafeliche area.

Table 7.—M**easurements of** *Megacricetodon primitivus*

M. primitivus	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
M1	1.28	1.41	1.54	0.055	56/75	0.76	0.87	0.96	0.037
M2	0.90	0.99	1.10	0.044	86/82	0.71	0.83	0.94	0.038
M3	0.64	0.67	0.70	0.030	3	0.67	0.70	0.72	0.025
m1	1.10	1.25	1.37	0.059	50/56	0.70	0.79	0.88	0.046
m2	0.89	1.00	1.09	0.042	83/81	0.71	0.81	0.91	0.039
m3	0.73	0.80	0.85	0.042	7	0.57	0.62	0.69	0.043

N = number of specimens; s. d. = Standard deviation.

Megacricetodon Fahlbush, 1964
Megacricetodon primitivus (Freudenthal, 1963)
(Plate 4, Figures 1-10)
Material and measurements: Table 7

Description

M1: The anterocone is unequally split in 58 specimens, while it is somehow symmetrical in other 15. A well- developed cingulum is present in the anterior part of the anterocone in 77 specimens, it is small in 10 and absent in 8. The protolophule is posterior in all specimens. However, in 9 of them a second anterior protolophule is present, although it does not connect completely the protocone and metacone. A paracone spur is present in 21 specimens (being small in 12 of them) and absent in 78. A well-developed cingulum that runs from the anterocone till the hypocone is present in 58 out of 92 specimens. The mesoloph is medium in 33, short in 57 and absent in 16 specimens. The metalophule is anterior in 92, posterior in 1 and transverse in 14.

M2: The protolophule is directed forwards in 78, transverse in 14 and double anterior in 4. The mesoloph is medium in 49, short in 24 and absent in 2 specimens. The metalophule is absent in one specimen, anterior in 66, posterior in 9 and transverse in 23. A paracone spur is present in 77 specimens, in 16 of which it is small, and absent in 16.

m1: The anteroconid consists generally of a single cusp, although in 6 unworn specimens a slightly split double anteroconid is present ('8' pattern). The mesolophid is short in 37, medium in 37, absent in 24. The anterosinusid is open in 38 and closed in 26. The lingual anterolophid is present in 39 out of 62 specimens. An anterostylid is also present in 55 out of 77 specimens. This anterostylid is well developed in 32 of these 55 specimens.

m2: The lingual anterolophid is absent in 16 specimens, very short in 47, short in 32 and medium in 1. The mesolophid is of medium length in 6, short in 47 and is absent in 45.

Remarks

The general morphological pattern of the material from La Retama is similar to that of the type material of Valtorres and other samples described by Daams y Freudenthal (1988b). The main difference observed is the lower frequency of long and medium mesolophs and mesolophids of the sample from La Retama. This difference could be due to ecological conditions, since the development of this character could be related to humidity as pointed out by Daams *et al.* (1999c). The size of the *Megacricetodon primitivus* from La Retama is relatively small compared to the other populations of this species. Nevertheless, we think that this size difference could also be due to a lower productivity of the environment on which this species was living.

Megacricetodon sp. nov.
(Plate 4, Figures 11-17)
Material and measurements: Table 8

Description

M1: The anterocone is unequally split in 3 specimens, while it is rather symmetrical in other 3. A well-developed cingulum is present in the anterior part of the anterocone in 4 specimens and it is small in 3. The protolophule is posterior in all specimens. A paracone spur is present in 5 specimens (in 2 of them it is small) and absent in 3. A well-developed cingulum that runs from the anterocone till the hypocone is present in 2 out of 6 specimens. The mesoloph is of medium length in 7 and short in 1 specimen. The metalophule is posterior in all specimens.
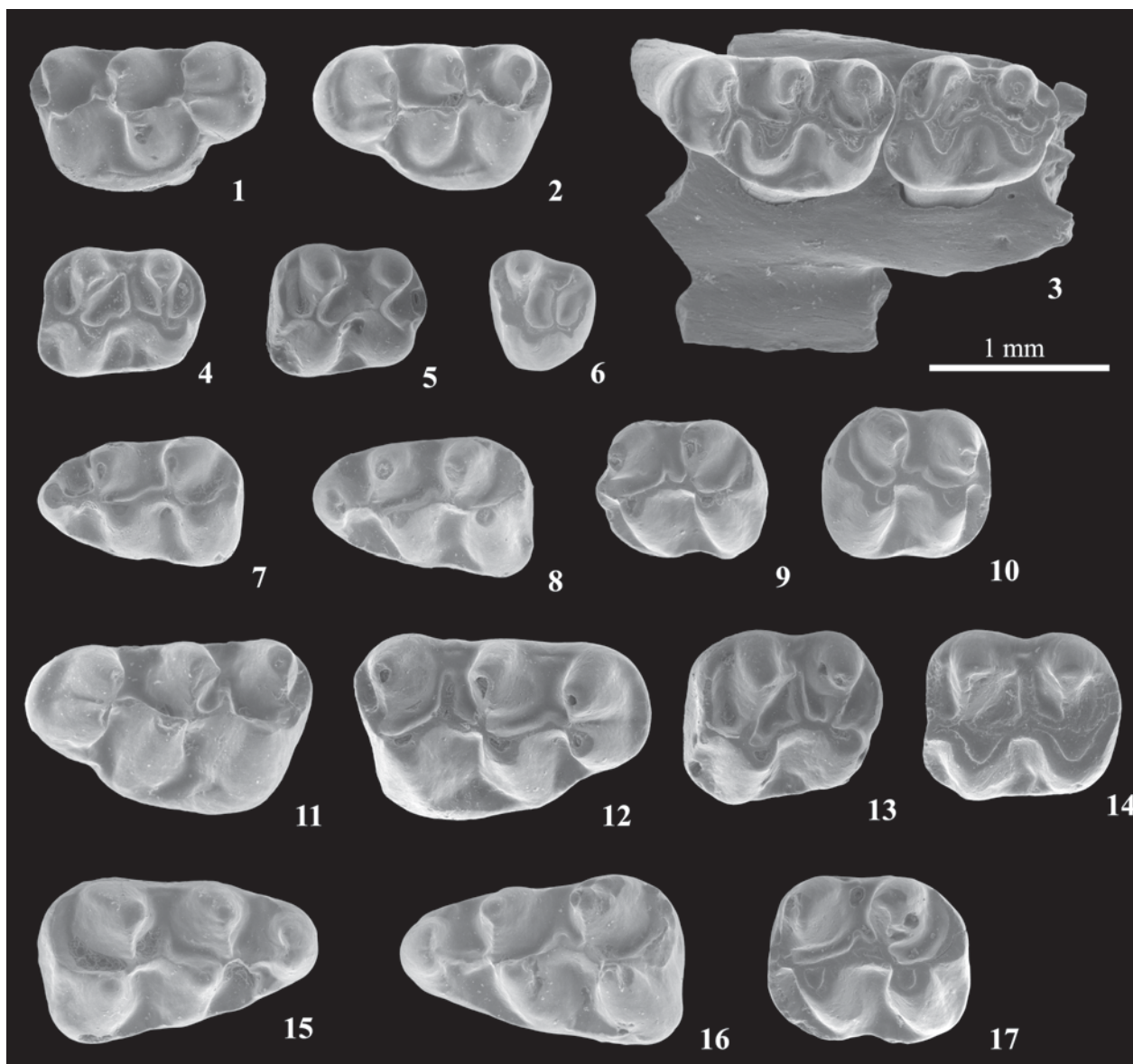
Plate 4.—Figures 1-10 *Megacricetodon primitivus* (Freudenthal, 1963); 1. M1 right, (REM- 84); 2. M1 left, (REM- 1); 3. M1, M2 left, (REM- 8); 4. M2 left, (REM- 128); 5. M2 left, (REM- 153); 6. M3 left, (REM- 229); 7. m1 left, (REM- 255); 8. m1 left, (REM- 241); 9. m2 left, (REM- 334); 10. m2 right, (REM- 418); Figures 11-17 *Megacricetodon* sp. nov.; 11. M1 left, (REM- 18); 12. M1 right, (REM- 119); 13. M2 left, (REM- 149); 14. M2 left, (REM- 138); 15. m1 right, (REM- 320); 16. m1 left, (REM- 250); 17. m2 left, (REM- 340).

M2: The protolophule is directed forwards in 2 and is transverse in 1. The mesoloph is medium in all specimens. The metalophule is anterior in one and transverse in two. A paracone spur is present in the two specimens on which this structure can be observed.

m1: The anteroconid consists of a single cusp in 4 specimens and in another 3 unworn specimens a double anteroconid slightly split is present ('8' pattern). The mesolophid is short in 7 and absent in one. The anterosinusid is open in six and closed in two specimens. The lingual anterolophid is present in five out of seven specimens. An anterostylid is also present in four out of seven specimens. This anterostylid is well developed in two of the four specimens where it is present.

m2: The lingual anterolophid is absent in two specimens and very short in another four. The mesolophid is short in five specimens and it is absent in one.

Table 8.—**Measurements of *Megacricetodon* nov. sp**

Megacricetodon nov. sp.	Length				N	Width			
	Min.	Mean	Max.	s.d.		Min.	Mean	Max.	s.d.
M1	1.58	1.68	1.78	0.085	7/8	0.94	1.05	1.15	0.071
M2	1.13	1.17	1.23	0.051	3/2	1.07	1.08	1.08	0.007
M3	0.81	0.84	0.89	0.044	3	0.85	0.87	0.89	0.021
m1	1.56	1.62	1.68	0.042	8/7	0.90	0.97	1.00	0.034
m2	1.11	1.19	1.25	0.055	6	0.97	1.01	1.05	0.030
m3	0.96	0.98	1.00	0.028	2	0.79	0.81	0.82	0.021

N = number of specimens; s. d. = Standard deviation.

Remarks

The general pattern of the material from La Retama is somewhat different from that of *Megacricetodon primitivus*. It shows a higher frequency of slightly split anteroconids and, in average shorter mesolophs and mesolophids. The morphology is similar to the *M. gersii* material from biozone F and G1 of Daams *et al.* (1999a). Daams *et al.* (1999a) also include a new *Megacricetodon* species from biozone Db that has not yet been described. Its morphology is very similar also to the material from La Retama and probably all these samples could be included in a new species that will be described in a separate paper, which is in preparation. The scarce material from La Retama does not allow a detailed statistical comparison and therefore we refrain from a specific assignation at this point.

This species is easily distinguished from *M. primitivus* from La Retama by its much larger size.

Erinaceomorpha Gregory, 1910
Erinaceidae Fischer von Waldheim, 1817
Galericinae Pomel, 1848
Galerix Pomel, 1848
Galerix cf. *symeonidisi* Doukas, 1986
(Plate 5, Figures 1-8)
Material and measurements: D3 (1.54 x 1.10); C (1.54 x 0.67); P3 (2.04 x 1.55); M1 (2.16 x 2.88), M2 (1.92 x 2.48); p2 (1.46 x 0.96); p3 (1.42 x 0.77); p4 (1.85 x 1.25).

Description

D3: The D3 has a relatively low paracone, with a slightly curved posterocrista. The protoconal flange appears as a bulge in the outline, lingually of the tip of the paracone. The small conical protocone is the starting point of a ridge, which continues as a strong anterolingual cingulum. There is a shelf-like posterolingual cingulum. On the labial side the cingular development is patchy.

C: The upper canine is a slender unicuspid, with its slightly backwards-inclined tip at the centre of the tooth. There is a small posterior flattening which bears a minute cuspule.

P3: The paracone of the P3 has a long posterocrista. The lingual flange bears a clear hypocone, which is about half the size and height of the protocone.

M1: The protoconule of the M1 appears as a club-shaped ending of the anterior arm of the protocone. There is no protocone-metaconule connection, but the protocone-hypocone ridge passes close by the lingual side of the metaconule. The posterior arm of the metaconule ends short of the posterior cingulum. There are well-developed cingula on the anterior, labial and posterior side.

M2: The M2 does not have a protoconule. Here too, the protocone-metaconule connection is absent, and the posterior arm of the metaconule ends without reaching the posterior cingulum. The cingula are somewhat less developed than in the M1.

p2-p3: Two isolated premolars have been found, which are interpreted as the p2 and p3. The p2 has an elliptical outline, whereas the p3 has a straight posterior side. This premolar is lingually longer than labially. In the p3 the tip of the main cusp lies in the centre of the tooth, in the p2 just in front of this point. Both premolars have tiny accessory cuspules at the front and at the back.

p4: The p4 consists of a trigonid with a short posterior flattening. The metaconid is well developed. The paraconid is blade-like. Since the anterior side of the protoconid is rounded, a true paralophid is not developed.
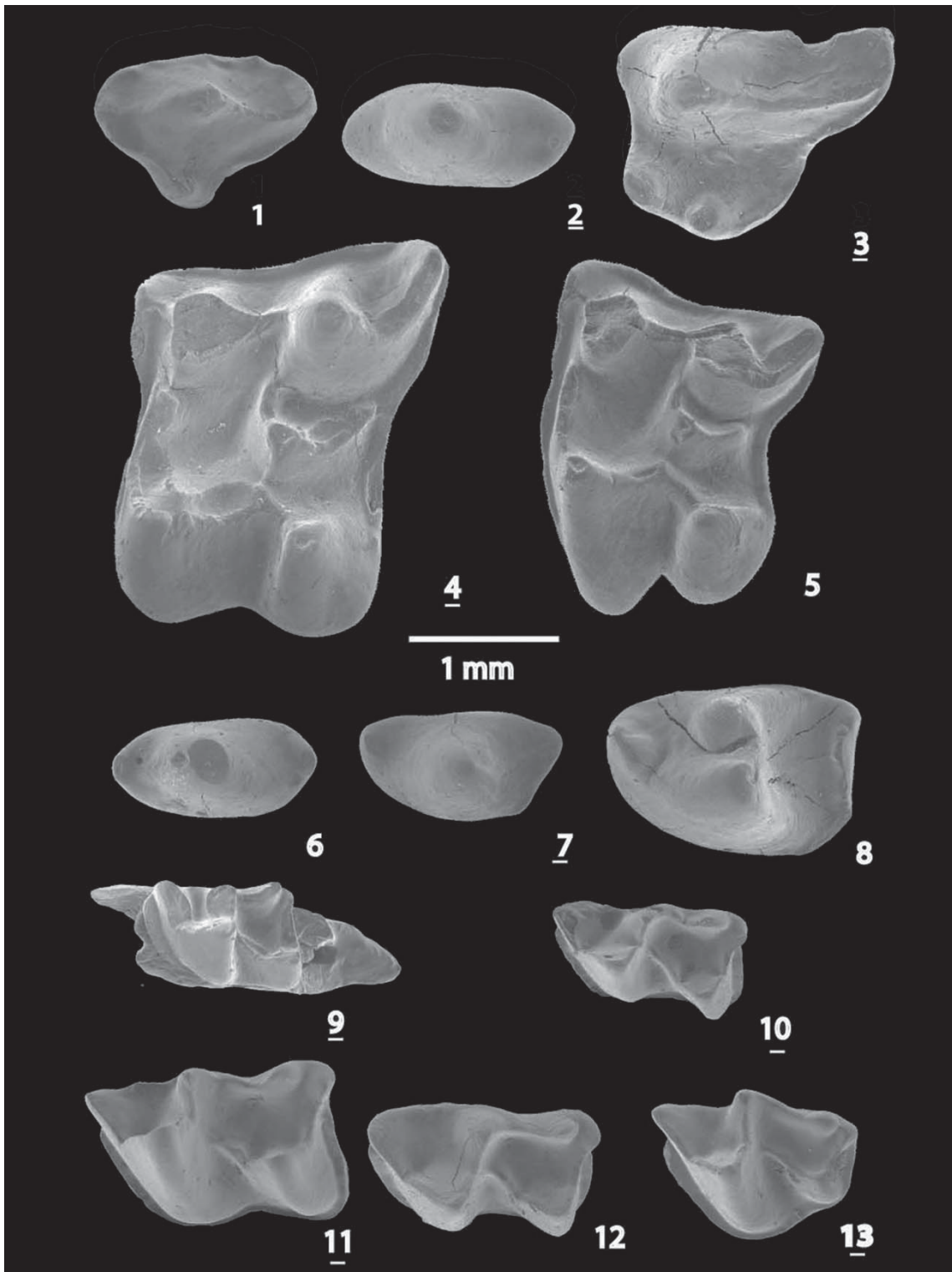
Plate 5.—Figures 1-8 *Galerix* cf. *symeonidisi* Doukas, 1986; 1. D3 left, (REM-451); 2. C right, (REM-452), reversed; 3. P3 right, (REM-453), reversed; 4. M1 right, (REM-454), reversed; 5. M2 left, (REM-455); 6. p2 left, (REM-456); 7. p3 right, (REM-457), reversed; 8. p4 left, (REM-458); Figure 9 *Soricidae* gen. et sp. indet.; 9. m1 right, (REM-459), reversed; Figure 10 *Asellia mariaetheresae* Mein, 1958; 10. m1 right, (QREM-460), reversed; Figures 11-13 *Hipposideros* (*Pseudorhinolophus*) sp.; 11. m1 left, (QREM-462), reversed; 12 m2 right, (QREM-463); 13. m3 right, (QREM-466), reversed.

Remarks

The genus *Galerix* is a very common element in the European Early and Middle Miocene faunas. In the Middle Miocene it is mainly represented by two wide-spread species, *G. symeonidisi* and *G. exilis*. Initially these were believed to represent a single evolutionary lineage, in which through an increase in size, the gradual loss of the hypocone on the P3 and the reduction of the protocone-metaconule connection *G. symeonidisi* evolved into *G. exilis* (Ziegler y Fahlbusch, 1986). This view was contested by van den Hoek Ostende and Doukas (2003) on the basis of the Galerix assemblages from the Aragonian type section (Daroca-Calamocha area, Zaragoza). Some of these assemblages showed a variation in size that was too large to be comfortably fitted into one species. They believed that the pattern was better explained by assuming gradual replacement of *G. symeonidisi* by *G. exilis*. This replacement theory is now assumed to be the most plausible model (Ziegler, 2005). However, the actual presence of two species in one assemblage could still not be proven in the absence of sufficiently large assemblages to demonstrate a bimodal distribution in size.

Van den Hoek Ostende and Doukas (2003) assumed that *Galerix symeonidisi* disappeared in zone Db. In that zone the minimum size abruptly increased, indicating that the smaller species was no longer present.

The only P3 found in La Retama has a hypocone, the various elements are relatively small, and both upper molars lack the protocone-metaconule connection. The small size and hypocone on the P3 are characteristic for *Galerix symeonidisi*, whereas the absence of a protoconule-metaconule connection is more common in this species than in *G. exilis*. In view of the scantiness of the material, it is tentatively assigned to the species. La Retama is among the youngest occurrences of *G. symeondisi*.

Soricomorpha Gregory, 1910
Soricidae Fischer von Waldheim, 1817
Soricidae gen. et sp. indet.
(Plate 5, Figure 9)
Material and measurements: m1 (1.20 x 0.69 x 0.73).

Description

m1: The only shrew molar is preserved in a mandible fragment. The trigonid is somewhat wider and longer than the talonid. The oblique cristid ends against the middle of the posterior wall of the trigonid. The entocristid closes the talonid basin at the lingual side. The hypolophid runs behind the entoconid and is separated from it by a narrow valley. The cingulum is wide on the anterior side, and well developed on the labial and posterior sides.

Remarks

With only a single lower molar available, shrews are difficult if not impossible to identify. *Miosorex* is often used as a dustbin for isolated Middle Miocene shrews in Spain, but pending a more comprehensive review of the Early and Middle Miocene shrews, it seems wiser to refrain from identifying single molars even at the genus level.

Chiroptera Blumenbach, 1799
Hipposideridae Gray, 1831
Hipposideros Gray, 1831
Brachipposideros Sigé, 1968
Hipposideros (Brachipposideros) collongensis (Dépèret, 1892)
(Plate 6, Figures 1-5)
Material and measurements: Table 9

Description

C: The only upper canine preserved in La Retama is badly damaged, the crown is partially broken and the root is missing. However, its shape, long and narrow, can be appreciated; the lingual surface is convex, the labial surface almost flat. On the distal edge, a distinct secondary cusp can be observed. It is rounded, short and does not diverge much from the main cusp. Practically no cingulum is preserved, though it seems to be developed at least to a certain extent on the distal part of the labial side.

P4: Only one specimen preserved, in which the heel is missing. The main cusp is high; the postparacrista is high and slightly bent. The labial cingulum is thin; on the mesial side it is thicker; at the labio-mesial angle a cusplet is observed.

M3: In occlusal view, the outline is triangular, with the distal region only slightly reduced. The metacone is present, as well as a short postmetacrista. The length of the latter seems to be variable; in three specimens the postmetacrista is no longer than a third of the premetacrista; however, in a fourth, the postmeta-

Table 9.—**Measurements of *Hipposideros (Brachipposideros) collongensis***

H. (Brachipposideros) collongensis	Length			N	W			w
	Min.	Mean	Max.		Min.	Mean	Max.	
Upper canine		1.30		1		0.54		
P4		1.17		1/0				
M3	0.92	0.99	1.10	4/5	1.27	1.36	(1.45)	
m1-2		(1.27)		1		(0.75)		(0.80)

N = number of specimens). Estimated values in parentheses. In the lower molars, two widths were measured, W= width measured at the trigonid; w = width measured at the talonid.

Table 10.—**Measurements of *Hipposideros (Pseudorhinolophus)* sp.**

H. (Pseudorhinolphus) sp.	Length			N	W			w
	Min.	Mean	Max.		Min.	Mean	Max.	
Uper canine		1.57		1		1.25		
M1	(1.42)	1.51	1.60	2	1.78	1.84	1.90	
p4		1.07		1			0.90	
m1-2	(1.50)		(1.60)	2	(0.83)		(1.00)	(0.91)
m3	(1.42)		(1.43)	2/2/1	0.97	1.00	(1.03)	(0.63)

N = number of specimens). Estimated values in parentheses. In the lower molars, two widths were measured, W = width measured at the trigonid; w = width measured at the talonid.

crista is about two thirds the length of the premetacrista. The fifth specimen is damaged at that region.

m2: This tooth presents the typical morphology of the group. Though the entoconid and a part of the entocristid are missing, it can be clearly observed that it is nyctalodont (Menu *et al.*, 1971). The labial cingulum is thin and regular in thickness; on labial view it runs downwards drawing a convexity that reaches its deepest point at mid-length of the tooth. An important difference in the height of the labial and lingual cusps is observed, the latter being remarkably higher. On the lingual side, the metaconid is the highest cusp; on the labial side, it is the protoconid. All the cristids present a deep notch.

Remarks

This material agrees with the morphology and size of *Hipposideros (Brachipposideros) collongensis*. It has been described in several Miocene localities of Europe ranging in age from MN3 to MN7/8, such as Vieux-Collonges, the type locality of the species (Mein, 1958), La Grive St Alban (Guérin *et al.*, 1971), La Serre de Verges (Meurisse *et al.*, 1969), Cases de Pène (Mein *et al.*, 1973), Bouzigues (Sigé, 1968), Crémat (Sigé *et al.*, 1991) and Stubersheim 3 (Ziegler, 1994). It is the first time this species is described from a Spanish locality.

Hipposideros (Brachipposideros) collongensis differs from other species of the subgenus *Brachipposideros* in the relatively less reduced third molars; *H. (B.) aguilari* is smaller and *H. (B.) dechaseauxi* is larger. *H. (B.) branssatensis* from Coderet-Branssat (Hugueney, 1965) is similar in size to *H. (B.) collongensis*, but presents a distinct paraloph in the M3.

Pseudorhinolophus Schlosser, 1887
Hipposideros (*Pseudorhinolophus*) sp.
(Plate 5, Figures 11-13 and Plate 6, Figures 6-9)
Material and measurements: Table 10

Description

C: The upper canine is long and narrow, the crown flattened on the lingual side and slightly concave on the labial side. On lateral view, the crown is curved toward the rear; the distal edge is worn up to a certain distance from the cingulum, where it forms the distinct angle of the upper canines of the bats of the subgenus *Pseurhinolophus*. The cingulum is thick and well developed on the lingual side. It narrows and gets apart from the base of the crown towards the distal edge, where it forms a small platform. On the labial side the cingulum is thin and weak.
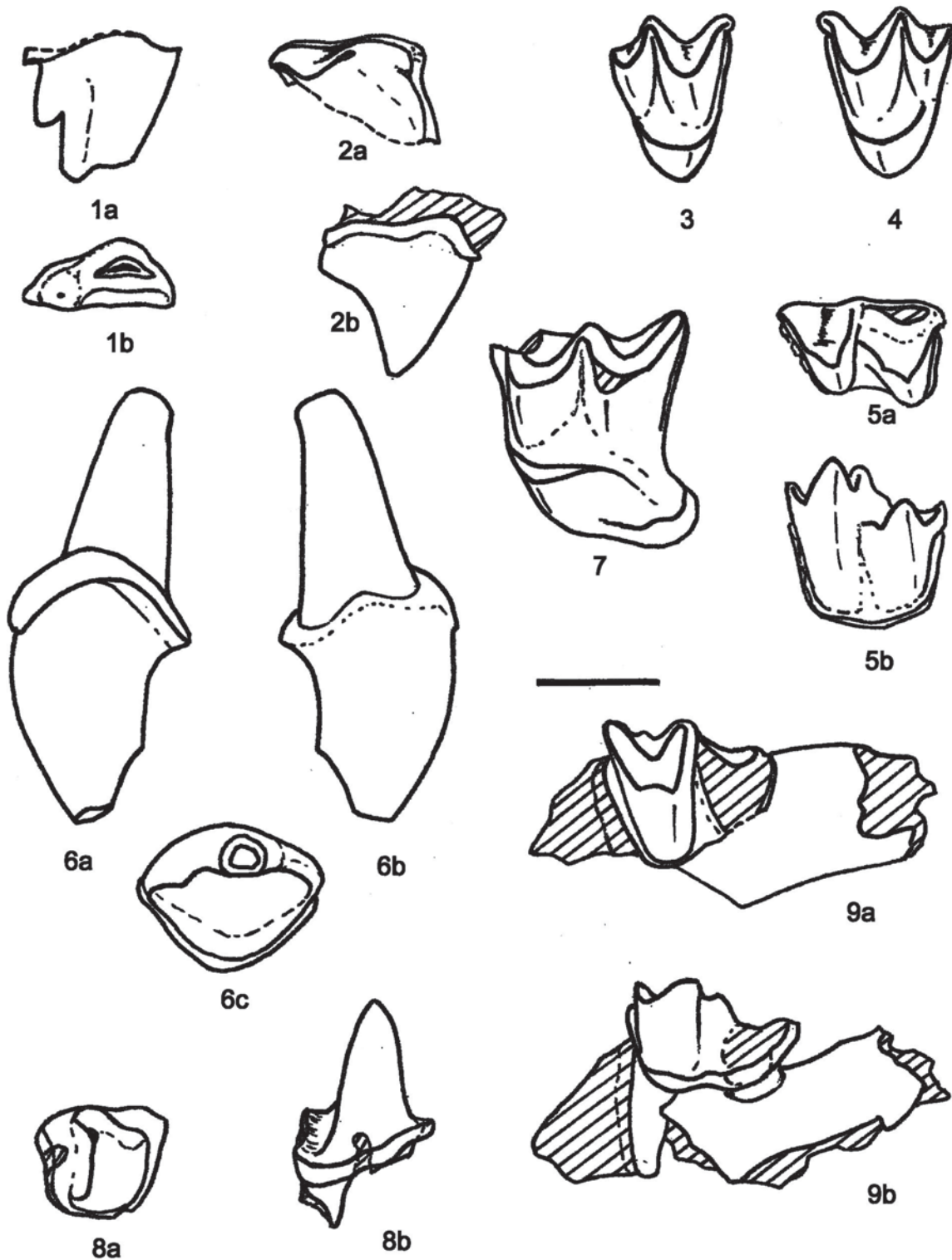
Plate 6.—Figures 1-5 *Hipposideros* (*Pseudorhinolophus*) *collongensis* (Deperet, 1892); 1. C right, (QREM-34) a: labial view; b: occlusal view; 2. P^4 right, (QREM-9), occlusal view; 3. M^3 right, (QREM-13), occlusal view; 4. M^3 left, (QREM-18), occlusal view; 5. M_2 right, (QREM-29), a: occlual view; b: labial view; Figures 6-9 *Hipposideros* (*Pseudorhinolophus*) sp.; 6. C right, (QREM-1) a: lingual view; b: labial view; c: occlusal view; 7. M^1 right, (QREM-36) occlusal view; 8. P_4 right, (QREM-19) a: occlusal view; b: labial view; 9. M_3 left, (QREM-17) a: occlusal; b: labial. Scale: 1mm.

M1: The first upper molars has a sub-quadrate occlusal outline. The paracone and metacone are wide; the valley between both cusps is narrow and deep. The protocone is placed as mesial as the paracone and presents no basal cingulum. The preprotocrista connects the anterior cingulum; the postprotocrista is short; there is no paraloph nor a metaloph. A well-developed heel provided by a thick cingulum is present. The distal cingulum is thin and ends at the base of the metacone. A fourth small root is present on the base of the heel.

p4: There is a single specimen that agrees in morphology and size with the species of the subgenus *Pseudorhinolophus*. Only the crown and the base of the distal root are preserved. The occlusal outline is subtriangular; the posterior and lingual surfaces of the crown are concave, the labial surface is convex. On the disto-lingual edge of the main cusp a distinct angle is observed with the swelling of a secondary cusp. The cingulum is thin and continuous all around the base of the crown. On the distal part it develops a small concave platform with a small tubercule on the disto-lingual angle. A small triangular platform without tubercules is observed on the antero-lingual angle.

m1-2: The general appearance of these teeth agrees with the morphology of other species of the subgenus; nyctalodont, the labial cingulum is thin to intermediate and distinct notches are observed on the paralophid and crista obliqua. The hypoconulid is well developed and stands well apart from the entoconid. The entocristid is slightly concave in occlusal view.

m3: this tooth differs from the anterior molars in the reduction of the talonid. The entoconid occupies a more labial position and the hypoconid is lingually displaced. Thus, the talonid is reduced both in length and width. The hypoconulid is well developed.

Remarks

The Hipposideridae belonging to the subgenus *Pseudorhinolophus* are characterised for having single cusped upper canines, differing thus from other subgenera of *Hipposideros*, which present a secondary distal cusp, developed to a different degree depending on the subgenus. The fossil species of *Hipposideros (Pseudorhinolophus)* are mainly distributed in the Oligocene, *H. (P.) bouziguensis* being up to now the only species recorded in the Miocene. This Miocene species is characterised by its large size and derived characters (Legendre, 1982a) and has been recorded in several localities such as Bouzigues (Sigé, 1968) and Port-la-Nouvelle (Legendre, 1982a and b) in France.

Hipposideros (Pseudorhinolophus) bouziguensis and the material of La Retama differ in a number of important characters. The first species is quite larger, with more massive teeth and shows advanced characters absent in the specimen from La Retama. In *H. (P.) bouziguensis* the third molars are strongly reduced; the preparacrista in the upper molars is unconnected to the precingulum; whereas the cingulum of the talon is continuous with the postcingulum. Therefore, the species represented in La Retama must belong to an undescribed species of the subgenus *Pseudorhinolophus* that retains certain primitive characters.

The upper canine referred to "*Rhinolophus*" from the MN4 locality of Córcoles (Alférez et al, 1982, plate 1, fig. 8) is in fact the upper canine of a hipposiderid of the subgenus *Pseudorhinolophus*. Although no measurements are given, measurements taken from the figure indicate a similar size as the specimen from La Retama, and therefore the Córcoles canine might belong to the same species.

The isolated p4 described in Crémat (Sigé *et al.*, 1991) is considered by the authors as belonging to a new undescribed species of *Hipposideros (Pseudorhinolophus)*; no measurements are given, but the Crémat premolar seems similar in size to *H. (P.) bouziguensis*, and is therefore larger than the species of La Retama.

Asellia Gray, 1838
Asellia mariaetheresae Mein, 1958
(Plate 5, Figure 10; Plate 7, Figures 1-7)
Material and measurements: Table 11

Description

P4: Slender, with a well-developed lingual heel; straight paracrista; the cingulum that surrounds the crown is thin and presents no swellings; a small concavity develops on its medio-distal side.

M1: Sub-quadrate, without hypocone and with a well-developed heel. Preprotocrista continuous with the precinculum; postprotocista directed to the base of the metacone. A weak paraloph is observed in one of the specimens. The heel presents a thick cingulum, unconnected to the postcingulum. Four roots are observed on this tooth.

M2: similar to the first molar, but easily distinguished for its shorter heel. The cingulum of the

Table 11.—**Measurements of *Asellia mariaetheresae***

| *Asellia mariaetheresae* | Length | | | | W | | | w |
	Min.	Mean	Max.	N	Min.	Mean	Max.	
P4	0.92	0.97	1.02	1/0		1.27		
M1		1.40		1		1.54		
M2		1.34		1/2	1.54		1.60	
M3		0.80		1		1.40		
m1	(1.30)	1.38	(1.45)	3	(0.66)	0.76	0.94	0.81
m2		1.37		1/1/2		0.72		0.80
m3	1.22	1.24	1.27	3	0.75	0.83	1.00	0.79

N = number of specimens. Estimated values in parentheses. In the lower molars, two widths were measured, W = width measured at the trigonid; w = width measured at the talonid.

heel is not as thick as in M1, and connects in the two specimens with the distal cingulum.

M3: small, strongly reduced on its distal part. There is no metacone, nor a premetacrista, and even though a mesostyle is present, the postparacrista is shortened to about a half the length of the preparacrista. The protocone is low, close to the lingual side and presents no cingulum. The precingulum connects the preprotocrista; the postprotocrista ends at about the mid-distal margin of the tooth.

m1-2: Nyctalodont, the labial cingulum is thin. In m1, the trigonid is narrower and slightly longer; the paraconid and metaconid stand wider apart than in m2. The three main lingual cusps are, of approximately the same height. The hypoconulid is small but distinct and stands well apart from the entoconid. Distinct notches are observed on all of the cristids. The entocristid is slightly bent.

m3: Similar in morphology to the anterior molars except for the reduction in the talonid. The position of the entoconid is displaced towards the labial side and closer to the trigonid, thus resulting in a shorter and narrower talonid. The hypoconulid shows no reduction when compared with m1 and m2.

Remarks

Asellia mariaetheresae is the best represented species of Chiroptera in La Retama. This species was first described in Vieux-Collonges (Mein, 1958) and since then has been found in other Miocene Mediterranean localities ranging from MN4 to MN15, such as the French localities of Port-la-Nouvelle (Legendre, 1982), La Grive St Alban (Guérin *et al*., 1971), Cases de Pène (Mein *et al*., 1973) or Brisighella in northern Italy (Kotsakis *et al*., 1989). The material from La Retama does not show any significant morphological differences with the

material of *Asellia mariaetheresae* described in other localities. With regard to the size, the M1 and M2 in La Retama are slightly narrower and the lower molars somewhat shorter when compared to the material from Port-la-Nouvelle. However, this species seems to present a relatively wide range of variability in the size of the teeth.

A broken p4 (QREM-5), in which only the mesial half of the crown is preserved, agrees with the size and morphology expected for *Asellia mariaetheresae* and might be referred with caution to this same species.

The single lower molar from the Spanish middle Miocene locality of Casetón 1A (Sevilla, 2002), referred to Hipposideridae indet., though within the range of variation in size observed in *Asellia mariaetheresae*, differs with the material from this species in La Retama in the proportions of the tooth, the thickness of the cingulum and in the absence of notches in the metacristid and entocristid.

The single M3 referred to cf. *Asellia* sp. from the French locality of Crémat (Sigé *et al*., 1991) differs from *Asellia mariaetheresae* in the degree of distal reduction of the tooth, as well as in the development of the parastyle.

Vespertilionidae Gray, 1821
Myotis Kaup, 1829
Myotis sp.
(Plate 7, Figures 8, 9)
Material and measurements: P4 (0.87 x 0.95); M2 ((1.20) x 1.56);

Description

P4: Small, relatively wide, with a sub-elliptical occlusal outline, slightly concave on its medio-dis-

tal side; parastyle absent; the cingulum is strong and continuous; on the mesio-lingual side it develops a small tubercle.

M2: this tooth is partially damaged: both the parastyle and a part of the metacone are missing. In occlusal view, the outline of the tooth is close to rectangular. Both a paraloph and a metaloph are present, though weakly developed. The swelling of a small hypocone on the postprotocrista is visible. On the anterior side of the tooth, the cingulum, of intermediate width, connects with the preprotocrista. The basal cingulum is briefly interrupted at its mid point and connects the distal cingulum, which ends close to the metastyle; at the distal base of the protocone it gets thicker and develops a small platform.

Remarks

The fossils referred to the genus *Myotis* are relatively frequent in the Miocene. Apart from size, the characters that differ in the upper molars of these species are mainly the development of a hypocone, protoconule and metaconule, the presence of a paraloph and a metaloph as well as characteristics of the postprotocrista.

Thus, the upper molars of *Myotis antiquus* from La Grive St. Alban (Mein, La Grive), *M. murinoides* and *M. elegans* described in Sansan (Baudelot, 1972) and *Myotis* sp. II of Bouzigues (Sigé, 1968) present in addition to the hypocone a distinct protoconule and metaconule. *Myotis sanctialbani* presents no hypocone, but distinct protoconule and metaconule, whereas *M. salobrensis* and *M. boyeri* Lissieu (Mein, 1964) lack these three elements. Furthermore, the latter species presents the postprotocrista connected to the distal cingulum, a characteristic quite unusual among the species of the genus.

Myotis bavaricus described in Petersbuch (Ziegler, 2003) is also close in size to *Myotis* sp. from La Retama. However, its P4 is slightly larger, with less concave distal outline and occasionally with both mesio-labial and mesio-lingual cingular tubercles. The M2 is similar in length but wider; a large and curved ectoloph is present and the basal cingulum is continuous.

Myotis sp. from La Retama resembles more closely several other species described in the Miocene, but the scanty material preserved in La Retama does not permit to establish a more precise determination. Thus, it agrees with the morphology and size of the M2 referred to *Myotis* sp. in the Spanish loca-

lity of Fuenmayor (Martínez- Salanova, 1987); to *Myotis* sp. I from the French locality of Bouziges (Sigé, 1968), also described in the Spanish locality of Rincón del Bu (Murrelaga et al, 2004), or to *Myotis* aff. *minor* from Casetón 1A (Sevilla, 2002).

Molossidae Gill, 1872
Tadarida Rafinesque, 1814
Tadarida sp.
(Plate 7, Figure 10)
Material and measurements: 1 upper canine (1.42 x 1.14)

Description

This tooth presents an occlusal outline intermediate between triangular and semicircular. On lateral view, the crown forms a slight angle with the root. The lingual surface of the crown is strongly concave; anterior and labial surfaces convex, separated by a deep groove that extends from the base to the apex; a similar groove develops near the distal angle of the crown. The cingulum is thick and continuous; on lateral view it bends slightly towards the root at the mid point of the labial side; on the lingual side it is fairly straight, and develops a small platform.

Remarks

Molossids present sexual dimorphism in the canines; for this reason, they have wider ranges of variability in the size of these teeth than other Chiroptera. The morphology of the upper canine of the Molossid from La Retama agrees with that described by Rachl (1983) for *Tadarida engesseri* from the locality of Steinberg (MN6) and falls within the size of the larger specimens of this species. It fits too with the size of the smaller specimens of *Tadarida helvetica* from Port-la-Nouvelle (Legendre, 1982b and c). Therefore, in the absence of additional material, it is not possible to relate the specimen of La Retama to any of these two species in particular.

Molossidae are rare in Spanish Neogene localities. They were already present in the Iberian Peninsula at least since MN3, since the upper molar from the lower Miocene locality of Barranco del Fraile (Murelaga *et al.*, 2004) is without doubt a molossid. Another tertiary record of this group in Spain is ?*Nyctinomus* sp. from Buñol (MN4) (Adrover, 1968).
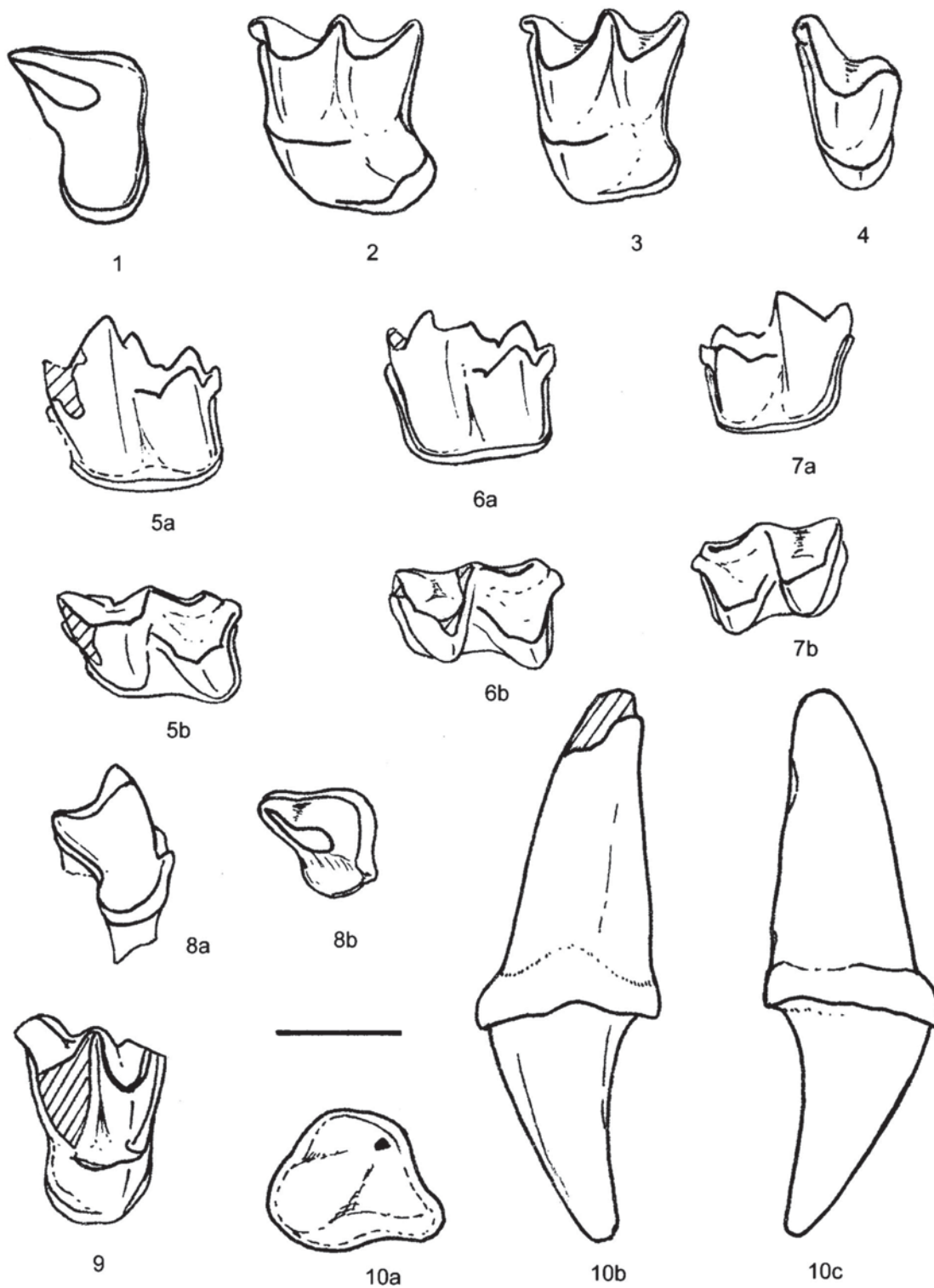
Plate 7.—Figures 1-7 *Asellia mariaetheresae* Mein, 1958; 1. P^4 right, (QREM-8), occlusal view; 2. M^1 left, (QREM-35), occlusal view; 3. M^2 left, (QREM-22), occlusal view; 4. M^3 left, (QREM-15), occlusal view; 5. M$_1$ left, (QREM-10), a: labial view, b: occlusal view; 6. M$_2$ left, (QREM-25), a: labial view, b: occlusal view; 7. M$_3$ right, (QREM-32), a: labial view, b: occlusal view; Figures 8-10 *Myotis* sp.; 8. P^4 right, (QREM-30), a: lingual view, b: occlusal view; 9. M^2 left, (QREM-11), occlusal view; Figure 19 *Tadarida* sp.; 10: C left, (QREM-2), a: occlusal; b: labial; c: lingual. Scale: 1mm.

Biochronological conclusions

The micromammal faunal list of La Retama is as follows:

Heteroxerus rubricati Crusafont, Villalta y Truyols, 1955
Heteroxerus grivensis (Forsyth Major, 1893)
Armantomys aragonensis de Bruijn, 1966
Armantomys jasperi Daams, 1991
Pseudodryomys ibericus de Bruijn, 1966
Pseudodryomys simplicidens de Bruijn, 1966
Microdyromys koenigswaldi de Bruijn, 1966
Democricetodon decipiens Freudenthal and Daams, 1988
Megacricetodon primitivus (Freudenthal, 1963)
Megacricetodon sp. nov.
Galerix cf. *symeonidisi* Doukas, 1986
Soricidae gen. et sp. indet.
Hipposideros (Brachipposideros) collongensis (Deperet, 1892)
Hipposideros (Pseudorhinolophus) sp.
Asellia mariaetheresae Mein, 1958
Myotis sp.
Tadarida sp.

Daams (1991) studied the hypsodont Gliridae including the *Armantomys* material from La Retama. In this work he assigned this fauna to the biozone D1 of Daams and Freudenthal (1988a). Later studies based on mammal material from La Retama correlate this fossil assemblage with local biozone D (among others Morales *et al*., 1993, 1999).

A new biostratigraphic framework for the Aragonian of the Calatayud-Daroca and other central Spanish basins has been proposed by Daams *et al*. (1998 and 1999a). The latter authors proposed a new division of the previous zone D. According to these authors the zone Db (early MN5) is characterized by the presence of two *Megacricetodon* species, of which the large one has not been yet defined. In La Retama there are two *Megacricetodon* species. The small one assigned to *M. primitivus* and the large one to *Megacricetodon* nov. sp. The general morphological pattern of the material of *Megacricetodon primitivus* from La Retama is similar to that of the type material of Valtorres and other samples described by Daams and Freudenthal (1988b). The second species has been compared with the material from Db localities of the Aragonian type area. The morphology and size are very similar and, as discussed before, we think that all these samples could belong to the same taxon.

This correlation is supported by other taxa as the glirids. *Pseudodryomys simplicidens* from the type area of the Aragonian has been extensively studied and discussed by García Paredes (2006), showing trends toward size increase of the molars, simplification of the p4 and simplification of the posterior part in the m3. The morphology and size of the material from La Retama correspond to that of the material from localities of equivalent age (Db) in the type area of the Aragonian. Other taxa with *a priori* good biochronological connotation, such as *Democricetodon*, do not contributed significantly to the age assignation of La Retama. The size of the *Democricetodon* material from La Retama agrees best with *D. decipiens* from Buñol and the younger populations of the species in the Villafeliche area. The morphology of the material is not conclusive since it agrees with that of *D. decipiens* and the younger *D. moralesi*. These two species belong to the lineage *D. hispanicus- D. lacombai* defined by van der Meulen *et al*. (2003). The small size of some rodents from La Retama is a quite normal pattern since it is observed in *Heteroxerus rubricati*, *Megacricetodon primitivus* and *D. decipiens*, we think that it could be related to the local environmental conditions of this basin during the middle Aragonian. Therefore, we based our correlation mainly on the presence of the two *Megacricetodon* species despite the fact that *D. decipiens* has been recorded in older localities in other Spanish basins.

The other rodent species do not precise the age but contribute to a better knowledge of their temporal distribution. On the one hand, *Armantomys jasperi* from La Retama is one of the youngest records of this species (Daams, 1991; García Paredes, 2006). On the other hand, *Pseudodryomys ibericus* is rare among the Gliridae material from La Retama. In the type area of the Aragonian (Calatayud-Montalbán Basin), *P. ibericus* becomes less frequent after zone Db (García Paredes, 2006), localities which have similar age as La Retama (Morales *et al*., 1999). The erinaceid *Galerix symeonidisi* disappears after zone Db all together (van den Hoek Ostende y Doukas, 2003), and its presence in La Retama is among the youngest occurrences.

In spite of being poorly represented, the Chiroptera in La Retama are quite interesting. On the first place, two species are added to the poorly known Spanish record of bats: *Hipposideros (Brachipposideros) collongensis* and *Asellia mariaetheresae*, unknown up to now in the Spanish Neogene, but well known in other European Miocene localities.

Considering the composition of species represented in La Retama, there are affinities with some French localities, for instance Port-la-Nouvelle and Bouzigues. However, the record of a species of the genus *Asellia* in a non-karstic locality is a novelty, since all the known fossils of this genus had been described exclusively from karstic localities (Sigé *et al*., 1983; Sigé *et al*., 1991; Kotsakis *et al*., 1989).

Palaeoenvironmental conclusions

Morales *et al*. (1993 and 1999) interpreted the environment of La Retama as a riparian habitat consisting of an open landscape with shallow permanent water bodies of limited extensions, under seasonal warm climatic conditions. The detailed study of the micromammals contributes to a better understanding of the possible environment in which the fauna probably lived.

Recent species of *Hipposideros* and *Asellia* are distributed in warm, dry regions, mainly with shrub-land vegetation; though some species of the genus *Tadarida* can be found in temperate regions with short and mild winters, molossids are mainly distributed and are more diverse in regions with a warm climate. The genus *Myotis* is very diverse and is widely distributed, from tropical regions to high latitudes where winters are long and cold, during which they hibernate. Thus, the association of bat species in La Retama suggests a landscape of subtropical dry climate with an open landscape of shrub-land vegetation for this period in the basin. This interpretation, based on the Chiroptera information, fits the one based on the Gliridae. On the one hand, there is a predominance of simple glirids such as *Armantomys aragonensis* and *Pseudodryomys simplicidens* which are supposed to be open country and dry conditions inhabitants (Daams y van der Meulen, 1984), and on the other hand, the low diversity of glirids (only five species have been recorded) and the low relative abundance of the somehow more complicated ones, could indicate the predominance of relatively open and dry conditions in the La Retama area. Such a landscape would be unfavourable for insectivores, which are indeed very rare in the locality.

Other faunal arguments that could support this environmental interpretation are the presence of *Megacricetodon* species with shorter mesolophs and mesolophids that the cospecific populations from other areas. The length of the mesoloph and mesolophids have been used by Daams *et al*. (1999b) to infer relative humidity conditions, longer mesolophs and mesolophids are taken as indicative of more humid conditions. In addition the presence of relatively smaller representatives of known species such as *H. rubricati*, *M. primitivus* and *D. decipiens*, could be indicative of a low plant productivity related to the low humidity conditions.

References

Adrover, R. (1975). Principales yacimientos paleomastológicos de la provincia de Teruel y su posición estratigráfica relativa. *Trabajos Neóg.-Cuatern.*, 4: 31-48.

Alcalá, L., Cerdeño, E., Montoya, P., Morales, J., Pérez, B. y Soria, D. (1990). Composición Taxonómica y Anatómica de los restos de Macrovertebrados del Mioceno inferior continental de Loranca del Campo (Cuenca). *Com. I Reunión de Tafonomía y Fosilización*, 7-12.

Alcalá, L., Daams, R. y Morales, J. (1992). Faunal composition and taphonomy of the Early Miocene mammal fauna of Loranca del Campo (Cuenca, Spain). *EPA Work. Taphonomy: processes and products*. Strassbourg, 19.

Alférez, F., Molero, G., Brea, P. y Santafé, J. V. (1982). Precisiones sobre la geología, fauna, cronoestratigrafía y paleoecología del yacimiento mioceno de Córcoles. *Rev. Real Acad. Cienc. Exact. Físic. Nat. Madrid*, 76: 249-276.

Álvarez Sierra, M. A., Daams, R. y Peláez-Campomanes, P. (1994). Synthesis of Late Oligocene/Early Miocene micromammal faunas of the Loranca Basin (Province of Cuenca, Spain). *Comunicaciones de las X Jornadas de Paleontología*, 18-21.

Baudelot, S. (1972). *Etude des Chiroptères, Insectivores et Rongeurs du Miocène de Sansan (Gers)*. Tesis Doctoral. Université Paul Sabatier de Toulouse, Francia, 364 págs.

Bruijn, H. de (1966). Some new Miocene Gliridae (Rodentia, Mammalia) from the Calatayud area (prov. Zaragoza, Spain): I. *Proc. Kon. Ned. Akad. Wetens.* Series B, 69: 58-71.

Cerdeño, E. (1992a). Spanish Neogene Rhinoceroses. *Palaeontology*, . 35: 297-308.

Cerdeño, E. (1992b). New remains of the Rhinocerotid Hispanotherium matritense at La Retama site: Tagus Basin, Cuenca, Spain. *Geobios*, 25: 671-679.

Cerdeño, E. (1996). Lartetotherium (Rhinocerotidae) en la fauna con Hispanotherium del Mioceno medio de La Retama, Cuenca. *Rev. Esp. Paleont.*, 11:.193-198.

Cuenca Bescós, G. (1988). Revisión de los Sciuridae del Aragoniense y del Rambliense en la Fosa de Calatayud-Montalbán. *Scripta Geol.*, 87: 1-116.

Daams, R. (1981). The dental pattern of the Dormice Dryomys, Myomimus, Microdyromys and Peridyromys. *Utrecht micropaleont. bull. Special publ.*, 3: 1-113.

Daams, R. (1991). Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and the Oligocene-Miocene boundary interval of Spain. *Scripta Geol.*, 95: 1- 62.

Daams, R., Álvarez-Sierra, M. A., van der Meulen, A. J. y Peláez-Campomanes, P. (1996). Paleoecology and paleoclimatology of micromammal faunas from Upper Oligocene-Lower Miocene sediments in the Loranca Basin, Province of Cuenca, Spain. In: *Tertiary basins of Spain, the stratigraphic record of crustal kinematics.* (P. F. Friend y C. J. Dabrio, Edit.) Cambridge University Press, Cambridge, 295-299.

Daams, R. y Freudenthal, M. (1988a). Synopsis of the Ducht-Spanish collaboration program in the Aragonian type area, 1975-1986. *Scripta Geol.* Special Issue 1: 3-18.

Daams, R. y Freudenthal, M. (1988b). *Megacricetodon* (Cricetidae) from the Aragonian and the Lower Vallesian of the Calatayud-Teruel basin. *Scripta Geol.* Special Issue 1: 39-132.

Daams, R., Lacomba, J. I. y López-Martínez, N. (1986). Nuevas faunas de micromamíferos del Terciario continental de la Depresión Intermedia (provincia de Cuenca, España centro-oriental). *Estudios Geol.*, 42: 181-186.

Daams, R. y Meulen, A. J. van der (1984). Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the upper Oligocene and Miocene of north central Spain. In: *Paleoenvironnements continentaux en Méditerranée au Néogène et évolution paléoclimatique* (Meulenkamp, J. edit.). *Paléobiol. Continent.*, 14: 241-257.

Daams, R., Meulen, A. J. van der, Álvarez-Sierra, M. A., Peláez-Campomanes, P., Calvo, J. P., Alonso Zarza, M. A. y Krijgsman, W. (1999a). Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). *Newslett. Strat.*, 37: 103-139.

Daams, R., Meulen, A. J. van der, Peláez-Campomanes, P. y Álvarez-Sierra, M. A (1999b). Trends in rodent assemblages from the Aragonian (Early Middle Miocene) of the Calatayud-Daroca Basin (Aragón, Spain). In: *Hominoid Evolution and Climate Change in Europe. 1 The Evolution of Neogene Terrestrial Ecosystems in Europe* (Agusti, J. Rook, L. and Andrews, P., edit.). Cambridge University Press, Cambridge, 127-139.

Díaz-Molina, M. y López-Martínez, N. (1979). El Terciario continental de la Depresion intermedia (Cuenca); bioestratigrafia y paleogeografia. *Estudios Geol.*, 35: 149-167.

De Miguel, I., Fraile, S., Nieto, M., Pérez, B., Soria, D., Alcalá, L., Montoya, P. y Morales, J. (1996). Factores de control en la composición anatómica de las asociaciones de mamíferos miocenos de la Depresión Intermedia (Cuenca, Castilla-La Mancha, España). *Com. II Reunión de Tafonomía y Fosilización*, 225-232.

Freudenthal, M. (2006). The status of *Democricetodon, Fahlbuschia, Pseudofahlbuschia* and *Renzimys* (Cricetidae, Mammalia). A reply to van der Meulen *et al.* (2004). *Geobios*, 39: 43-55.

Freudenthal, M., Hugueney, M. y Moissenet, E. (1994). The genus Pseudocricetodon (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). *Scripta Geol.*, 104: 57-114.

García Paredes, I. (2006*). Patrones evolutivos de los Gliridae (Rodentia, Mammalia) del Mioceno inferior y medio del área tipo del Aragoniense (Cuenca de Calatayud-Montalbán)*. Tesis Doctoral. Universidad Complutense de Madrid, 676 pp.

Ginsburg, L., Morales, J. y Soria, D. (1987). Nouvelles faunes de grands mammifères d'âge Miocène inférieur dans la partie orientale du bassin du Tage (Espagne). Conséquences stratigraphiques. *C. R. Acad. Sci. Paris.* (Série II), 305: 629-632.

Guérin, C. y Mein, P. (1971). Les principaux gisements de mammifères miocènes et Pliocènes du domaine rhodanien. *Doc. Lab. Géol. Fac. Sci. Lyon.*, 49: 131-170.

Hoek Ostende, L. W. van den (2003). Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area. *Col. Paleont.* Vol. Ext., 1: 281-310.

Hoek Ostende, L. W. van den y Doukas, C. (2003). Distribution and evolutionary history of the Early Miocene erinaceid Galerix symeonidisi Doukas, 1986. - In: *Distribution and migration of Neogene mammals in Eurasia* (Reumer, J. W. F. y Wessels, W., edit.). Deinsea, Rotterdam,10: 287-303.

Hugueney, M. (1965). Les Chiroptères du Stampien supérieur de Coderet-Branssat (Allier). *Doc. Lab. Géol. Fac. Sci. Lyon.*, 9: 97-127.

Kotsakis, T. y Masini, F. (1989). Late Turolian bats from Brisighella (Northern Italy). *Boll. Soc. Paleont Italia.*, 28: 281-285.

Legendre, S. (1982a). Hipposideridae (Mammalia: Chiroptera) from the mediterranean middle and late Neogene, and evolution of the genera *Hipposideros* and *Asellia*. *J. Vert. Paleont.*, 2: 372-385.

Legendre, S. (1982b). La faune de micromammifères du gisement burdigalien de Port-la-Nouvelle (Aude). Compléments et indications paléoécologiques. *Bull. Soc. Géol. France*, 24: 383-387.

Legendre, S. (1982c). Étude anatomique de *Tadarida helvetica* (Chiroptera, Molossidae) du gisement burdigalien de Port-la-Nouvelle (Aude): denture et squelette appendiculaire. *Zool. Jahrb. Anat.*, 108: 263-292.

Martínez-Salanova Sánchez, J. (1987). Estudio Paleontológico de los micromamíferos del Mioceno inferior de Fuenmayor (La Rioja). *Publ. Inst. Est. Riojanos. Ciencias de la Tierra, Paleontología.* 10, 99 pp.

Mein, P. (1958). Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouv. Arch. Muséum d'Hist. Nat. Lyon.*, 5: 1-22.

Mein, P. (1964). Chiroptera (Miocene) de Lissieu (Rhone). *C.R. 89ème Cong. Soc. Savantes, Sec. Sciences Lyon.*, 5: 237-253.

Mein, P. y Cornet, C. (1973). Les incidences de la découverte d'un remplissage karstique fossilifère sur l'interpretation morphologique de la surface d'abrasion du Vingrau (Pyrénées Orientales). *C. R. Somm. Soc. Géol. France*, 2: 54-55.

Menu, H. y Sigé, B. (1971). Nyctalodontie et myotodontie, important charactères de grades évolutifs chez les chiroptères entomophages. *C. R. Acad. Sci. Paris*, 272: 1735-1738.

Meulen, A. J. van der, Peláez-Campomanes, P. y Daams, R. (2003). Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in The Calatayud-Teruel basin (Zaragoza, Spain). *Col. Paleont.* Vol. Ext., 1: 385-441.

Meurisse, M., Michaux, J. y Sigé, B. (1969). Un remplissage karstique à micromammifères du Miocène inférieur à la Serre de Vergès, près Saint-Arnac (Pyrénées Orientales). *C. R. Somm. Soc. Géol. France*, 5: 166-167.

Morales, J. (1989). Los yacimientos de grandes mamíferos del Terciario de Cuenca. In: *La fauna del Pasado en Cuenca* (Sanz, J. L., edit.). Instituto Juan de Valdés, Cuenca, 1: 167-188.

Morales, J., Alcalá, L., Hoyos, M., Montoya, P., Nieto, M., Pérez, B. y Soria, D. (1993). El yacimiento del Aragoniense medio de La Retama (Depresión Intermedia, provincia de Cuenca, España): significado de las faunas con *Hispanotherium*. *Scripta Geol.,* 103: 23-39.

Morales, J., Nieto, M., Peláez-Campomanes, P., Soria, D., Álvarez, M. A., Alcalá, L., Amezua, L., Cerdeno, E., Daams, R., Fraile, S., Guillem, J., Hoyos, M., Merino, L., De Miguel, I., Monparler, R., Montoya, P., Pérez, B., Salesa, M. J. y Sánchez, I. M. (1999). Vertebrados continentales del terciario de la cuenca de Loranca (provincia de Cuenca). In: *La huella del pasado; fosiles de Castilla-La Mancha* (Aguirre, E. y Rábano, I., edit.). Patrimonio histórico de Castilla-La Mancha, Toledo, 237-260.

Murelaga, X., Astibia, H., Sesé, C., Soria, D. y Pereda-Suberbiola, X. (2004). Mamíferos del Mioceno Inferior de Las Bárdenas Reales de Navarra (Cuenca del Ebro, Península Ibérica). *Munibe*, 55: 7-102.

Rachl, R. (1983). *Die Chiroptera (Mammalia) aus dem Mittelmiozänen Kalken des Nördlinger Rieses (Süddeutschland).* Tesis Doctoral. Universidad de Munich, Alemania, 285 pp.

Sevilla, P. (2002). Quirópteros fósiles del Aragoniense medio de Casetón (Teruel, España). *Rev. Esp. de Paleont.*, 17: 257-268.

Sigé, B. (1968). Les Chiroptères du Miocène infèrieur de Bouzigues. I. Étude systématique. *Palaeovertebrata,* 1: 65-133.

Sigé, B., Aguilar, J. P., Marandat, B. y Astruc, J. G. (1991). Extension au Miocène inférieur des remplissages phosphatés du Quercy. La faune de Vertébrés de Crémat (Lot, France). *Géobios*, 24: 497-502.

Sigé, B., Crochet, J. Y., Sudre, J., Aguilar, J. P. y Escarguel, G. (1997). Nouveaux sites d'âges variés dans les remplissages karstiques du Miocène inférieur de Bouzigues (Hérault, sud de la France). Partie I: sites et faunes 1 (insectivores, chiroptères, artiodactyles). *Géobios, Mém. Spéc.*, 20: 477-483.

Sigé, B. y Legendre, S. (1983). L'histoire des peuplements de chiroptères du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôts fluvio-lacustres. *Mém. Biospéol.*, 10: 209-225.

Ziegler, R. (1993). Die Chiroptera (Mammalia) aus dem Untermiozän von Wintershof-West bei Eichstätt (Bayern). Mitt. *Bayer. Strat. Paläont. Hist. Geol.*, 33: 119-154.

Ziegler, R. (1994). Die Chiroptera (Mammalia) aus dem Untermiozän von Stubersheim 3 (Baden-Württemberg). *Münch. Geowiss. Abh. (A)*, 26: 97-116.

Ziegler, R. (2000). The Miocene Fossil-Lagerstätte Sandelzhausen, 17. Marsupialia, Lipotyphla and Chiroptera (Mammalia). *Senckenbergiana Leth.*, 80: 81-127.

Ziegler, R. (2005). Erinaceidae and Dimylidae (Lipotyphla) from the Late Middle Miocene of South Germany.- *Senckenbergiana Leth.*, 85: 131-152.

Ziegler, R. y Fahlbusch, V. (1986). Kleinsäuger-Faunen aus der basalen Oberen Süßwasser-Molasse Niederbayerns. – *Zitteliana*, 14: 3-80.