Insectivora from the Upper Aragonian and the Lower Vallesian of the Daroca-Villafeliche area in the Calatayud-Teruel Basin (Spain)

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In this study the insectivores from the Upper Aragonian and the Lower Vallesian of the Daroca-Villafeliche area in the Calatayud-Teruel Basin (Spain) are described and compared with related insectivore species from other European localities.
The paleoecological significance of the insectivores is evaluated. The species described are: *Galerix exilis, Galerix socialis, Desmanella crusafonti, Miosorex grivensis,* and *Crusafontina endemica.* An attempt is made to separate *G. exilis* from *G. socialis* on the basis of size and morphology.

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Introduction

The teeth have been measured by means of a Leitz Orthoplan Microscope (ocular 8 ×, objective 4 ×) with mechanical stage and measuring-clocks. All measurements are in 1 mm units. Photographs have been taken by means of an JEOL 35c (25 kv) scanning electron microscope.

The material is listed and stored at the Rijksmuseum van Geologie en Mineralogie, Leiden (catalogue numbers RGM 334 415 – 335 582).

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Systematic descriptions

Family Erinaceidae Bonaparte, 1838
Subfamily Echinosoricinae Cabrera, 1925
Tribe Galericini Pomel, 1848

Galerix Pomel, 1848

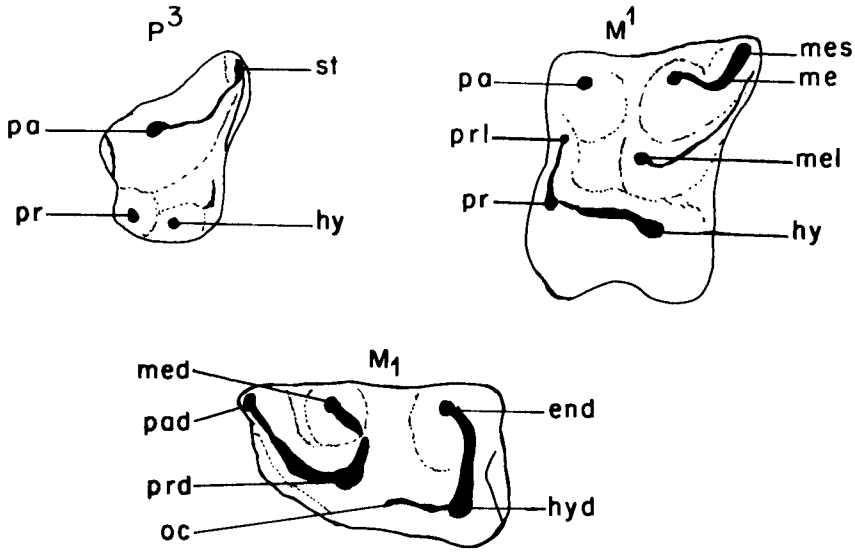
Introduction — De Blainville (1840) described a small hedgehog-like mammal (Erinaceidae) from Sansan under the name *Viverra exilis*. Pomel (1848) introduced the genus name *Galerix* for the hedgehog-like mammals from Sansan. According to Pomel, de Blainville's determination was inadequate. On the basis of the same material, Pomel described it as *Galerix viverroides*. Von Meyer (1865) described a similar form from Steinheim (Germany) as *Parasorex socialis*. Filhol (1891) described the galericid from Sansan as *Galerix exilis*. He synonymized *Parasorex socialis* von Meyer, 1865 from Steinheim with *G. exilis*, the latter one prevailing. From La Grive (France) Gaillard (1929) described two galericid species: *Galerix exilis* and *Pseudogalerix stehlini*. Viret (1938) confirms the conclusions of Gaillard (1929). Baudelot (1972) described two hedgehog-like mammals from Sansan: *Pseudogalerix exilis* and *Galerix sudrae*.

Engesser (1972) compared the two species (*Pseudogalerix stehlini* and *Galerix exilis*) from Sansan recognized by Gaillard (1929) and Viret (1938). *Pseudogalerix* was supposed to be characterized by the P^3 having one lingual cusp, by the high and sharp P_4 and by the connection between the protocone and the protoconule in M^2. However, according to Engesser (1972) these features are present in *G. exilis* as well. In spite of size differences between the two supposed species, he recognizes only one (*G. exilis*).

Baudelot (1972) mentions two species from La Grive: *Pseudogalerix stehlini* and *Galerix* sp., the latter species being the one referred to as *G. exilis* by Gaillard (1929) and Viret (1938). Engesser's (1972) opinion is not in agreement with that of Baudelot (1972): he refers *Galerix* sp. and *Pseudogalerix stehlini* in Baudelot (1972) to *Galerix socialis* and *Galerix exilis*, respectively.

Ziegler (1983) agrees with Engesser (1972) on the assignment of the species from Sansan and Steinheim (Table 1), but he disagrees on that of La Grive. *G. socialis* in Engesser (1972) is assigned to *G. exilis*; and *G. exilis* in Engesser (1972) to *G. stehlini*.

In the Upper Aragonian and Lower Vallesian of the Daroca-Villafeliche area two *Galerix* species (*G. socialis* and *G. exilis*) are recognized, following the concepts of Engesser (1972). The differences are summarized below:



hy = hypocone
me = metacone
mel = metaconule
mes = metastyle
pa = paracone
pr = protocone
prl = protoconule
st = style
end = entoconid
hyd = hypoconid
med = metaconid
oc = oblique cristid
pad = paraconid
prd = protoconid

Fig. 1. Nomenclature used for parts of the erinaceid cheek teeth (after Ziegler, 1983).

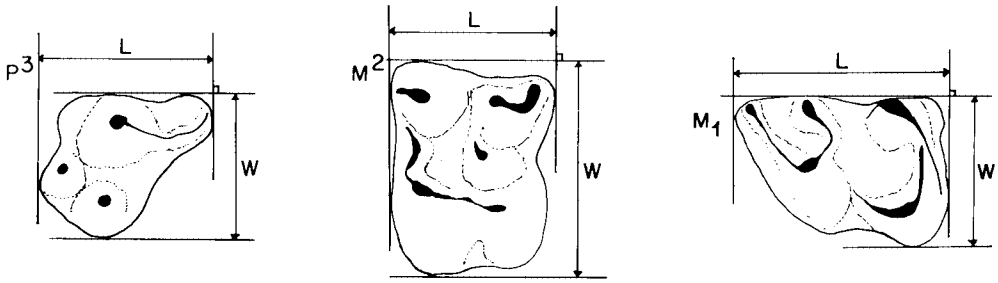


Fig. 2. Method of measuring the teeth in *Galerix* species.

G. exilis

The P_3 is shorter than the P_2. In our material this is only evident in monospecific samples. In heterogeneous associations this can only be discerned when the teeth are in the mandible.

The P_4 is high and canine-shaped. The protoconid is high and sharp.

The paraconid is well individualized and a small valley separates it from the protoconid.

The P^3 has one lingual cusp.

In M^2 the protocone is connected to the metaconule, and in M^1 this connection is generally present as well.

Table 1. Survey of the history of the nomenclature of the *Galerix* species from Sansan, Steinheim, and La Grive.

Author	Locality Sansan	Steinheim	La Grive
de Blainville, 1840	*Viverra exilis*		
Pomel, 1848	*Galerix viverroides*		
von Meyer, 1865		*Parasorex socialis*	
Filhol, 1891	*Galerix exilis*	*Galerix exilis*	
Gaillard, 1929	*Galerix exilis*	*Galerix exilis*	*Pseudogalerix stehlini* *Galerix exilis*
Viret, 1938			*Pseudogalerix stehlini* *Galerix exilis*
Baudelot, 1972	*Pseudogalerix exilis* *Galerix sudrae*	*Pseudogalerix* sp. *Galerix* sp.	*Pseudogalerix stehlini* *Galerix* sp.
Engesser, 1972	*Galerix exilis*	*Galerix socialis*	*Galerix exilis* *Galerix socialis*
Ziegler, 1983	*Galerix exilis*	*Galerix socialis*	*Galerix stehlini* *Galerix exilis*

The distal branch of the metacone of M^1 and M^2 ends at the base of the metacone.
M^1 and M^2 have a quadratic outline.
In localities where both species are present the specimens of *G. exilis* are larger than those of *G. socialis*.

G. socialis
The P_3 is longer than the P_2.
The P_4 has a well-developed trigonid and the protoconid is relatively low and blunt (as compared with *G. exilis*).
The paraconid is connected to the protoconid by a narrow ridge.
The P^3 has two lingual cusps.
There is a ridge between protocone and hypocone. A valley separates the metaconule from the protocone and the hypocone.
The distal branch of the metacone of M^1 and M^2 ends labially at the base of the metastyle.
M^1 and M^2 are generally longer than wide.
In localities where both species are present the specimens of *G. socialis* are smaller than those of *G. exilis*.

Ziegler (1983) too compared *G. exilis* with *G. socialis*, but his results are different from ours, except for the above mentioned differences in P_4 and P^3. According to this author the paralophid of the lower molars is higher and better individualized in *G. socialis* than it is in *G. exilis*. In our Spanish material this differential feature is not present. Ziegler (1983) also mentions that the P_3 is longer than the P_2 in *G. socialis*, and that this would be the reverse in *G. exilis*. In the Spanish *Galerix* material this is only evident when the premolars are still in mandible. Due to a considerable size overlap, isolated P_2 and P_3 cannot be separated on this basis. A third differential feature mentioned by Ziegler (1983), is the distal branch of the metaconule of M^1 and M^2. In *G. socialis* this branch would be absent. In our Spanish material the distal branch of the metaconule is present in *G. socialis*, and it is absent in *G. exilis*. However, the figures in Ziegler (1983, p. 136) do not correspond to the mentioned difference.

Galerix socialis (H. von Meyer, 1865) and
Galerix exilis (de Blainville, 1839)
Pl. 1; Pl. 2, figs. 1-6; Pl. 3, figs. 1-4.

Localities — All localities in this study.

Measurements — See Tables 2-17.

Description

P_1 — The first premolar has an extended oval shape. The labial side is straight or slightly concave and lingually it has a rounded outline. The morphology of the P_1 is dominated by the protoconid. The protoconid is anteriorly connected to a small stylid by a low ridge. In lingual view the protoconid is triangular and its posterior border is straight or slightly concave. At the postero-lingual side there is a small conical to ridge-shaped cusp. The P_1 has one oval-shaped root.

P_2 — The P_2 is less wide than the P_3 and it is also shorter. The anterior and posterior borders are rounded, the labial and lingual sides are straight. The dominant part of the premolar is the canine-like protocone, situated somewhat anteriorly. Posteriorly the protocone is straight or concave, anteriorly it is slightly convex. The posterior base is lower than the anterior one. On each of these bases there is a low stylid near the lingual border of the tooth. In some specimens the posterior stylid is connected to the base of the protoconid by a low and rounded ridge. Generally there is much variation of size (Table 2) and morphology. The P_2 has two parallel roots. Both are situated straight under the crown.

P_3 — This element shows much morphological variation. In occlusal view the shape of the P_3 varies between triangular, oval and square. The rather cone-shaped protoconid is situated centrally. Anteriorly and posteriorly there are stylids which are situated somewhat above the base, in most specimens. There is much variation in the shape of the stylids. In some cases they are weakly developed, or they are nearly absent. In most specimens, however, the anterior stylid has a cusp-like shape and it is situated lingually, whereas the posterior stylid is ridge-shaped. This ridge is connected to the base of the protoconid by a small ridge. In the P_3 two parallel roots are present. Besides the morphological variation there is much size variation too (Table 3).

P_4 — The predominant feature of this premolar is the high and sharp protoconid. The talonid is small, and in some specimens it is strongly reduced. The trigonid is rather large. It consists of the anteriorly concave protoconid, the metaconid, and the paraconid. In lateral view the metaconid is situated halfway the protoconid. The paraconid is a well-individualized cusp, in some cases connected to the protoconid by a low ridge, which runs along the labial border. The trigonid is lingually open. The talonid has a transverse ridge along the posterior border. This ridge is higher at the lingual side. The P_4 is two-rooted.

M_1 — In the first lower molar the talonid is slightly wider than the trigonid, and they are of equal length. The protoconid and the metaconid are of similar size and they are the highest cusps. The protoconid is pyramidal and one rib is part of the V-shaped ridge that connects the protoconid to the conical metaconid. The protoconid is connected by a ridge to the well-developed, slightly convex, paralophid. The paraconid is a low cusp of about the same height as the pyramidal entoconid. The entoconid is connected to the base of the metaconid by a very narrow ridge. The hypoconid is the lowest cusp. There is a weak oblique cristid, ending labially at the internal base of the protoconid. The talonid

Table 2. Measurements of the P_2 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	3	1.05	1.16	1.24	3	0.66	0.66	0.66	s
Carrilanga 1	7	1.24	1.34	1.45	7	0.66	0.71	0.87	e,s
Solera	4	1.40	1.52	1.64	4	0.82	0.85	0.89	e
Las Planas 5H	1	—	1.53	—	1	—	0.77	—	e
Toril	3	1.47	1.55	1.74	3	0.75	0.83	0.93	e
Villafeliche 9	1	—	1.83	—	1	—	0.97	—	e
Valalto 2C	2	1.57	1.57	1.57	2	0.98	0.99	0.99	e

Table 3. Measurements of the P_3 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	22	1.50	1.52	1.53	3	0.86	0.90	0.95	s
Carrilanga 1	25	1.70	1.82	1.98	25	0.82	1.04	1.17	e,s
Solera	14	1.40	1.56	1.78	17	0.86	0.97	1.07	e
Las Planas 5H	1	—	1.38	—	1	—	0.96	—	e
Toril	3	1.48	1.57	1.66	3	0.83	0.89	0.97	e
Valalto 2C	1	—	1.57	—	1	—	0.98	—	e

Table 4. Measurements of the P_4 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	4	1.81	1.85	1.90	4	1.20	1.26	1.30	s
Carrilanga 1	23	1.86	2.04	2.20	23	1.22	1.33	1.45	e,s
Solera	6	2.11	2.19	2.25	9	1.21	1.31	1.39	e
Las Planas 5H	1	—	2.26	—	1	—	1.35	—	e
Toril	1	—	2.19	—	3	1.24	1.26	1.29	e
Borjas	3	2.07	2.13	2.16	3	1.11	1.18	1.27	e
Valalto 2C	1	—	2.13	—	1	—	1.20	—	e

Table 5. Measurements of the M_1 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	1	—	2.99	—	1	—	1.82	—	s
Carrilanga 1	31	2.74	2.93	3.19	36	1.48	1.82	1.98	e,s
Solera	5	2.87	3.06	3.23	7	1.76	1.82	2.04	e
Toril	5	2.41	2.66	2.99	9	1.57	1.76	1.99	e
Villafeliche 9	1	—	3.08	—	1	—	1.77	—	e
Borjas	2	2.90	2.90	2.90	4	1.69	1.79	1.85	e
Valalto 2C	1	—	3.09	—	6	1.75	1.90	2.27	e

Table 6. Measurements of the M_2 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	3	2.43	2.56	2.68	7	1.64	1.75	1.93	s
Carrilanga 1	34	2.15	2.41	2.57	33	1.51	1.68	1.86	e,s
Solera	14	2.44	2.54	2.66	16	1.44	1.66	1.81	e
Las Planas 5H	1	—	2.48	—	1	—	1.56	—	e
Toril	2	2.39	2.43	2.46	9	1.45	1.56	1.69	e
Villafeliche 9	2	2.37	2.40	2.42	2	1.59	1.64	1.69	e
Borjas	3	2.31	2.38	2.46	3	1.39	1.51	1.57	e
Las Planas 5B	1	—	2.61	—	1	—	1.71	—	e
Valalto 2C	2	2.60	2.63	2.65	7	1.57	1.69	1.83	e

Table 7. Measurements of the M_3 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	1	—	2.00	—	1	—	1.20	—	s
Carrilanga 1	28	1.77	1.96	2.26	28	0.87	1.05	1.32	e,s
Solera	10	1.91	2.02	2.07	11	0.95	1.05	1.20	e
Las Planas 5H	2	2.00	2.04	2.07	2	0.95	0.95	0.95	e
Toril	7	1.89	2.01	2.05	7	1.03	1.07	1.09	e
Las Planas 5K	2	1.83	1.90	1.96	2	0.97	.98	0.99	e
Borjas	2	1.89	1.89	1.89	2	0.96	0.96	0.96	e
Valalto 2C	2	2.08	2.11	2.14	4	1.07	1.12	1.18	e

Table 8. Measurements of the P^2 of *G. exilis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Toril	1	—	1.15	—	1	—	1.93	—

Table 9. Measurements of the P^3 of *G. exilis* and *G. socialis*.
e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	3	1.95	2.06	2.12	4	1.56	1.79	2.09	s
Carrilanga 1	27	1.65	2.01	2.25	29	1.51	1.81	2.06	e,s
Carrilanga 1	4	1.67	1.77	1.84	4	1.41	1.46	1.54	e
Solera	8	1.90	2.04	2.31	9	1.31	1.47	1.55	e
Toril	5	1.63	1.80	1.86	5	1.29	1.38	1.46	e
Alcocer 2	1	—	1.79	—	1	—	1.31	—	e
Villafeliche 9	1	—	1.95	—	1	—	1.38	—	e
Las Planas 5B	2	2.08	2.13	2.17	2	1.48	1.51	1.53	e
Valalto 2C	6	1.68	1.97	2.26	6	1.25	1.52	1.68	e

Table 10. measurements of the P^4 of *G. exilis* and *G. socialis*. e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	1	—	2.55	—	1	—	2.25	—	s
Carrilanga 1	47	1.80	2.61	2.96	49	1.98	2.35	2.69	e,s
Solera	2	2.52	2.56	2.59	2	2.78	2.82	2.86	e
Villafeliche 9	2	1.81	1.94	2.07	3	2.44	2.51	2.56	e
Borjas	1	—	2.44	—	1	—	2.46	—	e
Valalto 2C	1	—	3.20	—	1	—	2.74	—	e

Table 11. Measurements of the M^1 of *G. exilis* and *G. socialis*. e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	3	1.92	2.04	2.13	2	2.74	2.77	2.80	s
Carrilanga 1	23	2.10	2.33	2.60	24	2.78	3.02	3.19	e,s
Carrilanga 1	7	2.11	2.44	2.62	7	2.94	3.14	3.41	e
Solera	6	2.28	2.61	2.85	5	2.96	3.25	3.52	e
Toril	6	2.43	2.50	2.60	7	3.24	3.29	3.38	e
Villafeliche 9	3	2.44	2.51	2.56	3	3.15	3.27	3.38	e
Borjas	1	—	2.57	—	2	2.93	3.25	3.57	e
Las Planas 5B	2	2.11	2.24	2.37	2	2.79	2.86	2.96	e
Valalto 2C	3	2.48	2.61	2.87	1	—	3.38	—	e

Table 12. Measurements of the M^2 of *G. exilis* and *G. socialis*. e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	3	2.01	2.08	2.22	1	—	2.85	—	s
Carrilanga 1	35	1.83	1.98	2.21	39	2.23	2.66	2.87	e,s
Carrilanga 1	9	1.82	2.03	2.30	9	2.41	2.74	2.93	e
Solera	15	1.99	2.19	2.37	15	2.64	2.85	3.01	e
Las Planas 5H	1	—	2.12	—	1	—	2.91	—	e
Toril	13	1.86	2.06	2.25	14	2.27	2.68	2.86	e
Villafeliche 9	2	2.05	2.14	2.23	2	2.99	3.13	3.27	e
Borjas	5	2.01	2.13	2.22	4	2.63	2.78	2.90	e
Valalto 2C	5	1.99	2.08	2.14	4	2.60	2.79	2.90	e

Table 13. Measurements of the M^3 of *G. exilis* and *G. socialis*. e = *G. exilis*, s = *G. socialis*

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.	Sp.
Pedregueras 2A	5	1.16	1.26	1.42	4	1.76	1.90	2.06	s
Carrilanga 1	24	1.16	1.24	1.33	25	1.76	1.88	2.00	e,s
Solera	17	1.15	1.35	1.50	16	1.72	2.00	2.22	e
Las Planas 5H	1	—	1.23	—	1	—	1.88	—	e
Toril	10	1.12	1.28	1.42	9	1.59	1.88	2.06	e
Alcocer 2	1	—	1.16	—	1	—	1.77	—	e
Villafeliche 9	3	1.05	1.15	1.24	3	1.78	1.83	1.91	e
Borjas	3	1.27	1.31	1.39	3	1.76	1.88	2.07	e
Las Planas 5B	2	1.13	1.16	1.19	2	1.75	1.86	1.97	e
Valalto 2C	7	1.25	1.31	1.38	6	1.62	1.90	2.05	e

Table 14. Measurements of the M^1 of intermediate form 1.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Carrilanga 1	1	—	2.62	—	1	—	3.41	—
Solera	1	—	2.58	—	1	—	3.26	—

Table 15. Measurements of the M^1 of intermediate form 2.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Carrilanga 1	2	2.47	2.53	2.59	2	2.94	3.08	3.22

Table 16. Measurements of the M^2 of intermediate form 1.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Carrilanga 1	5	1.90	2.02	2.14	5	2.52	2.69	2.82

Table 17. Measurements of the M^2 of intermediate form 2.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Carrilanga 1	3	1.96	2.07	2.17	3	2.68	2.79	2.92
Solera	1	—	2.16	—	1	—	2.71	—
Toril	1	—	2.17	—	1	—	2.93	—

basin is closed, the trigonid is open lingually. A moderately developed cingulum runs along the base of the paralophid. A cingulum is situated along the bases of the protoconid and the hypoconid. A cingulum is situated in the middle of the anterior side, parallel to the base of the crown. There are two parallel roots, somewhat inclined posteriorly with respect to the crown.

M_2 — The talonid and the trigonid are of equal size. The metaconid is the highest cusp. The protoconid and the entoconid are of equal height, but they are lower than the metaconid. The paraconid and the hypoconid are of equal height. The paraconid is not individualized. The shape of the trigonid is similar to that of the first lower molar except for the paralophid and the paraconid, which have a concave labial and anterior border in the M_2. The talonid is similar to that of the M_1. The oblique cristid is situated slightly more lingually. As in the first lower molar the talonid is closed and the trigonid is open lingually. The anterior and labial cingulums are similar to those in the M_1. The shape of the posterior cingulum is similar too, but its position is somewhat more labial in the M_2. Both shape and position of the roots in the M_2 are similar to those of the M_1.

M_3 — The talonid is shorter and narrower than the trigonid. The metaconid is the highest cusp. The protoconid and the entoconid are of equal height, but they are lower than the metaconid. The paraconid and the hypoconid are the smallest cusps. The paraconid is weakly individualized. The trigonid is similar to that of the M_2. The talonid only differs from the talonid of M_2 by the position of the hypoconid, which is situated

slightly more anteriorly in the M_3. The labial and posterior cingulums are absent. The anterior cingulum is similar to that in the M_2. The shape and the position of the roots are the same as in the other two molars.

P^3 (*G. exilis*) — The P^3 mainly consists of the high and conical paracone. From the top of the paracone a sharp style runs to the posterior base. The length and width of the style are variable. The anterior part of the paracone is steep. The shape of the protocone varies between blunt and conical to sharp and oval. In some specimens there is a cingulum along the anterior border, running from the protocone base to the paracone base. The labial border is straight or, occasionally, slightly curved. The P^3 is three-rooted: two labial roots and one lingual root.

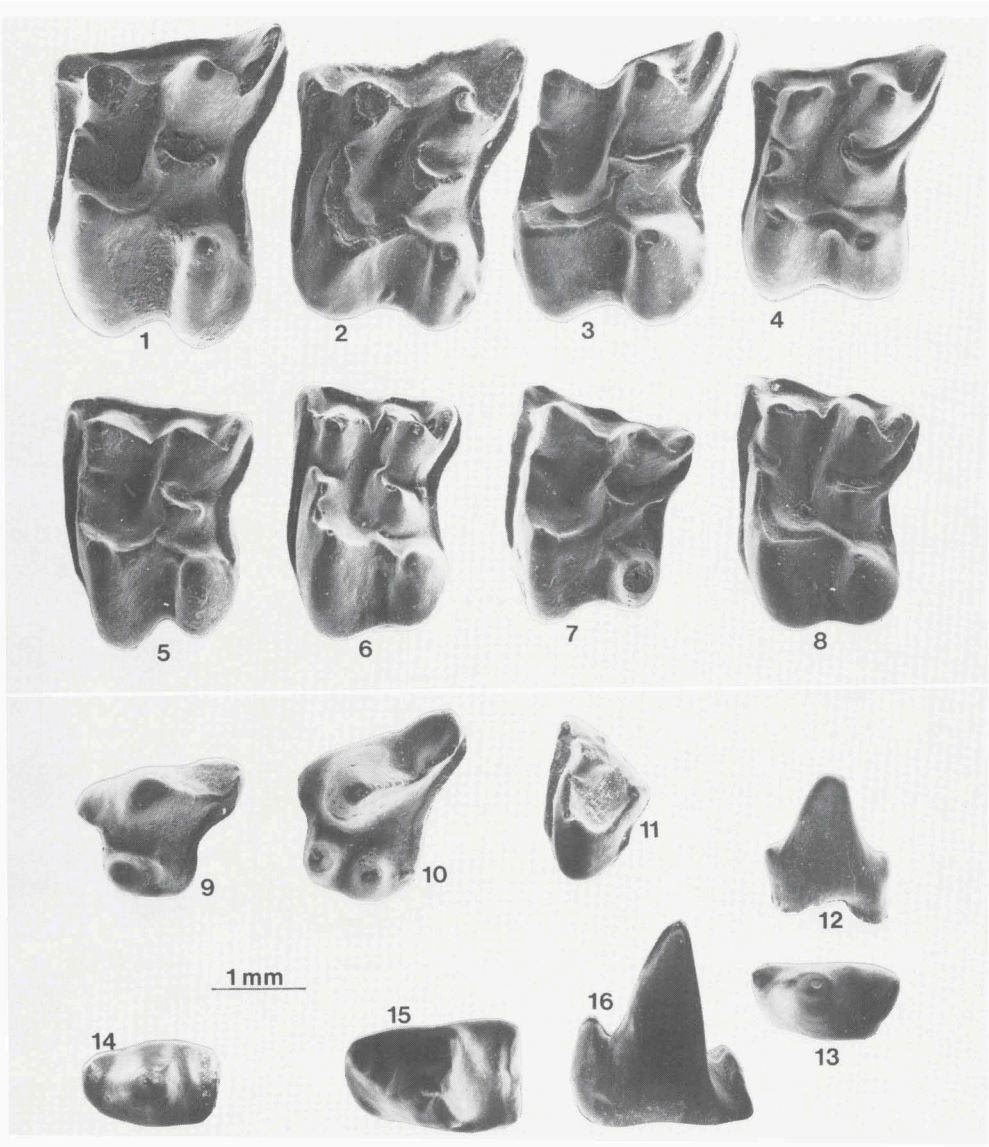
P^3 (*G. socialis*) — The P^3 of *G. socialis* differs from that of *G. exilis* by the presence of the hypocone. The paracone is the largest cusp. The protocone is situated slightly anteriorly of the paracone. The P^3 of *G. socialis* is wider than that of *G. exilis*. All other features are similar to those in *G. exilis*. The distribution of the morphotypes is shown in Fig. 3.

P^4 — The P^4 is more robust and larger than the P^3. The paracone is by far the largest cusp. It is conical and postero-labially connected to the somewhat extended style. Anteriorly there is a parastyle of similar morphology as in the P^3 but much smaller. The conical protocone is connected to the anterior base of the paracone by a ridge running parallel to the anterior border. The anterior border is concave. The conical hypocone is the lowest cusp. The posterior border has a variable outline. It may be slightly concave, slightly convex, or straight. There is a cingulum along the posterior border, running from the posterior hypocone base to the posterior base of the style. The P^4 is three-rooted: two labial roots and one broad and strong lingual root which is incompletely split.

M^1 (*G. exilis*) — The M^1 has an extended metastyle, giving this element an asymmetrical shape in contrast to the rectangular M^2. There are six cusps of which the smallest one is the protoconule, situated at the lingual base of the paracone. The protoconule is hardly visible if the molar is slightly worn. In this case it becomes part of the anterior transverse ridge. The protocone is the largest cusp. There is a Y-shaped connection between the protocone, the hypocone, and the metaconule. The posterior branch of the protocone is the lowest and widest part of this Y-shaped ridge pattern. The lingual metaconule-branch is weakly developed. The cone-shaped hypocone is well individualized. Its lingual part is rounded and slightly extended. The labial slopes of the protocone and hypocone are steeper than the lingual slopes. The hypocone is higher and better developed than the metaconule, but lower than proto-, para-, and metacone which are of equal height. The metaconule has a triangular pyramidal morphology because of its lingual, posterior and postero-labial branches. The postero-labial branch ends at the antero-lingual base of the metacone. The paracone and the metacone are of similar shape, but the metacone is somewhat more voluminous. Posteriorly a ridge connects the metacone to the postero-labially extended metastyle. There is a cingulum along the anterior border, running from the parastyle to the middle of the protocone base. Anteriorly there is a cingulum running from the labial base of the hypocone to the posterior base of the metastyle. The moderately developed labial cingulum connects the parastyle to the metastyle. This cingulum may be very weak. The M^1 is three-rooted: one large lingual root and two labial roots of which the posterior one is the largest.

M^2 (*G. exilis*) — In contrast to the M^1 the posterior metacone-branch in the M^2 is just slightly extended. The lingual protocone base extends somewhat further than in M^1. Lingually the hypocone is slightly oval. The hypocone-branch and the lingual metaconule-branch may be relatively shorter. The well-developed labial cingulum is connected to the parastyle and the metastyle. Roots and other features are similar to those of the M^1.

Plate 1



Galerix exilis/Galerix socialis
Fig. 1. M^1 sin., *G. exilis*, Solera, RGM 334 641.
Fig. 2. M^1 sin., Intermed. 1, Carrilanga 1, RGM 335 263.
Fig. 3. M^1 sin., Intermed. 2, Solera, RGM 334 638.
Fig. 4. M^1 sin., *G. socialis*, Carrilanga 1, RGM 335 266.
Fig. 5. M^2 sin., *G. exilis*, Borjas, RGM 334 918.
Fig. 6. M^2 sin., Intermed. 1, Carrilanga 1, RGM 335 333.
Fig. 7. M^2 sin., Intermed. 2, Solera, RGM 334 657.
Fig. 8. M^2 sin., *G. socialis*, Carrilanga 1, RGM 335 332.
Fig. 9. P^3 sin., *G. exilis*, Solera, RGM 334 573.
Fig. 10. P^3 sin., *G. socialis*, Carrilanga 1, RGM 335 192.

Galerix exilis (de Blainville, 1839)
Fig. 11. M^3 sin., Carrilanga 1, RGM 335 377.
Fig. 12. P_2 sin., in labial view, Solera, RGM 334 584.
Fig. 13. Idem, in occlusal view.
Fig. 14. P_3 sin., Solera, RGM 334 593.
Fig. 15. P_4 sin., Solera, RGM 334 606.
Fig. 16. Idem, in labial view.

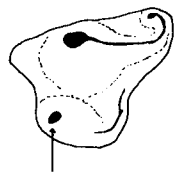
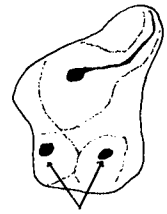
Morphotypes P^3 / Localities	 G.exilis	 G.socialis
Pedregueras 2A		3
Carrilanga 1	4	30
Solera	3	
Toril	5	
Alcocer 2	1	
Villafeliche 9	1	
Las Planas 5B	2	

Fig. 3. Distribution of the morphotypes of the P^3 of *Galerix*.

M^1 and M^2 (*G. socialis*) — In general the characters of the M^1 and the M^2 are similar to those of the same elements of *G. exilis*. However, there are some differences which are already stressed in the introduction of this chapter. The mentioned differences are the following:
The posterior branch of the metaconule is extended and it ends at the posterior base of the metastyle.
The M^1 of *G. socialis* has a more rectangular shape than the relatively quadratic M^1 of *G. exilis*.

Plate 2

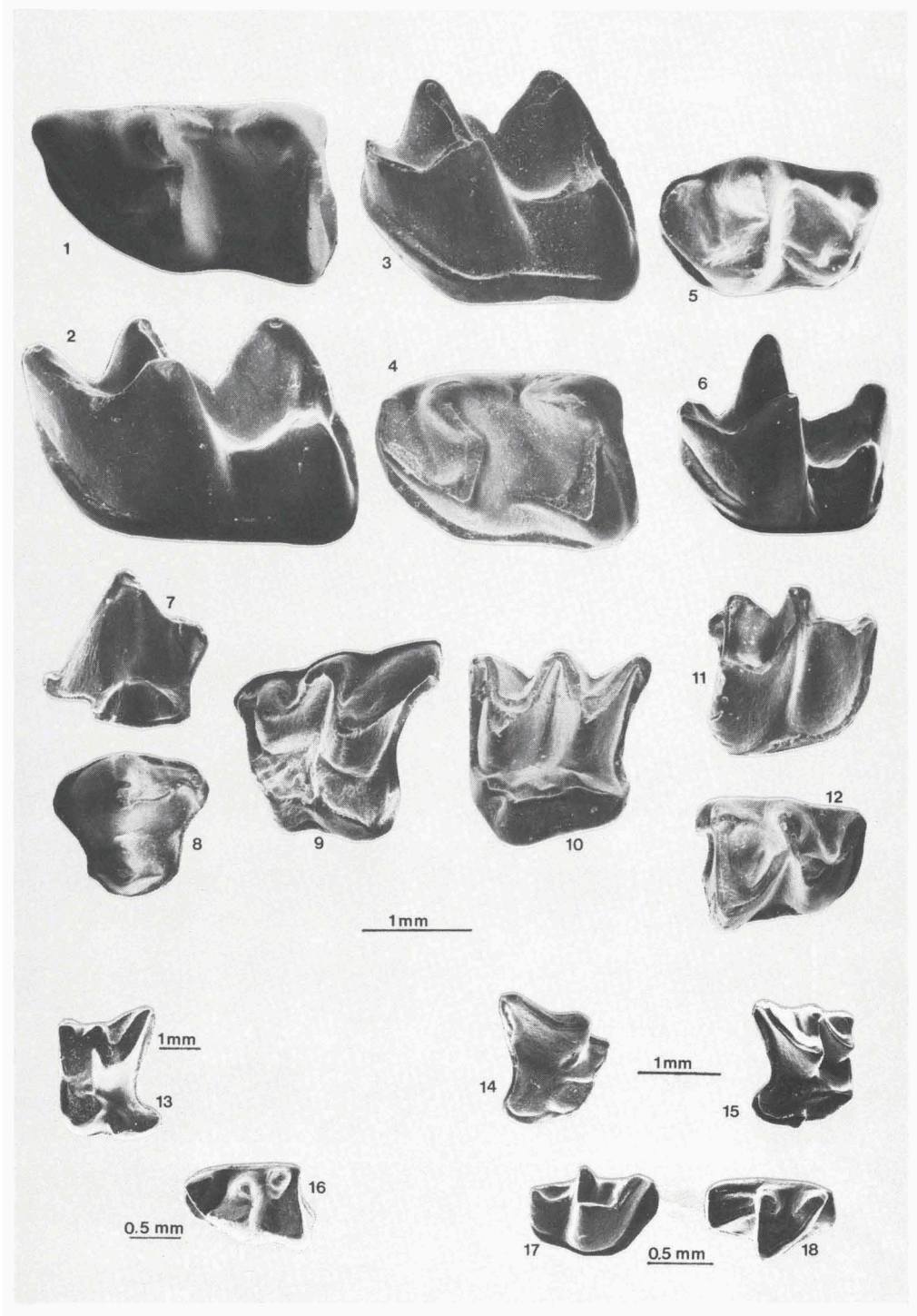
Galerix exilis/Galerix socialis
Fig. 1. M_1 sin., Carrilanga 1, RGM 335 418.
Fig. 2. Idem, in labial view.
Fig. 3. M_2 sin., Carrilanga 1, RGM 335 387.
Fig. 4. Idem, in labial view.
Fig. 5. M_3 sin., Toril, RGM 335 057.
Fig. 6. Idem, in labial view.

Desmanella crusafonti Rümke, 1974
Fig. 7. P^4 sin., lingual view, Pedregueras 2A, RGM 334 486.
Fig. 8. Idem, in occlusal view.
Fig. 9. M^1 sin., Pedregueras 2A, RGM 334 489.
Fig. 10. M^2 sin., Pedregueras 2A, RGM 334 492.
Fig. 11. M_1 dext., Pedregueras 2A, RGM 334 516.
Fig. 12. Idem, in labial view.

Crusafontina endemica Gibert, 1974
Fig. 13. M^1 sin., Carrilanga 1, RGM 335 587.

Miosorex aff. *grivensis* (Depéret, 1892)
Fig. 14. P^4 dext., Las Planas 5H, RGM 334 951.
Fig. 15. M^1 dext., Las Planas 5H, RGM 334 956.
Fig. 16. M_1 sin., Alcocer 2, RGM 335 172.
Fig. 17. M_3 dext., in labial view, Villafeliche 9, RGM 334 805.
Fig. 18. Idem, in occlusal view.

Plate 2



The protocone is connected to the hypocone by a ridge. The metaconule is separated from the protocone and the hypocone by a V-shaped valley.
The posterior cingulum is situated between the bases of the hypocone and the metaconule.

M^3 — This element is smaller than the other upper molars, and it has a subtriangular shape. The highest cusp is the conical paracone. The lowest cusp is the metacone, which is connected to the protocone by a small ridge. All cusps are connected by ridges: a closed, rounded basin is situated in the centre of the M^3. The paracone is anteriorly connected to the well-developed parastyle by a narrow ridge. A cingulum is present between the parastyle and the protocone base. Between the metacone and the protocone there is a narrow and low cingulum. This cingulum is of variable length. In some specimens it runs along the entire lingual side, in other ones it is completely absent. The same variation is present in the labial cingulum. The M^3 is three-rooted: the lingual root is the strongest one, the other two are situated labially and are of equal size.

Distribution of the morphotypes of M^1 and M^2 (Figs. 4, 5)
Four standard morphotypes are distinguished in the M^1:
In the first type the protocone is connected to the metaconule and the posterior metaconule branch is relatively short.
In the second type the protocone is connected to the hypocone and it is isolated from the metaconule. The posterior branch of the metaconule is relatively short.
In the third type the protocone is also connected to the hypocone. From the top of the metaconule a ridge descends towards the protocone-hypocone connection. The posterior metaconule branch is longer than in the two previous types.
In the fourth type the protocone is connected to the hypocone as well, the metaconule is an isolated cusp, and its posterior branch is long.

The standard morphotypes of the M^2 are basically the same as those of M^1 with the exception of the third type. In this type of M^2 the hypocone is an isolated cusp.

Figs. 4 and 5 show that the Upper Aragonian localities only contain *G. exilis*, that in Carrilanga 1 (zone H, Lower Vallesian) both species are present, and that in Pedregue-

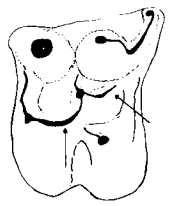
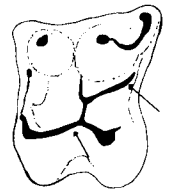
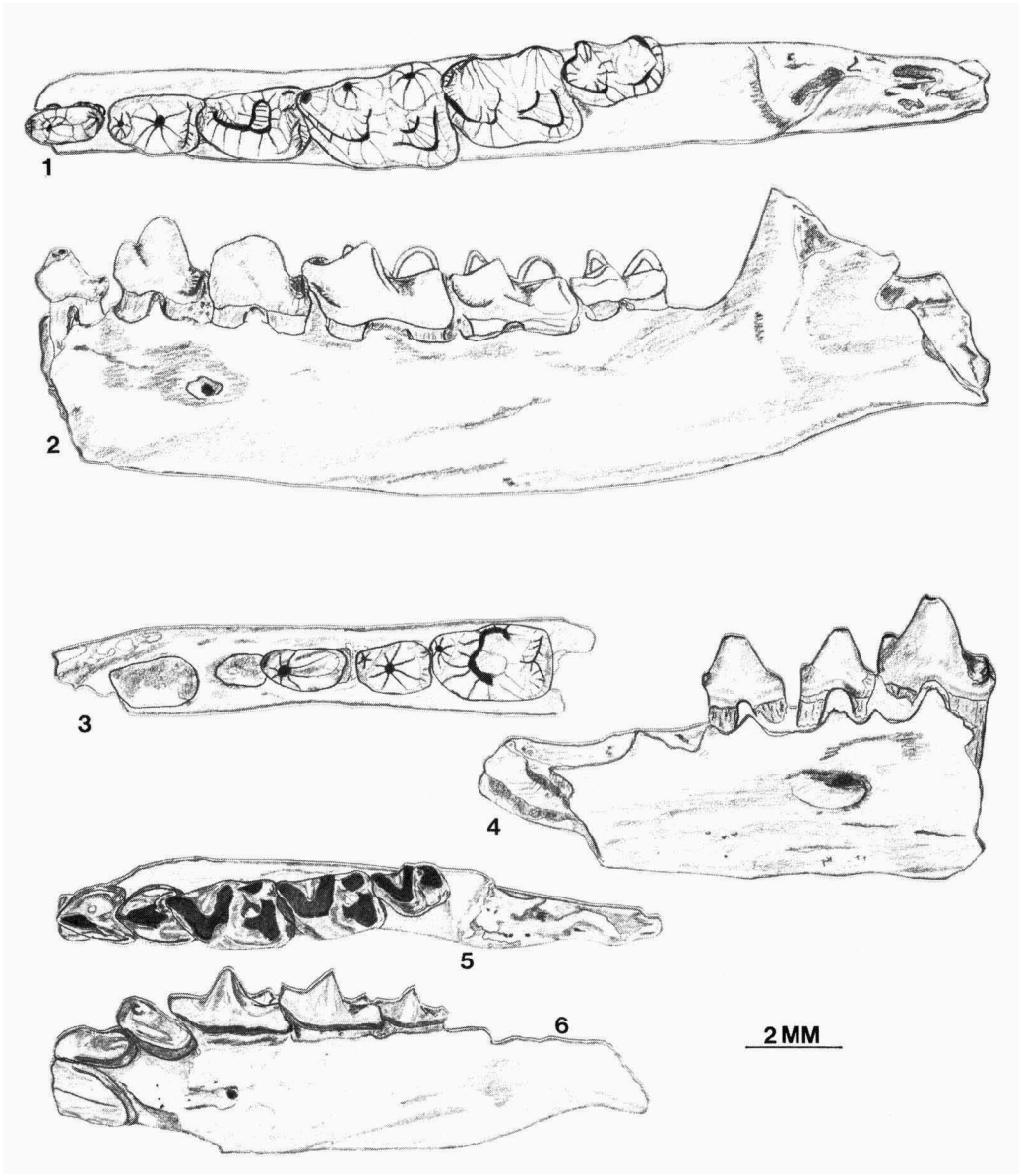
Morphotypes M¹ / Localities	 G.exilis	 intermed.1	 intermed.2	 G.socialis
Pedregueras 2A				2
Carrilanga 1	4	1	2	29
Solera	7	1		
Las Planas 5H	1			
Toril	8			
Alcocer 2	1			
Villafeliche 9	4			
Borjas	1			
Las Planas 5B	2			
Valalto 2C	3			

Fig. 4. Distribution of the standard morphotypes of M^1 of *Galerix*.

Plate 3



Galerix socialis (H. von Meyer, 1865)
Fig. 1. Mandible sin., P_2-M_3, Carrilanga 1, RGM 335 482.
Fig. 2. Idem, in labial view.

Galerix exilis (de Blainville, 1839)
Fig. 3. Mandible sin., P_2-P_4, Las Planas 5H, RGM 334 942.
Fig. 4. Idem, in labial view.

Crusafontina endemica Gibert, 1974
Fig. 5. Mandible sin., I-M_3, Carrilanga 1, RGM 335 555.
Fig. 6. Idem, in labial view.

Morphotypes M^2 / Localities	G.exilis	intermed.1	intermed.2	G.socialis
Pedregueras 2A				2
Carrilanga 1	6	5	3	49
Solera	19		1	
Las Planas 5H	5			
Toril	16		1	
Alcocer 2	1			
Villafeliche 9	2			
Borjas	5			
Valalto 2C	3			

Fig. 5. Distribution of the standard morphotypes of M^2 of *Galerix*.

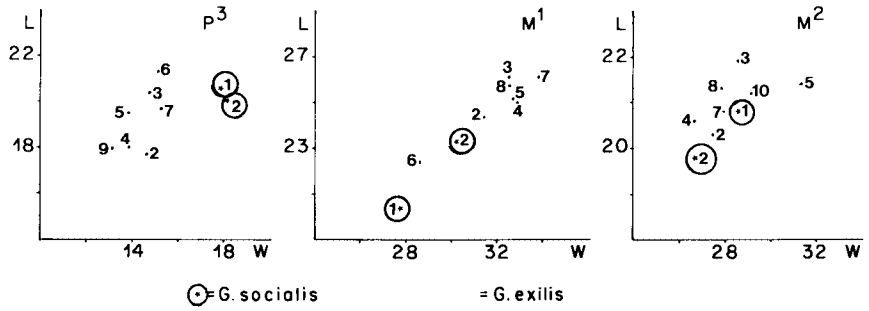


Fig. 6. Mean measurements of P^3, M^1 and M^2 of *Galerix* of various localities from the Daroca-Villafeliche area (x 0.1 mm).
1 = Pedregueras 2A; 2 = Carrilanga 1; 3 = Solera; 4 = Toril; 5 = Villafeliche 9; 6 = Las Planas 5B; 7 = Valalto 2C; 8 = Borjas; 9 = Alcocer 2; 10= Las Planas 5H.

ras 2A (zone I, Lower Vallesian) only *G. socialis* is represented. The intermediate morphotypes in Carrilanga 1 are not assigned to either species. Moreover, size differences among the four standard morphotypes of M^1 and M^2 are not of such an extent that they may serve for specific separation.

Size — From Fig. 6 it appears that the P^3 in *G. socialis* is wider than in *G. exilis*. The M^1 of *G. exilis* is smaller than it is in *G. exilis* with the exception of *G. exilis* from Las Planas 5B. In M^2 the size differences are very small. In P^4, M^3 and the lower molars there are no significant size differences between *G. exilis* and *G. socialis* (Tables 5-7, 10, 13).

In *G. socialis* P_2 is shorter than P_3 and in *G. exilis* P_3 is shorter than P_2. In our material this feature was present in localities with only one of the two species. Whenever both species were present in the same locality size ranges were very much overlapping in P_2 and P_3 (Tables 2 and 3). This fact, combined with a strong variation in morphology in P_2 and P_3 made it impossible to distinguish between *G. exilis* and *G. socialis*.

Comparison of sizes — The sizes of *G. exilis* and *G. socialis* from the Daroca-Villafeliche area are compared with those from other localities in Western Europe (Figs. 7a, b). In

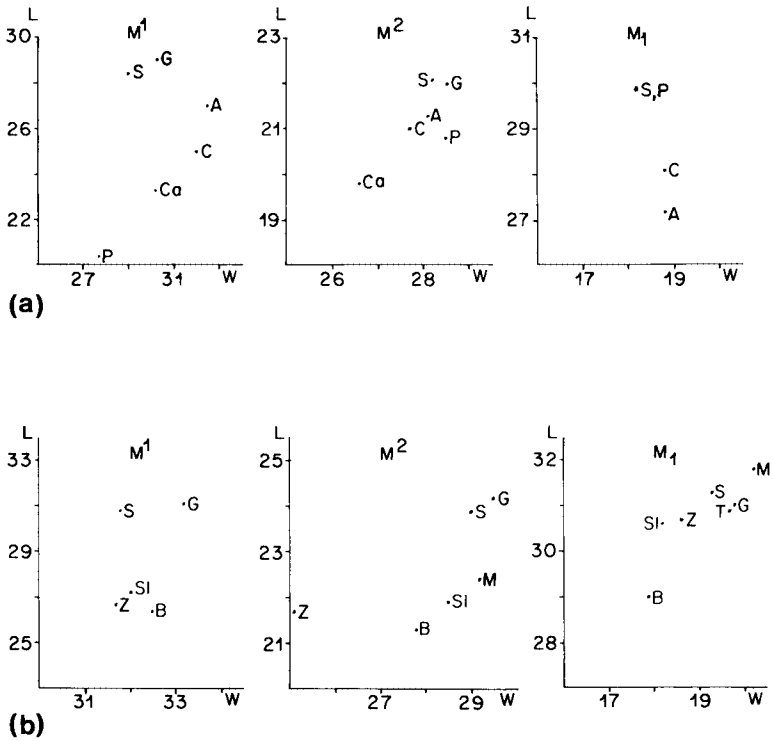


Fig. 7. Comparative measurements of M^1, M^2 and M_1 of *Galerix socialis* (a) and *G. exilis* (b) from various localities (x 0.1 mm).
S = Sansan; D = Daroca; G = La Grive; A = Anwil; C = Can Ponsic; T = Steinheim; Z = Goldberg; M = Manchones 1 + 2.

order to facilitate the comparison of the size of our Spanish material with that from other Miocene localities in Western Europe, we used the mean values of all assemblages.

It appears from Fig. 7b that *G. exilis* from the Daroca-Villafeliche area is considerably smaller than the same species from the other localities, with the exception of the M^2 from Goldberg (Germany). In *G. socialis* from the Daroca-Villafeliche area the upper teeth are small. In the lower elements there are not many size differences, except for the somewhat greater length of the M_1 from the Daroca-Vilafeliche area (Fig. 7a). Concluding it can be said that *G. socialis* from the Daroca-Villafeliche area is a small form in comparison with the same species from other West European localities.

Family Talpidae Fischer von Waldheim, 1817
Subfamily Uropsilinae Dobson, 1883
Desmanella Engesser, 1972

Desmanella crusafonti Rümke, 1974
Pl. 2, figs. 7-12; Pl. 4, figs. 1-13.

Material and measurements

Element	Measure	n	min.	mean	max.
P_4	L	1	—	1.09	—
	W	3	0.82	0.84	0.85
M_1	L	5	1.57	1.61	1.68
	W_1	6	0.76	0.98	1.11
	W_2	7	1.03	1.18	1.29
M_2	L	3	1.77	1.84	1.95
	W_1	3	1.21	1.23	1.25
	W_2	5	1.22	1.27	1.29
M_3	L	3	1.40	1.43	1.45
	W_1	6	0.89	0.91	0.93
	W_2	8	0.66	0.69	0.73
P^4	L	5	1.49	1.57	1.66
	W	4	1.42	1.47	1.55
M^1	L_1	2	2.21	2.23	2.25
	L_2	4	1.32	1.44	1.50
	W	2	1.86	1.88	1.90
M^2	L_1	2	1.67	1.69	1.71
	L_2	7	1.37	1.44	1.49
	W	2	2.03	2.07	2.10
M^3	L	4	1.08	1.13	1.17
	W	1	—	1.64	—

Description

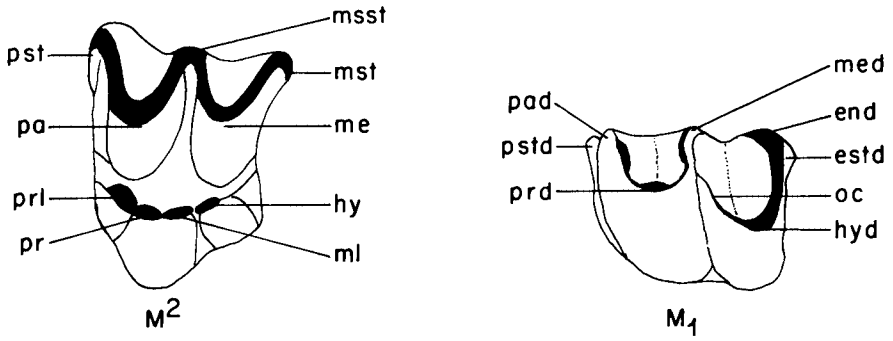
P_4 — The P_4 consists of a high and sharp paraconid, which is straight at the labial side and slightly concave at the lingual one. Postero-lingually a low ridge encloses a narrow talonid valley. This ridge is connected to the top of the paraconid. A cingulum runs along the posterior, labial and anterior sides of the tooth. Posteriorly there is a small cusp on the cingulum; it is connected to the base of the paraconid by a narrow ridge.

Lower molars — In all lower molars the trigonid is lingually open, while the talonid is partly closed by the ento- and the metaconid.

M_1 — The talonid is wider than the trigonid, but of the same length. Both paraconid and metaconid are rather conical although the metaconid is flattened at the talonid side. The paraconid is the lowest cusp. The protoconid is slightly more inclined to the lingual side than the hypoconid. The metaconid and the entoconid are of subequal height. At the postero-lingual corner of the crown a well-developed entostylid is present. The oblique cristid ends halfway the protoconid-metaconid crest. Antero-labially there is a cingulum. This cingulum ends labially at the base of the hypoconid. A posterior cingulum runs from the base of the hypoconid to the base of the entostylid.

M_2 — The talonid and the trigonid are of equal size. A weak parastylid and an entostylid are present. The protoconid is higher than the other cusps and it has the same lingual inclination as the hypoconid. The metaconid is higher than the entoconid and the low paraconid. The metaconid is conical except for the talonid side which is slightly concave. The oblique cristid ends just below the top of the metaconid. The anterior part of the cingulum is wider than in the M_1. All other characters are similar to those of the M_1.

M_3 — The talonid is shorter than the trigonid. The protoconid is somewhat higher than the metaconid. The entoconid and the paraconid are the lowest cusps. The shape of the metaconid is similar to that of the M_2. The paraconid and the entoconid are both blade-like. The oblique cristid ends at the base of the metaconid. The anterior cingulum



hy = hypocone
me = metacone
ml = metaconule
msst = mesostyle
mst = metastyle
pa = paracone
pr = protocone
prl = protoconule
pst = parastyle
end = entoconid
estd = entostylid
hyd = hypoconid
med = metaconid
oc = oblique cristid
pad = paraconid
prd = protoconid
pstd = parastylid

Fig. 8. Nomenclature used for parts of the upper and lower molars of *Desmanella* (based on Rümke, 1974).

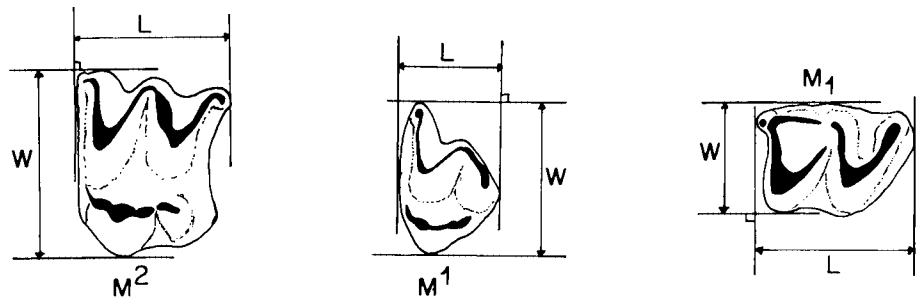


Fig. 9. Method used for measuring the upper and lower molars of *Desmanella* (after Rümke, 1974).

and the parastylid are like in M_2. The posterior cingulum is very weak. The labial cingulum is similar to that of the M_2.

P^4 — The paracone is conical except for the posterior side, which has a sharp posterocrista. The cusp is somewhat inclined posteriorly. The protocone is very small and it is not connected to the paracone. The anterocrista and posterocrista are weakly developed. A cingulum runs around the base of the crown, which is interrupted halfway the labial side. The cingulum is very narrow halfway the lingual side and it is slightly extended posteriorly and anteriorly. In some specimens a narrow vertical ridge is present on the labial side of the paracone. This ridge is connected to the cingulum.

M^1 — The postero-labial branch of the metacone is moderately elongated. The paracone has a conical shape. The protocone is well individualized. It is situated anteriorly. A protoconule and a hypocone are present, both well individualized. These cusps are connected by a narrow ridge, which ends at the base of the parastyle. Posteriorly this ridge is connected to the cingulum. The antero-lingual outline of the protoconule is rounded. The long posterior branch of the metacone and the elongated hypoconal flange cause a concave posterior border. The moderately developed mesostyle

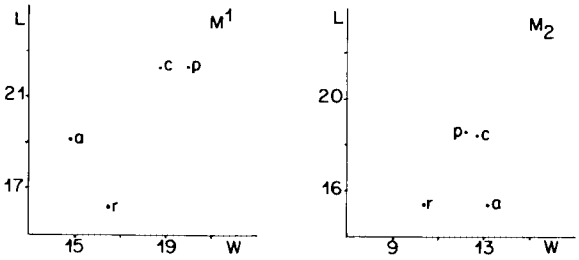


Fig. 10. Average sizes of M^1 and M_2 of three related Miocene *Desmanella* species.
a = Anwil (*D. stehlini*); c = Concud 3 (*D. crusafonti*); p = Pedregueras 2A (*D. crusafonti*); r = Rubielos de Mora 2 (*D. fejfari*).

may be slightly divided. The weak metastyle consists of the posterior part of the metacone branch together with the posterior cingulum. A posterior cingulum, and a short lingual cingulum at the base of the valley between the protocone and the protoconule are present. Very narrow cingulums connect the parastyle and the metastyle to the base of the mesostyle.

M^2 — This element is more symmetrical than the M^1. This is mainly due to the labial cusps which are of equal shape and size. The metacone is slightly higher than the paracone. The lingual cusps are much lower, and less individualized than in the M^1. The protocone is situated in the middle of the labial side and somewhat extended labially. The protoconule is lower than the hypocone. As in the M^1 the lingual cusps are connected by a narrow ridge. Anteriorly this ridge ends at the base of the parastyle, posteriorly it is connected to the cingulum. This ridge widens slightly between the protocone and the hypocone, indicating the position of the metaconule. The hypocone forms a hypoconal flange but is less developed than in M^1. The posterior border is somewhat concave. The metastyle consists of the posterior branch of the metacone and the posterior cingulum.

Plate 4

Desmanella crusafonti Rümke, 1974; Pedregueras 2A.
Fig. 1. P_4 sin., RGM 334 510.
Fig. 2. Idem, in labial view.
Fig. 3. M_1 dext., RGM 334 516.
Fig. 4. Idem, in labial view.
Fig. 5. M_2 dext., RGM 334 520.
Fig. 6. Idem, in labial view.
Fig. 7. M_3 dext., RGM 334 505.
Fig. 8. Idem, in labial view.
Fig. 9. P^4 sin., RGM 334 486.
Fig. 10. Idem, in lingual view.
Fig. 11. M^1 sin., RGM 334 489.
Fig. 12. M^2 sin., RGM 334 492.
Fig. 13. M^3 sin., RGM 334 500.

Miosorex aff. *grivensis* (Depéret, 1892)
Fig. 14. M_1 sin., Alcocer 2, RGM 335 172.
Fig. 15. Idem, in labial view.
Fig. 16. M_2 sin., Las Planas 5K, RGM 334 988.
Fig. 17. Idem, in labial view.
Fig. 18. M_3 sin., Las Planas 5K, RGM 334 991.
Fig. 19. Idem, in labial view.

Plate 4

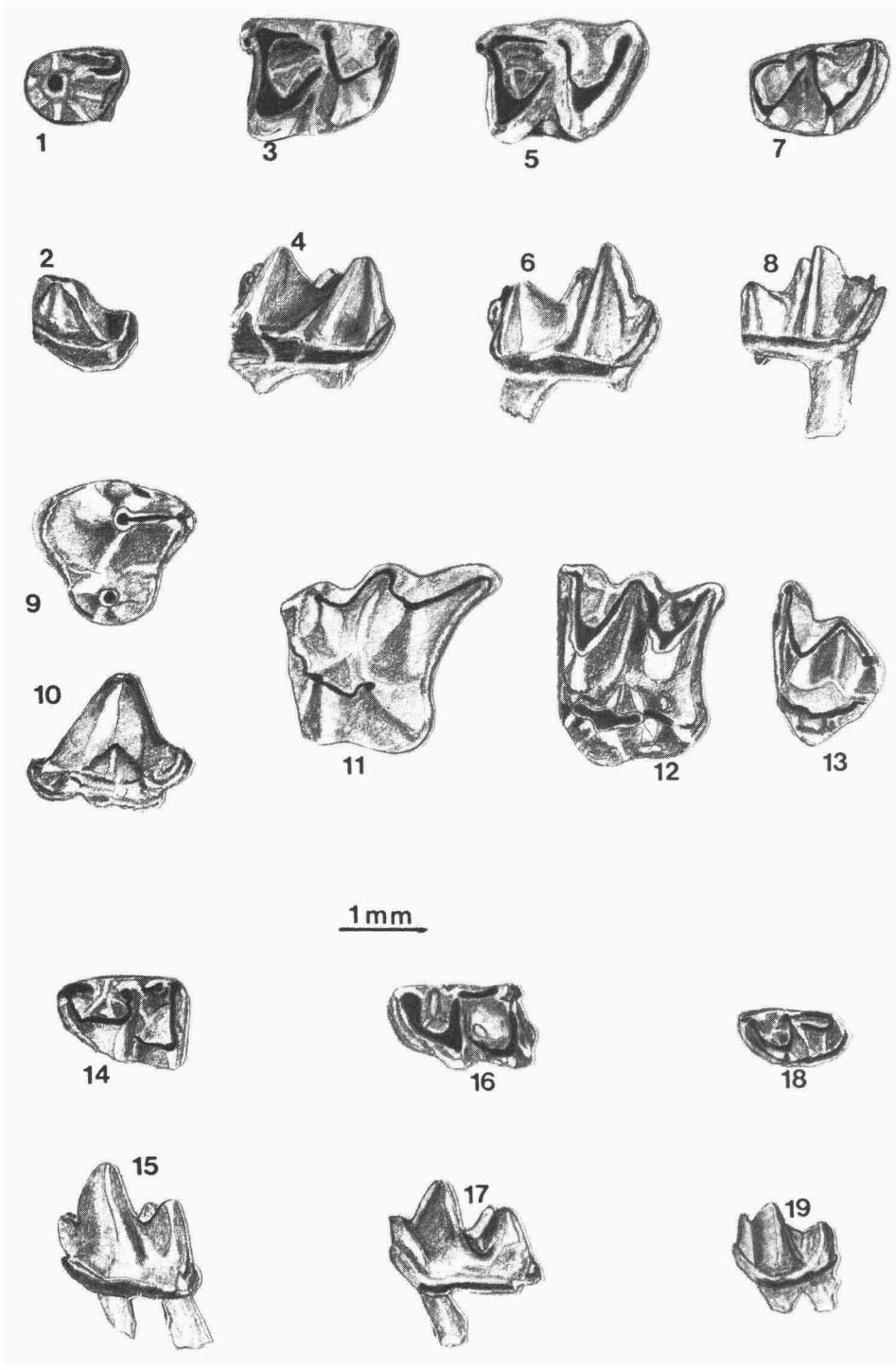


Table 18. Measurements of several dental elements of three Miocene *Desmanella* species.

Measurement		*D. stehlini* Anwil		*D. crusafonti* Concud		*D. fejfari* Rubielos de Mora 2		*D. crusafonti* Pedregueras 2A	
		n	size	n	size	n	size	n	size
M_1	L	1	1.52	43	1.80	1	1.36	5	1.61
	W_2	1	1.16	43	1.32	1	0.96	7	1.18
M_2	L	2	1.52	30	1.86	1	1.52	3	1.84
	W_2	2	1.26	30	1.22	1	1.04	5	1.27
P^4	L	0	—	71	1.68	2	1.16	5	1.57
	W	0	—	71	1.51	2	1.02	4	1.47
M^1	L_1	1	1.92	43	2.23	3	1.62	2	2.23
	W	1	1.48	43	2.00	3	1.65	2	1.88
M^2	L_1	1	1.44	51	1.70	1	1.28	2	1.69
	W	1	1.72	51	2.17	1	1.60	2	2.07

The mesostyle is not divided. A weak parastyle is present. A cingulum runs along the posterior border. A short lingual cingulum is present at the base of the valley between the protocone and the hypocone.

M^3 — As in the M^1 and the M^2 the labial part of the M^3 is well developed. The paracone and the metacone are well-developed cusps. The paracone is, in unworn specimens, the highest cusp. The protocone is the highest lingual cusp. Its anterocrista is slightly widened at the position of the protoconule. The protocone is slightly extended labially. the hypocone is weakly developed. The mesostyle is not divided. There is a weak parastyle. Anteriorly there is a ridge that connects the protocone to the base of the parastyle.

Discussion — *Desmanella crusafonti* from Pedregueras 2A resembles *D. crusafonti* from Concud 3 (Rümke, 1974), but some differences must be mentioned. The posterior cingulum of the M^1 from Concud 3 is weak, while this cingulum is well developed in the Pedregueras 2A material. In the M^2 from Pedregueras 2A the protocone is lingually less extended than in Concud 3. In the M^2 from Pedregueras 2A the lingual cingulum at the base of the valley between protocone and hypocone is better developed. The labial cingulum of the lower molars from Pedregueras 2A is not interrupted at the base of the protoconid. The M_1 from Concud 3 has a parastylid, in Pedregueras 2A a parastylid is absent. *D. crusafonti* from Pedregueras 2A and Concud 3 are of similar size (Fig. 10) with the exception of the smaller M_1 in Pedregueras 2A. *D. fejfari* from Rubielos de Mora and *D. stehlini* from Anwil are of different size and both are smaller than *D. crusafonti*.

Family Soricidae Gray, 1821
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Amblycoptini Kormos, 1926
Crusafontina Gibert, 1974

Crusafontina endemica Gibert, 1974
Pl. 2, fig. 13; Pl. 3, figs. 5-6.

Locality — Carrilanga 1: the material consists of one fragmentary mandible with P_3-M_3 and some isolated teeth.

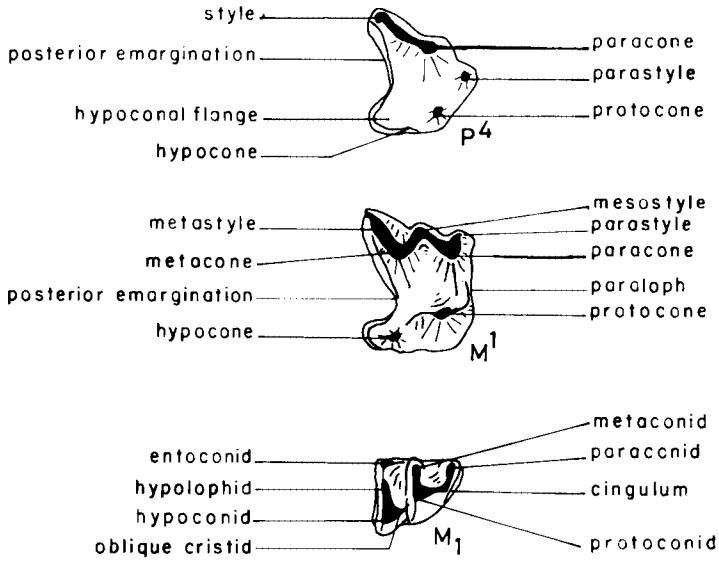


Fig. 11. Nomenclature used for parts of the cheek teeth of the Soricidae (based on Reumer, 1984).

Measurements

Element	Measure	n	min.	mean	max.
P_3	W	1	—	1.06	—
P_4	W	1	—	1.16	—
M_1	L	1	—	2.23	—
	W_1	1	—	1.17	—
	W_2	1	—	1.26	—
M_2	L	3	1.75	1.82	1.88
	W_1	3	1.02	1.06	1.11
	W_2	3	1.02	1.04	1.07
M_3	L	2	1.25	1.33	1.40
	W_1	2	0.74	0.75	0.75
	W_2	2	0.65	0.70	0.74
M^1	L_1	1	—	1.95	—
	L_2	1	—	2.07	—
	W	1	—	2.50	—
M_1-M_3	L	1	—	5.23	—

Description

P_4 — At the posterior side there is a postero-lingual basin which is L-shaped and connected to the posterior cingulum. At the lingual and labial sides there is a well-developed cingulum. A weaker cingulum is present at the posterior side. The postero-labial part is somewhat extended and it bends down slightly, covering part of the root.

M_1 — The talonid is slightly wider than the trigonid. The talonid is shorter than the trigonid. The oblique cristid ends at the base of the protoconid, which is the highest cusp. An entoconid crest is present but it is very low. The hypolophid is not connected to the entoconid, but it ends at the posterior base of the entoconid. The paralophid is long and the lingual valley is very wide, and shallow. The re-entrant valley is situated relatively

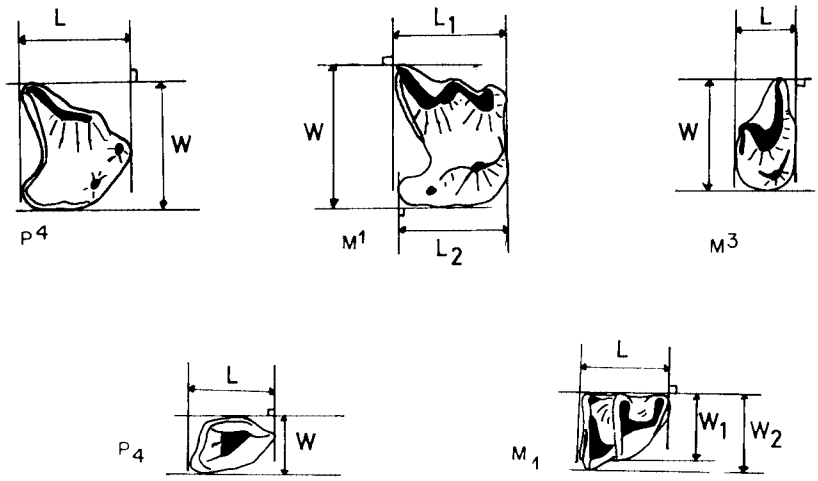


Fig. 12. Methods used for measuring cheek teeth of the Soricidae (based on Reumer, 1984).

high above the labial cingulum and it is weakly developed. There is no lingual cingulum. There are posterior and labial cingulums but they are weak.

M_2 — The trigonid is shorter than in the M_1. The talonid is narrower than the trigonid. The paralophid is shorter and the re-entrant valley is narrower than in the M_1. Both the lingual and the labial valleys are deeper than in M_1. The oblique cristid ends more lingually than in the first lower molar. The other characters are the same as in M_1.

M_3 — The talonid is narrower and shorter than the trigonid. The trigonid is similar in shape to that of the M_2. The labial and lingual valleys end almost at the base of the molar. There is an entoconid and a hypoconid. The oblique cristid ends halfway the base of the metalophid. The entoconid crest is hardly developed. There is a cingulum around the base of the molar except at the lingual side.

M^1 — The lingual part is longer than the labial part. This difference is mainly due to the well-developed talon. The metacone is the highest cusp. The protocone and the paracone are of equal height. The metacone and the paracone have the same shape. The hypocone is present but it is smaller than the protocone. There is an open valley between the hypocone and the protocone. There is no cingulum along the talon. Posteriorly there is a narrow cingulum which becomes little wider at the base of the metastyle. There is a narrow cingulum at the labial base of the protocone.

Subfamily Soricinae Fischer von Waldeim, 1817

Miosorex Kretzoi, 1959

Genotype — *Sorex pusillus* var. *grivensis* (Depéret, 1892)

Miosorex aff. *grivensis* (Depéret, 1892)
Pl. 2, figs. 14-18; Pl. 4, figs. 14-19; Pl. 5.

Localities — All localities in this study.

Measurements — See Tables 19-28.

Description

P_4 — The P_4 is asymmetrical in occlusal view. There are indications that the premolar is two-rooted but there is no evidence. The cusp of the P_4 is triangular. When the cusp is not very much worn it has a Y-shape. Postero-lingually and postero-labially there are crests. The labial crest is the best developed one. It has a secondary cuspule, situated somewhat underneath the top. Lingually, between the two crests, there is a basin. There is an anteriorly interrupted cingulum. The postero-labial cingulum slightly hangs over the posterior root of the P_4. The posterior cingulum has a narrow and sharp ridge which is connected to the postero-labial crest.

M_1 — The talonid and the trigonid are of almost equal size. The talonid is slightly shorter than the trigonid, but it is somewhat wider. The protoconid and the entoconid are of equal height and they are the lowest cusps. The metaconid and the hypoconid are of equal height. The paraconid is conical, which is, however, only visible in elements that did not suffer much wear. In unworn elements the protoconid is situated closely to the

Table 19. Measurements of the P_3 of *Miosorex grivensis*.

		Length				Width		
Localities	n	min.	mean	max.	n	min.	mean	max.
Las Planas 5K	3	0.73	0.79	0.84	3	0.65	0.66	0.68
Borjas	0	—	—	—	1	—	0.66	—

Table 20. Measurements of the P_4 of *Miosorex grivensis*.

		Length				Width		
Localities	n	min.	mean	max.	n	min.	mean	max.
Pedregueras 2A	2	1.01	1.14	1.27	2	0.75	0.77	0.78
Toril	1	—	1.05	—	1	—	0.70	—
Las Planas 5K	3	0.92	0.96	0.98	3	0.60	0.65	0.72
Borjas	2	0.97	1.01	1.05	2	0.64	0.64	0.64
Las Planas 5B	1	—	1.04	—	1	—	0.68	—
Valalto 2C	2	0.93	1.01	1.09	2	0.68	0.69	0.69

Table 21. Measurements of the M_1 of *Miosorex grivensis*.

		Length				Width		
Localities	n	min.	mean	max.	n	min.	mean	max.
Pedregueras 2A	6	1.46	1.55	1.64	8	0.93	0.97	1.02
Solera	15	1.29	1.40	1.48	16	0.78	0.91	0.99
Toril	3	1.21	1.24	1.27	3	0.78	0.81	0.84
Alcocer 2	1	—	1.24	—	1	—	0.88	—
Villafeliche 9	21	1.20	1.31	1.45	19	0.77	0.88	0.98
Las Planas 5K	5	1.21	1.31	1.43	5	0.84	0.88	0.93
Borjas	9	1.14	1.26	1.39	10	0.75	0.85	0.97
Las Planas 5B	6	1.22	1.32	1.41	7	0.81	0.91	0.97
Valalto 2C	5	1.27	1.32	1.38	5	0.78	0.87	0.97

Table 22. Measurements of the M_2 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Pedregueras 2A	7	1.27	1.44	1.57	8	0.88	0.94	1.01
Solera	6	1.27	1.32	1.36	7	0.81	0.87	0.93
Las Planas 5H	3	1.12	1.27	1.38	2	0.82	0.85	0.88
Toril	2	1.31	1.32	1.32	3	0.81	0.83	0.86
Alcocer 2	3	1.16	1.24	1.28	4	0.75	0.83	0.91
Villafeliche 9	16	1.20	1.31	1.44	17	0.71	0.83	0.97
Las Planas 5K	5	1.27	1.33	1.36	6	0.75	0.82	0.87
Borjas	8	1.18	1.32	1.44	8	0.77	0.84	0.96
Las Planas 5B	6	1.19	1.37	1.48	9	0.73	0.84	0.89
Valalto 2C	2	1.24	1.29	1.34	2	0.75	0.83	0.90

Table 23. Measurements of the M_3 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Pedregueras 2A	4	1.19	1.22	1.25	4	0.41	0.46	0.51
Solera	5	1.04	1.09	1.19	5	0.38	0.43	0.52
Las Planas 5H	2	1.08	1.10	1.12	2	0.35	0.40	0.44
Villafeliche 9	11	0.95	1.07	1.20	11	0.30	0.34	0.40
Las Planas 5K	3	0.99	1.06	1.12	3	0.31	0.38	0.43
Borjas	5	0.96	1.08	1.16	5	0.29	0.36	0.41
Las Planas 5B	3	1.06	1.09	1.11	3	0.39	0.42	0.44
Valalto 2C	6	1.00	1.08	1.13	5	0.30	0.35	0.39

Table 24. Measurements of the P^4 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
.Carrilanga 1	1	—	1.45	—	1	—	1.33	—
Las Planas 5H	2	1.59	1.62	1.64	3	1.35	1.38	1.43
Toril	0	—	—	—	2	1.43	1.43	1.43
Villafeliche 9	7	1.33	1.57	2.07	4	1.34	1.44	1.65
Las Planas 5K	3	1.37	1.44	1.49	2	1.32	1.32	1.32
Borjas	1	—	1.54	—	0	—	—	—
Valalto 5B	2	1.52	1.54	1.55	2	1.37	1.50	1.63

Table 25. Measurements of the M^1 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Solera	5	1.41	1.45	1.50	2	1.76	1.84	1.93
Las Planas 5H	1	—	1.36	—	1	—	1.85	—
Toril	3	1.20	1.29	1.38	2	1.66	1.68	1.69
Villafeliche 9	10	1.22	1.38	1.44	5	1.71	1.81	1.94
Las Planas 5K	10	1.07	1.36	1.46	10	1.61	1.69	1.81
Borjas	6	1.29	1.35	1.40	6	1.68	1.76	1.82
Las Planas 5B	6	1.27	1.31	1.52	7	1.53	1.69	1.77
Valalto 2C	1	—	1.49	—	1	—	1.85	—

Table 26. Measurements of the M^2 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Solera	1	—	1.29	—	2	1.73	1.75	1.76
Toril	2	1.17	1.21	1.25	2	1.61	1.62	1.63
Alcocer 2	1	—	1.28	—	0	—	—	—
Villafeliche 9	5	1.16	1.26	1.43	3	1.63	1.65	1.69
Las Planas 5K	5	1.21	1.25	1.30	2	1.66	1.66	1.66
Borjas	4	1.29	1.32	1.36	4	1.59	1.70	1.76
Las Planas 5B	6	1.27	1.29	1.33	6	1.49	1.59	1.67
Valalto 2C	1	—	1.33	—	1	—	1.59	—

Table 27. Measurements of the M^3 of *Miosorex grivensis*.

Localities	Length n	min.	mean	max.	Width n	min.	mean	max.
Carrilanga 1	2	0.79	0.80	0.80	2	1.41	1.43	1.44
Las Planas 5H	1	—	0.72	—	1	—	1.40	—
Villafeliche 9	3	0.60	0.67	0.71	3	1.19	1.26	1.32
Las Planas 5B	2	0.68	0.70	0.72	2	1.27	1.31	1.34

Table 28. Measurements of the individual M_1-M_3 distances in mandible fragments of *Miosorex grivensis*.

	Locality	Distance M_1-M_3
RGM 334 810	Villafeliche 9	3.62
RGM 334 818	Villafeliche 9	3.82
RGM 334 823	Villafeliche 9	3.68
RGM 334 827	Villafeliche 9	3.42
RGM 334 831	Villafeliche 9	3.84
RGM 334 835	Villafeliche 9	3.40
RGM 334 895	Borjas	3.65
RGM 335 152	Valalto 2C	3.26

metaconid. The entoconid crest is weak. The oblique cristid is situated labially, ending at the base of the protoconid. The labial re-entrant valley opens moderately high above the cingulum. The trigonid basin is deep and ends slightly above the base of the molar. The hypolophid is separated from the entoconid by a narrow sulcus. The lingual part of the hypolophid is somewhat bent posteriorly. There is a cingulum around the posterior, labial, and anterior borders. The anterior cingulum is welldeveloped but it does not surpass the most anterior part of the paraconid.

M_2 — The talonid and the trigonid are of equal size. The entoconid crest is lower than in M_1. The oblique cristid is situated more lingually and the re-entrant valley ends closer to the cingulum than in the first molar. The labial valley is narrower than in M_1. There is a cingulum along the anterior, labial and posterior borders. The anterior cingulum is well developed and surpasses the anterior part of the paraconid. All other characteristics are similar to those of the first molar.

M_3 — The talonid is reduced but it has a closed talonid basin. In lingual view the oblique cristid is considerably higher than the entoconid crest. The entoconid is very low. The hypoconid, the paraconid and the metaconid are of equal height. The protoconid is

the highest cusp. The lingual re-entrant valley is wide, ending at the base of the molar. The trigonid valley is similar to that of the M_2. The cingulum is similar to that of M_2.

P^4 — The P^4 is characterized by a well-developed paracone, two small cusps (the parastyle and the protocone) and a postero-lingual emargination. This moderately developed emargination and the postero-labially elongated style give the posterior border a concave shape. The paracone is separated from the parastyle by a U-shaped valley. The protocone and the parastyle are connected by a very low and narrow ridge. A small hypocone is present. There is a cingulum-like ridge along the hypoconal flange, ending at the base of the protocone. There is a wide posterior cingulum, which ends at the postero-labial corner.

M^1 — As in the P^4 there is a moderate posterior emargination. The metastyle is longitudinally elongated. The metacone is the highest cusp, the protocone is the second highest. The paracone is lower and somewhat smaller than the metacone. The labial crests of the M^1 have an asymmetrical W-shape. The external metacone-valley is longer and wider than the external paracone-valley. The paraloph, running along the anterior border, connects the protocone to the base of the paracone. The sulcus between para- and metacone is rather deep. There is a cingulum along the hypoconal flange. Postero-labially the cingulum becomes wider and it ends at the posterior base of the metastyle.

M^2 — The dental pattern of the M^2 is more or less similar to that of M^1. I will mention the differences only. The M^2 is longer and narrower than the M^1. The metastyle is shorter than in the first molar, and the W-shape is more symmetric. The talon is less developed. The external sulci are of the same size and shape.

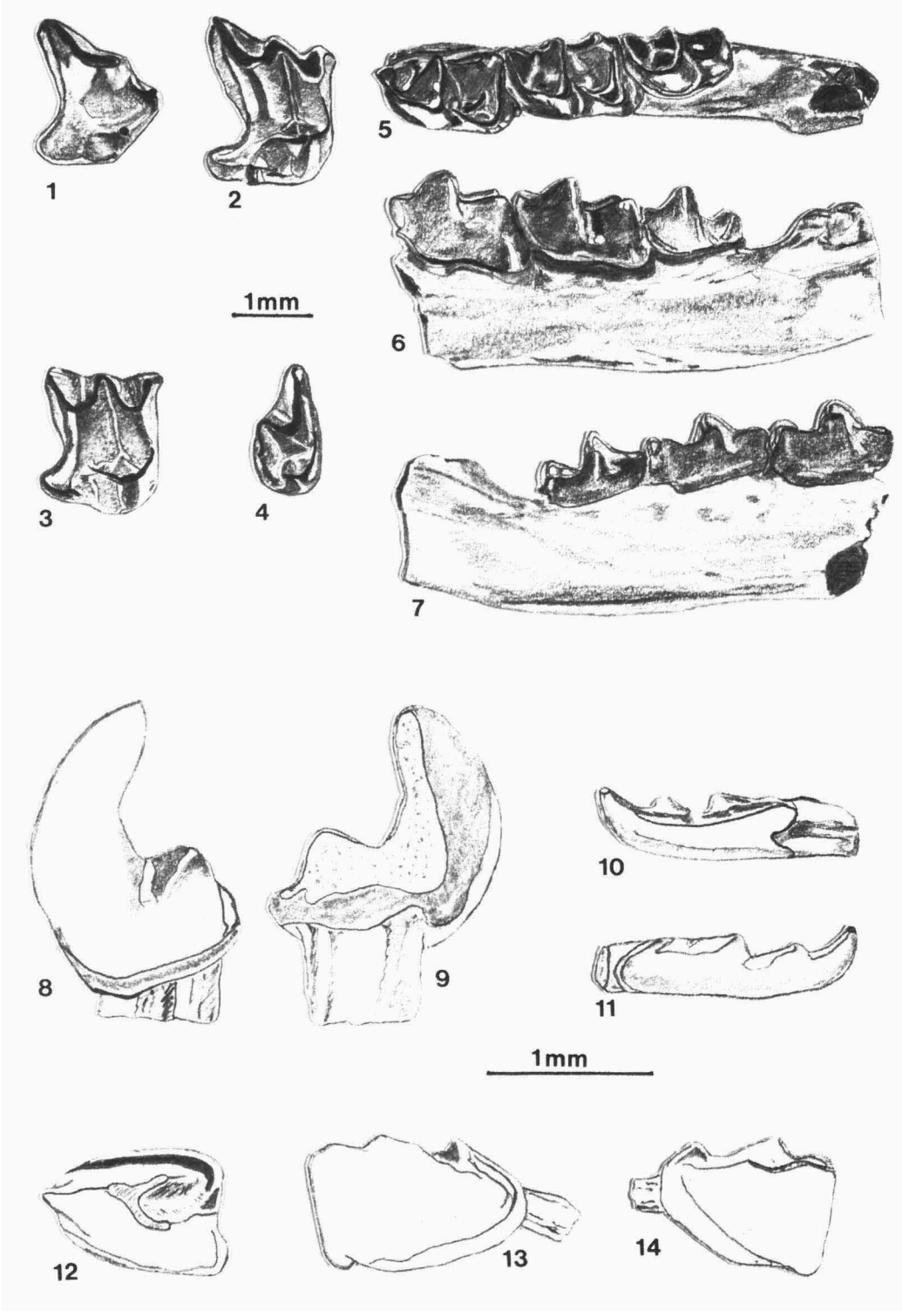
M^3 — The protocone is smaller and lower than the paracone. Metacone and hypocone are absent. The parastyle is well developed and elongated labially. There is a well-developed postmesocresta. There are no cingulums.

Discussion — The identification of the species described above as *Miosorex grivensis* is open to some doubt. This is due to the very subtle characteristics of the Miocene shrews and to the lack of sufficient knowledge of the European shrews from this period. Between *Crocidosorex antiquus* (Stehlin, 1940) and *Miosorex grivensis* there seems to be much resemblance. The mental foramen in *C. antiquus* is situated below the middle of P_4 (Stehlin, 1940), like it is in a number of mandibles of *M. grivensis*. The length of the tooth row M_1-M_3 is 3.25 mm (Viret & Zapfe, 1951). The main differences between the two

Plate 5

Miosorex aff. *grivensis* (Depéret, 1892)
Fig. 1. P^4 dext., Las Planas 5H, RGM 334 951.
Fig. 2. M^1 dext., Las Planas 5H, RGM 334 955.
Fig. 3. M^2 dext., Villafeliche 9, RGM 334 767.
Fig. 4. M^3 dext., Las Planas 5H, RGM 334 932.
Fig. 5. Mandible sin., M_1-M_3, Villafeliche 9, RGM 334 818.
Fig. 6. Idem, in labial view.
Fig. 7. Idem, in lingual view.
Fig. 8. I sup. dext., in labial view, Villafeliche 9, RGM 335 581.
Fig. 9. Idem, in lingual view.
Fig. 10. I inf. dext., in lingual view, Villafeliche 9, RGM 335 582.
Fig. 11. Idem, in labial view.
Fig. 12. P_4 sin., Las Planas 5K, RGM 334 976.
Fig. 13. Idem, in labial view.
Fig. 14. Idem, in lingual view.

Plate 5



species are: the bigger talonid of M_3, the presence of a hypoconulid in the lower molars, and the square shape of the upper molars in *C. antiquus*. In our material *M. grivensis* is larger than *C. antiquus* (Table 28). The dental elements of *C. antiquus* are pigmented if adequately fossilized (de Bruijn & Rümke, 1974). There is no pigmentation in *M. grivensis* from the Calatayud-Teruel Basin. The posterior border of the P^4 of *M. grivensis* is more concave than that of *C. antiquus*.

M. grivensis in Gibert (1974) is slightly larger than our material, although this difference may be due to different measuring techniques. The mental foramen is situated below the posterior root of P_4.

Baudelot (1972) described *Miosorex desnoyersianus* (Lartet, 1851) from Sansan. This species differs from *M. grivensis* by the following features: the oblique cristid of the first lower molar of *M. desnoyersianus* ends halfway the proto- and metaconid. In *M. grivensis* the oblique cristid is situated more labially. The talonid of the M_3 is less reduced in *M. desnoyersianus*, and the Sansan species is smaller.

Engesser (1972) recognized three groups of shrews in Anwil, none of which are determined down to the species level. He separates the groups on the basis of several characters among which are size, position of the mental foramen, and pigmentation. He supposes the middle-sized group to be *Miosorex grivensis*, which has three alveoli between the I_2 and the M_1. The mental foramen is situated below the distal root of P_4. The dental morphology and the size are similar to those of *M. grivensis* in this study. In our material the position of the mental foramen is variable. There is no relation between the position of the foramen and the stratigraphic level of the locality.

Paleoecology

Before discussing our results, it is worthwhile to consider the ecological conditions of extant insectivores. The majority of this group is living in areas with much vegetation. They avoid deserts (Grzimek, 1968) and prefer humid biotopes. According to Mares (1980) insectivores are of minor importance in dry ecosystems.

An other important feature of our paleoecological interpretation is the species diversity of all mammals within a certain ecosystem. A higher diversity depends on the following conditions (MacArthur, 1972):
more niche-diversity;
more complex biotope;
more favourable climate;
more stable climate;
more predation causes room for more species;
lower chance of catastrophes, such as fires and floods which may change the species composition (Delany, 1974).

The value of the insectivores as paleoecological indicators is generally not very great. It appears that there is a large variation of the occupied niches (Engesser, 1980). It is, for instance, not exceptional to find bovids, rhinoceroses and other arid-savannah-dwelling animals in combination with insectivores that indicate a wet biotope.

In this chapter an attempt will be made to give a paleoecological and paleoclimatic interpretation of the quantitative information of the insectivores from the Daroca-Calatayud area (Figs. 13, 14). The succession of the insectivore faunas is compared with the faunal succession of rodents in Daams & van der Meulen (1984). Van de Weerd &

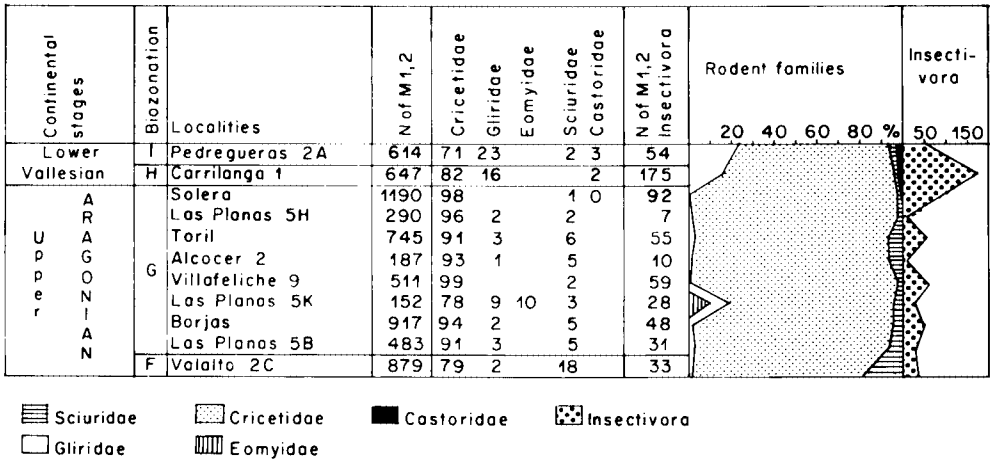


Fig. 13. Distribution of rodent families and insectivores (emended after Daams & Freudenthal, 1981).

Daams (1978) made some fundamental assumptions on the habitat of various rodent groups. These are:

1) Eomyidae were forest dwellers.
2) Beavers require streams permanently filled with water.
3) Ground squirrels live in dry open country.

In zones F and G, with the exception of Solera, the insectivores are represented by soricids and erinaceids in relatively low frequencies. According to Daams & van der Meulen (1984) zone E/F represents a relatively dry and warm interval, and in zone G there would be a trend towards a more humid and colder climate.

In the Upper Aragonian of the Daroca-Villafeliche area the insectivores are scarcely represented. There is a maximum of 18 % in Las Planas 5K and a minimum of 2 % in Las Planas 5H. In Las Planas 5K Eomyidae and a relatively large number of Glirinae are present, which are characteristic of wooded biotopes. The relatively high frequency of insectivores in Las Planas 5K coincides with a relatively large number of forest-dwelling Eomyidae and Glirinae. According to Daams & van der Meulen (1984) the Las Planas 5K fauna would represent a moister biotope than the other faunas of the Upper Aragonian.

In the uppermost Aragonian and the Lower Vallesian the relative frequency of the insectivores is higher than in the other localities. This coincides with a frequency increase of dormice (Gliridae), the entry of beavers (Castoridae) (Fig. 13), and scarcity ground-squirrels (Sciuridae). This interval is supposed to have represented a moister climate than the previous interval (Daams & van der Meulen, 1984).

The fossil Echinosoricidae sometimes have occupied the same niches as the extant species do (Engesser, 1980). The resemblance between *Galerix* and Echinosoricidae is minimal. There is only one recent species (*Uropsilus soricipes*) of Uropsilinae known. Its habitat is restricted to wooded areas above 1250 m and below 4500 m in East Asia. The fossil Uropsilinae in this study belong to *Desmanella*. In other paleoecological investigations there is some evidence that *Desmanella* inhabited wooded areas, probably with open water present (Engesser, 1980).

An increase (Fig. 14) in insectivore species number is observed in the Lower Vallesian (the presence of Talpidae and of *Crusafontina endemica*). This change may be

Continental stages	Biozonation	Localities	N of M1,2	Talpidae	Erinaceidae	Soricidae
Lower Vallesian	I	Pedregueras 2A	54	43	26	31
	H	Carrilanga 1	175		95	5
Upper ARAGONIAN	G	Solera	92		66	34
		Las Planas 5H	7		43	57
		Toril	55		78	22
		Alcocer 2	10		20	80
		Villafeliche 9	59		10	90
		Las Planas 5K	28		4	96
		Borjas	48		31	69
		Las Planas 5B	31		6	94
	F	Valalto 2C	33		67	33

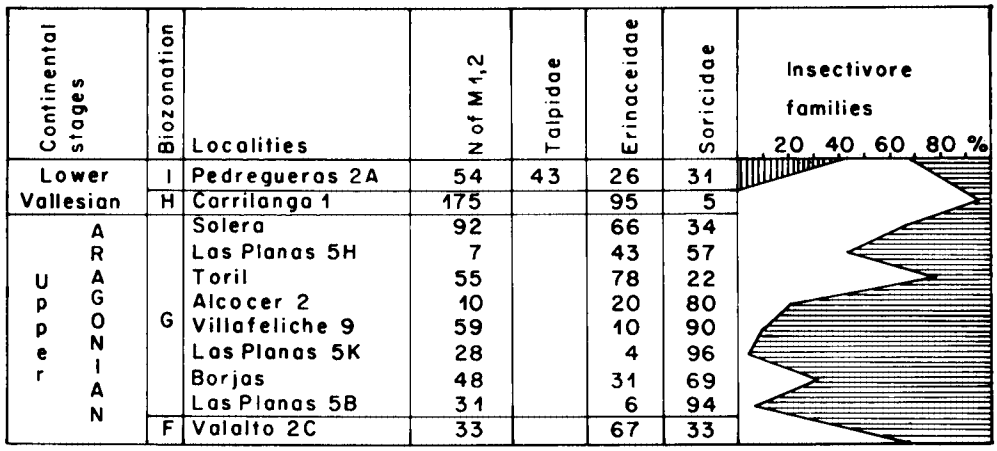


Fig. 14. Distribution of the insectivore families.

caused by the supposed climatic trend, towards lower mean annual temperatures and towards a higher humidity. The presence of the watermole *Desmanella crusafonti* in the Lower Vallesian corroborates this trend.

For *Galerix* and *Desmanella* the presence of water and trees is likely. Ziegler (1983) suggests the paleoclimate in the Miocene (Goldberg, Germany) to be comparable to that of the present Mediterranean area because of the ecology of *Galerix* species. Engesser (1980) suggests an environment of gallery forests for the Turkish Neogene on the basis of *Schizogalerix*. Concludingly it can be said that climatic trends in the Late Aragonian and Early Vallesian, deduced from the fossil record by Antunes & Pais (1984) and by Daams & van der Meulen (1984) fit well with the relative frequencies and species diversity of the insectivores.

Low insectivore species diversity and low frequencies are present in the larger part of the relatively dry and warm Late Aragonian and higher species diversity and frequencies are observed in the relatively humid and cool Early Vallesian.

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