

## Insectivores (Lipotyphla, Mammalia) from the Ramblian of the Daroca-Calamocha area

### *Insectívoros (Lipotyphla, Mammalia) del Ramblense del área de Daroca-Calamocha*

Lars W. van den Hoek Ostende<sup>1</sup>

**Abstract:** The insectivore assemblages from the Ramblian stratotype near Calamocha (Spain) are described, as well as those from San Roque 4A and 4B, two Ramblian localities near the Aragonian stratotype. Two new species are described, the erinaceid *Galerix remmerti*, and the shrew *Clapasorex alvarezae*. Both the percentages and the diversity of insectivores are higher in the Lower Ramblian, suggesting more humid conditions in zone Z than in zone A. This is in contradiction with the palaeoenvironmental reconstructions based on rodents.

**Key words:** Ramblian, Miocene, Insectivora.

**Resumen:** Se describen las asociaciones de insectívoros del estratotipo del Ramblense cerca de Calamocha (Teruel, España), junto de las de San Roque 4A y 4B, dos yacimientos Ramblenses del área-tipo del Aragoniense. Se describirán dos especies nuevas, el erinacéido *Galerix remmerti*, y la musaraña *Clapasorex alvarezae*. Tanto el porcentaje de insectívoros como su diversidad son mayores en el Ramblense inferior que en el Ramblense superior. Esto indica condiciones más húmedas en la zona Z que en la zona A, lo cual contradice las reconstrucciones paleoambientales basadas en roedores.

**Palabras clave:** Ramblense, Mioceno, Insectivora.

#### INTRODUCTION

The Lower Miocene continental stage Ramblian was defined by DAAMS *et al.* (1987) with its stratotype in northern Teruel. The Ramblian contains the Spanish assemblage zones Z and A. The latter had originally been included in the Aragonian, on the basis of the entry of the horse *Anchitherium* (DAAMS *et al.*, 1977). However, the near-absence of this animal in the type section made it in retrospect an unfortunate choice. Therefore the lower boundary of the Aragonian was redefined on the basis of the first entrance of the modern cricetid *Democricetodon*. Meanwhile, *Democricetodon* has been found in low numbers in the youngest localities of zone A, San Roque 4A and 4B. However, since these assemblages otherwise clearly belong to zone A, they are included in the Ramblian as well. The lower limit of the Ramblian was placed at the extinction level of an ancient group of Eomyidae (*Rhodanomys-Ritterneria*).

DAAMS *et al.* (1987) correlated the oldest two localities, Navarrete del Rio and Ramblar 1 with Laugnac, the reference locality of MN 2b, and Ramblar 4 with the French MN 3 locality of Estrepouy. Thus, in terms of MN-zonation the Ramblian encompasses the uppermost part of MN 2 and MN 3.

In many respects the Ramblian represents an interesting time frame. It contains the so-called Cricetid Vacuum, the only period in the European Neogene in which Muroidea did not dominate the rodent faunas. In fact, only one cricetid is present in this period, viz. *Melissiodon*. The period ends with the immigration of modern cricetids, an event that according to FAHLBUSCH (1989) is "the most remarkable change in the history of Lower Miocene rodents of Europe."

Unfortunately, surprisingly little is known of the smaller mammals from this period. Much of our knowledge comes from the work on the lagomorphs and rodents of the stratotype of the Ramblian, which, with the exception of the beavers have all been des-

<sup>1</sup> National Museum of Natural History, Naturalis, PO Box 9517, 2300 RA Leiden The Netherlands, E-mail: Hoek@Naturalis.NNM.NL

cribed. Papers have appeared on the Ochotonidae (LÓPEZ MARTINEZ, 1984), the Gliridae (DAAMS, 1985; 1989; 1990) the cricetids *Eucricetodon* and *Melissiodon* (SESÉ, 1987), the Eomyidae (ALVAREZ SIERRA, 1987) and the Sciuridae (CUENCA, 1988). From other parts of Europe, few extensive descriptions of rodents from this time frame exist. Favourable exceptions are the reference fauna of MN 3, Wintershof-West, on which various papers were published (HRUBESCH, 1957; FAHLBUSCH, 1970, MAYR, 1979; WU, 1993) and the French locality of Estrepouy (BAUDELOT & COLLIER, 1982; BULOT, 1980). Rodents have also been described extensively from the Anatolian MN 3 locality of Keseköy (DE BRUIJN & SARAC, 1991, 1992; DE BRUIJN *et al.*, 1993; ÜNAY, 1994, 1996; THEOCHAROPOULOS, 2000). However, at the time of this fauna Anatolia clearly belonged to a different bioprovince than Western Europe.

The non-rodent smaller mammals of the Ramblian type area, viz. the marsupials, the insectivores and the bats, have not been described. In this paper we describe the insectivores of the Ramblian stratotype. The insectivore faunas of San Roque 4A and 4B, which are found directly below Lower Aragonian strata in the vicinity of the Aragonian stratotype are also included in this study. Like in the rodents, the best comparative literature for this time frame comes from southern Germany (DOBEN-FLORIN, 1964; MÜLLER, 1967; ZIEGLER, 1989, 1990 ab, 1994). In addition to the insectivores of Wintershof-West, Ziegler described in his papers the assemblage of Stu bersheim 3. Unfortunately, the rodents of this MN 3 locality still await publication. The insectivores of Keseköy were also extensively described (VAN DEN HOEK OSTENDE, 1992, 1995ab, 1997, 2001ab).

## MATERIAL AND METHODS

The material from the Ramblian stratotype and adjacent areas described here was collected during excavations in the period 1976-1983 by the National Museum of Natural History, Leiden and the Museo Nacional de Ciencias Naturales, Madrid. A description of the geology of the area and the geographical and stratigraphical position of the various localities is given by DAAMS *et al.* (1987). The localities San Roque 4A and 4B were sampled in 1992-1994 by a team of the Museo Nacional de Ciencias Naturales and the Institute of Earth Sciences of Utrecht Uni-

versity. The locality Valhondo 3 has not been included in the study. I did not find any insectivores from this locality. Given the sample size (183 M1/M2 of rodents) it is unlikely that not one single insectivore element was found, and I suspect therefore that the insectivores of this locality have been lost.

The terminology for parts of molars of the Erinaceidae follows ENGESSER (1980); the orientation of the elements of this family for measuring follows DE JONG (1988). Terminology and way for measuring for the Soricidae largely follows REUMER (1984), with the exception of the oblique crest and entoconid crest which are here called oblique cristid and entocristid respectively. The terminology and measuring method for the Talpidae follows VAN DEN HOEK OSTENDE (1989).

Measurements were taken using a Reflex measuring microscope. All measurements are in mm. The width given for the lower molars is always the talonid width. The length and width given for the M1 and M2 of Soricidae are the buccal length and posterior width, respectively, measured according to REUMER (1984). Since these are generally the maximum length and width, the data are thus comparable with literature that uses length and width only.

All elements have been illustrated as if coming from the left side. Inversed images are indicated by an underlined number in both captions and plates.

The material from the localities Navarrete del Rio (Nav), Valhondo 1 (VH 1), Ramblar 3, 4, 5, and 7 (Ra 3, 4, 5, 7), La Dehasa (Deh), Agreda (Agr), and San Roque 4A and 4B (SR 4A and 4B) is stored in the Museo Nacional de Ciencias Naturales, Madrid. The material from Ramblar 1, Bañon 2, 5 and 11 (Bn 2, 5, and 11), and Moratilla 1 (Mor 1) is kept in the National Museum of Natural History, Leiden.

## SYSTEMATIC PART

*Lipotyphla* HAECKEL, 1866

*Erinaceidae* FISCHER VON WALDHEIM, 1817

*Galericinae* POMEL, 1848

*Galerix* POMEL, 1848

*Galerix remmerti* nov. sp.

(Plate I; figs. 1-13)

*Derivatio nominis:* The species is named in honour of the late Prof. Dr. Remmert Daams, who, together with others, collected of the material described here.

*Diagnosis:* *Galerix remmerti* is a medium sized species of *Galerix* (m2 2,5). The metaconid of the p4 is well developed, the paraconid more or less free standing. The P3 usually bears one lingual cusp only. A protocone-metaconule connection on the M1 and M2 is invariably present.

*Differential diagnosis:* *Galerix remmerti* is morphologically very close to *G. aurelianensis*. It differs from this species in being about 10 % smaller. In size, *G. remmerti* is similar to *G. exilis*. It differs from this species in having invariably a protocone-metaconule connection on the M1 and M2.

*G. remmerti* is larger than *G. symeonidis*, *G. saratji*, and *G. uenayae*. Furthermore, it differs from *G. symeonidis* in usually having a protocone only on the P3, and from *G. uenayae* and *G. nanus* in having a well-developed metaconid on the p4. *G. remmerti* is clearly smaller than *G. africana*, from which it differs further in the presence of a posterior arm of the metaconule in the M1 and M2. *G. remmerti* is somewhat smaller than *G. stehlini*, and differs from this species in having a well-developed metaconid on the p4.

*Parasorex socialis*, *P. ibericus* and *P. depereti* are commonly attributed to *Galerix*, but were transferred to a separate genus. The morphological differences with *G. remmerti* are those between the genera *Parasorex* and *Galerix* as given by VAN DEN HOEK OSTENDE (2001d). *Tetracus*, synonymised with *Galerix* by VAN DEN HOEK OSTENDE (2001d), is here considered a separate genus. For the differences with *Galerix* see discussion and HUGUENEY & ADROVER (this volume).

*Type locality:* Ramblar 1 (Zone Z)

*Other localities with Galerix remmerti:* Valhondo 1, Ramblar 3, Ramblar 7, Ramblar 5, La Dehesa, Bañon 5, San Roque 4 A, San Roque 4 B.

*Holotype:* M2 dext. RGM 410026 (Plate I, fig. 11)

*Description of the holotype:* The holotype is an almost unworn M2. The outline of the occlusal surface is sub-rectangular. The anterior side is wider than the posterior side. The protocone is the largest cusp. The protoconule is discernible as a small thickening in the anterior arm of the protocone. The posterior arm of the protocone connects to the metaconule. A ridge from the hypocone connects to the flank of the protocone-metaconule connection. The metaconule is crescent-shaped. The anterior arm of this cusp connects to the base of the metacone; the posterior arm either connects to the base of the metacone or ends freely just short of the base of that cusp. The hypocone is cone-shaped.

The paracone and the metacone are about the same size. A centrocrista runs over the tips of the lingual cusps, forming one ridge with a sharp notch at the position of the mesostyle. The posterior arm of the metacone, which forms the posterior part of this ridge, bends sharply to the posterolabial corner of the M2. A small, non-protruding parastyle lies directly in front of the paracone. There are well-developed cingulums on the anterior, labial and posterior sides.

*Measurements:* Measurements are listed in Table 1.

#### DESCRIPTION

*d3.* The d3 is much longer than it is wide. The outline of the occlusal surface is sub-triangular. The specimen from Ramblar 1 (RGM 410.010) has a rather rectangular outline, due to the unusually strong development of the parastyle. The lingual and labial sides are straight to slightly concave. The milk molar consists mainly of the large triangular protoconid. The tip of this cusp lies in the centre of the d3. In front of the protoconid lies a low but distinct parastyle. At the back of the milk molar lies a short flattening, which bears an indistinct cusp in the middle of the posterior side.

*d4.* The d4 is somewhat longer than it is wide. It consists of a trigonid with a long posterior flattening. The protoconid is only somewhat higher than the metaconid. The two cusps stand close together and are connected by a short ridge. The anterior flange of the protoconid-metaconid crest slopes down gently to towards the paraconid. The latter is a distinct and low cusp in the anterolabial corner. The anterior flange of the protoconid-metaconid crest make an abrupt angle with the lingual side, thus providing an indistinct ridge connecting the protoconid to the paraconid. The posterior flange of the protoconid-metaconid crest is much more steep than the anterior flange. The posterior flattening slopes down to the lingual side. It widens lingually and is bordered at the back by a posterior ridge. A faint central ridge may be present on the posterior flank of the postero-metaconid crest. The only cingulum is the -very- weak antero-lingual cingulum along the base of the paraconid.

*p4.* The outline of the occlusal surface is subrectangular. The p4 consists of a trigonid with a short posterior flattening. The protoconid is the highest cusp. It is rather bulbous. As a result, there is no true trigonid valley. The metaconid lies as a well-developed cusp on the lingual flank of the protoconid. Its tip

element	locality	N	length		width	
			range	mean	range	mean
D3	Ra 4	1		2,36		1,47
	VH 1	1		1,84		1,24
	Ra 1	1		1,99		1,34
D4	Ra 1	1		2,63		2,46
P3	SR 4A	1		1,87		1,42
	Ra 7	2	2,04-2,13	2,09	1,51-1,57	1,54
	Ra 3	3	1,99-2,18	2,11	1,55-1,80	1,65
	VH 1	5	1,62-1,93	1,74	1,32-1,45	1,37
	Ra 1	1		1,81		1,72
P4	SR 4A	1		2,48		2,80
	VH 1	1		2,82		2,32
M1	Ra 7	2	2,67-2,75	2,71	3,16-3,35	3,26
	VH 1	3	2,20-2,41	2,32	2,91-3,05	3,00
	Ra 1	2	2,51-2,55	2,53	3,05-3,15	3,10
M2	Ban 5	1		1,84		2,43
	Ra 7	3	2,14-2,21	2,17	2,71-2,83	2,78
	Ra 3	1		2,08		2,80
	VH 1	14	1,81-2,07	2,03	2,43-2,69	2,59
	Ra 1	3	1,99-2,10	2,06	2,59-2,85	2,70
M3	SR 4B	1		1,35		2,04
	SR 4A	3	1,26-1,34	1,30	1,87-1,93	1,90
	Ra 7	5	1,14-1,29	1,23	1,72-1,90	1,81
	Ra 3	3	1,20-1,31	1,26	1,72-1,92	1,85
	VH 1	4	1,16-1,25	1,21	1,65-1,79	1,74
	Ra 1	2	1,25-1,29	1,27	1,81-1,83	1,82

element	locality	N	length		width	
			range	mean	range	mean
d3	Ra 7	3	1,85-1,95	1,91	0,99-1,09	1,05
	VH 1	1		1,71		0,99
	Ra 1	1		1,87		1,05
d4	Ra 7	1		1,78		1,38
	Ra 1	3	2,01-2,03	2,02	1,29-1,67	1,43
p4	Ra 7	3	1,99-2,22	2,11	1,25-1,39	1,34
	VH 1	1		1,87		1,32
m1	Ra 5	1		3,06		2,09
	Ra 7	2	2,99-3,03	3,01	1,92-2,07	2,00
	RA 3	1		3,07		2,06
	VH 1	2	2,94-2,96	2,95	1,87-1,89	1,88
	Ra 1	1		2,93		1,98
m2	SR 4A	2	2,52-2,78	2,65	1,69-1,82	1,76
	Ra 7	4	2,34-2,72	2,58	1,62-1,89	1,74
	Ra 3	3	2,49-2,57	2,54	1,77-1,82	1,79
	VH 1	1		2,34		1,57
	Ra 1	9	2,46-2,61	2,53	1,69-1,81	1,72
m3	SR 4A	3	1,94-2,02	1,99	1,01-1,12	1,07
	Deh	2	1,77-1,94	1,86	0,98-0,98	0,98
	Ra 7	1		1,78		0,98
	Ra 3	2	1,86-1,96	1,91	1,03-1,15	1,09
	VH 1	1		1,77		0,92
	Ra 1	1		1,72		1,13

Table 1.- Measurements for the upper and lower dentition of *Galerix remmerti* n.sp.Table 1.- Medidas de la dentición superior e inferior de *Galerix remmerti* n.sp.

is clearly lower than that of the protoconid. The paraconid is well developed. It is connected to the protoconid at its base only. It is the lowest cusp of the trigonid. The posterior flattening is bordered at its back by a strong ridge. A faint transverse ridge may be present halfway the posterior flattening.

*m1*. The outline of the occlusal surface is rectangular. The trigonid and talonid have about the same length. The talonid is slightly wider than the trigonid. The paraconid lies at the end of a slightly curved paralophid. The ridge connecting the protoconid and metaconid is notched deeply halfway. The trigonid basin is narrow and runs parallel to the protoconid-metaconid crest. The oblique cristid ends just lingually of the base of the protoconid. The entocristid ends just labially of the base of the metaconid. The talonid basin is large and deep. The hypolophid curves slightly outward above the posterior cingulum, then curves back and connects to the entoconid. The anterior cingulum runs along the base of the paralophid and is strong. The posterior cingulum is strong and short. In two specimens from San Roque 4A (SR 4A I 5 and I7), and one specimen from Ramblar 7 (Ra 7 I 15) this cingulum connects to the posterior arm of the entoconid. A small labial cingulum is present between the hypoconid and protoconid.

*m2*. The outline of the occlusal surface is rectangular. The trigonid and talonid are of similar length and width. The paraconid is blade-like and is incorporated in the curved paralophid. The ridge between protoconid and metaconid is sharply notched halfway. The trigonid basin is Y-shaped, with the short arms running towards the notches in the paralophid and the protoconid-metaconid crest. The oblique cristid ends lingually of the base of the protoconid. The entocristid is well developed and connects to a very small metacristid just behind the metaconid. One specimen from San Roque 4A (SR 4A I 9) lacks the metacristid. The talonid basin is wide and deep. The hypolophid is curved in a similar way as in the *m1*. The anterior cingulum is well developed; the posterior cingulum is short and strong. In one specimen from Ramblar 1 (RGM 410.015) the posterior cingulum is connected to the posterior arm of the entoconid. A small labial cingulum borders the tiny re-entrant valley.

*m3*. The trigonid is longer and wider than the talonid. The paralophid, incorporating the blade-like paraconid is relatively short and low, making the trigonid basin more open than in the *m2*. The proto-

nid-metacnid crest is notched halfway. The cusps of the talonid are low. The oblique cristid and the ento-cristid end near the base of the protoconid and metacnid, respectively. The anterior cingulum is narrow. There are no other cingulums.

*D3*. The D3 is much longer than wide. The outline of the occlusal surface is roughly triangular. The paracone is the largest cusp. Its tip lies in the front part of the milk molar. The front face of the paracone is rounded. The posterocrista runs from the tip of the paracone backwards, over the tip of the metacone and curves to the posterolabial corner of the D3. The metacone is about half the height of the paracone and clearly smaller. In the worn specimen from Valhondo 1 the metacone is completely incorporated in the posterocrista. In front of the paracone lies a very large but low parastyle. A small lingual flange lies off the tips of the paracone and metacone. The flange bears no cusp. The flange continues posteriorly as a wide cingulum along the flange of the posterocrista.

*D4*. The labial part of the milk molar consists of the high and large paracone. The tip of this cusp lies halfway the length of the D4. The anterior face of the paracone is rounded. The posterocrista is sharp. It has a slight bend at about two-thirds its length. In front of the paracone lies a protruding parastyle, which is connected to the anterior face of the paracone by a low ridge. The large and conical protocone lies anterolingually of the tip of the paracone. The protocone is about half as high as the paracone. The paracone and protocone are separated by a wide valley. The conical hypocone lies posterolingually of the protococone. At the base the two cusps are merged. The hypocone is about half as high as the protocone. Directly behind the hypocone lies a small accessory cusplet. Paracone, protocone and hypocone flank a posterior basin, which is posteriorly bordered by a faint ridge. There is a short lingual cingulum along the flank of the paracone and a short labial cingulum along the side of the posterocrista of the paracone.

*P3*. The premolar consists of a large paracone with a large lingual flange. The anterior face of the paracone is rounded. The tip lies just in front of the middle of the P3. A sharp posterocrista runs from the tip backwards. The posterocrista curves at its end to the labial side. The lingual side of this crest is rather steep. The labial side slopes down more gently, particularly at its posterior end, where a labial flattening is present. A small parastyle lies in front of the paracone. The lingual flange bears a low, conical protocone.

The protocone is connected to the parastyle by an indistinct ridge. An equally indistinct ridge runs from the protocone backwards. In one specimen from Ramblar 3 (Ra 3 I 28) a faint cusplet (hypocone) appears as a thickening. In the only P3 from Ramblar 1 (RGM 410021) the hypocone is a tiny, distinct cusplet directly behind the protocone. The posterior ridge borders the lingual flange at the back, and continues as a cingulum along the lingual flank of the posterocrista of the paracone. The only other cingulum of the P3 is the cingulum along the posterolabial flattening

*P4*. The outline of the occlusal surface is irregularly quadrangular. The paracone is the largest cusp. Its anterior face is rounded. A sharp posterocrista runs from the tip of paracone backwards. The posterocrista bends sharply halfway and ends in the posterolabial corner of the premolar. In front of the paracone lies a small, slightly protruding parastyle.

The lingual cusps are cone-shaped and well developed. The protocone is about twice the height of the hypocone. The two cusps are usually connected by a short, straight ridge. One of the specimens from San Roque 4A (SR 4A I 20) lacks this feature. The anterior arm of the protocone usually runs in the direction of the parastyle, but connects to the base of the paracone in one specimen from Valhondo 1. There is a well-developed anterior cingulum between the parastyle and the protocone and a well-developed posterior cingulum all along the posterior side, which is more or less emarginated.

*M1*. The outline of the occlusal surface is subrectangular. The protocone is the largest cusp. The protocone is incorporated in the anterior arm of the protocone, but clearly discernible in all but the very worn specimens. The anterior arm of the protocone ends freely near the parastyle or connects to the paracone. The posterior arm of the protocone divides into two equally strong ridges, connecting to the hypocone and the metaconule, respectively. In one specimen from Ramblar 1 (RGM 410024) the posterior arm of the protocone connects to the metaconule, with a ridge from the hypocone connecting to the flank of this ridge. The hypocone is cone-shaped and about half the height of the protocone. The metaconule is crescent-shaped. The anterior arm ends against the base of the metacone. The posterior arm either ends against the base of the metacone or ends freely near the posterior cingulum.

The parastyle is low and protrudes slightly. The anterior face of the paracone is rounded. The posterior arm of the paracone is straight and connects to

the base of the metacone. The metacone is clearly larger and higher than the paracone. Its anterior face bears a faint ridge. The posterior arm of the metacone is curved and extends to the posterolabial corner of the M1. The molar has well-developed cingulums on the anterior, labial and posterior sides.

*M2*. The other M2 resemble the holotype closely. The protoconule disappears quickly with wear. The posterior arm of the protocone is often separated in two equally strong branches connecting to the metaconule and hypocone, respectively.

*M3*. The outline of the occlusal surface is triangular. The protocone is the largest cusp. The paracone is somewhat smaller, but higher than the protocone. The metacone is clearly the smallest cusp. The two arms of the protocone connect to the paracone and metacone, respectively. In some specimens these arms are notched. The posterior arm of the paracone and the anterior arm of the metacone meet halfway the labial side. The parastylid is very well developed. It lies anterolabially of the paracone and is connected to this cusp by a ridge. This ridge may either continue as a centrocrista over the tip of the paracone or end against the base of the paracone. In the latter case the anterior side of the paracone is rounded. There is a well-developed anterior cingulum. A faint labial cingulum may be present. The development of the posterior cingulum varies from a short patch halfway the posterior side to a well-developed cingulum between the bases of the protocone and metacone.

*Galerix* sp.  
(Plate I, fig. 14-18)

*Locality*: Moratilla 1, ?Ramblar 4

*Measurements*: Measurements are listed in Table 2.

DESCRIPTION

*d3*. The milk molar is much longer than it is wide. It is wider at the back than at the front. The protoconid is a large, triangular cusp. Its lingual and labial faces are rather steep; its posterior face slopes down gently to the back of the d3, more or less forming a posterior shelf. In one of the three specimens there is a small bulge on the edge between the labial and posterior sides. In front of the protoconid lies a parastylid, which is well developed in two specimens, weak in the third. There is a small cuspule on the posterolabial corner of the milk molar.

element	locality	N	length		width	
			range	mean	range	mean
d3	Mor 1	3	1,91-2,11	2,01	1,15-1,24	1,19
m1	Mor 1	1		3,40		2,22
m2	Mor 1	1		2,73		1,91
m3	Mor 1	3	1,96-2,16	1,96	1,15-1,25	1,19
D3	Ra 4	1		2,36		1,47
P3	Mor 1	4	1,97-2,20	2,10	1,35-1,58	1,45
M2	Mor 1	1		2,66		3,45
M3	Mor 1	3	1,36-1,50	1,44	2,10-2,16	2,12

Table 2.- Measurements of *Galerix* sp.

Tabla 2.- Medidas de *Galerix* sp.

*m1, m2*. The first two lower molars have been found associated in a piece of mandible. Judging from this fragment the lower jaw must have been quite robust. Both molars are very worn, particularly in the area of the hypoconid, which is worn down to the level of the talonid basin. The metaconid of the m1 is damaged. In both molars the trigonid and talonid are about the same length. In the m1 the talonid is slightly wider than the trigonid; in the m2 the talonid and trigonid are the same width. The oblique cristid ends just lingually of the base of the protoconid. A small metacristid is found both in the m1 and in the m2. The anterior cingulum is weak in both molars, which may be partly due to wear.

*m3*. The trigonid is somewhat wider and clearly longer than the talonid. The protoconid and the metaconid are the best-developed cusps of the last lower molar. They are similar in size and height. The paraconid is completely incorporated in the paralopid, which is very low and poorly developed. The hypoconid and the entoconid are much reduced, but still discernible as cusps. The oblique cristid ends near the base of the protoconid. Together with the hypolophid and the entocristid it forms a low ridge bordering a shallow talonid basin.

*D3*. The single D3 from Ramblar 4, except for a p1 the only element of *Galerix* found in this locality, stands out because of its large size. The outline of the occlusal surface is subtriangular. The largest cusp is the paracone, which lies in the front part of the milk molar. Directly behind the paracone lies the metaco-

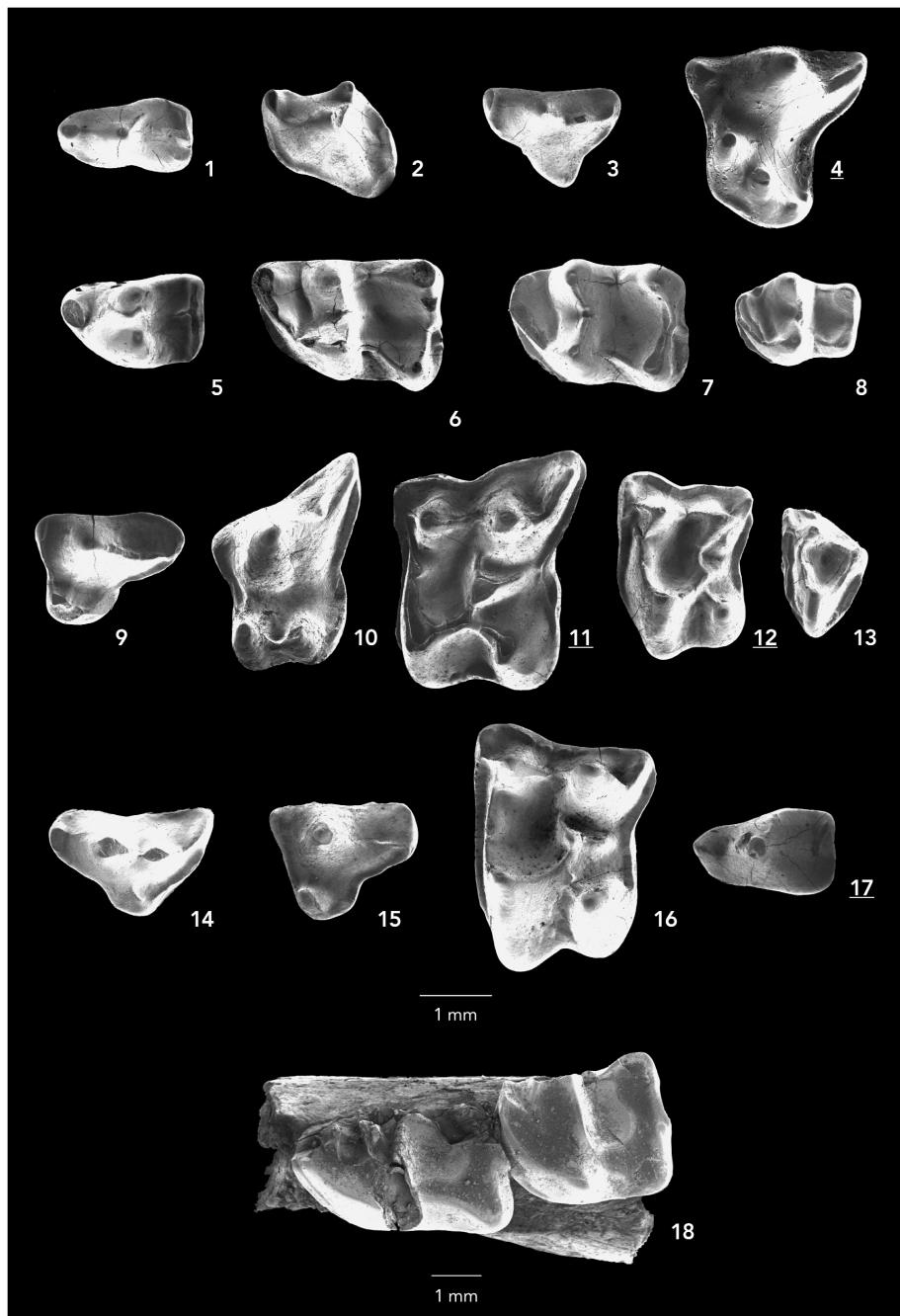


Plate I

*Galerix remmerti* 1. d3 sin. (Ra 7, I 2); 2 d4 sin. (Ra 1, RGM 410005); 3. D3 sin. (Ra 1, RGM 410021); 4. D4 dext. (Ra 1, RGM 410023); 5. p4 sin. (Ra 7, I 12); 6. m1 sin. (Ra 1, RGM 410011); 7. m2 sin. (Ra 1, RGM 4100127); 8. m3 sin. (Ra 3, I 17); 9. P3 sin. (Ra 7, I 21); 10. P4 sin. (VH 1, I 19); 11. M1 dext. (Ra 7, I 25); 12. M2 dext. (holotype, Ra 1, RGM 410026); 13. M3 sin. (Ra 7, I 40). (all fig. 11.5x)

*Galerix* sp. 14. D3 sin. (Ra 4, I 2); 15 P3 sin. (Mor 1, RGM 410126); 16. M2 sin. (Mor 1, RGM 4101310); 17. d3 dext. (RGM 410112)(11.5x); 18. Mandible with m1,m2 sin. (Mor 1, RGM 410122) (8x).

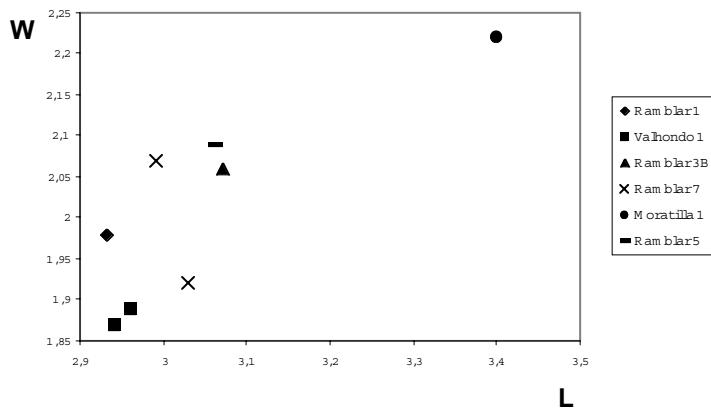


Figure 1.- Length (L) / Width (W) diagram for the m1 of *Galerix* sp. (Moratilla 1) and *G. remmerti* nov. sp. (all other localities).

Figura 1.- Diagrama de Longitud (L) / Anchura (W) para el m1 de *Galerix* sp. (Moratilla 1) y *G. remmerti* nov. sp. (las demás localidades).

ne, which is clearly smaller and about half the height of the paracone. The anterior flank of the paracone is rounded. From the tip of this cusp runs a posterocrista, which runs over the tip of the metacone and then curves to the posterolabial corner of the D3. A very low but large parastyle lies in front of the paracone. There is a small lingual extension, lingually of the notch separating paracone and metacone. A postero-lingual cingulum continues from this flattening to the back of the milk molar.

*P3*. The outline of the occlusal surface is hook-shaped. The paracone is the highest cusp. The posterocrista is rather faint. It slopes down quickly and than continues more or less horizontally to the back of the premolar. The protocone is well developed and conical. It lies anterolingually of the tip of the paracone. The parastyle is a very low, ridge-shaped cuspule on a somewhat protruding extension in front of the paracone. From it, a faint ridge runs along the

anterior side to the base of the protocone. The back of the P3 is also bordered by a faint ridge, which runs from the base of the protocone backwards.

*M2*. The outline of the occlusal surface is subrectangular. The anterior side is only somewhat wider than the posterior side. The protocone is the largest cusp. Its anterior arm connects to the paracone. The protoconule is incorporated in the anterior arm of the protocone and appears as a small elevation. The posterior arm of the protocone connects to the crescent-shaped metacone. The hypocone is cone-shaped. A sharp ridge runs from the hypocone to the middle of the flank of the protocone-metacone crest. The anterior arm of the metacone ends against the base of the metacone; the posterior arm ends just short of the metacone.

The paracone is somewhat smaller than the metacone. In front of the paracone lies a non-protruding parastyle. The centrocrista of the paracone connects to the parastyle in front and to the undivided mesostyle

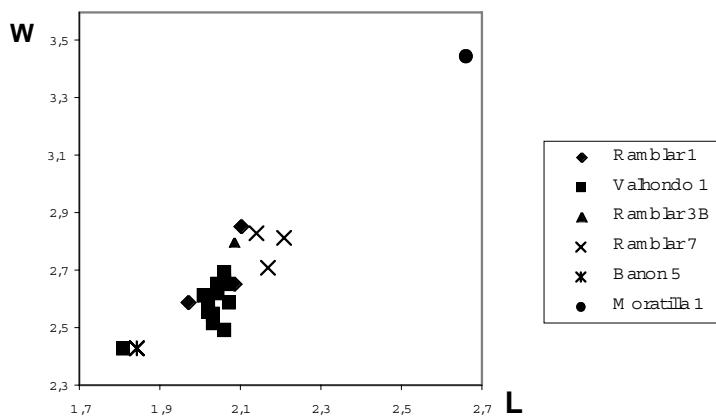


Figure 2.- Length (L) / Width (W) diagram for the M2 of *Galerix* sp. (Moratilla 1) and *G. remmerti* nov. sp. (all other localities).

Figura 2.- Diagrama de Longitud (L) / Anchura (W) para el M2 de *Galerix* sp. (Moratilla 1) y *G. remmerti* nov. sp. (las demás localidades).

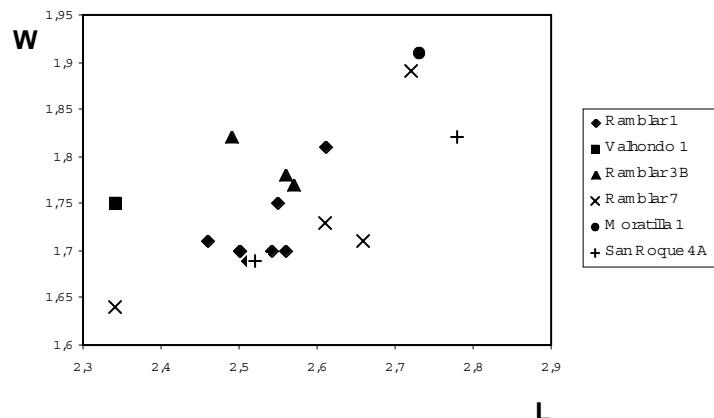


Figure 3.- Length (L) / Width (W) diagram for the m2 of *Galerix* sp. (Moratilla 1) and *G. remmerti* nov. sp. (all other localities).

Figura 3.- Diagrama de Longitud (L) / Anchura (W) para el m2 de *Galerix* sp. (Moratilla 1) y *G. remmerti* nov. sp. (las demás localidades).

at its end. The metacone also bears a sharp centrocrista. Near its end it bends abruptly to the posterolabial corner of the M2. The molar has well-developed cingulums on the anterior, labial and posterior sides.

?*Galerix symeonidis* DOUKAS, 1986

*Locality:* San Roque 4B

*Measurement:* M3 (1,07 x 1,52)

*Description:* One of the M3 from San Roque 4B is considerably smaller than the other M3 found. Morphologically it falls within the variation of all *Galerix* M3 and is therefore not described separately.

*Remarks:* Recently, in a review of the Galericini, I synonymised the Oligocene genus *Tetracus* with the Miocene genus *Galerix* (VAN DEN HOEK OSTENDE, 2001d). Since I did not have the benefit of own mate-

rial, this conclusion was based on literature only. The diagnosis for *Tetracus* given by CROCHET (1975) indicated no differences with *Galerix*. Following the classification proposed in my paper, *Galerix* would appear in the lowermost Oligocene of Europe. However, HUGUENEY & ADROVER (this volume) present new, extensive descriptions of *Tetracus*. They also consider *Tetracus* and *Galerix* to be very similar, but still note some differences, which could be used to distinguish between the two genera. Since the differences involve the P3 and M3, traditionally important elements in the taxonomy of the Galericinae, I now consider synonymising *Tetracus* with *Galerix* an unfortunate choice. At least for the time being, as indicated by Hugueney and Adrover, it seems wiser to retain *Tetracus* as a separate genus.

Following this classification, the oldest record of *Galerix* is found in the lowermost Miocene of Anatolia (DE BRUIJN ET AL., 1992; VAN DEN HOEK OSTEN-

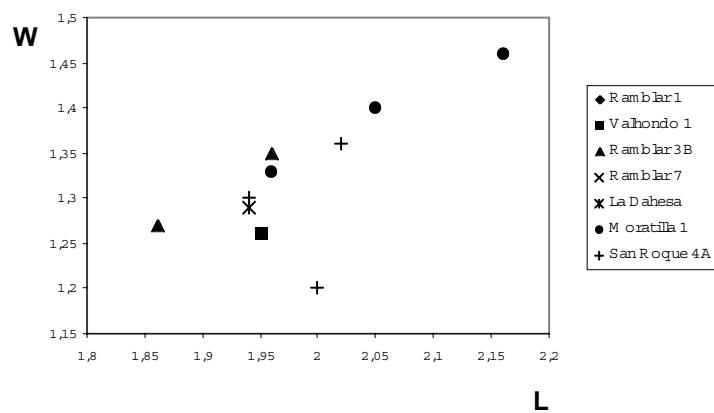


Figure 4.- Length (L) / Width (W) diagram for the m3 of *Galerix* sp. (Moratilla 1) and *G. remmerti* nov. sp. (all other localities).

Figura 4.- Diagrama de Longitud (L) / Anchura (W) para el m3 de *Galerix* sp. (Moratilla 1) y *G. remmerti* nov. sp. (las demás localidades).

Species	Locality	N m1/m2	m1/m2 ratio
<i>G. aurelianensis</i>	Erkertshofen 2	4/2	1,28
	Peterbuch 2	44/23	1,21
	Stubersheim 3	1/5	1,27
<i>Galerix</i> sp.	Moratilla 1	1/1	1,25
<i>Galerix remmerti</i>	Ramblar 7	2/4	1,17
	Ramblar 3	1/3	1,21
	Valhondo 1	2/1	1,26
	Ramblar 1	1/9	1,16
<i>G. saratji</i>	Harami 3	6/8	1,15
	Harami 1	11/17	1,18
	Kilcak 3B	4/2	1,19
	Kilcak 0"	2/8	1,26
<i>G. uenayae</i>	Keseköy	18/27	1,23

Table 3.- m1/m2 ratio for various species of *Galerix*.  
Tabla 3.- relación m1/m2 para varias especies de *Galerix*.

DE, 1992). The genus is, like all other Galericinae, not found in the European lowermost Miocene. *Galerix* first appeared in Europe in MN 3. ZIEGLER (1990a) described *G. aurelianensis* from the German localities Stubersheim 3 (MN 3) and Petersbuch 2 and Erkertshofen 2 (MN 4). Later the presence of the species was also noted in the reference locality of MN 3, Wintershof-West (ZIEGLER, 1994). Ziegler assumed that *Galerix* was an immigrant, a conclusion which I endorsed (VAN DEN HOEK OSTENDE, 1992, 2001c). My conclusions were partly based on the assemblages presented in this paper, which, however, had hitherto remained undescribed.

The taxonomy of *Galerix* is difficult because of the high morphological variation. Characters are rarely unequivocal, and there always seem to be exceptions to the rule (VAN DEN HOEK OSTENDE, 2001d). A good overview of the morphological variation within a *Galerix* species was given by ZIEGLER (1983) in his description of *G. exilis* from Steinberg. Morphological characters used to distinguish between species are the presence or absence of a hypocone on the P3, the development of the metacoenid and the paralophid of the p4, and the development of the ridges between protocone, hypocone and metaconule. Apart from these characters species are of course also recognised on the basis of their sizes.

The *Galerix* material from the Ramblian localities is tentatively assigned to three species. Most of the material represents *G. remmerti* n. sp. Moratilla 1 yield-

ded a surprisingly large species of *Galerix*, whereas a single M3 from San Roque 4B on the basis of its size probably presents an early entry of *G. symeonidis*.

*Galerix remmerti* is morphologically very similar to *G. aurelianensis*. One of the characteristics of *G. aurelianensis* is that a protocone-metaconule connection is present in a vast majority of the specimens, and is often equally developed as the protocone-hypocone connection (ZIEGLER, 1990a). This feature is also found in *G. remmerti*, in which the protocone-metaconule connection is even invariably present. The only difference between the Spanish and the German species lies in the sizes. *G. remmerti* is about 10 % smaller than *G. aurelianensis*, with almost no overlap in the size ranges of the various elements. This places *G. remmerti* in the same size category as *G. exilis*, which according to ZIEGLER (1990a) is morphologically very close to *G. aurelianensis* and thus also to *G. remmerti*. We believe, however, that the invariable presence of a protocone-metaconule connection on the upper molars in *G. remmerti* is a sufficient character to distinguish it as a separate species. In *G. exilis* such a connection is present in only c. 35 % of the M1 and c. 75 % of the M2 (ZIEGLER, 1983).

VAN DEN HOEK OSTENDE (1992) suggested that the Early Miocene *Galerix saratji* from Anatolia would make a plausible ancestor to *G. aurelianensis*, since the two differ in size only. Likewise, it would make a good ancestor to *G. remmerti*. It seems a differentiation in sizes between the Central European and Spanish *Galerix* evolved as the genus immigrated into Europe near the MN 2/MN 3 transition, presumably from Anatolia (VAN DEN HOEK OSTENDE, 1992, 2001c).

The m1 and the M2 from Moratilla 1 stand out because of their sizes (fig. 1, 2). The difference in size is much less in other elements, such as the m2 and m3 (fig. 3, 4). Here the elements from Moratilla 1 fall in the uppermost part of the size variation of *Galerix remmerti*. Since the m1 and m2 from Moratilla 1 were found associated in a mandible fragment, it is clear that the large elements belong to the same species as the relatively smaller ones. Figures 1 and 3 suggest a different m1/m2 ratio for *Galerix* sp. and *G. remmerti*. In order to test the taxonomical value of this ratio, it has been calculated for a number of Lower Miocene *Galerix* assemblages (tab. 3). The table shows a relatively high m1/m2 ratio for *G. aurelianensis*. However, the ratio varies considerably between the various assemblages of *G. remmerti*. Presumably this is a result of the small sample sizes.

The single m1 from Ramblar 3 is one of the larger ones found, whereas the single m2 from Valhondo 1 happens to be one of the smaller ones of the species. In both cases this leads to a high m1/m2 ratio. Thus, although our results are not clear-cut, I believe that the value of relative size between elements as a taxonomical character is worth further investigation, provided one has suitably large assemblages. This would not need to be confined to the m1/m2 ratio. For instance, like in the Desmaninae (RÜMKE, 1985), the p2/p3 ratio may also prove to be useful. After all, the relative size of these premolars is already used to distinguish between the genera of Galericini (VAN DEN HOEK OSTENDE, 2001d), and differences in the anterior dentition are already used to distinguish species in the tribe (e.g. in *Parasorex ibericus* (MEIN & MARTIN-SUAREZ, 1994) and in *Tetracus daamsi* (HUGUENEY & ADROVER, this volume).

The presence of a different *Galerix* species in Moratilla 1 is not understood, but presumably ecologically controlled. Moratilla 1 is the only locality that contains the eomyid *Ligerimys freudenthalii*, which makes up for even 27 % of the rodent fauna.

One of the two M3 from San Roque 4B is too small to belong to *Galerix remmerti*, and probably represents an early occurrence of *G. symeonidis*, which is found in the area in zones B-Da (VAN DEN HOEK OSTENDE & DOUKAS, in press). This early occurrence of this species, which is otherwise known from MN 4 and the lowermost part of MN 5 only, is as such not surprising. San Roque 4A and 4B also already contain *Democricetodon*, announcing the faunal change at the Ramblian/Aragonian boundary. Apparently the migrations leading to this faunal change were already underway for some species. Alternatively, *G. symeonidis* may have already been present throughout MN 3. ZIEGLER (1994) also found two small *Galerix* M3 in Wintershof-West, which he tentatively assigned to *G. symeonidis*. In combination with our M3 from San Roque 4B, this could lead to the suggestion that *G. symeonidis* was already present in MN 3. Comparison with our measurements of *G. symeonidis* shows that the two M3 from Wintershof-West are intermediate in size between those of *G. aurelianensis* and *G. symeonidis*. Thus, though the M3 are somewhat too small to be comfortably assigned to *G. aurelianensis*, they do not seem to fit in *G. symeonidis* either. In view of the stratigraphical distribution of the two *Galerix* species, it seems more logical to consider them outliers of *G. aurelianensis*.

Talpidae FISCHER VON WALDHEIM, 1817

*Desmanodon* ENGESSER, 1980

*Desmanodon* aff. *daamsi* VAN DEN HOEK

OSTENDE, 1997

(Pl. II, figs. 1-7)

#### DESCRIPTION

Since the *Desmanodon* material of the Ramblian localities, together with that from the Lower and Middle Aragonian, has been extensively described by VAN DEN HOEK OSTENDE (1997), we will only give a short description here.

*Lower dentition.* The p4 consists of a high triangular protoconid with a small bulge on the anterior side, bordered by a posterior cingulum. The specimen from Ramblar 7 has a short talonid between the posterior cingulum and the protoconid. In the m1, the m2, and the m3 the trigonid and talonid are of similar length. In the m1 the talonid is wider than the trigonid, in the m2 trigonid and talonid are of the same width, whereas the talonid is narrower than the trigonid in the m3. The oblique cristid ends against the middle of the protoconid-metacristid crest, although a more lingual position is found in two m1, from Valhondo 1 and Moratilla 1, respectively. The entocristid is usually well developed, but is lacking in two m1, from Ramblar 1 and Moratilla 1, respectively. The anterior cingulum is well developed. The labial cingulum is well developed on the m1, weak on the other two lower molars. The posterior cingulum is well developed on the m1 and m2.

*Upper dentition.* The P4 has an S-shaped posterocrista and a very small protocone (morphotype C sensu VAN DEN HOEK OSTENDE, 1989). The posterolingual side may be either slightly concave or straight, depending on the development of the posterolingual cingulum. The M1 and M2 invariably lack the protoconule. The hypocone is a weak cusp, particularly on the M1 where it can easily disappear with wear. On the M3, the hypocone is well developed and lies against the metacone. The division of the mesostyle is incomplete in about 60 % of the M1, 65 % of the M2 and about 25 % of the M3.

*Measurements:* Measurements are listed in Table 4.

*Remarks:* The *Desmanodon/Paratalpa* finds from the Daroca-Calamocha area, including that from the Ramblian localities, were already discussed by VAN DEN HOEK OSTENDE (1997). The finds are problema-

element	locality	N	length		width	
			range	mean	range	mean
P4	Ram 7	1		1.66		1.12
	VH 1	1		1.51		1.03
	Nav	1		1.60		1.28
M1	SR 4A	1		2.33		1.66
	Mor 1	2	2.51-2.56	2.54	1.52-1.58	1.55
	Ban 2	1		2.42		1.55
	Agr	2	2.61-2.64	2.63	1.53-1.58	1.56
	Ram 7	1		2.63		1.57
	VH 1	3	2.45-2.61	2.53	1.52-1.61	1.55
	Ram 1	1		2.60		1.61
	Nav	3	2.39-2.41	2.40	1.49-1.70	1.59
M2	SR 4B	1		1.76		1.98
	SR 4A	1		1.74		1.87
	Mor 1	1		1.92		2.24
	Ban 2	2	1.78-1.83	1.81	2.05-2.06	2.06
	Agr	8	1.75-1.99	1.91	1.76-2.21	2.09
	Ram 5	1		1.75		2.01
	Ram 7	1		1.74		2.15
	VH 1	5	1.58-1.81	1.71	2.00-2.19	2.07
	Ram 1	1		1.78		2.08
M3	Ban 2	2	1.03-1.04	1.04	1.50-1.55	1.53
	Agr	5	1.05-1.22	1.11	1.50-1.79	1.64
	VH 1	8	0.94-1.10	1.03	1.59-1.73	1.65
	Ram 1	5	0.93-1.08	1.02	1.45-1.58	1.52
	Nav	3	1.05-1.12	1.09	1.58-1.63	1.61

element	locality	N	length		width	
			range	mean	range	mean
p4	Mor 1	1		1.27		0.87
	Agr	2	1.21-1.27	1.24	0.76-0.76	0.76
	Ram 7	1		1.25		0.81
	VH 1	3	1.23-1.36	1.31	0.76-0.84	0.79
m1	Mor 1	2	1.70-1.89	1.80	1.27-1.29	1.28
	Agr	3	1.90-2.02	1.95	1.24-1.36	1.31
	Ram 7	1		1.87		1.26
	VH 1	4	1.75-2.01	1.90	1.14-1.28	1.23
	Ram 1	4	1.70-1.83	1.80	1.14-1.22	1.17
m2	Mor 1	4	1.89-1.97	1.92	1.23-1.25	1.24
	Ram 7	1		2.08		1.18
	VH 1	3	1.96-1.98	1.97	1.21-1.24	1.22
	Ram 1	2	1.89-1.94	1.92	1.14-1.29	1.22
	Nav	1		1.83		1.27
m3	Mor 1	5	1.36-1.61	1.50	0.78-0.90	0.85
	Agr	2	1.49-1.57	1.53	0.81-0.90	0.86
	VH 1	2	1.40-1.45	1.43	0.71-0.75	0.73
	Ram 1	3	1.36-1.46	1.41	0.77-0.81	0.79

Table 4.- Measurements for the upper and lower dentition of *Desmanodon* aff. *daamsi*.Tabla 4.- Medidas de la dentición superior e inferior de *Desmanodon* aff. *daamsi*.

tic, in that only elements of the dentition were found. In order to distinguish between Early Miocene *Desmanodon* and *Paratalpa* humeri are needed, since the dental morphology of the two genera is very much alike (VAN DEN HOEK OSTENDE, 1989, 1997; ZIEGLER, 1990b). Unfortunately, no humeri of either genus have been found in European MN 3 localities. The youngest finds of a *Paratalpa* humerus dates from MN 2, the earliest finds of *Desmanodon* humeri in Europe date from MN 4. Since there is no break in the morphology in the series of *Desmanodon/Paratalpa* assemblages from the Daroca-Calamocha area, which ranges from the uppermost of zone Z (Navarrete del Rio) to zone Db (La Col D), I assumed that they all belong to the same species. The time frame in which this mole is found in Daroca-Calamocha partly overlaps with the period in which *Desmanodon* is found in Germany (viz. MN 4), and is younger than the oldest occurrence of *Paratalpa*. Thus I suggested that the species from Daroca-Calamocha probably is referable to *Desmanodon* (VAN DEN HOEK OSTENDE, 1997), which implies that the genus migrated into Europe at the same time as *Galerix* (VAN DEN HOEK OSTENDE, 2001d). ZIEGLER (1990b) also tentatively suggested that *Desmanodon* might be an MN 3 immigrant in the European faunas.

Recently, a *Desmanodon* humerus was discovered in the collection of the Museo Nacional de Ciencias Naturales, Madrid. The humerus was found in the locality of Vargas 4BB. A search in the collections of the Natural History Museum Naturalis in Leiden yielded various fragmentary *Desmanodon* humeri from the locality of Vargas 1. Both localities are placed in zone C and are too young to provide direct evidence for the generic identity of the Ramblian finds. Nevertheless, they confirm that the Aragonian fossils belong to *Desmanodon* rather than *Paratalpa*, and since there are no differences in dental morphology between the Ramblian and Aragonian talpids of the area, it is a additional indication that the older finds belong to *Desmanodon* as well.

VAN DEN HOEK OSTENDE (1997) described *Desmanodon daamsi* from the Spanish locality Rubielos del Mora. In that paper the differences between this species and the Daroca-Calamocha talpid were stressed, i.e. somewhat wider upper molars, a weaker division of the mesostyle, and a weaker development of the hypocone. However, the newly found humerus also indicates similarities. The humerus of *D. daamsi* is characterised by its relatively long shaft, a fea-

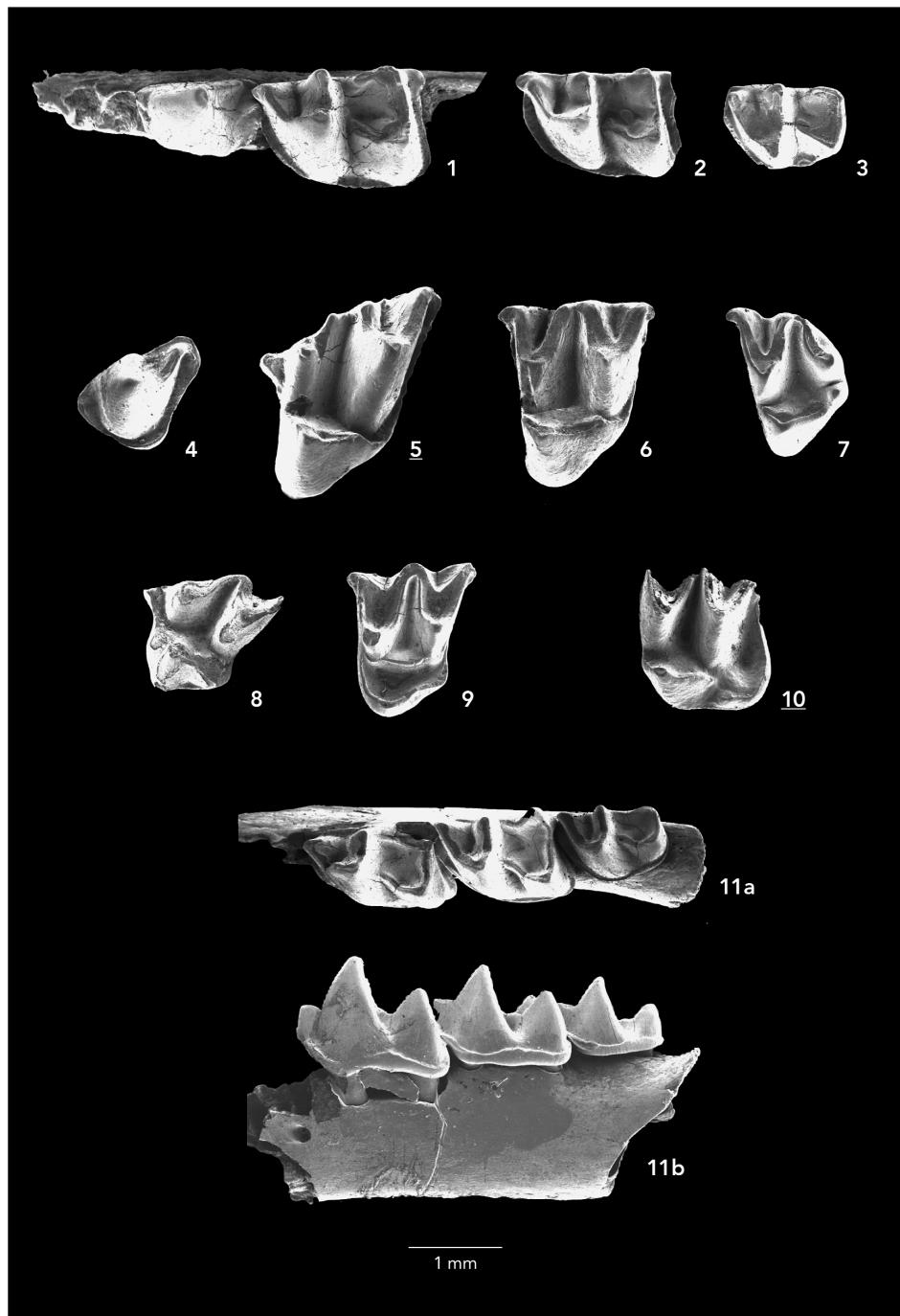


Plate 2

*Desmanodon* aff. *daamsi*. 1. Mandible with p4, m1 sin. (VH 1, I 83); 2. m2 sin. (VH 1, I 87); 3. m3 sin. (VH 1, I 91); 4. P4 sin. (VH 1, I 94); 5. M1 dext. (VH 1, I 98); 6. M2 sin. (VH 1, I 105); 7. M3 (VH 1, I 110).  
*Myxomysale* sp. 8. M1 dext. (Ra 1, RGM 410070); 9. M2 sin. (Ra 1, RGM 410071);  
*Heterosorex* sp. 10. M2 dext. (Ra 1, RGM 410069);  
*Soricella discrepans* 11. Mandible with m1-m3 (Ra 1, RGM 410033) a. occlusal view, b. lingual view. (all fig. 15x)

re that is also found in the humerus from Vargas 4BB. Furthermore, although the hypocone of the upper molars is better developed in our material than in *D. daamsi*, it is weaker than in the other European *Desmanodon* species, *D. antiquus* ZIEGLER, 1985 and *D. meuleni* DOUKAS, 1986. This also indicates a close relationship between the finds of the Daroca-Calamocha area and *D. daamsi*. Of course, the differences still stand and our material is therefore best classified as *D. aff. daamsi*.

#### *Myxomygale* FILHOL, 1890

*Myxomygale* cf. *hutchisoni* (ZIEGLER, 1985)  
(Pl. II fig. 8, 9)

*Locality:* Ramblar 1

*Measurements:* M2 = 1,46 x 1,63

#### DESCRIPTION

*M1.* The only specimen is damaged, lacking the posterolabial corner. The protocone is large. A small protoconule is incorporated in the anterior arm of this cusp directly in front of the tip of the protocone. The anterior arm of the protocone connects to the protruding parastyle, which is well developed. The parastyle is separated from the paracone by a wide valley. The posterior arm of the protocone runs parallel to the lingual side. The presence of a well-developed hypocone is indicated by a large bulge at the end of the posterior arm. Unfortunately, the enamel is abraded in this area, so that the hypocone itself cannot be observed properly. At the position of the hypocone there is a bulge in the posterior outline of the molar, making it slightly emarginated between the hypocone and the base of the metacone. The lingual face of the protocone is concave between the tip of the protocone and the tips of the protoconule and hypocone.

The posterior arm of the paracone is slightly curved. It connects to the undivided mesostyle. The anterior arm of the metacone is straight. The posterior arm of the metacone is longer than the anterior arm, but due to the damage in the area it cannot be assessed by how much. The only cingulum is a small patch between the bases of the protocone and the hypocone.

*M2.* The only specimen is extremely worn. The outline of the occlusal surface is subrectangular, with a concave posterolingual corner. The lingual complex is reduced to a deep basin bordered by enamel

ridges. The concave posterolingual side suggests that, in addition to a large protocone, a hypocone was present, situated lingually of the base of the metacone. The development of the hypocone, and whether or not a protoconule was present, cannot be assessed from this specimen. The labial cusps are of similar size. The anterior arms of the paracone and the metacone are slightly shorter than their respective posterior arms. The anterior arm of the paracone and the posterior arm of the metacone bend slightly at their ends, forming the parastyle and metastyle, respectively. The mesostyle is undivided. Although this may partly be due to wear, the division must have been incomplete at the most in unworn specimens. The only cingulum is a very narrow patch in the concave posterolingual corner of the molar.

*Discussion:* The two molars from Ramblar 1 are the first elements of *Myxomygale* described from Spain. In the lower Miocene of Europe, three species of this genus are known, *M. hutchisoni* (ZIEGLER, 1985), *M. engesseri* DOUKAS, 1986, and *M. minor* ZIEGLER, 1990. A fourth species, *M. antiqua* FILHOL, 1890 is known from the Oligocene of France only.

The material from Ramblar 1 is certainly not referable to *Myxomygale antiqua*, which is much larger than all the other representatives of the genus. It can also not be included in *M. engesseri*, a species that is characterised by the near absence of a hypocone on the M2. The bulge in the outline of the M2 from our locality suggests that a hypocone was at least present, and probably well developed.

*Myxomygale minor* and *M. hutchisoni* are both known from S. Germany. ZIEGLER (1990b) described *M. minor* from the MN 2 locality Ulm-Westtangente. Material from the uppermost Oligocene localities Eggingen-Mittelhart 1+2, which had previously been described as *M. cf. engesseri* (VAN DEN HOEK OSTENDE, 1989), was partly classified by Ziegler as *M. aff. minor*. *M. hutchisoni* was described as *Palurotrichus hutchisoni* by ZIEGLER (1985) and was based on material from the MN 4 fissure fillings Petersbuch 2 and Erkertshofen 1 + 2. VAN DEN HOEK OSTENDE (1989) transferred the species to *Myxomygale*, an opinion that was endorsed by ZIEGLER (1990b). Later ZIEGLER (1990b, 1994) included material from the MN 3 localities Stubersheim 3 and Wintershof-West in *M. hutchisoni*.

The main difference between *Myxomygale minor* and *M. hutchisoni* is the larger size of the latter. Although ZIEGLER (1990b) indicates that the species is

"much larger", his figures and measurements suggest that there is a small overlap in size at least. Furthermore, the dimensions of the material from Stubersheim 3 and Wintershof-West falls in the lower part of the size range of *M. hutchisoni* and are only somewhat larger than *M. minor*, thus taking an intermediate position between the material from MN 2 and MN 4. The M2 from Ramblar 1 is of similar size as those from the German MN 3 localities. Since our material is damaged or worn it is best classified as *Myxomysgale* cf. *hutchisoni*.

*Heterosoricidae* VIRET & ZAPFE, 1951  
*Heterosorex* VIRET & ZAPFE, 1951

*Heterosorex* sp.  
(Pl. II, fig. 10)

Locality: Ramblar 1

#### DESCRIPTION

*M2*. The only element of *Heterosorex* preserved is the M2. It is represented by three specimens, unfortunately all of which are damaged. One specimen lacks the paracone and the other two are damaged on the labial side. The protocone is large. Its anterior arm ends against the base of the paracone. The posterior arm runs parallel to the lingual side. The hypocone is incorporated in the posterior arm of the protocone as a small elevation in two specimens. In the third the posterior arm of the protocone ends freely between the ridge-shaped hypocone and the base of the metacone. The two labial cusps appear to be of similar size. Their cusps are high and pointed, their arms long and sharp. The mesostyle, which can only be observed in one of the three specimens, is undivided. The trigon basin is deep. An equally deep basin is formed between the metacone and the well-developed posterior ridge.

*Discussion:* ADROVER (1972, 1975) listed *Heterosorex neumayrianus* in his faunal list of Naverette del Rio. However, he neither described nor illustrated the material. Our collection from Navarette yielded no heterosoricid elements. The only *Heterosorex* material found in our collections from the Ramblian sections consists of the three fragmentary M2 from Ramblar 1.

Two species of *Heterosorex* are known from the European Lower Miocene. *H. neumayrianus* has been

found in various localities in S. Germany, ranging in age from MN 2 to MN 4 (ZIEGLER, 1989). *H. ruemkiae* is known from the Greek MN 4 locality Aliveri only (DOUKAS, 1986). The latter species differs from *H. neumayrianus* in its smaller size. Unfortunately, due to the damage our material cannot be measured and can therefore not be compared with either species. It is therefore best classified as *Heterosorex* sp.

Soricidae FISHER VON WALDHEIM, 1917  
Crocidosoricinae REUMER, 1987

*Clapasorex* CROCHET, 1975  
and  
*Oligosorex* KRETZOI, 1959

The taxonomy of the smaller Late Oligocene and Early Miocene shrews is still very problematic. This section is intended to give an insight in these problems. Of course, standard procedure in studies like this would be presenting the results of the taxonomical study of the two small shrews in the Ramblian section as clear-cut conclusions. But since our doubts may be equally useful to other authors as our conclusions, we prefer to give an insight in how those conclusions came to be. Thus, before describing the material we identified as *Oligosorex* and *Clapasorex*, we will give a short overview of the literature on the Early Miocene shrews and then discuss how we came to our identifications.

The problems in the taxonomy of the smaller shrews from this period are well illustrated by ZIEGLER (1989), who described the shrews from four Upper Oligocene localities under the heading *Crocidosorex* cf. *thauensis*, reaching the conclusion that the material probably represents two new species. Despite having a large number of isolated teeth, he also identified a small shrew from Ulm-Westtangente as *Crocidosorex* sp. VAN DEN HOEK OSTENDE (2001b) encountered similar problems, publishing three out of five small shrews from the Lower Miocene of Anatolia in open classification.

The main problem is that soricid taxonomy is largely based on the number of antemolars. The absence of complete mandibles hampers the identification of a species. Molar morphology is generally regarded as a less useful criterion, and as a result adequate description of the molars are relatively rare. Furthermore, in order to use morphological criteria, these have first to be linked with certainty to a taxon, for which

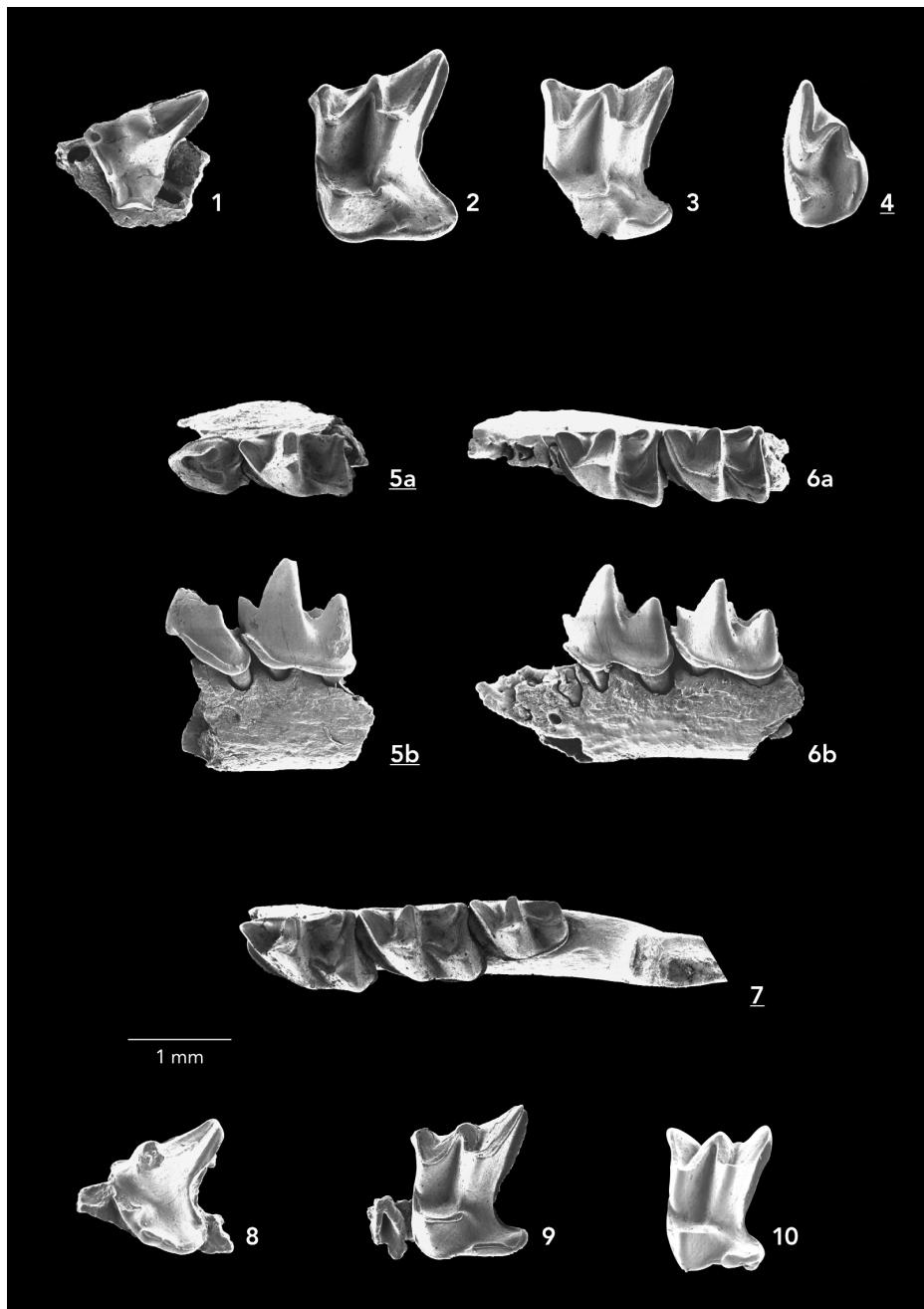


Plate3

*Soricella discrepans*. 1. P4 sin. (Ra 1, RGM 410033); 2. M1 dext. (Ra 1, 410048); 3. M2 sin. (Ra 1, RGM 410051); 4. M3 dext. (Ra 1, 410066).

*Clapasorex alvarezae* n.sp. 5. Mandible p4-m1 dext. (Nav, I 14) a. occlusal view, b. lingual view; 6. Mandible m1, m2 sin. (holotype, Ra 3, I 48) a. occlusal view, b. lingual view; 7. Mandible m1-m3 dext. (Nav, I 11); 8. P4 sin. (VH 1, 72); 9. M1 sin. (Ra 1, RGM 410057); 10. M2 sin. (Ra 1, RGM 410065). (all fig. 15x)

one needs localities that also yield complete mandibles. And then of course, the more characteristic but usually rarer upper molars, have to be linked correctly to the lower dentition.

Three genera of Early Miocene small shrews are recognised: *Oligosorex*, *Clapasorex* and *Carposorex*. *Oligosorex* has been considered a synonym of *Crocidosorex* by many authors, but should be retained as a separate genus according to VAN DEN HOEK OSTENDE (2001b). The only species retained in *Crocidosorex* should be the somewhat enigmatic type species *C. piveteaui* LAVOCAT, 1951, which is known from the Upper Oligocene of France. *Oligosorex* contains *O. antiquus* (POMEL, 1853), *O. thauensis* (CROCHET, 1975) and *O. reumeri* Van den Hoek Ostende, 2001. These three species share the presence of a vestigial p3 directly in front of beside the anterior part of the p4. *Carposorex* and its type species *C. sylviae* CROCHET, 1975 is characterised by wrinkled enamel. *Clapasorex* is known from two species, *C. bonisi* CROCHET, 1975 and *C. sigei* CROCHET, 1975.

Since shrews are similar in the morphology of the molars, even recognising the number of species present in a sample is by no means easy. In the case of the study of the Ramblian material, the presence of more than one species was first suspected on the basis of minor differences in the morphology of the m1. Some of these seem to have a narrower trigonid relative to the talonid. The hypolophid in these m1 runs closer by the entoconid and the general appearance is a bit more massive than the other. In the m2 too the hypolophid seems to run closer to the entoconid in the more massive specimens. The mandibles confirm that these differences indeed indicate the presence of two species. Though both species possess four antemolars, there are differences in the relative sizes of the alveoles. The three anterior alveoles are of subequal size in the species with the more massive molars, which we designate species A for the time being. In the other species (B) the third alveole is tiny and merges with the anterior alveole of the p4.

Finding the corresponding upper molars of the two species was a painstaking business. A single M1 from Ramblar 1 stands out because of its very small, ridge-shaped hypocone. Most of the M2 have a small ridge-shaped hypocone, but in some specimens the hypocone seems to be smaller still. In these M2 the anterior arm of the paracone and the posterior arm of the metacone seem to be somewhat less elongated than in others. Both these M1 and M2 with a tiny

hypocone and the lower molars of species A are found in the older localities only, so that the association of the two seems to be certain. Differences between the P4 from the various localities are slight, but here too two types seem to be represented. The two differ in the direction of the lingual flange, which results in a lesser degree of emargination and a larger angle between the lingual and labial sides in one type. Again based on the stratigraphical distribution, the P4 with a stronger emargination seem to be associated to species A.

Having established the presence of two different species, the next question is their generic affinity. Species B shows a vestigial p3, which is considered characteristic for *Oligosorex*. The morphology of the molars is in accordance with this identification. Since the alveoles of the antemolars are of sub-equal size species A, it is no *Oligosorex*. *Carposorex* is characterised by wrinkled enamel, which is not found in our species. This leaves *Clapasorex* as the only described genus. Unfortunately, the diagnosis of *Clapasorex* (CROCHET, 1975) provides few useful features. According to this diagnosis, the trigonid basin is relatively closed, but this character is not supported by the illustrations given by Crochet. These illustrations resemble well our material. Our material also agrees with other features mentioned in the diagnosis: massive cusps, well-developed labial cingulums on the lower molars, lingual cingulum on the m1, m3 relatively poorly reduced, hypocones weaker than in *Oligosorex*. However, whether or not these characters are suitable for diagnosing a genus, is open to doubt. The relative size of the m1 and m2 is also mentioned as a diagnostic character. In the material from Navarete del Rio we find two mandibles, in which the m1 is larger than the m2 in the one, but smaller in the other.

The lower anterior dentition is not mentioned in the generic diagnosis of *Clapasorex*, but they are used in the diagnosis of its type species, *C. sigei* (the anterior dentition of the other species *C. bonisi* is not known). Like our species, *C. sigei* has four lower antemolars. In the type species the alveoles of the antemolars are confluent, with the exception of that of the posterior root of the p4. In our species, both the alveoles of the first two antemolars, and that of the anterior root of the p4 and the third antemolars are confluent. However, the alveoles of the second and third antemolars are separated. This configuration thus resembles that found in *C. sigei*. Combined with

the similarities in the molar morphology, this allows our species to be identified as a *Clapasorex*, at least for the time being.

*Clapasorex alvarezae* nov. sp.  
(Pl. III, figs. 5-10)

*Derivatio nominis:* The species is named in honour of Dr. Marian Álvarez Sierra, who described the Eomyidae of the Ramblian type section.

*Diagnosis:* Small-sized Crocidosoricine (m<sub>2</sub> 1,17). The m<sub>1</sub> is on average slightly larger than the m<sub>2</sub>. Four lower antemolars. The alveoles of the anterior three antemolars of sub-equal size, and partly confluent. The m<sub>1</sub> and m<sub>2</sub> have a lingual cingulum, which is better developed in the m<sub>1</sub>. Hypocones of the upper molars poorly developed.

*Differential diagnosis:* *Clapasorex alvarezae* is clearly larger than *C. bonisi* and somewhat larger than *C. sigei*. In addition, it differs from the latter species by having a separation between the alveoles of the second and third lower antemolar.

*Clapasorex alvarezae* differs from all species of *Oligosorex* by having alveoles of similar size for the front three lower antemolars. It differs from *Carpolestes* in not having wrinkled enamel.

*Type locality:* Ramblar 3 (Zone Z)

*Other localities with Clapasorex alvarezae:* Navarette del Rio, Ramblar 1, Valhondo 1.

*Holotype:* Ra 3 I 48. Mandible fragment with m<sub>1</sub>, m<sub>2</sub> and the alveoles of the anterior dentition (m<sub>1</sub> = 1,18 x 0,79, m<sub>2</sub> = 1,17 x 0,77) (Pl. III, fig. 6).

*Description of the holotype:* The mandible fragment with m<sub>1</sub> and m<sub>2</sub> shows the alveoles of the anterior dentition. Apparently this fragment is broken off at the posterior end of the alveole of the lower incisor. Five smaller alveoles are present in front of the m<sub>1</sub>. The last one of these is the largest and belonged to the posterior root of the p<sub>4</sub>, which is still in place. The alveole directly in front of it also contains the remnants of a root, presumably the anterior root of the p<sub>4</sub>. The remaining three alveoles are of similar size as that of the anterior alveole of the p<sub>4</sub>. The first two are coalescent, as are the third and the fourth. There is a small foramen mentale directly below the anterior alveole of the p<sub>4</sub>, above the centre of the ramus horizontalis.

The trigonid of the m<sub>1</sub> is longer and somewhat narrower than the talonid. The paraconid is low and lies at the end of a long paralophid. The paralophid is

bent at about two-thirds of its length. The trigonid basin is very open. The protoconid-metaconid crest is notched slightly halfway. The oblique cristid ends just lingually of the base of the protoconid. The hypolophid runs behind the entoconid and is more or less separated from this cusp by a narrow valley. The entocristid is very well developed and ends high against the posterior flank of the metaconid. The anterior cingulum is strong. It ends just below the paraconid. The labial cingulum is well developed and the posterior cingulum is strong. There is a lingual cingulum, which is better developed near the trigonid basin than near the talonid basin. The trigonid and talonid of the m<sub>2</sub> are of the same width. The trigonid is longer than the talonid. The paralophid is long. The protoconid and metaconid stand far apart. The oblique cristid ends near the centre of the protoconid-metaconid crest. The hypolophid runs behind the entoconid. The entocristid is well developed and ends against the posterior flank of the metaconid. The anterior cingulum is well developed. The posterior cingulum is still rather wide at its labial side, but becomes labially quickly narrower. The labial cingulum is well developed; the lingual cingulum is weak.

*Measurements:* Measurements are listed in Table 5.

element	locality	N	length		width	
			range	mean	range	mean
p4	Ra 1	1		0,81		0,56
	Nav	1		0,83		0,63
m1	Ra 3	2	1,18-1,21	1,20	0,77-0,79	0,78
	VH 1	4	1,14-1,23	1,20	0,71-0,77	0,75
	Nav	2	1,21-1,27	1,24	0,81-0,84	0,83
m2	Ra 3	2	1,17-1,19	1,18	0,72-0,77	0,75
	VH 1	5	1,08-1,19	1,14	0,69-0,75	0,72
	Ra 1	1		1,14		0,77
	Nav	2	1,21-1,25	1,23	0,74-0,81	0,78
m3	Ra 3	2	0,94-1,00	0,97	0,39-0,48	0,44
	Ra 1	1		0,92		0,40
	Nav	2	0,97-1,02	1,00	0,41-0,43	0,42
P4	VH1	2	1,26-1,35	1,31	1,11-1,14	1,13
M1	Ra 1	1		1,20		1,44
	Nav	1		1,19		1,47
M2	Ra 3	1		0,95		1,33
	Ra 1	2	1,08-1,09	1,09	1,37-1,42	1,40

Table 5.- Measurements of *Clapasorex alvarezae* nov. sp.

Tabla 5.- Medidas de *Clapasorex alvarezae* nov. sp.

## DESCRIPTION

*p4*. The premolar has the rough heart-shape typical for soricid *p4*. The wear surface of the paraconid is Y-shaped. The two arms are equally long; the labial arm is somewhat better developed than the lingual arm. The two arms border a well-defined sulcus, at the bottom of which lies a small but distinct, ridge-shaped cusplet. The labial and lingual cingulums are well developed. The lingual cingulum connects to the posterior cusplet; the labial cingulum ends against the flank of this cusplet.

*m1, m2*. See description holotype

*m3*. The trigonid is somewhat longer and wider than the talonid. It resembles the trigonid of the *m2*, but is much smaller. The talonid is reduced. The hypoconid is the only discernible cusp. It forms together with the oblique cristid, the hypolophid, the entoconid, and the entocristid a continuous ridge bordering a very shallow talonid basin. The oblique cristid ends lingually of the middle of the protoconid-metacanid crest, leaving a very large re-entrant basin. The anterior cingulum is strong and the labial cingulum is well developed. There is a weak lingual cingulum near the trigonid basin.

*P4*. The labial part of the premolar is occupied by the large and high paracone. The cusp has a long and sharp posterocrista, reaching to the postero-labial corner of the *P4*. The parastyle and protocone, positioned anteriorly and anterolingually of the tip of the paracone, respectively, are of about the same height. The protocone is somewhat larger than the parastyle. The two cusplets are connected by a ridge. There is no parastylar crest. The short posterior arm of the protocone ends freely on the large lingual flange. A tiny hypocone lies postero-lingually of the protocone. The hypocone forms the starting point of a low ridge that borders the lingual flange and continues to the posterolabial corner of the premolar. This ridge is best developed on the lingual side and near its posterior end. There is a well-developed labial cingulum.

*M1*. The *M1* is only somewhat wider than it is long. The posterior emargination is moderate to strong (PE-ratio= 0,27-0,31). The anterior arm of the protocone ends against the base of the paracone. The posterior arm of the protocone ends freely near the base of the metacone. There is no true hypocone, just a ridge-shaped elevation on the lingual side of the hypoconal flange. This elevation is the starting point of a narrow ridge that runs along the back of the

molar. The paracone is clearly smaller than the metacone. Its posterior arm is only somewhat longer than its anterior arm, whereas the posterior arm of the metacone is much longer than the anterior arm of this cusp. The mesostyle is undivided. The only cingulum is the well-developed posterior cingulum along the base of the posterior arm of the metacone.

*M2*. The molar is clearly wider than it is long. The posterior emargination is moderate (PE-ratio=0,21-0,23). The labial cusps are about the same size and height. Both arms of the paracone and the anterior arm of the metacone are of similar length; the posterior arm of the metacone is somewhat longer. The mesostyle is undivided.

The anterior arm of the protocone connects to the base of the paracone. The posterior arm of the protocone runs more or less parallel to the lingual side and ends lingually of the metacone. The hypocone is very small and ridge-shaped. The only cingulum is the posterior cingulum, which is very narrow near the posterior emargination, wider near its labial end.

*Remarks*: The genus *Clapasorex* was defined by CROCHET (1975) for small-sized shrews from Paulhiac (France, MN 1) and Bouzigues (France, MN 2). The latter locality yielded the type species, *C. sigei*, whereas the *Clapasorex* from Paulhiac was described as *C. bonisi*. The genus was diagnosed: Soricinae primits. Prefossile de *m1* relativement fermée, entocristide des molaires plutôt courte, cupides épaisses, crête oblique remontant légèrement la muraille postérieure du trigonide. Cingulums antérieurs non élargis sous les paraconides. Bourrelets cingulaires latéraux bien formés et présents lingualement sur *m1*. *m2* plus petite que *m1*. *M3/m3* assez peu réduits. Foramen mentonnier sous *p4*. Hypocône des molaires peu ou mal cuspidé, éperon le supportant peu développé par rapport à *Crocidosorex* [= *Oligosorex*]. Contour lingual des molaires supérieur souligné par un cingulum.

Thus the number of antemolars is not included in the diagnosis of the genus, probably because it is not known for the older species, *C. bonisi*. However, it is known for the type species *C. sigei*, which has four antemolars. The alveoles of these, with the exception of the one for the posterior root of the *p4*, are coalescent. This configuration resembles the one found in *C. alvarezae*. Here there is a similar coalescence, with the exception of the alveoles of the second and third lower antemolar. Our species also agrees with the *Clapasorex sigei* in the massive aspect of the

lower molars and the poor development of the hypocone. The main difference with the type species of *Clapasorex* is the somewhat larger size, the Spanish species being about 10 % larger than *C. sigei*. Thus the three species of *Clapasorex*, described from MN 1 (*C. bonisi*), MN 2 (*C. sigei*), and MN 3 (*C. alvarezae*) show a size increase which may represent a evolutionary lineage.

*Clapasorex alvarezae* is the first record of its genus outside of France. It is also the youngest record of *Clapasorex*. The species is only found in assemblages from Zone Z. Possibly *Clapasorex* became extinct afterwards.

*Oligosorex thauensis* (CROCHET, 1975)  
(Pl. IV, figs. 1-8)

*Localities:* *Oligosorex thauensis*: Ramblar 1, Valhondo 1, Ramblar 3, Ramblar 7; *Oligosorex aff. thauensis*: Agreda, Bañon 2, Moratilla 1, San Roque 4A.

*Measurements:* Measurements are listed in table 6.

DESCRIPTION

*Mandible.* One mandible fragment from Ramblar 3B (I 47) shows a foramen mentale below the p4. This foramen lies just above the middle of the ramus horizontalis. The fragment is broken off in line with the anterior root of the p4. It shows a second, equally small alveole just (antero-)lingually of the anterior p4 alveole, presumably belonging to a small p3. Below these two alveoles lies a cross-section of the large alveole of the lower incisor. A relatively complete ramus horizontalis from Ramblar 7 (I 51) shows what at first sight seem to be four alveoles in front of the m1. The largest of these is partly covered by the m1 and belongs to the posterior root of the p4. The alveole in front this appears too large for just the small anterior root of the p4. On the posterior side this alveole shows a slight indentation. From this, and from the cross-section described above, this alveole is interpreted as the merger of the alveoles of the p3 and the anterior root of the p4.

p4. The lingual and labial sides of the p4 are concave, the posterior side is emarginated. The labial side of the premolar is much deeper than the lingual side. The wear surface of the paraconid has the typical Y-shape of Crocidosoricinae. The labial arm is somewhat shorter than the lingual arm. The two arms

border a shallow sulcus. The lingual cingulum is well developed; the labial cingulum somewhat less. The posterior cingulum is conspicuously strong.

m1. The trigonid is somewhat longer and clearly narrower than the trigonid. The paraconid stands at the end of a long paralophid, which is bent at about two-thirds its length. The protoconid and metaconid stand close together. The trigonid basin is very open. The oblique cristid ends lingually of the base of the protoconid. The hypolophid runs behind the entoconid, connecting to the lingual cingulum. A small valley separates the hypolophid from the entoconid. The entocristid is well developed and ends against the posterior flank of the metaconid. The anterior cingulum is well developed. It ends against the front of the paraconid. The labial and posterior cingulums are rather weak. There is a continuous lingual cingulum, which is conspicuously well developed in one speci-

element	locality	N	length		width	
			range	mean	range	mean
p4	Ra 3	1		0,87		0,62
m1	SR 4A	1		1,12		0,71
	Mor 1	2	1,12-1,18	1,15	0,81-0,85	0,83
	Bn 2	1		1,18		0,69
	Agr	1		1,21		0,84
	Ra 7	3	1,06-1,21	1,14	0,71-0,76	0,73
	Ra 3	2	1,13-1,27	1,20	0,78-0,84	0,81
	VH 1	2	1,15-1,24	1,20	0,72-0,77	0,75
	Ra 1	3	1,12-1,21	1,17	0,81-0,82	0,81
m2	SR 4A	2	1,20-1,24	1,22	0,76-0,76	0,76
	Mor 1	1		1,25		0,77
	Agr	7	1,21-1,31	1,27	0,69-0,87	0,77
	Ra 7	1		1,13		0,73
	Ra 3	4	1,10-1,20	1,15	0,69-0,75	0,71
	VH 1	1		1,12		0,72
	Ra 1	6	1,13-1,25	1,18	0,70-0,78	0,74
P4	Mor 1	1		1,37		1,33
	Ra 7	1		1,35		1,15
	Ra 3	1		1,31		1,17
	Ra 4	1		1,36		1,23
M1	Ra 7	2	1,13-1,14	1,14	1,36-1,46	1,41
	Ra 3	2	1,21-1,30	1,26	1,53-1,62	1,58
	Ra 1	6	1,17-1,30	1,22	1,44-1,69	1,54
M2	Agr	1		1,01		1,30
	Ra 7	2	0,95-1,03	0,99	1,23-1,37	1,30
	Ra 3	2	1,08-1,10	1,09	1,35-1,40	1,38
	Ra 4	2	1,09-1,11	1,10	1,30-1,32	1,31
	Ra 1	5	1,08-1,19	1,12	1,31-1,48	1,38

Table 6.- Measurements of *Oligosorex aff. thauensis*.  
Table 6.- Medidas de *Oligosorex aff. thauensis*.

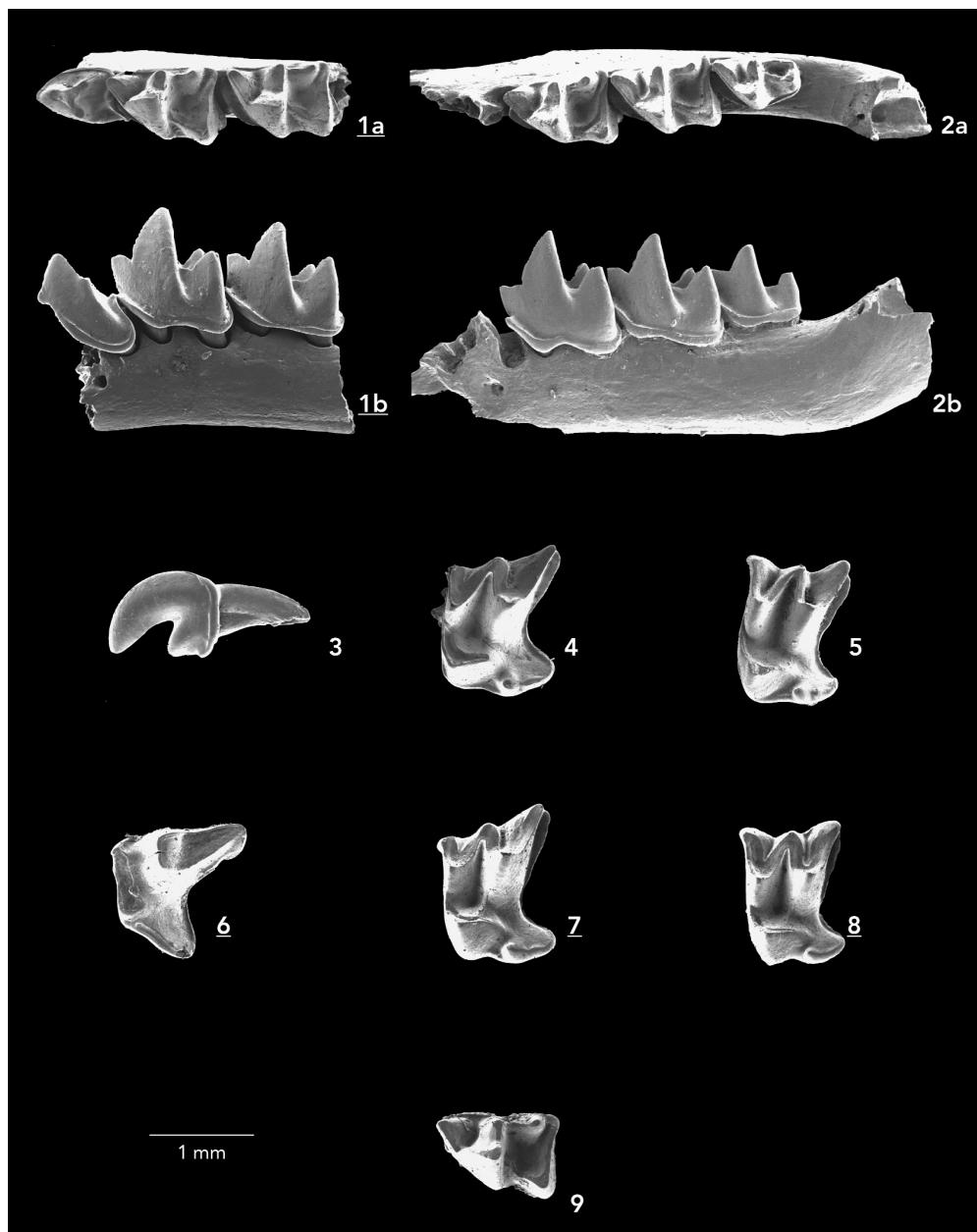


Plate 4

*Oligosorex thauensis*. 1. Mandible p4-m2 dext. (Ra 3, I 47) a. occlusal view, b. lingual view; 2. Mandible m1-m3 sin. (Ra 7, I 51) a. occlusal view, b. lingual view. 3. I1 sin. (Ra 3, I 45); 4. M1 sin. (Ra 1, RGM 410056); 5. M2 sin. (Ra 1 RGM 401064); 6. P4 dext. (Mor 1, RGM 410138); 7. M1 dext. (Ra 7, I 57); 8. M2 dext. (Ra 7, I 60).  
Crocidosoricinae gen. et sp. indet. 9. m1 sin. (Bn 5, RGM 410097). (all fig. 15x)

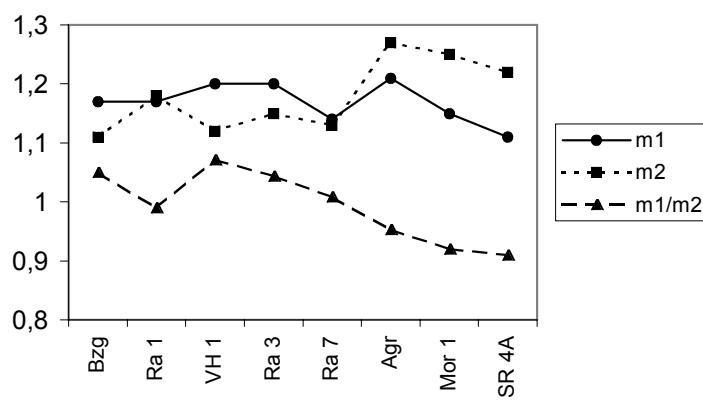


Figure 5.- Average length of the m1 and m2, and the m1/m2 ratio for the various assemblages of *Oligosorex* (aff.) *thauensis* in the Daroca-Calamocha area. The data of the type locality Bouzigues (Bzg) have been added for comparison.

Figura 5.- Longitud media del m1 y m2, y relación m1/m2 para varios yacimientos de *Oligosorex* (aff.) *thauensis* en el área de Daroca-Calamocha. Se han añadido los datos de la localidad tipo, Bouzigues (Bzg), para comparación.

men from Agreda (Agr I 5) and one from Banon 2 (RGM 410099).

*m2*. The trigonid is somewhat narrower than the talonid. The trigonid and talonid are of similar length. The paraconid is only somewhat lower than the metaconid; the protoconid is clearly higher than the metaconid. The oblique cristid ends against the protoconid-metaconid crest, labially of its centre. The hypolophid runs behind the entoconid, and is separated from this cusp by a small valley. It connects to the lingual cingulum. The entocristid is well developed and ends against the posterior flank of the metaconid. The anterior cingulum is wide. The posterior cingulum is rather wide at its labial end, but narrow on the lingual side. The labial and lingual cingulums are narrow.

*M1*. The M1 is somewhat wider than it is long. The anterior arm of the protocone ends against the base of the paracone. The posterior arm of the protocone ends freely near the base of the metacone. The development of the hypocone varies. It is usually present as a small but distinct cusplet, but in some specimens it is nearly absent. A ridge runs from the hypocone along the posterior side of the molar. The paracone is much smaller than the metacone. The posterior arm of the paracone is somewhat longer than its anterior arm. The posterior arm of the metacone is c. 30% longer than the anterior arm. The mesostyle is undivided. There is a short lingual cingulum between the base of the protocone and the hypocone.

*M2*. The M2 is much wider than it is long. The posterior emargination is moderate. The metacone is somewhat larger and higher than the paracone. The

two arms of the paracone are of similar length. The anterior arm is slightly bent near its end. The posterior arm of the metacone is somewhat longer than the anterior arm. The latter connects to the posterior arm of the paracone at the undivided mesostyle. The protocone is large. Its anterior arm ends against the anterior flank of the paracone near the base of that cusp. The posterior arm of the protocone ends freely, lingually of the base of the metacone. A small hypocone lies lingually of the end of the posterior arm of the protocone. A posterior ridge runs from the hypocone backwards and continues as the posterior cingulum, which becomes very narrow near the posterior emargination.

*Remarks*: *Oligosorex thauensis* was described by CROCHET (1975) from the French MN 2 locality Bouziges. A characteristic feature of this species is the combined alveole of the p3 and the anterior root of the p4, in which the p3 is situated next to the anterior root of the last premolar. This configuration is in our material preserved in mandibles for Ramblar 3 and Ramblar 7.

Another character Crochet used in his diagnosis, is the relatively size of the m1 with respect to the m2, the latter being smaller. He had the benefit of a suitable large assemblage to observe this character. Unfortunately, our assemblages are much smaller, which provides a certain uncertainty when calculating length ratios between elements. In fig. 5 we have plotted the average lengths of the m1 and m2, as well as the m1/m2 ratio for all assemblages containing both these elements. The values for the type locality Bouzigues have been added for comparison. With the exception of the assemblage of Ramblar 1, figure 5

suggests a trend in which the m1/m2 ratio becomes increasingly smaller. The low value for Ramblar 1 may be due to chance, although it is in fact one of the larger assemblages available. Like in Ramblar 1, the m1/m2 ratio is lower than 1 in the three younger assemblages. This seems to be the consequence of an increase in the length of the m2, whereas the m1 is similarly sized with respect to the older assemblages.

Due to the small sample size, one has to be cautious about any conclusions, but there are indications that some change in the m1/m2 ratio occurred between Ramblar 7 and Agreda. Unfortunately, we do not have any mandibles with the alveoles of the anterior dentition for the younger assemblages. Therefore we can not check whether there are changes in the anterior dentition accompanying the presumed reversal of the m1/m2 ratio. There are no changes in the molar morphology. However, it is noteworthy that the M2 from Ramblar 7 and Agreda are about 10 % shorter than in the older localities, while retaining the same width, suggesting a change of proportions in the upper dentition as well. Because of the larger m2 in Agreda, Moratilla 1 and San Roque 4A the younger assemblages are provisionally classified as *Oligosorex* aff. *thauensis*.

#### *Soricella* DOBIN-FLORIN, 1964

*Soricella discrepans* DOBIN-FLORIN, 1964  
(Pl. II, fig. 11; Pl. III figs. 1-4)

Localities: Navarrete del Rio, Ramblar 1.

#### DESCRIPTION

**Mandible.** Two jaw fragments show that at least four alveoles were present in front of the m1. The hindmost two alveoles, of which the anterior one is clearly smaller than the posterior one, belong to the p4. The remaining two alveoles are in size comparable to that of the posterior root of the p4. There is a large foramen mentale below the alveoles of the p4.

**m1.** The trigonid is clearly longer and somewhat narrower than the talonid. The two arms of the protoconid are nearly perpendicular to one another. The paralophid is long. It bends sharply just past its middle. The trigonid basin is very open. The oblique cristid ends just labially of the middle of the protoconid-metacristid crest. The hypolophid connects to the entoconid. It slightly bends backwards at its end,

making a tiny bulge in the posterior outline just posterolabially of the entoconid. The entocristid slopes down sharply from the entoconid, connecting to a relatively low metacristid. The anterior cingulum is strong but short, ending well short of the paraconid. The labial cingulum is narrow and slopes up slightly near the re-entrant valley. The posterior cingulum is well developed on the labial side. It narrows quickly lingually. The lingual cingulum is weak.

**m2.** The talonid is shorter and somewhat narrower than the talonid. In contrast to the m1 the two arms of the protoconid form an acute angle. The protoconid-metacristid crest is straight; the paralophid slightly bent. The oblique cristid ends against the middle of the protoconid-metacristid crest or just labially of that point. The hypolophid ends against the entoconid. It bends slightly at its end, forming a small bulge in the posterior outline of the m2. The entocristid slopes down sharply from the tip of the entoconid and connects to a low metacristid. The anterior cingulum ends just short of the paraconid. It is strong, becoming narrower towards the labial side. The labial cingulum is narrow to well-developed. In contrast to the m1, it does not slope upwards near the re-entrant valley. The posterior cingulum is well developed, but becomes narrow near the lingual side. A weak lingual cingulum may be present near the trigonid basin.

**m3.** The trigonid is shorter and wider than the talonid. The two arms of the protoconid are relatively straight. The hypoconid and entoconid are reduced, but still discernible as cusps. Together with the oblique cristid, hypolophid, entocristid and a very small metacristid they form a ridge bordering the talonid basin. The oblique cristid connects to the protoconid-metacristid crest just lingually of the middle of this crest. The anterior cingulum, which ends just short of the paraconid is strong. It continues labially as the well-developed labial cingulum. There is a narrow posterior cingulum. A very weak lingual cingulum is found near the trigonid basin.

**P4.** The only available specimen is damaged, lacking the posterolingual corner of the premolar. The anterior side is slightly concave; the posterior side is emarginated. The tip of the paracone lies just in front of the middle of the labial side. Its posterocrusta is high and sharp. The parastyle is a small conical cuspule in front of the paracone. There is no parastylar crest. A short anterior crest runs from the base of the parastyle along the anterior side, without reaching the protocone. The protocone is low and crescent-shaped,

with its arms bending to the lingual side. There is a short and narrow anterior cingulum in front of the protocone. Due to the damage the presence or position of the hypocone cannot be ascertained.

*M1*. The M1 is moderately emarginated (PE-ratio= 0,18-0,28). The protocone is large. Its anterior arm ends against the base of the paracone. The posterior arm end freely between the base of the metacone and the hypocone. A faint, transverse ridge runs between the end of the posterior arm of the protococone and the base of the metacone. There is an even fainter ridge between the hypocone and the flank of the posterior arm of the protocone. In one specimen from Ramblar 1 (RGM 410050) the ridge connecting to the metacone is well developed, whereas the faint ridge near the hypocone is absent. The hypocone is very small and is incorporated in a ridge that borders the hypoconal flange and continues as the posterior cingulum. The posterior arms of the labial cusps are longer than their respective anterior arms. The metacone is much larger than the paracone. The mesostyle is undivided. There is a weak cingulum along the base of the posterior arm of the protococone. A weak labial cingulum may be present.

*M2*. The only available specimen is damaged, lacking the major part of the protococone. The posterior arm of the protococone ends freely between the base of the metacone and the hypocone. A transverse ridge connects the end of the posterior arm of the protococone to the base of the metacone. The hypocone is very small and ridge-shaped. From its tip runs a posterior ridge bordering the hypoconal flange and continuing as the posterior cingulum. The paracone is somewhat smaller than the metacone. In both labial cusps the posterior arm is somewhat longer than the anterior arm, in the metacone more so than in the paracone. The mesostyle is undivided. There are no cingulums on the anterior, labial and lingual sides.

*M3*. The anterior side of the M3 is straight, the posterior side is rounded. The protococone is small. It has an anterior arm only, which continues as a narrow anterior cingulum that ends against the anterior flank of the paracone. The paracone is the largest cusp. Its anterior arm is nearly twice the length of the posterior arm. The posterior arm of the paracone is about the same length as the anterior arm of the metacone. The two arms meet at the incompletely divided mesostyle. The metacone is ridge-shaped and continues to the lingual side of the M3. The trigon basin is wide. It opens to the lingual side between the protococone and the metacone.

*Remarks*: The genus *Soricella*, and its type species *S. discrepans* were described by DOBEN-FLORIN (1964) from the S. German fissure filling Wintershof-West (MN 3). The lower molars of the genus are very characteristic, since the hypolophid connects, unlike in other shrews, to the entoconid. More material from S. Germany was described by ZIEGLER (1989), with assemblages from Ulm-Westtangente (MN 2), Stübersheim 3 (MN 3), and Erkertshofen 2 and Petersbuch 2 (MN 4). Ziegler found the metrical variation between the various assemblages to be large. Ulm-Westtangente yielded the smallest dimensions, Wintershof-West the largest. The other assemblages, including the younger ones, take an intermediate position. Thus it was clear, that the variation in size is not part of a phylogenetical increase. Since *Soricella discrepans* from Ulm-Westtangente was clearly smaller than that from the type locality Wintershof-West, without showing any morphological differences, Ziegler classified the MN 2 assemblage as *Soricella cf. discrepans*. This suggests, however, that additional material would further clarify the taxonomical position of the Ulm-Westtangente assemblage. Since the assemblage is suitably large (185 elements), the metrical difference with the younger assemblages is better expressed by classifying the *Soricella* from Ulm-Westtangente as *S. aff. discrepans*.

Apart from *Soricella discrepans*, Petersbuch 2 yielded a number of *Soricella* elements that are too large to be included in this species (ZIEGLER, 1989). In the absence of morphological differences to endorse the difference in size, Ziegler refrained from naming the species and listed it as *Soricella* sp.

Extensive descriptions and measurements of *Soricella* are known from Germany only, but finds of *S. discrepans* have been noted from elsewhere. ZIEGLER (1989) mentions the presence of the species in Dolnice (MN 4, Czech Republic), HUGENEY (1974) lists it for Montaigu-Chavroches (MN 2, France), and ADROVER (1972, 1975) already noted the presence of *S. discrepans* in Navarete del Rio.

A remarkable difference between the descriptions given above and the descriptions made by ZIEGLER (1989), is that I, like DOBEN-FLORIN (1964), consider the hypocone to be present, whereas Ziegler describes it as being absent. This is not a true difference, but a mere difference in interpretation. From my point of view, the illustrations given by ZIEGLER (l.c. pl. 4, figs 7, 8, and 10) clearly show the presence of a small hypocone. These illustrations also show the

MN	zone	Locality	N M1M2	percentage	<i>Galerix remmerti</i>	<i>Galerix</i> sp.	<i>Galerix cf. symeonidis</i>	<i>Desmanodon aff. deamsi</i>	<i>Myosorex</i> sp.	<i>Heterosorex</i> sp.	<i>Soricella discrepans</i>	<i>Clapasorex alvarezae</i>	<i>Oligosorex thauensis</i>	<i>Oligosorex aff. thauensis</i>	Soricide gen. et sp. indet	N Species	Diversity
3	A	San Roque 4B	3	3,8%													
		San Roque 4A	16	1,5%												3	2,7
		Moratilla 1	21	1,7%												4	2,7
		Bañon 11	1	0,4%													
		Bañon 2	8	2,7%													
		Bañon 5	2	1,5%													
		Agreda	27	1,6%												2	1,9
		La Dahesa	1	0,9%													
2	Z	Ramblar 5	2	2,0%													
		Ramblar 7	24	3,2%												3	2,6
		Ramblar 3	28	2,3%												4	3,0
		Ramblar 4	3	0,8%	?												
		Valhondo 1	57	11,5%												4	3,3
		Ramblar 1	59	7,0%												7	4,9
		Navarrete	16	4,9%												3 (4)	2,7

Figure 6.- Stratigraphical distribution of the Ramblian insectivores of the Daroca-Calamocha area. The number of species and diversity index (1/Spi 2) have been given for the larger assemblages only. *Heterosorex* is listed for Navarrete on the basis of literature (ADROVER, 1972; 1975), but was not found in our samples.

Figura 6.- Distribución estratigráfica de los insectívoros del Ramblense del área de Daroca-Calamocha. Se muestran el número de especies y el índice de diversidad (1/Spi 2) sólo para los yacimientos más ricos. *Heterosorex* es incluido en función de la bibliografía (ADROVER, 1972, 1975), pero no ha sido encontrado en nuestras muestras.

presence of the faint transverse ridges between the end of the posterior arm of the protocone and the base of the metacone and the hypocone, respectively. This feature was not included in Ziegler's descriptions, but was already mentioned by DOBEN-FLORIN (1964).

*Soricella discrepans* is only found in the older assemblages of the sections, indicating that the species disappeared from the area. In contrast to *Clapasorex alvarezae*, this cannot be a true extinction, since the species continues into MN 4 in German localities.

*Soricid gen. et sp. indet.*

Localities: Bañon 5, Moratilla 1

Measurements: Bn 5: m1 = 1,34 x 0,84; Mor 1: m1 = 1,39 x 0,85.

#### DESCRIPTION

m1. The trigonid is longer and narrower than the talonid. The protoconid and metaconid stand close together. The paraconid stands at the end of a long and relatively straight paralophid. The oblique cristid ends close to the base of the protoconid. It is slightly notched before reaching the protoconid. The hypolophid runs behind the entoconid and connects to the lingual cingulum in the specimen from Bañon 5, against the posterolingual side of the entoconid in the specimen from Moratilla 1. The hypolophid and entoconid are well separated. A well-developed entocristid borders the talonid basin lingually.

The specimen from Bañon 5 shows a lingual cingulum only. The cingulum is strong along the trigonid valley, very weak along the entocristid. The

absence of other cingulums may be due to slight damage at the bottom of the crown. The specimen from Moratilla 1 shows a similar development of the lingual cingulum, with the exception that here the cingulum is lacking along the entocristid. In this specimen the anterior cingulum is well developed, but does not reach up to the paraconid area. The posterior cingulum is narrow and the labial cingulum is weak.

*Discussion:* The two m1 described above stand out because of their relatively large size. A remarkable morphological feature is the very strong lingual cingulum near the trigonid basin, and the weak development of the labial cingulum. Due to the scarcity of the material, and identification below the family level is not possible.

#### PALAEOECOLOGICAL REMARKS

The Ramblian faunas from the Daroca-Calamocha area are not particularly rich in insectivores (Fig. 6). The highest percentages are found in the older assemblages. Navarrete del Rio, Ramblar 1 and Valhondo 1 have yielded 4,9%, 7,0% and 11,5% respectively. In the other assemblages the percentage of insectivores is below 3%, with the exception of the assemblage of Ramblar 7 (3,2%).

In species richness also the older assemblages compare favourably to the younger ones. The highest number, seven species of insectivore, is found in Ramblar 1. Two faunal elements are known from this assemblage only, *Heterosorex* sp. and the mole *Myxomysale* sp. Although not present in our samples, *Heterosorex* was also reported from Navarrete del Rio by ADROVER (1972, 1975). Adding that to our faunal list would bring the number of insectivore species from this locality to four. A notable absentee in the fauna is the erinaceid *Galerix*. This genus is believed to have immigrated into Europe near the MN 2/MN 3 transition (VAN DEN HOEK OSTENDE, 2001c) and was thus not yet present at the time. This may also account for the lower percentage of insectivores in Navarrete relative to Ramblar 1 and Valhondo 1, as the niche for the larger insectivore remained unoccupied. Another absentee in the Navarrete del Rio assemblage is *Oligosorex thauensis*, which is found in most other localities. Apart from Ramblar 1, Navarrete is the only locality in our study that contains *Soricella discrpans*, which is believed to have disappeared from the area afterwards.

*Clapasorex alvarezae* too is a shrew found in the older localities only, but it continues longer than *Soricella* and is also found in Valhondo 1 and Ramblar 3. The latter two assemblages both contain four species of insectivore. The other three species are *Galerix remmerti*, *Desmanodon* aff. *daamsi* and *Oligosorex thauensis*. These are the lineages that continue through zone A, in which *O. thauensis* becomes *O. aff. thauensis*. Absence of one of these species in the younger faunas can usually be explained by insufficient sample size, with two exceptions. *Galerix* is missing from the assemblage of Agreda. Since the sample from this locality is suitably large (over 1000 M1/M2 of rodents were retrieved), this absence is believed to be real. *Galerix* is present in Moratilla 1, but is represented by another species than in the other localities. This very large species may also be present in Ramblar 4, where a single large D3 of *Galerix* was found. Moratilla 1 also contains a large soricid, which is otherwise only found in Bañón 5. A small M3 of *Galerix* in San Roque 4A may represent an early entry of this species, which is found in zones B-Da (VAN DEN HOEK OSTENDE & DOUKAS, in press). The stratigraphic occurrence of the various species of insectivore is summarised in Fig 6. The table also lists the number of insectivore M1M2, and the percentage of insectivore M1M2 calculated on the basis of the rodent M1M2. For the localities in which the number of insectivore M1M2 > 15 the number of species and the diversity of the insectivore assemblage is given, calculated as the reciprocal of the Simpson-index ( $1/p_i^2$ ; in which  $p_i$  is the proportion of various insectivore species).

In comparison to the known insectivore faunas from the same period, the absence of Dimylidae in the Spanish faunas is remarkable. Dimylidae are quite common in the lower Miocene of both southern Germany (MÜLLER, 1967; ZIEGLER, 1990a) and Anatolia (VAN DEN HOEK OSTENDE, 1995b), although they make up only a minor fraction of the insectivore assemblages of Stubersheim 3 and Keseköy. Another remarkable difference is the low diversity in talpids. Stubersheim 3 and Keseköy both have four mole species, whereas, with the exception of two *Myxomysale* molars in Ramblar 1, only one species is found in the Spanish Ramblian faunas.

At first sight, the insectivore assemblage of Stubersheim 3 with its eleven species of insectivores seems more diverse than the Spanish assemblages. However, the German assemblage is strongly domi-

nated by the shrews *Miosorex pussiliformes* and *Sorex discrepans*, and has a low diversity index ( $D_i = 2,5$ ). Unfortunately, we do not know the proportion taken by the insectivores in the total smaller mammal fauna, since the rodents from Stubersheim 3 have not yet been studied. The Anatolian MN 3 locality Keseköy has yielded nine insectivore species (VAN DEN HOEK OSTENDE, 2001c). It is rich in insectivores ( $> 25\%$ ), and has a higher diversity than Stubersheim 3 ( $D_i = 3,4$ ). The proportion of the insectivores found in Keseköy is much higher than in the Spanish locality, but this is not surprising since the Anatolian assemblage was collected in a lignite mine and local conditions there probably favoured insectivores. However, the diversity index is comparable to that of Valhondo 1 and even lower than that of Ramblar 1. Thus, the Spanish assemblages are not very rich in insectivores and have clearly less species than the known coeval insectivore assemblages. Nevertheless, particularly the assemblages from zone A are still pretty diverse and probably represent a palaeoenvironment well suitable for insectivores.

Generally, a suitable environment for insectivores is considered to be fairly humid. The litter layers of forests provide, with its fauna of detritus feeders, a good food source for insectivores. Since the percentages, species richness and diversity of insectivores drop in zone A, it would on the basis of our results be considered to represent a dryer period than zone Z. This is direct contradiction to the findings of DAAMS & VAN DER MEULEN (1984) and VAN DER MEULEN & DAAMS (1992), who consider zone A "definitely more humid than Zones Z and B". Their arguments are threefold:

1. Zone A shows a peak in Eomyidae, which are generally considered to be forest-dwellers.
2. The percentages of hypodont Myomiminae (*Praearmatomys*/*Armantomys*), which are believed to represent a dry environment, peak in zones Z and B and are low in zones A and C.
3. Agreda (Zone A) is the only locality that contains a beaver.

Looking in closer detail, the contradiction between the ecological signal of the insectivores and the rodents becomes even worse. On the basis of the presence of the beaver, Agreda should be considered to

represent one of the wettest localities in the succession. However, as far as insectivores are concerned it has the lowest number of species, the lowest percentage and the lowest diversity. The total absence of *Galerix* in this well-sampled locality is remarkable. This might be taken as an indication that *Galerix remmerti* is a relatively dry element in the fauna. Although recent Galericinae prefer moist environments and may even be semi-aquatic, some species of *Galerix* are known to occur in localities that represent a dry environment (ZIEGLER, 1983; LUIS & HERNANDO, 2000). Considering *Galerix* a dry faunal element would, however, only partly solve the conflicting signal of insectivores and rodents. An overall analysis of the entire faunas might help to resolve the issue, but for now we have no explanation for this contradiction.

The assemblage from Moratilla 1 stands out by having a different species of *Galerix* and having a different species of soricid than commonly found in the other assemblages. Probably this is the result of an unknown local change in the environment. Over 25% of the rodent fauna from this locality consists of *Ligerimys freudenthalii*, an eomyid that is not found in any of the other localities.

#### ACKNOWLEDGEMENTS

The study of the Ramblian Spanish insectivores was suggested to me by the late Remmert DAAMS over ten years ago. He offered me the insectivore material of the Daroca-Calamocha area in the collections of the Museo Nacional de Ciencias Naturales, Madrid for study. At the same time Thijs FREUDENTHAL offered me the material from that same area in the National Museum of Natural History on loan. Both showed great patience with me, as the publication of articles for my PhD took priority over the study of the Spanish material, as did Marian ÁLVAREZ SIERRA, who continued the loan after Remmert's demise. All in all, the publication of the Spanish insectivores is long overdue. It is with pleasure that I dedicate this paper to Remmert DAAMS, mingled with sadness that he never saw the paper he initiated.

The SEM photographs were made by Jeroen GOUD of the National Museum of Natural History, Leiden. Niko Korenhof assembled the plates. Georgia HODGSON suggested some linguistic improvements, and Thijs FREUDENTHAL translated the summary in Spanish. As referees Jelle REUMER and

Marian ÁLVAREZ SIERRA scrutinised the paper. The help of all these colleagues is gratefully acknowledged.

## REFERENCES

- ADROVER, R., 1972. Yacimiento de micromamíferos en Navarrete del Rio (provincia de Teruel, España) (Nota preliminar). *Acta Geologica Hispanica*, **7**: 176-177.
- ADROVER, R. 1975. Principales yacimientos paleomastológicos de la provincia de Teruel y su posición estratigráfica relativa. In: A. M. TERESA & A. E. AGUIRRE *Actas I Coloquio internacional sobre bioestratigrafía continental del Neogeno superior y Cuaternario inferior. Trabajos Neogenos-Cuaternario*. **4**: 31-48
- ÁLVAREZ SIERRA, M.A. 1987. Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior español. *Scripta Geologica*, **86**: 1-207.
- BAUDELOT, S & A. COLLIER, 1982 Les faunes de mammifères du Haut-Armagnac (Gers, France); les Gliridés (Mammalia, Rodentia). *Géobios*, **15, 5**: 705-727.
- BULOT, C., 1980. Découverte de nouveaux Rongeurs dans le gisement d'Estrepouy (Gers). *Bulletin du Muséum National d'Histoire Naturelle. C: Sciences de la Terre: Paleontologie, Géologie, Mineralogie*, **2, 4**: 397-406.
- CROCHET, J.-Y., 1975. Diversité des Insectivores Soricidés du Miocène inférieur de France. *Colloque international C.N.R.S.*, **218**: 631-652.
- CROCHET, J.-Y., 1995. Le Gorouillas et les sites contemporains (Oligocène, MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertébrés. 4. Marsupiaux et insectivores. *Palaeontographica A*, **236**: 39-75.
- CUENCA, G., 1988. Revisión de los Sciuridae del Aragonense y del Ramblense en la fosa de Calatayud-Montalbán. *Scripta Geologica* **87** 1-116.
- DAAMS, R., 1985. Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain). *Scripta Geologica*, **77**: 1-20.
- DAAMS, R., 1989. Miscellaneous Gliridae from the Miocene of the Calatayud-Teruel Basin, Aragón, Spain. *Scripta Geologica*, **89**: 13-26.
- DAAMS, R., 1990. Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and the Oligocene-Miocene boundary interval of Spain. *Scripta Geologica*, **95**: 1-62.
- DAAMS, R., M. FREUDENTHAL & M.A. ÁLVAREZ, 1987. Ramblian; a new stage for continental deposits of early miocene age. *Geologie en Mijnbouw* **65**: 297-308.
- DAAMS, R., M. FREUDENTHAL & A. VAN DE WEERD, 1977. Aragonian, a new stage for continental deposits of Miocene age. *Newsletter of Stratigraphy*, **6, 1**: 42-55.
- DAAMS, R. & A.J. VAN DER MEULEN, 1984. Palaeoenvironmental and palaeoclimatic interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of north central Spain. *Palaeobiologie Continental*, **14**: 241-257.
- DE BRUIJN, H., V. FAHLBUSH, G. SARAÇ & E. ÜNAY, 1993. Early Miocene rodent faunas from the eastern Mediterranean area. Part III The genera *Deperetomys* and *Cricetodon* with a discussion of the evolutionary history of the Cricetodontini. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **96, 2**: 151-216.
- DE BRUIJN, H. & G. SARAÇ, 1991. Early Miocene faunas from the eastern Mediterranean area. Part I The genus *Eumyarion*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **94, 1**: 1-36.
- DE BRUIJN, H. & G. SARAÇ, 1992. Early Miocene rodent faunas from the eastern Mediterranean area. Part II *Mirabella*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **95, 1**: 25-40.
- DE BRUIJN, H., E. ÜNAY, L.W. VAN DEN HOEK OSTENDE & G. SARAÇ, 1992. A new association of small mammals from the lowermost Lower Miocene of Central Anatolia. *Géobios* **25, 5**: 651 - 670.
- DE JONG, F., 1988. Insectivora from the Upper Aragonian and Lower Vallesian of the Daroca-Villafeliche area in the Calatayud-Teruel Basin (Spain). In: M. FREUDENTHAL (ed.) *Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain)*. *Scripta Geologica, Special Issue*, **1**: 253-285.
- DOBEN-FLORIN, U., 1964. Die Spitzmäuse aus dem Alt-Burdigali von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, N.F.*, **117**: 1-82.
- DOUKAS, C., 1986. The mammals of the Lower Miocene of Aliveri (Island of Evia, Greece). Part 5. The insectivores. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **B 89, 1**: 15-38.
- ENGESSER, B., 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen*, **102**: 37-363.
- FAHLBUSCH, V., 1970. Populationsverschiebungen bei tertiären Nagetieren, eine Studie an oligozänen und miozänen Eomyidae Europas. *Abhandlungen Bayerische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, N.F.*, **145**: 1-136.
- FAHLBUSCH, V., 1989. European Neogen rodent assemblages in response to evolutionary, biogeographic, and ecologic factors. In: C.C. BLACK & M.R. DAWSON (eds.) *Papers on Fossil Rodents in honor of Albert Elmer Wood. National History Museum Los Angeles County, Science Series*, **33**: 129-138.
- HRUBESCH, K., 1957. Zahnstudien an tertiären Rodentia als Beitrag zu deren Stammesgeschichte. Über die Evolution der Melissiodontidae, eine Revision der Gattung *Melissiodon*. *Abhandlungen Bayerische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, N.F.*, **83**: 1-101.

- HUGUENEY, M., 1974. Gisements de petits mammifères (tertiaires) dans la région de Saint-Gerand-le-Puy *Revue Scientifique du Bourbonnais et du Centre de la France*, **1974**: 52-68.
- HUGUENEY, M. & ADROVER, R. Este Volumen. *Tetracus daamsi*, une nouvelle espèce de Galericinae (Erinaceidae, Mammalia) dans l'Oligocène de Majorque (Espagne). *Coloquios de Paleontología*.
- LÓPEZ MARTINEZ, N., 1984. Los lagomorfos (Mammalia) de la sucesión del Mioceno inferior de Calamocha (prov. de Teruel). *Coloquios de Paleontología*, **39**: 27-44.
- LUIS, A. & J.M. HERNANDO, 2000. Los microvertebrados del Mioceno Medio de Somosaguas Sur (Pozuelo de Alarcón, Madrid, España). *Coloquios de Paleontología*, **51**: 87-136.
- MAYR, H., 1979. Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. *Thesis University München*, 1-420.
- MEIN, P. & E. MARTIN-SUAREZ, 1994. *Galerix iberica* sp. nov. (Erinaceidae, Insectivora, Mammalia) from the late Miocene and early Pliocene of the Iberian Peninsula. *Geobios*, **26**, 6: 723-730.
- MÜLLER, A., 1967. Die Geschichte der Familie Dimylidae (Insectivora, Mammalia) auf Grund der Funde aus der terciären Spaltenfüllungen Süddeutschlands. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, N. F.*, **129**: 1-93.
- REUMER, J.W.F., 1984. Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (the Netherlands) and Hungary. *Scripta Geologica*, **73**: 1-173.
- RÜMKE, C.G., 1985. A review of fossil and recent Desmaninae (Talpidae, Insectivora). *Utrecht Micropalaeontological Bulletin, special publication* **4**: 1-241.
- SESÉ, C. 1987. *Eucricetodon* and *Melissiodon* (Cricetidae, Rodentia) from the Ramblian and Lower Aragonian of the Calamocha area (Calatayud-Teruel Basin, Spain). *Scripta Geologica* **83**: 1-17.
- THEOCHAROPOULOS, C., 2000. Late Oligocene-Middle Miocene Democricetodon and Spanocricetodon from the eastern Mediterranean area. *Gaia*, **8**: 1-90.
- ÜNAY, E., 1994. Early Miocene rodent faunas from the eastern Mediterranean area. Part V. The Gliridae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **97**, 4: 445-490.
- ÜNAY, E., 1996. On fossil Spalacidae (Rodentia). In: R. BERNOR, V. FAHLBUSH & H.-W. MITTMANN (eds.). *The Evolution of Western Eurasian Neogene Mammal Faunas*, Columbia University Press: 246-252.
- VAN DEN HOEK OSTENDE, L.W., 1989. The Talpidae (Insectivora, Mammalia) of Eggingen-Mittelhart (Baden-Württemberg, F.R.G.) with special reference to the *Paratalpa-Desmanodon* lineage. *Stuttgarter Beiträge zur Naturkunde, B.*, **152**: 1-29.
- VAN DEN HOEK OSTENDE, L.W., 1992. Insectivore faunas of the Lower Miocene of Anatolia. Part 1: Erinaceidae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **94**, 4: 437-467.
- VAN DEN HOEK OSTENDE, L.W., 1995a. Insectivore faunas from the Lower Miocene of Anatolia. Part 2: *Dinosorex* (Heterosoricidae). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **98**, 1: 1-18.
- VAN DEN HOEK OSTENDE, L.W., 1995b. Insectivore faunas from the Lower Miocene of Anatolia. Part 3: Dimylidae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **98**, 1: 19-38.
- VAN DEN HOEK OSTENDE, L.W., 1997. Insectivore faunas from the Lower Miocene of Anatolia. Part 4: The genus *Desmanodon* (Talpidae) with the description of a new species from the Lower Miocene of Spain. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **100**, 1/2: 27-65.
- VAN DEN HOEK OSTENDE, L.W., 2001a. Insectivore faunas from the Lower Miocene of Anatolia -- Part 5: Talpidae. *Scripta Geologica*, **122**: 1-45.
- VAN DEN HOEK OSTENDE, L.W., 2001b. Insectivore faunas from the Lower Miocene of Anatolia -- Part 6: Crocidosoricinae (Soricidae). *Scripta Geologica*, **122**: 47-81
- VAN DEN HOEK OSTENDE, L.W., 2001c. Insectivore faunas of the Lower Miocene of Anatolia. Part 8: Stratigraphy, palaeoecology, palaeobiogeography. *Scripta Geologica*, **122**: 101-122.
- VAN DEN HOEK OSTENDE, L.W., 2001d. A revised generic classification of the Galericini (Insectivora, Mammalia) with some remarks on their palaeobiogeography and phylogeny. *Geobios* **34**, 6: 681-695.
- VAN DEN HOEK OSTENDE, L.W. VAN DEN & C.D. DOUKAS, in press. The distribution of *Galerix symeonidis* Doukas, 1986. *Proceedings "Distribution and Migration of Tertiary Mammals in Eurasia"* Utrecht, 17-19 May, 2001. Deinsea
- VAN DER MEULEN, A.J. & R. DAAMS, 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**: 227-253.
- WU, W., 1993. Neue Gliridae (Rodentia, Mammalia) aus untermiozänen (orleanischen) Spaltenfüllungen Süddeutschlands. *Documenta Naturae*, **81**: 1-149.
- ZIEGLER, R., 1983. Odontologische und osteologische Untersuchungen an *Galerix exilis* (Blainville)(Mammalia, Erinaceidae) aus dem miozänen Ablagerungen von Steinberg und Goldberg im Nördlinger Ries (Süddeutschland). *Dissertation Universität München*: 1-244
- ZIEGLER, R., 1985. Talpiden (Mammalia, Insectivora) aus dem Orleanium und Asterium Bayerns. *Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie*, **25**: 131-175.
- ZIEGLER, R., 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozän und Untertermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde, B.*, **152**: 1-73.
- ZIEGLER, R., 1990a. Didelphidae, Erinaceidae, Metacondontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untertermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde, B.*, **158**, 1-99.

ZIEGLER, R., 1990b. Talpidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde, B.*, **167**: 1-81.

ZIEGLER, R., 1994. Bisher übersehene Insectivora (Mammalia) aus dem Untermiozän von Winterhof-West bei Eichstätt (Bayern). *Mitteilungen der Bayerische Staatsammlung für Paläontologie und historische Geologie*, **34**: 291-306.