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Upper Eocene rodents from the Almazán basin (Soria, Spain)

PABLO PELAEZ-CAMPOMANES¹

Key words: Rodents, Pseudosciuridae, Theridomyidae, Upper Eocene, Almazán basin, Spain, Paleocology, dental size

ABSTRACT

The rodent faunas from three Upper Eocene localities in the Almazán basin (province of Soria, Spain) are described: Mazaterón, Miñana and Deza 2. A new species of Issiodoromyinae (Theridomyidae), *Pseudoltinomys crebrum* is described from Mazaterón and Miñana. Comparison of the assemblages from the Almazán basin with other European Upper Eocene localities suggests an Early Late Eocene Age (MP 16) for Mazaterón and Miñana and a somewhat younger Age for Deza 2 (MP 17). The composition of the mammal assemblages from the Almazán basin and the dental morphology of some individual species suggest that the area was not densely forested during the Early Upper Eocene (MP 16). This is in sharp contrast to biotope reconstructions in continental basins elsewhere in Europe.

RESUME

Trois faunes de rongeurs de l'Eocène supérieur du Bassin d'Almazán (Province de Soria, Espagne) sont décrites: Mazaterón, Miñana et Deza 2. Une nouvelle espèce d'Issiodoromyinae (Theridomyidae), *Pseudoltinomys crebrum*, trouvée à Mazaterón et Miñana, est décrite. Les comparaisons des faunes du Bassin d'Almazán avec celles de l'Eocène supérieur de l'Europe suggèrent pour Mazaterón et Miñana un âge Eocène supérieur (MP 16) et pour Deza 2 un âge un peu plus jeune (MP 17). La morphologie dentaire et l'abondance relative des différents taxons du Mazaterón suggèrent l'existence dans cette région d'un milieu plus ouvert que dans autres régions Européennes à l'Eocène supérieur (MP 16).

1. Introduction

The Paleogene deposits of the Almazán basin have recently yielded mammalian faunas that are essentially different from those of France, Germany and England. The Perissodactyla (Cuesta 1992a, 1993), the Primates (Moyá-Solá & Köhler 1992), the Creodonta (Cuesta 1992b), the Insectivora (Pelaez-Campomanes et al. 1989) and the Rodentia (Pelaez-Campomanes et al. 1989, Pelaez-Campomanes 1992) have been published. Excavations and screenwashing carried out in 1990 yielded many small mammal remains from three late Eocene localities (Mazaterón, Miñana and Deza 2). The rodents in these assemblages will be described below. *Pairomys ibericus* from Mazaterón and Miñana has been included in the revision on the subfamilies Remyinae and Oltinomyinae (Vianey-Liaud et al., 1994).

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The aim is to update the fauna lists of the localities in the Almazán basin, to establish the biochronological position and to contribute to the reconstruction of the environment in this area during the early part of the Upper Eocene.

The Almazán basin is situated in the provinces of Soria and Zaragoza (North central Spain) and is the eastern prolongation of the Duero basin. The lithostratigraphy and sedimentology of the Almazán Basin have been studied by Guisado et al. (1988) and Armenteros et al. (1989). The localities of Mazaterón (Jimenez et al. 1989) and Miñana (Peláez-Campomanes et al. 1989) are situated in the Mazaterón Carbonatic Unit (Guisado et al. 1988). These two fossil assemblages come from an approximately 5 m thick dark-grey-marls with intercalation of small bodies of sand and conglomerate. The locality of Deza 2 is situated in the Deza Upper Carbonatic Unit (Armenteros et al. 1989). Deza 2 is an approximately 10 cm thick black marl with abundant freshwater mollusc remains that is situated some two meters stratigraphically above the large mammal locality of Deza (Jimenez et al. 1989). All the fossiliferous sediments belong to the tectono-sedimentary unit 1 (Armenteros et al. 1989).

The biochronological framework proposed at the Mainz Symposium (Schmidt-Kittler 1987) is used for correlating the fossil faunas studied.

The nomenclature used for parts of the cheek teeth of Pseudosciuridae is after Hooker (1986), for the Theridomyidae after Hartenberger (1973) and for the Gliridae after Daams (1981). The teeth were measured using a NIKON monocular measuring microscope with digital reading equipment. Measurements are given in 1.0 mm units. The length represents the maximal length and the width the maximal width taken at right angle to the length. The tooth height of the Issiodoromyinae is only measured in unworn teeth. It has been measured using the methodology proposed by Vianey-Liaud (1972) for Theridomyids.

The material is stored in the collections of the Department of Paleontology of the Universidad Complutense, Madrid (U.C.M.)

Tab. 1. Measurements of length and width of the cheek teeth of *Sciuroides cf. siderolithicus* from Mazaterón.

	LENGTH					N	WIDTH				
	MIN.	MED.	MAX.	S.D.	C.V.		MIN.	MED.	MAX.	S.D.	C.V.
D ₄	1.90	2.03	2.08	.076	3.75	5/4	1.28	1.45	1.53		
P ₄	2.12	2.23	2.35			4	1.71	1.78	1.85		
M ₁₋₂		2.60				1		2.23			
M ₃	2.58		2.70			2	2.11		2.18		
D ⁴						0/1		1.93			
P ⁴		1.85				1		2.11			
M ¹⁻²	2.18	2.29	2.40	.088	3.85	6	2.33	2.43	2.51	.071	2.93
M ³		2.50				1		2.34			

2. Systematic description

Pseudosciuridae ZITTEL, 1893

Sciuroides MAJOR, 1873

Sciuroides cf. *siderolithicus* (PICHET & HUMBERT, 1869)

(Pl. 1, Figs. 1–7)

Locality: Mazaterón (Soria, Spain)

Material and measurements: 5 D₄, 4 P₄, 1 M₁₋₂, 2 M₃, 1 D⁴, 1 P⁴, 6 M¹⁻² and 1 M³. (See Tab. 1 and Fig. 1)

Description

D₄: These teeth are long and narrow, with a pointed anterior outline. The protoconid is situated slightly posteriorly with respect to the metaconid. The well-developed ectolophid is complete. A crest runs from the metaconid along the lingual border without reaching the entoconid. Another irregular crest runs longitudinally from the metaconid into the central basin. The curved hypolophid and the hypoconid are not connected in some specimens. The lingual end of the posterolophid reaches the entoconid. The posteriorly directed sinusid is open and shallow.

P₄: The anteroconid is lower than the main anterior cusps and it has an antero-labial position. The metaconid is the highest cusp. The protoconid is hardly differentiated. The complete metalophid points obliquely backwards. The ectolophid is interrupted in one specimen. The mesolophid and mesoconid are absent. The basin of the trigonid shows low, irregular, and longitudinal accessory crests. The hypolophid is interrupted near the middle in one specimen. The lingual end of the curved posterolophid reaches the entoconid. The shallow sinus points obliquely backward.

M₁₋₂: Four main cusps and four transverse ridges are present. The anterolophid is the lowest crest. The anteroconid is small. The slightly oblique metalophid is interrupted near the middle in two specimens. A mesolophid is absent. The enamel of the central basin is wrinkled. The curved hypolophid is always complete. The well-developed posterolophid joins the entoconid. The shallow sinusid is directed towards the synclinid IV.

M₃: This tooth resembles the first two lower molars. The metalophid is interrupted near the middle. An accessory ridge runs from the protoconid towards the centre of the tooth.

D⁴: The only specimen present misses the anterior part of the tooth. The small protocone has a more labial position than the hypocone. The protoloph has accessory crests on either side. A well-developed mesostyle is present. The metalophule II is larger than the metalophule I. The long posteroloph is thin. It is lower than the other ridges. The sinus is very shallow.

P⁴: The premolar is smaller than the molars. The anteroloph is very short. The protocone is situated close to the hypocone, and is of the same height. The protoloph has accessory crests on its posterior side only. A mesostyle and an irregular mesoloph are present in the middle of the labial tooth border. The metalophule I and II do not join the hypocone. The sinus is shallow.

M¹⁻²: The anteroloph is longer than the posteroloph. The long protoloph shows a paraconule of variable size. The protoloph has frequently accessory crests on its anterior side. A short mesoloph sprouts from the mesostyle. The metalophule I and II may be either

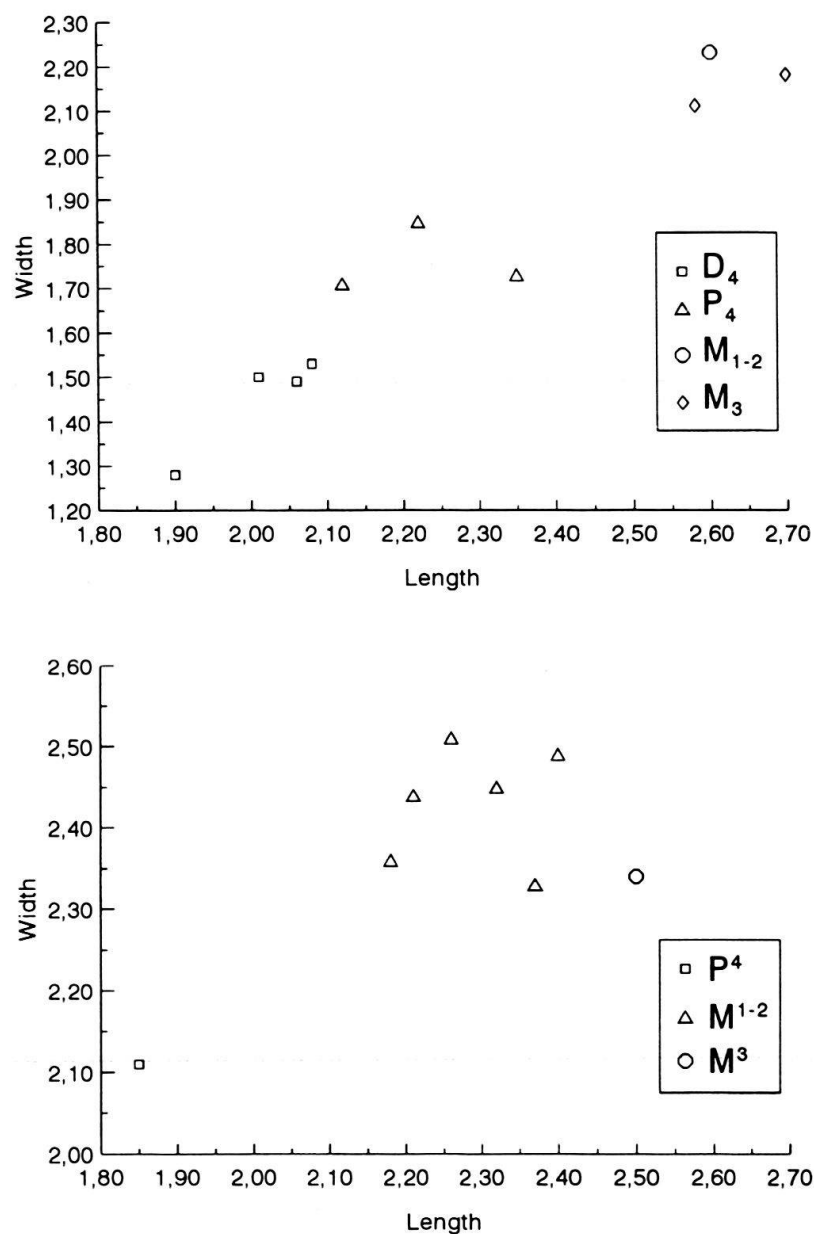


Fig. 1. Scatter diagrams giving length and width of the cheek teeth of the material of *S. cf. siderolithicus* from Mazaterón.

complete or interrupted. The well-developed metalophule I joins the hypocone. The enamel of the synclines is usually crenulated. The shallow sinus is transverse.

M³: This element has a sub-rounded outline. The protocone is the highest cusp. The posterior part is reduced. The shallow sinus is transverse.

Locality: Miñana (Soria, Spain)

Material: 1 D₄, 1 P₄ and 3 M¹⁻².

The poor preservation of this material makes it impossible to take measurements and to see details of the dental pattern. However, these teeth seem to be similar to the material from Mazaterón.

Discussion

Sciuroides cf. *siderolithicus* from Mazaterón is smaller than *S. russelli* (Hartenberger & Louis 1976) from Grisolles (MP 16), *S. ehrensteinensis* Schmidt-Kittler 1971 from Ehrenstein 1A (MP 18) and *S. rissonei* Hooker 1986 from Creechbarrow (MP 16). Furthermore, it is slightly smaller than *S. siderolithicus* (Pictet & Humbert 1969) from the upper Eocene localities of Mormont-Eclepens and the Quercy. The Robiac and Le Bretou material, described as *Suevosciurus (Suevosciurus) romani* by Hartenberger (1973, 1988), is also larger than the Mazaterón material. The size of our teeth is similar to that of *Suevosciurus (S.)* cf. *romani* from Pontils (Anadón et al. 1983).

These teeth assigned to *S. (S.) romani* and *S. (S.)* cf. *romani* are very similar to *Sciuroides siderolithicus*. Bosma (1974) having noted this similarity proposed to assign the species from Robiac to the genus *Sciuroides* rather than to *Suevosciurus*. Hooker (1986) followed Bosma and synonymized *Suevosciurus (Suevosciurus) romani* with *Sciuroides siderolithicus*. However, Hartenberger (1988) disagreed with the proposed synonymy on the basis of, among others, the different dental size ratios of the material from Mormont-Eclepens (type material of *S. siderolithicus*) and the *Suevosciurus (S.) romani* from Le Bretou. He used the measurements of the type material of *S. siderolithicus*, given by Schmidt-Kittler (1971), and justifies his decision by showing that *S. siderolithicus* has a relatively longer M₃. However, the table of cheek teeth measurements (Schmidt-Kittler, 1971, p. 33) shows an error in the length of M₁₋₂ (M₁–M₃: 8.56; M₁: 2.25; M₂: 2.27; M₃: 3.05). The total length of the lower dental range, given by Schmidt-Kittler in the same table appears to be correct considering the scatter-diagram of figure 13 (p. 36). In reality the teeth from Le Bretou and Mormont-Eclepens are of about the same size. We therefore follow Hooker (1986) and synonymize *Suevosciurus (Suevosciurus) romani* with *Sciuroides siderolithicus*.

The size ratios of the teeth from Mazaterón, Miñana and Pontils (Anadón et al. 1983) are slightly different from those of other European assemblages of *S. siderolithicus*. The Spanish material has deciduous and permanent premolars that are relatively smaller than in other European populations of the species. These differences in size ratio may be due to provincialism, or may be a primitive feature. Since the morphology of the material from Spain is virtually identical to the type material we include the material from Mazaterón and Miñana in *S. cf. siderolithicus*.

Theridomyidae ALSTON, 1876
 Issiodoromyinae LAVOCAT, 1951
Pseudoltinomys LAVOCAT, 1951

Pseudoltinomys crebrum n. sp.
 (Pl. 2 & Pl. 3)

Theridomys euzetensis (DEPÉRET, 1917), Peláez-Campomanes et al., 1989
Pseudoltinomys sp. PELÁEZ-CAMPOMANES, 1992

Type locality: Mazaterón (Soria, Spain)
 Holotype: M¹⁻² sin. (MAZ RT059); (Pl. 3, Fig. 5).

Derivatio nominis: From the latin *creber*: frequent, numerous. Because it is the most abundant rodent in the fauna of this locality.

Diagnosis: Buno-lophodont teeth with well-developed main cusps. The enamel of the anticlines and anticlinids is irregular. The mesoloph is less developed than the main crests and it is generally incomplete. The mesolophid is either absent or poorly developed. The lower molars have two roots. The enamel of the trigonid basin is crenulated. The premolars are smaller than the molars.

Differential diagnosis: *P. crebrum* differs from *P. cosetanus* Hartenberger, 1983 from the upper Eocene of Pontils and *P. mamertensis* Hartenberger, 1973 from the upper Eocene of Fons 4 by its larger and more hypsodont teeth.

P. crebrum n. sp. differs from *P. phosphoricus* Hartenberger, 1973 from Perrière by its lower crowned teeth, by its weak mesoloph and mesolophid and by its premolars which are relative to the molar smaller.

P. crebrum n. sp. differs from the rest of the *Pseudoltinomys* species by its smaller size and by its more bunodont teeth.

Material and measurements: 3 D₄, 7 P₄, 20 M₁₋₂, 5 M₃, 5 D⁴, 6 P⁴, 29 M¹⁻² and 8 M³. (See Tab. 2 and Fig. 2).

Tab. 2. Measurements of length, width and height of the cheek of *Pseudoltinomys crebrum* n. sp. from Mazaterón.

	LENGTH					N	WIDTH				
	MIN.	MED.	MAX.	S.D.	C.V.		MIN.	MED.	MAX.	S.D.	C.V.
D ₄	1.55		1.57			2/1		1.09			
P ₄	1.59	1.69	1.81	.094	5.57	6/7	1.22	1.31	1.36	.048	3.63
M ₁₋₂	1.67	1.76	1.84	.051	2.90	13/14	1.41	1.53	1.68	.070	4.55
M ₃	1.81	1.84	1.88			4	1.34	1.38	1.41		
D ⁴	1.29	1.37	1.43			4	1.30	1.40	1.49		
P ⁴	1.42	1.48	1.54			4	1.56	1.63	1.69		
M ¹⁻²	1.50	1.62	1.72	.058	3.58	19/20	1.64	1.75	1.95	.069	3.95
M ³	1.47	1.57	1.66			4	1.53	1.61	1.67		

	HEIGHT					N
	MIN.	MED.	MAX.	S.D.	C.V.	
D ₄		0.81				1
P ₄	0.97	1.04	1.12			4
M ₁₋₂	0.89	1.10	1.25	.113	10.26	7
M ₃		1.16				1
D ⁴	0.93	0.98	1.04			3
P ⁴	1.06	1.12	1.18			3
M ¹⁻²	1.19	1.31	1.44	.077	5.85	10
M ³	0.90	1.09	1.12			3

Description

D₄: The metaconid is larger than the protoconid. The metalophid is absent. One specimen shows a small anteroconid. Synclinid II is wide and shallow. The mesolophid is either very short or absent. The ectolophid is weak at the level of the sinus. The straight hypolophid is large. The posterolophid widens in its middle.

P₄: The anterior lobe is as long as the posterior one or slightly longer. A continuous ridge runs around the anterior half of the tooth. The protoconid and anteroconid are not distinct. A longitudinal crest runs between the metaconid and the synclinid III. The ectolophid is interrupted at level of the sinusid in two out of seven specimens. The sinusid is connected to the synclinid III in unworn teeth. The robust hypolophid has a large entoconid. Synclinid IV is closed lingually. The sinusid is narrow and shallow.

M₁₋₂: The teeth are robust. An anterior cingulum forms the border of a well-developed anterosinusid. These structures disappear progressively with wear. The metalophid is interrupted near the middle. The anterior arm of the protoconid points obliquely backwards. The mesoloph is short and low. The sinusid is confluent with the synclinid III in six specimens. The hypolophid and the posterolophid are the highest ridges. The sinus is narrow and shallow.

M₃: This element has a rounded posterior side. The morphology resembles that of the M₁₋₂. Synclinid II contains several accessory longitudinal crests. The mesolophid is low. The posterolophid is very robust. The sinusid is narrow and shallow.

D⁴: The crown is low and smaller than the P⁴. The anterior part is smaller than the posterior part. The protoloph has a paraconule in its middle. The short mesoloph does not reach the posterior arm of the protocone in 4 out of 5 specimens. The metaloph joins the posteroloph in 3 out of 5 specimens. The shallow sinus is confluent with the syncline II.

P⁴: The teeth are sub-quadrate. The anterior border is slightly concave. The anteroloph is almost absent. The mesoloph is interrupted near the middle in 2 out of 6 specimens. The robust metaloph may be connected to the posteroloph (3/6), to the hypocone (1/6) or it may be an isolated ridge (2/6). The sinus is transverse and shallow. It joins the syncline II in unworn teeth.

M¹⁻²: The synclines are shallow. The long anteroloph reaches the labial side of the tooth. The protoloph is crenulated on either side. The paraconule is usually well developed. The syncline II is confluent with the sinus. The mesoloph is low and irregular. It is interrupted in 18 out of 29 specimens. The metaloph is short and it has a crenulated anterior wall. The metaloph may be connected to the posteroloph (17/29), to the hypocone (1/29) or it may be an isolated ridge (11/29). The narrow sinus points slightly forwards.

M³: The anteroloph is long. The protoloph has crenulations on either side. The mesoloph is complete but thin and irregular. The metaloph and posteroloph are small. The narrow sinus is directed forwards. It joins the synclinid II in all specimens.

Locality: Miñana (Soria, Spain)

Material and measurements: 2 D₄, 1 P₄, 6 M₁₋₂, 5 M₃, 1 D⁴, 6 M¹⁻² and 1 M³. (See Tab. 3 and Fig. 2).

Tab. 3. Measurements of length and width of the cheek of *Pseudoltinomys crebrum* n. sp. from Miñana.

	LENGTH					N	WIDTH		
	MIN.	MED.	MAX.	S.D.	C.V.		MIN.	MED.	MAX.
D ₄		1.64				1/2	1.05		1.29
P ₄		1.72				1		1.40	
M ₁₋₂	1.66	1.72	1.78	.023	3.05	5/4	1.42	1.53	1.65
M ₃	1.71	1.86	1.96			3	1.45	1.47	1.50
D ⁴		1.36				1		1.47	
M ¹⁻²	1.55	1.62	1.67			4	1.57	1.72	1.85
M ³		1.63				1		1.69	

Remarks

The material of *P. crebrum* from Miñana is very similar to that of the type locality. Morphologically, the material from Miñana shows dental features that can be found in the type material from Mazaterón as well. The only difference between these two populations could be that some of the dental elements from Miñana have a size that is slightly larger than in Mazaterón.

Discussion

The material from Mazaterón and Miñana represents two different samples from the same bed. Therefore, the strong similarity between both samples is not surprising. In order to simplify the discussion, we will only discuss the richer assemblage from Mazaterón.

P. crebrum is a member of the group of small sized *Pseudoltinomys* species from the Upper Eocene of Western Europe. Its teeth are slightly smaller than those of *P. phosphoricus* from Malpérié and its type locality Perrière. *P. mamertensis* and *P. cosetanus* are distinctly smaller than *P. crebrum*.

P. crebrum from Mazaterón shows a height/length relation that is intermediate between that of *P. mamertensis* and *P. phosphoricus*. If we consider only the metrical characteristics as Hartenberger (1973) and Vianey-Liaud (1976) do, the assemblage from Mazaterón would represent an intermediate evolutionary stage between *P. mamertensis* and *P. phosphoricus*. However, the dental morphology does not fit this evolutionary stage. The dental features of *P. crebrum* may be interpreted as primitive because of its teeth show distinct main cusps and poorly developed ridges. The mesoloph is not as high as the other crests and is usually incomplete. The mesolophid is almost absent. *P. mamertensis* and *P. phosphoricus* have better developed anticlines and anticlinids than *P. crebrum* and their main cusps are less differentiated. Morphologically *P. crebrum* is similar to *P. cosetanus*. Both species have a similar stage of development of the main crests, with a low mesoloph and mesolophid, and enamel crenulation in the trigonid basin. This latter character has been used as diagnostic for *P. cosetanus* by Anadón et al. (1983).

P. crebrum does probably not belong to the *P. mamertensis* – *P. major* lineage proposed by Vianey-Liaud (1976) because of its special combination of primitive morphology and evolved metrical characteristics. However, both lineages may have *P. cosetanus* as a common ancestor.

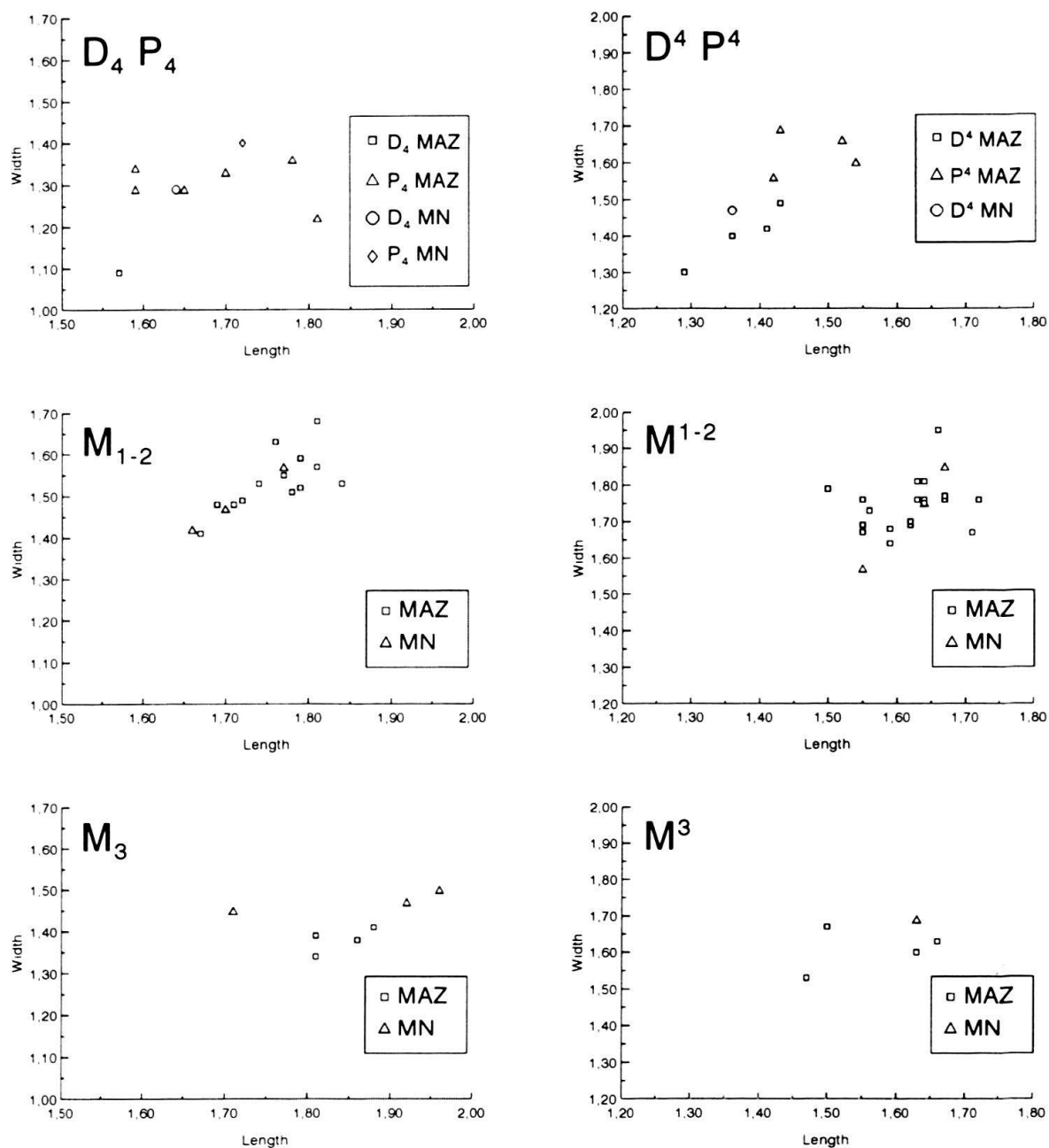


Fig. 2. Scatter diagrams giving length and width of the cheek teeth of the material of *P. crebrum* n. sp. from Mazaterón (MAZ) and Miñana (MN).

Theridomyinae ALSTON, 1876

Theridomys JOURDAN, 1837

Theridomys euzetensis (DEPERET, 1917)

(Fig. 3.1)

Locality: Deza 2 (Soria, Spain)

Material and measurements: 1 M₁₋₂ DEZ RT001: 2.08x1.96

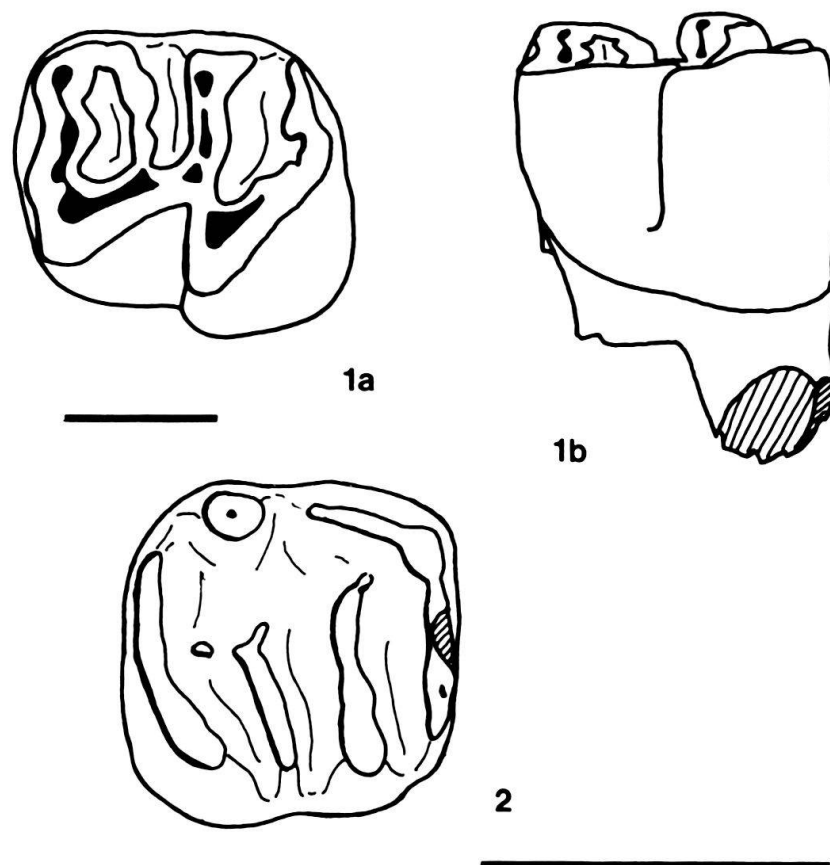


Fig. 3. 1: *Theridomys euzetensis* from Deza 2, M₁₋₂ Sin. (DEZ RT001), a. oclusal view, b. labial view. 2: *Glamys priscus* from Deza 2, M₁ Dex. (DEZ2 RG001). Graphic scale represents 1 mm.

Description

M¹⁻²: The crown is relatively low. The metalophid is sinuous. The anteroconid is absent. The mesolophid is the lowest crest. The synclinids are shallow. The enamel is thick and shows almost the same thickness around the various anticlinids. The sinus is wide and shallow.

Discussion

The dental pattern of this specimen is similar to that of *Theridomys euzetensis* from the Upper Eocene of Euzet, Fons 4, Malpérié, Perrière and Sosis (Hartenberger 1973). The size is similar to the larger teeth from these localities.

Gliridae THOMAS, 1897

Gliravinae SCHAUB, 1958

Glamys VIANEY-LIAUD, 1989

Glamys priscus (STEHLIN & SCHAUB, 1951)

(Fig. 3.2)

Locality: Deza 2 (Soria, Spain)

Material and Measurements: 1 M₁ (DEZ RG001) 0.91x0.95

Description

M₁: The tooth has a trapezoidal outline. The isolated metaconid is the highest cusp. The mesolophid is of medium length. The entoconid is also isolated. The hypoconid is robust.

3. Biochronology

The faunal lists of the Almazán localities are:

Mazaterón & Miñana

Pairomys ibericus

Sciuroides cf. *siderolithicus*

Pseudoltinomys crebrum n. sp.

Deza 2

Theridomys euzetensis

Glamys priscus

The biochronological positions of Mazaterón, Miñana and Deza have been discussed by several authors over the past years. Peláez-Campomanes et al. (1989) correlated the Miñana fauna to MP 17 on the basis of some dental fragments assigned to *T. euzetensis*. On the basis of the perissodactyl fauna, Jimenez (1992a) and Cuesta (1993) correlated the faunas of Mazaterón and Miñana to either MP 16 or MP 17 and Deza to either MP 17 or MP 18. Cuesta (op cit) mentioned that the perissodactyls from Mazaterón show a high degree of hypsodonty, similar to taxa from localities correlated to MP 17. However, the primitive dental morphology of the perissodactyls from Mazaterón is similar to that shown by taxa from the Rhenanian (MP 16). The same author remarks that the presence of the *Leptolophus* in Mazaterón would confirm the latter age. Vianey-Liaud et al. (1994) correlated Mazaterón and Miñana to MP 17 on the basis of features of *Pairomys ibericus*, a new species described by these authors.

On the score of our more extensive faunal list, the correlation of these localities has to be modified. The presence in Mazaterón and Miñana of *S.* cf. *siderolithicus* suggests an MP 16 age for these localities, since this taxon has only been recorded in Rhenanian localities (MP 15–16). This correlation is supported by the presence of *P. crebrum* n. sp. which shows a primitive dental pattern resembling that of *P. cosetanus* from Pontils and La Livinière 2 (MP 15).

The stratigraphic position of Deza 2 is higher than that of Mazaterón and Miñana (Armenteros et al. 1989). Because of the presence of *Theridomys euzetensis*, this locality is correlated to MP 17 (Headonian).

4. Paleoecology

The rodent faunas of Mazaterón and Miñana are very poor in species. Mazaterón yielded more than one hundred identifiable dental remains, which belong to three species only. Miñana contains fewer teeth but these represent the same three species. These two faunas are less diverse than all other Late Eocene rodent faunas from Europe. Most loca-

Species Diversity of Rodents

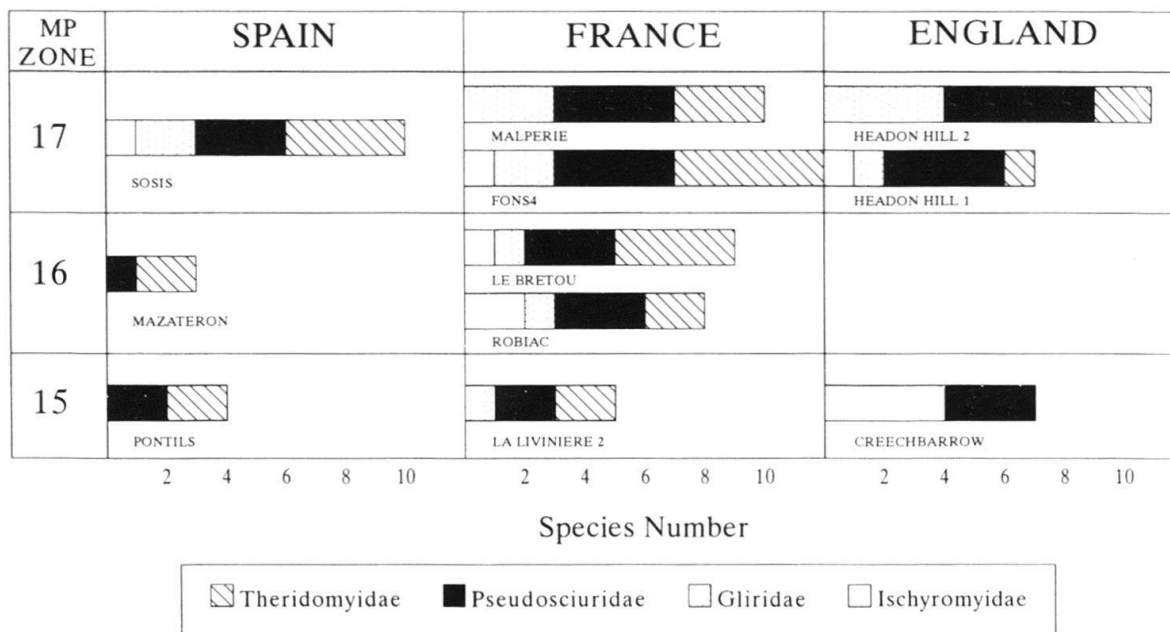


Fig. 4. Bar diagram giving the number of species belonging to the four main Eocene rodent families recorded in several European Eocene localities. The data has been obtained from: Pontils, Anadon et al. 1983; La livinière 2, Hartenberger 1973, Marandat 1987; Creechbarrow, Hooker 1986; Robiac, Fons 4, Sosis, Malpérié, Hartenberger 1973; Le Bretou, Hartenberger et al. 1974, Hartenberger 1988; and Headon Hill 1,2, Bosma 1974, Bosma & De Bruijn 1979, 1982.

lities in MP 15, such as La Livinière 2 (Reference level) and Pontils, have four or five species (Hartenberger 1973, Anadón et al. 1983); however, these collections contain very few teeth so the species richness is expected to increase with sample size. Localities of MP 16 are for example Creechbarrow (Hooker 1986), Robiac (Hartenberger 1973) and Le Bretou (Hartenberger 1973, 1988; Hartenberger et al. 1974). Robiac has eight rodent species, Le Bretou nine and Creechbarrow seven. The differences in species richness between associations of MP 15 and MP 17 are even larger. Fons 4 contains 12 species, Sosis at least 9 and Malpérié 10 (Hartenberger 1973).

The low species diversity of the Mazaterón's fauna may be due either to a taphonomic bias or to the existence of particular ecological conditions. It will be argued that there is evidence to assume peculiar ecological conditions for the region during the late Rhenanian.

Figure 4 shows the number of species of the four main rodent families (Ischyromyidae, Pseudosciuridae, Theridomyidae and Gliridae) in several european localities from the upper Rhenanian and lower Headonian. The total amount of dental remains used for the specific determinations is, for most of the localities, not detailed by the authors then it has not been included in figure 4. The associations from England show a high proportion of pseudosciurids species, While the first occurrence of theridomyids is at MP 17. In

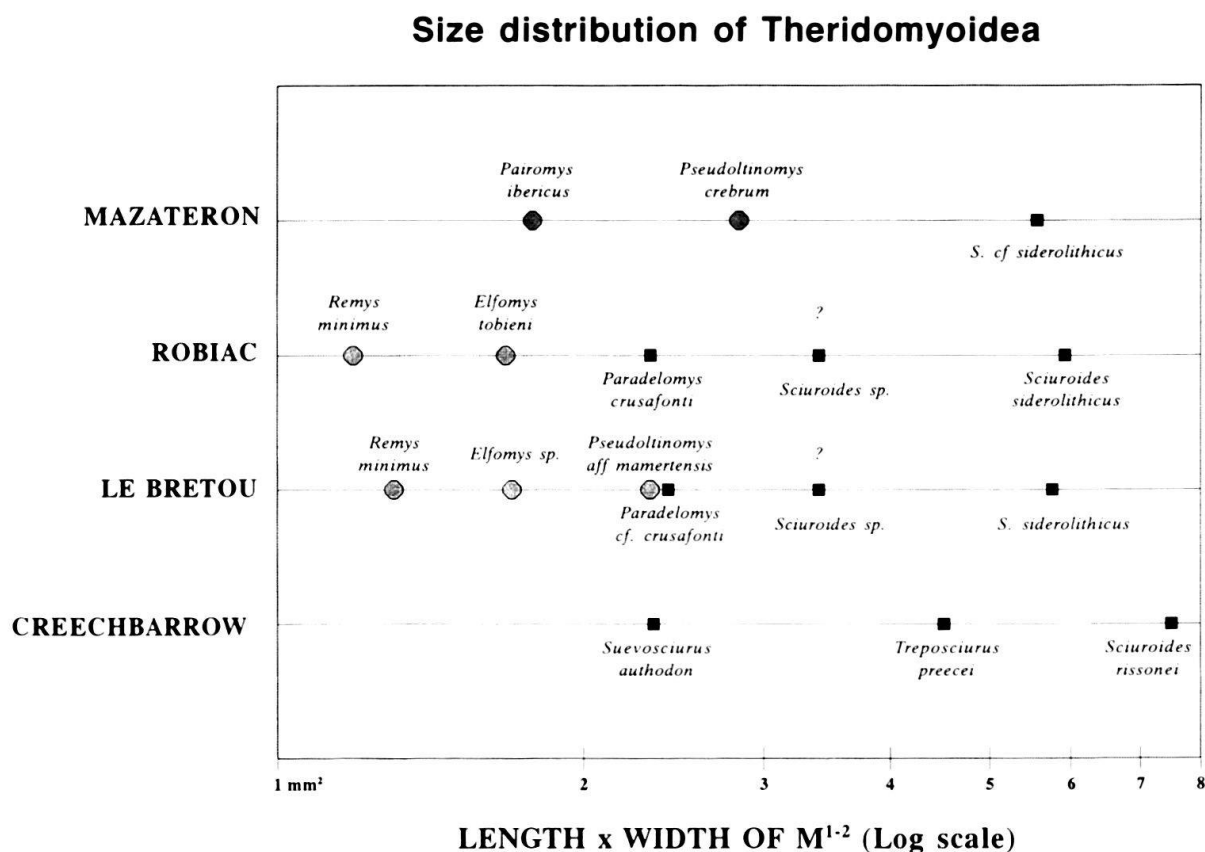


Fig. 5. Diagram giving the surface area (length x width) of the upper M1–2 of the Theridomyoidea recorded in some localities correlated with MP 16. The surface is represented in logarithmic scale. For the source of the data see legend of figure 4.

french and northern spanish localities the proportion of pseudosciurids and theridomyids (first occurrence in MP 14) are approximately the same. The localities from the Almazán basin show more species of theridomyids than of pseudosciurids, and glirids and ischyromyids are absent. In all three areas considered there is a general trend towards a higher number of theridomyid species from the Late Rhenanian to the Early Oligocene (Hartenberger 1973; Collinson & Hooker 1987, 1991; Vianey-Liaud 1991). This change in composition has been interpreted as a reaction to a change towards progressively more open environment (Collinson & Hooker 1991). According to Collinson & Hooker (1987) a low ratio small ground mammals/large ground mammals is typical for open environment. The fauna from Mazaterón is characterized by a high proportion of large ground mammals and, among rodents, a high proportion of theridomyids. Both are evidences of an open (either humid or dry) environment.

Figure 5 shows the size distribution of theridomyid species from several localities assigned to MP 16. There are differences between South England, France and central western Spain. In South England the size distribution of the pseudosciurids is similar to that of the french localities, which show three quite constant size groups. These three size groups of pseudosciurids are also present in younger localities such as Fons 4 or Sosis (Hartenberger 1973), therefore the absence in Mazaterón of the two small sized pseudo-

sciurids seems to be significant. Considering the theridomyids, there are also some differences between Mazaterón and the other localities. The theridomyids from Mazaterón have larger sizes than taxa of the same subfamily recorded from french localities. This is also true for the hypsodonty. *Pairomys* from Mazaterón is of larger size and more hypsodont than *Remys* from the french localities and it has the size of *Elfomys* from those faunas. *Pseudoltinomys* from Mazaterón is also larger and more hypsodont than *P. mamer-tensis* from Le Bretou. It seems that the theridomyids from Mazaterón are displaced towards larger sizes.

The larger size and hypsodonty of the theridomyids from Mazaterón comparing to those from Le Bretou and Robiac may be explained as an adaptation to a more coarse food. In other words, the herbivore component of the diet, related to the frugivore component, may have been higher in the theridomyids from Mazaterón than in those from french localities. This change in diet may have been the result of the lower fruit availability in this period. This explanation agrees with the low proportions of frugivore pseudo-sciurids (for dietary adaptations in theridomyoids see Collinson & Hooker 1987, 1991).

The perissodactyls from Mazaterón show also more hypsodont teeth than the related taxa of other european localities from MP 16 (Cuesta 1993). Therefore, the adaptations to a more coarse diet seem to be general in the Mazaterón fauna. The other vertebrates recorded in these localities are still under study or are not useful for paleoecological interpretations (see introduction).

During the Rhenanian the lacustrine sediments are less extended than during the Headonian in the Almazán basin (Bond 1996) which may be related with the differences observed between the faunas from these periods. However the studies on the sedimentology of the area are not conclusive.

Concluding, the structure and composition of the Mazaterón mammal assemblage suggest the existence of an open environment in central-western Spain during the late Rhenanian, with probably more severe ecological conditions than in other european regions.

The presence in Mazaterón of a high proportion of genera hitherto recorded in north-western Spain only, such as the perissodactyls *Cantabrotherium*, *Franzenium* and *Paran-chilophus* and the rodent *Pairomys*, may be explained by the existence of geographical barriers between central-western and north-eastern Spain (Casanovas & Santafé 1987, 1992; Cuesta 1992). However, the existence of a common pattern for rodents and perissodactyls, with primitive dental morphology and relatively high hypsodont teeth may be evidence of singular ecological conditions in this area, as it has been discussed before. Therefore, the endemic character may have been the result of the existence of ecological rather than geographical barriers.

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Plate 1-3

Plate 1

1–7 *Sciuroides* cf. *siderolithicus* from Mazaterón. 1. D⁴ Dex (MAZ RP040), 2. P⁴ Sin. (MAZ RP030), 3. M¹⁻² Sin. (MAZ RP034), 4. M³ Sin. (MAZ RP039), 5. D⁴ Sin. (MAZ RP010), 6. P⁴ Sin. (MAZ RP015), 7. M₃ Sin. (MAZ RP023). Graphic scale represents 0.5 mm.

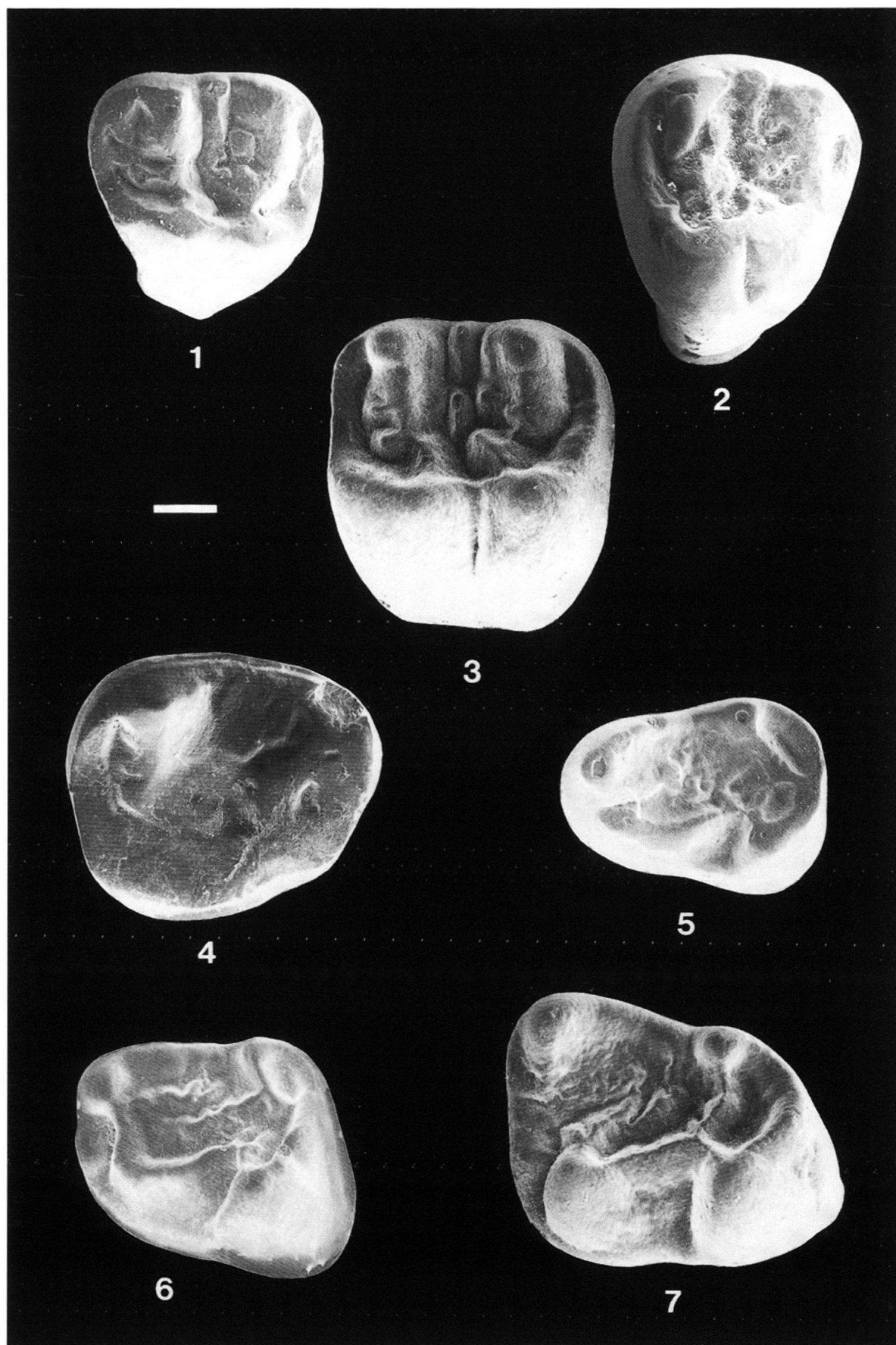


Plate 2

1–6. *Pseudoltinomys crebrum* n. sp. from Mazaterón. 1. D₄ Sin. (MAZ RT001), 2. P₄ Sin. (MAZ RT008), 3. P₄ Sin. (MAZ RT007), 4. M_{1–2} Sin. (MAZ RT013), 5. M_{1–2} Sin. (MAZ RT028), 6. M₃ Dex. (MAZ RT034). 7–8. *Pseudoltinomys crebrum* n. sp. from Miñana. 7. M_{1–2} Sin. (MN RT007), 8. M₃ Dex. (MN RT019). Graphic scale represents 0.5 mm.



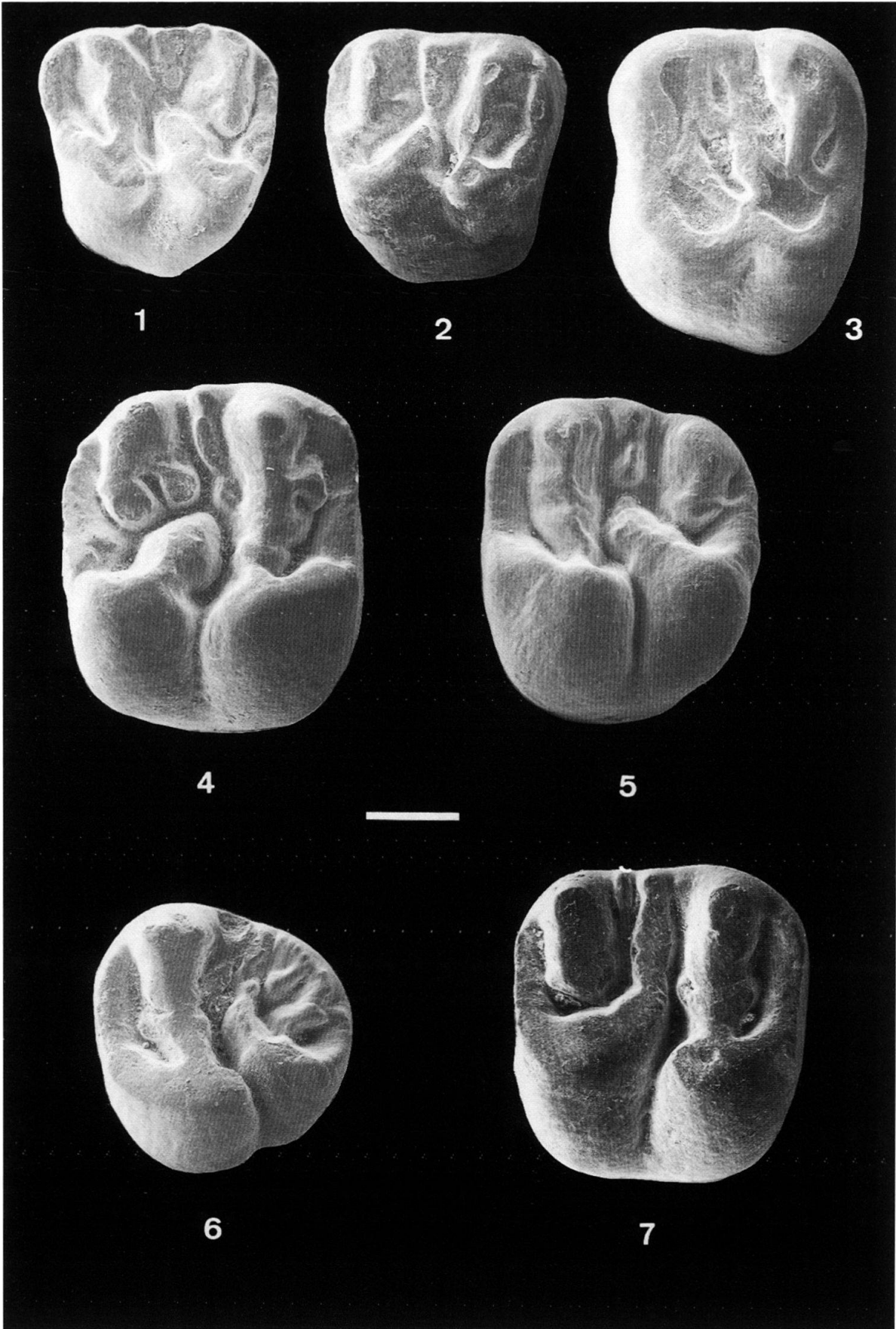


Plate 3

1–6. *Pseudoltinomys crebrum* n. sp. from Mazaterón. 1. D⁴ Sin. (MAZ RT040), 2. D⁴ Dex. (MAZ RT043), 3. P⁴ Sin. (MAZ RT045), 4. M¹⁻² Dex. (MAZ RT065), 5. M¹⁻² Sin. (MAZ RT059) Holotype, 6. M³ Sin. (MAZ RT091). 7. *Pseudoltinomys crebrum* n. sp. from Miñana, M¹⁻² Dex. (MN RT030). Graphic scale represents 0.5 mm.

