Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain)

E. Martín Suárez & M. Freudenthal

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The fauna of Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, SE Spain) contains species attributed to the genera *Huerzelerimys*, *Parapodemus*, and *Occitanomys*. The material described allows a detailed biostratigraphy of Upper Miocene deposits of SE Spain.

Key words: Rodentia, Late Miocene, Spain.

En este trabajo se estudian tres géneros de Muridae (*Huerzelerimys*, *Parapodemus* y *Occitanomys*) procedentes de varios yacimientos del Mioceno final de Crevillente (Alicante). Las faunas encontradas permiten precisar la bioestratigrafía de los depósitos del Turoliense inferior del SE de España.

Palabras clave: Rodentia, Miocene final, España.

E. Martín Suárez, Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain; M. Freudenthal, Nationaal Natuurhistorisch Museum, Postbus 9517, NL-2300 RA Leiden, The Netherlands, and Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain.

Introduction

The aim of this paper is the study of the Muridae from a large number of fossiliferous localities in the area of Crevillente. The first fossil micromammal faunas from this area were reported by Montenat (1973) in his Doctor's thesis, which was published in 1977. These faunas were studied by de Bruijn et al. (1975). Since 1986 we have discovered quite a number of new fossiliferous localities in the same area.

These localities are situated in two sections, that were published by Freudenthal et al. (1991a). The sedimentary complex shows an alternation of continental and marine beds. The continental beds are formed by alluvial fan deposits, and marls and clays deposited in an environment of very calm water with occasional emersions. The marine beds in general are witnesses of more troubled water.

The Cricetidae from the same localities were published by Freudenthal et al. (1991b), resulting in a zonation on the basis of Cricetidae that will be compared in this paper with the results obtained from the study of the Muridae.

The material from the new localities is kept in the collections of the Nationaal Natuurhistorisch Museum (National Museum of Natural History, Leiden, The Netherlands).

Acknowledgements

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Dental terminology and measurement method

Measurements of the specimens were taken by means of the Leitz Ortholux measuring equipment described by Freudenthal (1966). An attempt was made to measure the murid teeth by means of a Wild M5 binocular microscope with ocular micrometer at 25 × enlargement. Unfortunately this method has to be rejected, because of the poor degree of repeatability. Measurements taken by a single person on the same specimen frequently vary in the amount of 2 divisions of the micrometer, which – at 25 ×

enlargement – represents an error of 0.08 mm. We consider an error of 0.01 mm as good, and 0.02 mm as acceptable; 0.03 may occur incidentally and larger values should only be accepted in special cases. A value of 0.08 is always unacceptable, because it is far beyond the amount of accuracy required in the study of rodent molars. The best result obtainable in the mentioned Wild system is a discriminatory value of 0.5 division, equal to 0.02 mm, which we consider almost the maximum acceptable error. One of the present authors (M.F.) investigated the possibilities of the Wild MMS 235 ocular measuring system with displacement of cross-hairs. Results were even worse than in the above described method. These problems are evidently due to the oblique objectives, which make refocusing during the measuring track impossible. Only absolutely flat – and horizontally oriented – surfaces can be measured accurately.

It is sometimes said, that such a degree of measuring error is irrelevant in comparison with the error caused by the difficulty of orientation, and differences due to the stage of wear of the specimen. However, orientation is a matter of definition, and differences due to wear can be evaluated, and, if need be, adjusted or corrected.

Orientation in fact is one of the major problems in measuring small-mammal specimens. When we started measuring our murid material we tried out the orientation used by van de Weerd (1976, fig. 9). We soon realized that his orientation of the specimens is subjective, and that various persons measuring specimens according to his orientation came to results that differed as much as 7 %, or more than 0.10 mm. In fact, the problem is, that van de Weerd does give some figures to explain the orientation, but he doesn't describe what points he uses as reference. So, the method applied by him remains vague. Since no objective orientation criteria for murid molars have been published as far as we know, we will propose such a method:

For each element a reference line is defined along which the specimen should be oriented. In M_1 and M_2 the reference line is not necessarily identical or parallel to the longitudinal crest. Length and width are measured as the smallest circumscribed rectangle with sides parallel and perpendicular to the reference line (Fig. 1).

M_1 — The reference line runs through the middle of the tooth at the union of anteroconid with protoconid-metaconid, and through the middle of the posterior wall. This orientation is less exact than we wished it to be, but it is the best we could find. Generally the reference line makes an angle of c. 10° with the longitudinal crest, and in *Parapodemus* and *Huerzelerimys* it frequently is perpendicular to the posterior border. In our material, when the specimen is oriented correctly, the width can nearly always be measured in a straight line over hypoconid and entoconid, and not over protoconid or metaconid.

M_2 — The reference line is the base of the anterior border of the molar. When this border is curved the labial part of it is taken. When the anterior accessory cusp protrudes over the base it is not taken into account for orientation (of course it is taken into account for the actual measurement).

M_3 — The reference line is the anterior border of protoconid-metaconid at the level of the wear surface. When this is not an approximately straight line, the anterior border of the protoconid is taken.

M^1 — The reference line is the tangent to the borders of t3 and t9. In practice this line is almost parallel to the line that connects the centers of t2, t5, and t8.

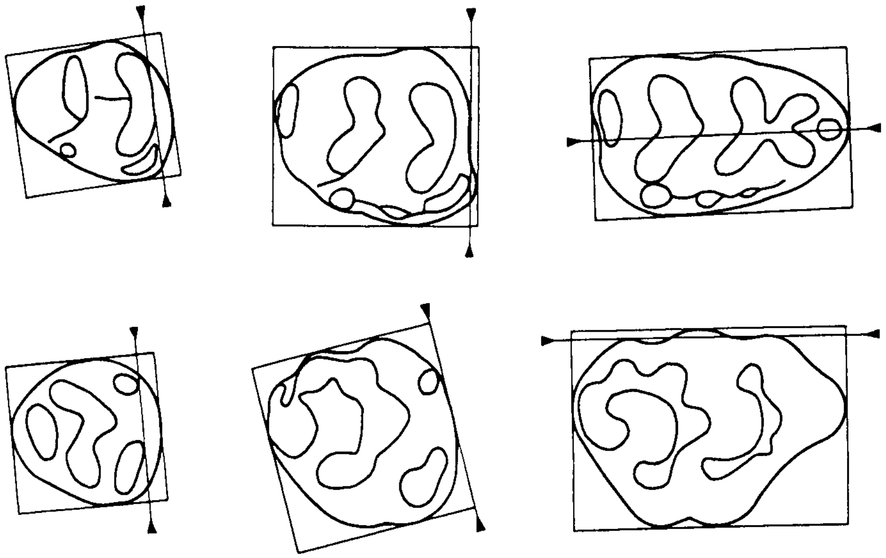

Fig. 1. Measuring method. The reference lines are indicated by triangles.

M^2 — The reference line is the tangent to the base of the anterior wall of the tooth, or, when this border is convex, the tangent to the labial part of this border.

M^3 — The reference line is the anterior border of the molar at the level of the wear surface.

Abbreviations

The following abbreviations for locality names are used:

ACE	Casa del Acero (Agustí et al., 1981)
AGUA	Los Aguanaces (Adrover, 1986)
ALJB	Aljezar B (Adrover, 1986)
AGUA	Aguanaces (Adrover, 1986)
AMB2C	Ambérieu 2C (Mein et al., 1993)
BAC	Baccinello V-1 (Engesser, 1989)
CC3	Concud 3 (van de Weerd, 1976)
CR	Crevillente (2, 4B, 7, 8, 15, 17: our data)
CCBL	Cascante-Cubla (Mein et al., 1993)
CUC	Cucalón (Mein et al., 1993)
DD	Dorn-Dürkheim (Franzen & Storch, 1975)
ECK	Eichkogel (Daxner-Höck, 1977)
LM	Los Mansuetos (van de Weerd, 1976)
MDV	Masada del Valle 2 and 5 (van de Weerd, 1976)
ML	Mollon (data in van de Weerd, 1976)
PERE	Peralejos E (van de Weerd, 1976)
PIK	Pikermi (de Bruijn, 1976)
PM	Puente Minero (Alcalá et al., 1991)
TO	Tortajada (van de Weerd, 1976)

TOA	Tortajada A (van de Weerd, 1976)
VDC3	Valdecebro 3 (van de Weerd, 1976)
VP	Vivero de Pinos (Adrover, 1986)

Taxonomic descriptions

Family MURIDAE Gray, 1821
Subfamily MURINAE Gray, 1821

Genus *Huerzelerimys* Mein, Martín Suárez & Agustí, 1993

Huerzelerimys vireti (Schaub, 1938)
Pl. 1, figs. 7-19.

Original reference — *Parapodemus? vireti* Schaub, 1938, pp. 24-26.

Type locality — Mollon (Dept. Ain, France).

Holotype — An isolated M^1 sin, P.L.61, deposited in the 'Naturhistorisches Museum', Basel.

Localities with H. vireti in the Crevillente area — Crevillente 2 (CR2), Crevillente 4B (CR4B); Crevillente 1, 2 and 3 in de Bruijn et al. (1975).

Measurements — See Tables 1-2 and Fig. 2.

Description of the material from Crevillente 2

M_1 — A small tma is present, which in 30 % of the specimens is a mere enamel fold. The anteroconid is symmetrical; its lingual lobe is generally connected to the metaconid. The labial cingulum is continuous and wide, with a very voluminous c1 and two more large cusps (in one specimen there are even three). The terminal heel is oval, smaller than c1. Among the specimens with roots, 37.5 % have only two roots, the other 62.5 % have a small third root between the main ones; this accessory root may occupy a central position or be placed slightly towards the labial border of the tooth.

M_2 — The anterolabial cuspid is very voluminous, isolated, and protrudes forward with respect to the anterior wall of the tooth. The labial cingulum is continuous, with a big c1 (though smaller than in M_1), and a second cuspid at the base of the protoconid; this second cuspid may be very small, or also larger than c1. The posterior heel is oval, bigger than c1 and smaller than the anterolabial cusp. There are two roots.

M_3 — The anterolabial cusp is well developed and isolated. The c1 is small or absent. The hypoconid-entoconid complex is slightly shifted towards the lingual side of the tooth. There are two roots.

M^1 — The t1 is placed slightly backwards, its internal wall forms an almost right angle with the posterior wall of the t2-t3 pair; it is column-shaped and not connected to the t5. At the anterior base of t2 there may be a small flange of enamel. Cusps t4 and t8 are connected by a high crest in 18 % of the specimens only; in the rest of the cases that connection is low. Cusps t6 and t9 are close together and convergent; in only 63 % of the specimens t6 and t9 are connected, in the rest of the cases the connection comes into existence at an advanced degree of wear. The t12 is voluminous and not integrated in the t9-t8 cingulum. There are three main roots, and a very small one under t5-t6.

M^2 — Rounded teeth; t1 and t3 isolated; t3 reduced. A high connection between t4 and t8 is present in 16.6 % of the cases. The connection t6-t9, present in 71 % of the specimens, is higher than in M^1; t9 is a bit smaller than t6; t12 is isolated and large (though smaller than it is in M^1). Generally there are four roots, occasionally there are three, in which case the lingual root is double.

M^3 — The t1 is large and isolated; t3 is small, but clearly distinguishable. The t8 is also isolated, and remains so until a very advanced degree of wear. There are three roots, none of them double.

Description of the material from Crevillente 4B

In order not to repeat the descriptions, we will only mention the differences existing between the material from CR2 and CR4B.

M_1 — The tma is present in half the material, absent in the other half. The labial lobe of the anteroconid is slightly smaller than the lingual one; the latter one is connected to the metaconid, except for two cases. The labial cingulum and accessory cusps are somewhat more reduced than in CR2. There are two main roots and a small central one in the four specimens in which roots are conserved.

M_2 — The anterolabial cusp is slightly more reduced than in the specimens from CR2. In all other respects the material is identical with that from CR2.

M_3 — The anterolabial cusp is a bit smaller than the CR2 material. In all other

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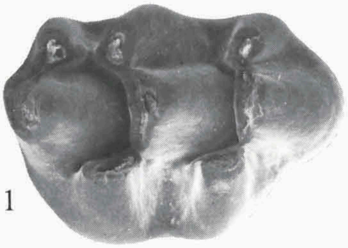
Plate 1

Huerzelerimys turoliensis (Michaux, 1969) from Crevillente 15
Fig. 1. M^1 dext., RGM 403 833.
Fig. 2. M^2 sin., RGM 403 848.
Fig. 3. M^3 dext., RGM 403 881.
Fig. 4. M_1 dext., RGM 403 760.
Fig. 5. M_1 dext., RGM 403 768.
Fig. 6. M_2 dext., RGM 403 784.

Huerzelerimys vireti (Schaub, 1938) from Crevillente 4B
Fig. 7. M^1 sin., RGM 404 046.
Fig. 8. M^2 sin., RGM 404 093.
Fig. 9. M^2 dext., RGM 404 121.
Fig. 10. M_1 sin., RGM 403 979.
Fig. 11. M_2 sin., RGM 404 005.
Fig. 12. M_3 sin., RGM 404 044.

Huerzelerimys vireti (Schaub, 1938) from Crevillente 2
Fig. 13. M^1 sin., RGM 402 373.
Fig. 14. M^1 dext., RGM 402 384.
Fig. 15. M^2 dext., RGM 402 393.
Fig. 16. M^3 sin., RGM 402 400.
Fig. 17. M_1 sin., RGM 402 325.
Fig. 18. M_2 dext., RGM 402 359.
Fig. 19. M_3 sin., RGM 402 363.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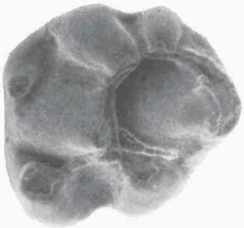
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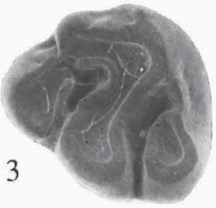
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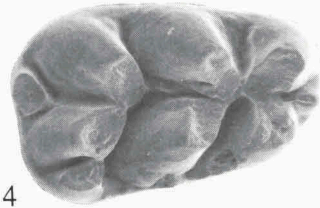
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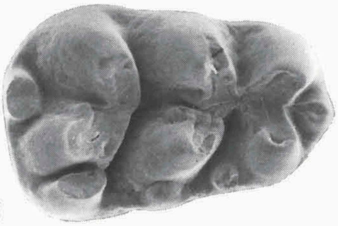
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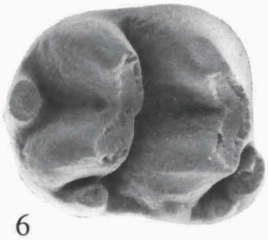
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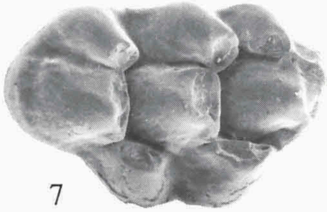
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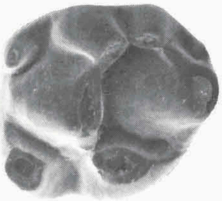
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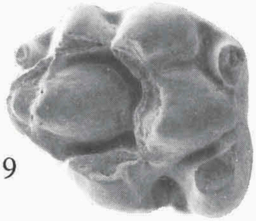
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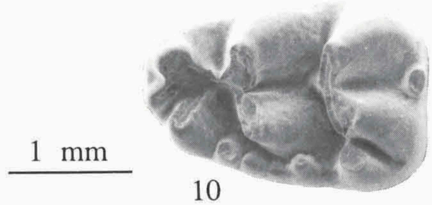

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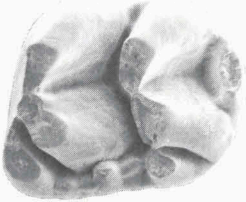
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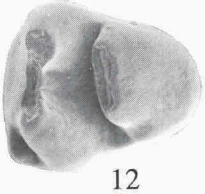
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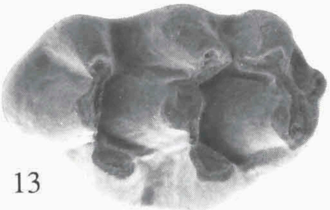
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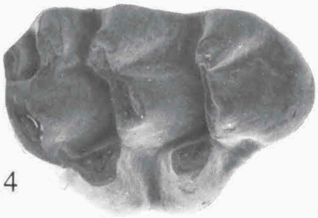
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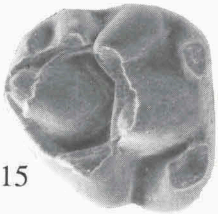
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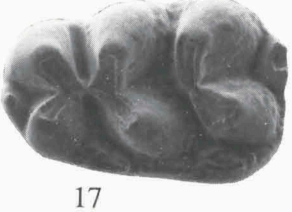
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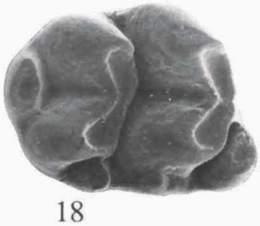
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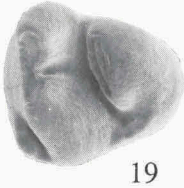
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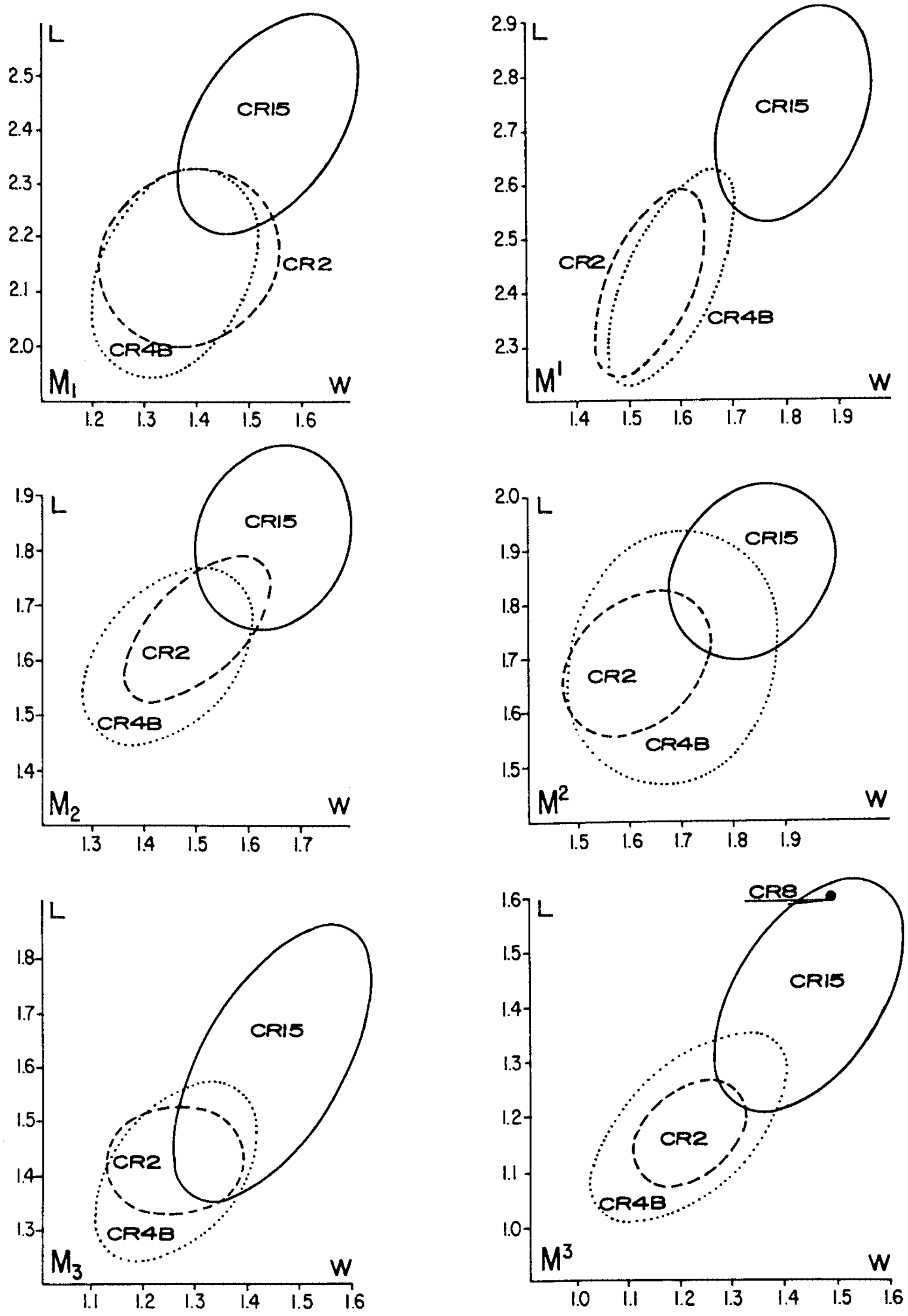


Fig. 2. Length/width diagrams of the molars of *Huerzelerimys vireti* from CR2 and CR4B, and *H. turoliensis* from CR15 and CR8. For explanation of symbols see Fig. 8.

Table 1. Measurements of the lower molars of *Huerzelerimys*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M_1													
CR15	20	2.26	2.398	2.58	13.22	0.093	23	1.43	1.520	1.67	15.48	0.075	1.58
CR4B	25	2.00	2.134	2.32	14.81	0.080	27	1.25	1.350	1.48	16.85	0.060	1.58
CR2	16	2.06	2.147	2.26	9.26	0.056	16	1.23	1.366	1.50	19.78	0.064	1.57
M_2													
CR15	21	1.67	1.857	1.97	16.48	0.073	22	1.53	1.639	1.74	12.84	0.056	1.13
CR4B	37	1.49	1.615	1.72	14.33	0.058	35	1.30	1.475	1.58	19.44	0.057	1.09
CR2	18	1.54	1.644	1.78	14.46	0.065	18	1.39	1.493	1.60	14.05	0.067	1.10
M_3													
CR15	15	1.39	1.592	1.81	26.25	0.117	15	1.32	1.425	1.62	20.41	0.082	1.12
CR4B	22	1.27	1.374	1.55	19.86	0.064	25	1.14	1.255	1.34	16.13	0.059	1.09
CR2	7	1.35	1.423	1.48	9.19	0.043	8	1.16	1.284	1.38	17.32	0.073	1.11

Table 2. Measurements of the upper molars of *Huerzelerimys*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M^1													
CR15	19	2.56	2.731	2.91	12.80	0.106	25	1.70	1.812	1.92	12.15	0.072	1.51
CR4B	22	2.24	2.422	2.61	15.26	0.090	24	1.49	1.575	1.69	12.58	0.049	1.54
CR2	8	2.26	2.466	2.56	12.45	0.094	8	1.46	1.566	1.62	10.39	0.051	1.57
M^2													
CR15	22	1.73	1.865	2.01	14.97	0.069	23	1.72	1.817	1.95	12.53	0.064	1.03
CR4B	36	1.47	1.683	1.83	21.82	0.075	40	1.45	1.566	1.74	18.18	0.056	1.07
CR2	14	1.57	1.668	1.78	12.54	0.056	14	1.52	1.593	1.71	11.76	0.063	1.05
M^3													
CR8	1		1.600				1		1.480				1.08
CR15	24	1.24	1.424	1.58	24.11	0.082	24	1.30	1.439	1.59	20.07	0.065	0.99
CR4B	19	1.06	1.185	1.28	18.80	0.076	18	1.05	1.228	1.36	25.73	0.083	0.96
CR2	9	1.11	1.174	1.25	11.86	0.050	9	1.12	1.207	1.28	13.33	0.059	0.97

respects the material is identical with that from CR2.

M^1 — In two specimens there is a short posterior spur at the base of t1, which reaches the base of the t5. The crest between t4 and t8 is found in 28 % of the specimens; t6 and t9 are connected in 71 % of the specimens. The t12 is somewhat more reduced in CR4B than in CR2, without, however, being integrated in the cingulum t9-t8.

M^2 — The crest connecting t4-t8 is found in 20 % of the specimens, slightly more frequent than in CR2. The t3 is present, and t12 is a bit more reduced than in the population from CR2.

M^3 — The t6-t8 connection is better developed than in CR2: it appears already in specimens with a lesser degree of wear.

Remarks — There are no significant differences between the populations from CR2 and CR4B. There are, however, some minor differences:

In the M_1 the anteroconid is somewhat asymmetrical in CR4B and more frequently connected to the metaconid than in CR2; there is a slight reduction of the cingulum and of the size of the accessory cuspids in the lower molars from CR4B. In the M_2 and M_3 from CR4B the anterolabial cuspid is smaller.

In the upper molars the connections t4-t8 and t6-t9 are more frequent in CR4B than in CR2. In CR4B the t12 is slightly reduced, but it is never integrated in the cingulum t9-t8. In M^2 the t3 is somewhat smaller in the material from CR4B. In the M^3 from CR4B the t8 looses its isolated state earlier: in similar wear stages the t8 is isolated in CR2 and connected to t6 in CR4B.

There are no differences in the number, nor in the shape and disposition of the roots.

The size is very similar in both populations, even slightly smaller in CR4B, which is the younger locality of the two (Fig. 2).

In both cases, the intrapopulational variability (morphologically and biometrically) is at least as high as the interpopulational variability.

Comparison of our material with other European populations

— With respect to various populations of *H. minor* Mein et al., (1993, this volume) the material from Crevillente is of larger size; the connections anteroconid-metaconid in M_1, and t4-t8 and t6-t9 in M^1 and M^2 are more frequent in *H. vireti* from CR2 and CR4B. The third root of M_1 is larger in the Crevillente populations.

— The M_1 of *Huerzelerimys vireti* from CR2 and CR4B have more frequently a tma than those from Puente Minero (Alcalá et al., 1991). The tma is also more frequent in CR2 and CR4B than in the populations from other localities near Teruel, that were studied by Adrover (1986) and van de Weerd (1976).

— In the lower molars from CR2 and CR4B the longitudinal connections between the pairs of cusps are less frequent than in the localities near Teruel. On the other hand the labial and posterior cingulums, as well as the anterolabial cuspid of M_2 and M_3, are better developed in the material from CR2 and CR4B.

— The roots of the lower molars show the same pattern both in the populations from Crevillente and from Teruel.

— In the M^1 and M^2 from CR2 and CR4B the lingual and labial longitudinal spurs (of t1 and t3) do hardly exist, whereas they are frequent in the populations from Teruel (see Adrover, 1986; Alcalá et al., 1991; van de Weerd, 1976). The frequency with which t6 and t9 are connected is similar in all these populations. The t12 is a distinct cusplet and bigger in Crevillente than it is in the Teruel populations.

— In M^3 the t3 is somewhat larger in Crevillente than in Teruel and the t8 remains isolated in a more advanced wear stage.

— There are no differences in the roots of the upper molars of the various populations.

— The dimensions of *Huerzelerimys vireti* from CR2 and CR4B are similar to those of the populations from Aguanaces and Vivero de Pinos (Adrover, 1986); from Mollon, the type-locality (Schaub, 1938, measurements after van de Weerd, 1976); Tortajada A, Alfambra and Valdecebro 4 (van de Weerd, 1976); Puente Minero (Alcalá et al., 1991), etc. (Fig. 3).

The populations of *Huerzelerimys vireti* from CR2 and CR4B show characters

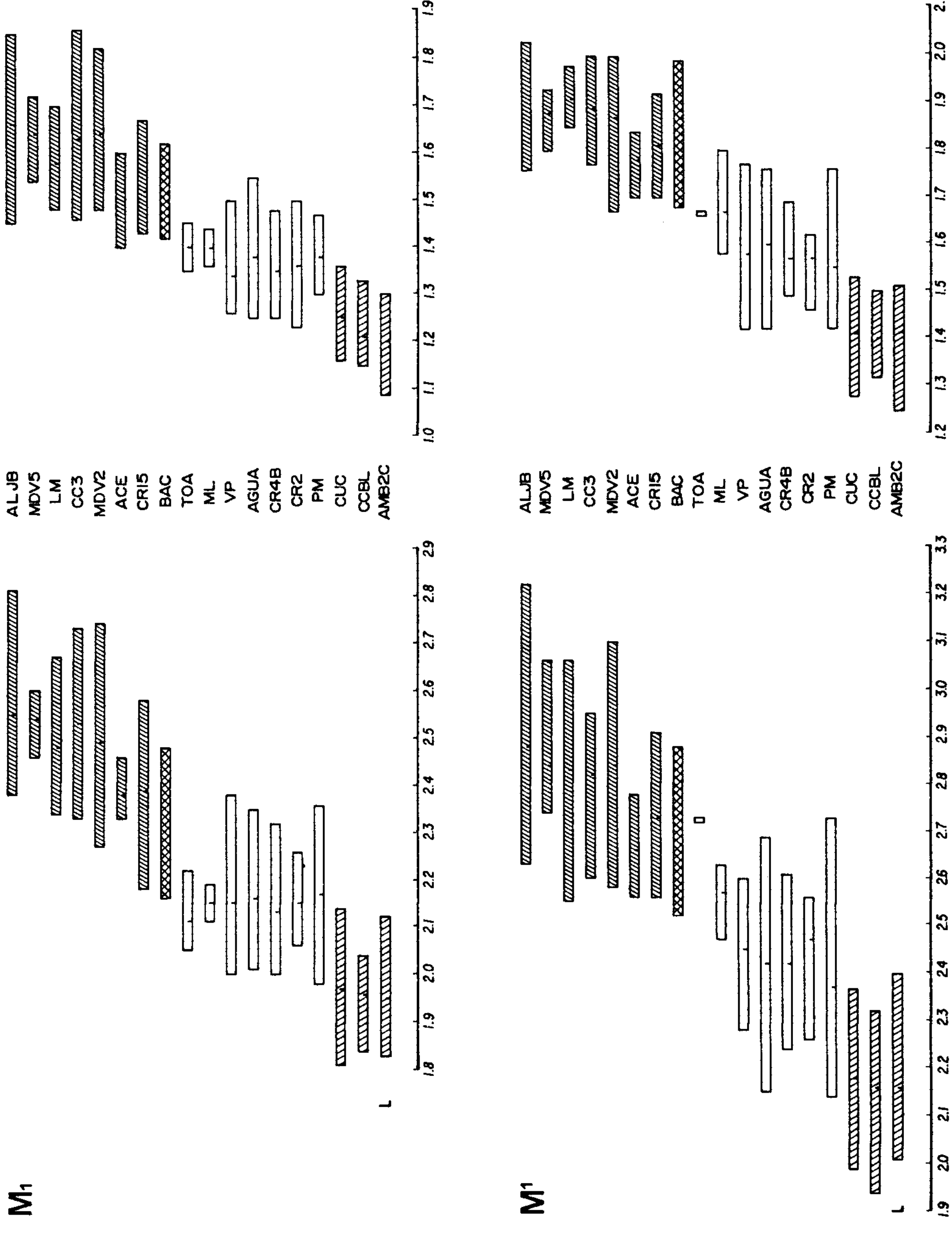


Fig. 3. Size ranges for length and width of the first molars of *Huerzelerimys* from several localities in Western Europe.

that may be considered as plesiomorphic in the evolution of the group, like the poor development of longitudinal connections between cusps (anteroconid-metaconid, t1-t5, t4-t8, t6-t9), well-developed t12, large accessory cuspids, etc. This, together with their dimensions which are similar to, or smaller than those of the other populations, makes us think, that CR2 and CR4B are, for the moment, among the oldest localities in which *Huerzelerimys vireti* has been found.

Huerzelerimys turoliensis (Michaux, 1969)
Pl. 1, figs. 1-6.

Original reference — *Valerymys turolienis* Michaux, 1969, p. 23.
Selected subsequent reference — *Anthracomys majori* Schaub, 1938 in Thaler (1966, p. 118).

Type-locality — Los Mansuetos (Teruel, Spain).

Holotype — A maxilla with M^1-M^2, RA 141, deposited in the 'Institut de Paleontologia Miquel Crusafont', Sabadell (Spain).

Localities with H. turoliensis in the Crevillente area — Crevillente 5A (CR5A), Crevillente 15 (CR15), Crevillente 8 (CR8), Crevillente 4 and 5 in de Bruijn et al., 1975.

Measurements — See Tables 1-2 and Fig. 2.

Description of the material from Crevillente 15

M_1 — A tma is present and well-developed in 86 % of the cases. The lingual lobe of the anteroconid is connected to the metaconid (except for one specimen), even in little-worn teeth. In 59 % of the molars either protoconid, or metaconid or both these cusps develop one or two enamel folds, that present themselves as very short posterior spurs, and taper out at the very base of the cusp. The labial cingulum is continuous, with a c1 of medium size or large. There may be up to two more accessory cusps, variable in shape, size and position. The terminal heel is very variable, high or very low, oval-rounded or blade-like, in the majority of the specimens rather reduced. There are two main roots and a small one under the protoconid.

M_2 — The anterolabial cuspid is big and isolated, somewhat protruding forward with respect to the anterior border of the tooth. Contrary to the situation in M_1, only one specimen has a small enamel fold on the posterolingual wall of the protoconid. The labial cingulum is reduced, with a rarely voluminous c1, and a small bulge of enamel at the base of the protoconid. The terminal heel is oval and similar in size to the anterolabial cuspid; it is absent in one specimen. There are two roots.

M_3 — The anterolabial cuspid is very well developed (67 %) or very much reduced (33 %). The c1 is very much reduced or absent. The high degree of size variability is caused by the varying size of the anterolabial cuspid. There are two roots. One specimen, RGM 403 799 is very large, and has rugose enamel; the hypoconid-entoconid complex is relatively broader than in the rest of the specimens.

M^1 — The t1 is placed backwards, in 28 % of the specimens there is a trace of a t1-t5 connection. Four specimens have a very small t1bis. There is a ridge at the base of the anterior wall of the t2 in 33 % of the cases. Cusp t4 is connected to t8 by a crest in 33 % of the specimens. Cusps t6 and t9 are of similar size, and united, although in some unworn specimens the tops are separated. The t12 is reduced to a widening of the t9-t8 cingulum. Among the specimens with preserved roots the following pattern is seen: the anterior, posterior and a small central root are always present; on the lingual side there may be a furrowed root (5 specimens) or two roots (4 specimens); so, the total number of roots is four of five.

M^2 — The t1 is isolated, only in two cases there is a trace of a longitudinal connection; t3 is small. The t4 is separated from the t8; in one specimen the t4 is split into two. Cusps t6 and t9 are generally connected; the t9 is reduced, of about the same size as the t3. The t12 is very much reduced or absent. Ten specimens have their roots preserved; eight of them have four, and two of them have three roots, the lingual root being grooved.

M^3 — The t1 is isolated; t3 is reduced or absent. In little-worn teeth the t8 may be connected to or separated from the t6. There are twelve specimens with roots; eight of them have four roots and the other four have three roots; in two of these four specimens the anterior root is grooved, in the other two the lingual root is grooved (Fig. 4).

Remarks — Crevillente 5A is a very poor locality, and has only yielded six specimens of *Huerzelerimys*; morphologically they are similar to the material from CR15.

Crevillente 8 has yielded a total of 192 specimens, among which one single M^3 belongs to *Huerzelerimys turoliensis*.

Comparison with the collection of *Huerzelerimys turoliensis* from its type-locality Los Mansuetos (coll. IVA, Utrecht) shows that the dimensions of the material from CR15 are slightly smaller (Fig. 3). In both populations small accessory cusps are frequent in various points of the M^1. In the M^2 from Los Mansuetos, the t9 is smaller than or equal to the t3, being somewhat more reduced than in CR15. In the M_1 from CR15 the tma is more frequent than in those from Los Mansuetos.

De Bruijn et al. (1975) describe a M^1 of *Huerzelerimys* from Crevillente 4, that they attribute to *H. vireti-turoliensis*, because its size is intermediate between both species. In our opinion this specimen should be attributed to *H. turoliensis*, with t12 reduced to a small widening of the cingulum t9-t8, and a longitudinal connection that runs from the t1 to the center of the lingual wall of t5; it is a small specimen, but some

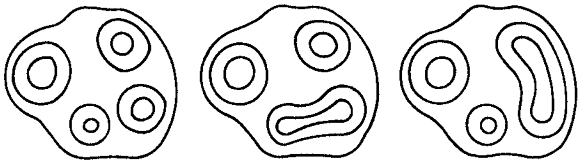


Fig.4. Roots of the M^3 of *Huerzelerimys turoliensis* from CR15.

specimens from CR15 are even smaller.

H. oreopitheci from Baccinello (Engesser, 1989) is somewhat smaller than *H. turoliensis*. Morphological differences are: the well-developed tma in the majority of the M_1 from CR15, the absence of t12 in the M^1 and M^2 from CR15, and the different number of roots in the upper molars. According to its author, *H. oreopitheci* has hypsodont molars as an adaptation to insular isolation (Engesser, 1989, p. 232).

In Sabadell we studied part of the collection from Casa del Acero on which the paper by Agustí et al. (1981) is based. This led to the conclusion, that *Huerzelerimys turoliensis* from Casa del Acero has molars with higher crowns. In the upper molars from Casa del Acero the transverse connections between the cusps, specially t1-t2 and t4-t5, are very high; in CR15, on the other hand, they are low. Half the M^1 from Casa del Acero have a spur that connects t1 with the center of the lingual wall of t5; such a connection is less frequent in CR15. In Casa del Acero there are no accessory cusps in the M^1, whereas such cusps are frequent in CR15 and in Los Mansuetos. In the M^2 from Casa del Acero there exists a very small fifth root, which is not present in CR15. All these differences seem to indicate that Casa del Acero is younger than CR15, although *H. turoliensis* from CR15 is larger.

Dr Adrover provided us with a collection from Aljezar B. *H. turoliensis* from Aljezar B is much larger than the material from CR15. However, there are hardly any morphological differences, except for the reduction of the tma, and the better developed connection t6-t9 in the M^1 of *H. turoliensis* from Aljezar B. 29 % of the M^2 from Aljezar B have five roots.

In CR8 we have found one single M^3, that is much larger than the specimens from CR15; morphologically it is identical, and its size agrees with the specimens of *H. turoliensis* from Aljezar B.

Discussion

From *Huerzelerimys vireti* (CR2 and CR4B) towards *H. turoliensis* (CR15) there is a considerable increase in size (Fig. 2) and several shifts of character states, but there is no clear-cut break. In the lower molars there is a certain reduction of the cingulums, specially of the terminal heel in M_1. There also is a slight trace of a longitudinal spur in *H. turoliensis*. The lower molars show no change in the pattern of the roots between these two species.

The upper molars show a slight trace of a t1-t5 connection in some specimens of *H. turoliensis*; the most significant differences are found in the t12; this cusp is individualized in *H. vireti*, and it is integrated in the cingulum in *H. turoliensis*. In the M^3 of *H. turoliensis* the t3 tends to disappear. There are clear differences in the disposition of the roots: in the M^1 of *H. turoliensis* the lingual root is grooved or subdivided. In the M^2 the size and disposition of the roots are alike in both populations. The M^3 of *H. vireti* from CR2 and CR4B have three roots, none of which is grooved or split; in *H. turoliensis* there are four roots or three roots, one of which is grooved (Fig. 4).

The localities CR2 and CR4B have yielded populations of *Huerzelerimys vireti*, that are very similar in size and morphology, though the size of the molars from

CR4B is somewhat less than in the case of CR2. This is an unexpected feature, in view of the stratigraphic position of the localities (see Freudenthal et al., 1991a): CR2 is lower than CR4B, and in-between them are beds with signs of a marine ingression. Between CR4B and CR15 there is also a bed that shows signs of a transgression; in the time elapsed between the deposition of these localities a faunal change takes place, that affects not only *Huerzelerimys*, but the entire fauna (for the Cricetidae see Freudenthal et al., 1991b).

The only localities younger than CR15 that have yielded *Huerzelerimys* are CR8 (only one M^3) and CR5 studied by de Bruijn et al. (1975), with a single M_3. We suppose that the deposition of these two levels (which may be identical) coincides with a decline of *H. turoliensis* before this species disappeared completely from the area.

'*Valerymys juniensis*' from Canteras de Jun is intermediate in size between *H. vireti* and *H. turoliensis* (Padial Ojeda et al., 1989), but its morphology is not intermediate, as we have been able to confirm through direct comparison, thanks to the kindness of Dr Ruiz Bustos. The faunal assemblage of Canteras de Jun (Brandy, 1979, Padial Ojeda, 1986, and our own collection) proves that this locality must be younger than Los Mansuetos, the type-locality of *H. turoliensis*; this means, that '*V. juniensis*' cannot be an intermediate form between *H. vireti* and *H. turoliensis*. In our opinion this species from Canteras de Jun is a large-sized *Parapodemus* form (see Mein et al., this volume).

The origin of the species included in *Huerzelerimys* must be sought in some population of *Progonomys cathalai*. At the beginning of the latest Vallesian various lineages arise from that species in Western Europe: on the one side *P. woelferi*, and on the other side *Huerzelerimys minor*, which stands at the basis of the evolution of the rest of the species of that genus (Mein et al., 1993). The theory that *Progonomys woelferi* be a possible ancestor of *Huerzelerimys* (van de Weerd, 1976) must be rejected, since *P. woelferi* has been found in later levels than the oldest localities with *Huerzelerimys*; moreover, the oldest populations of *H. minor* contain specimens of smaller size and with a more derived morphology than the contemporaneous and younger populations of *P. woelferi*.

In this way, the populations from CR2 and CR4B might be placed as descendants of *H. minor*, among the first representatives of *H. vireti*, in which the connection t6-t9 has gained importance, though it never becomes complete during the entire existence of the genus.

It is hard to say whether *Huerzelerimys turoliensis* from CR15 is a descendant in situ of *H. vireti* from CR4B or whether it is an immigrant in the region. The second hypothesis is more probable, since its appearance coincides with a complete renewal of the fauna.

Genus *Parapodemus* Schaub, 1938

Type-species — *Mus gaudryi* Dames, 1883. For details on this type-species see the discussion on p. 96.

Parapodemus lugdunensis Schaub, 1938
Pl. 2, figs. 1-14.

Original reference — *Parapodemus lugdunensis* Schaub (1938, pp. 26-27).

Holotype — An isolated M^1, P.L.63, deposited in the 'Naturhistorisches Museum', Basel.

Type-locality — Mollon (Dept. Ain, France).

Localities with P. lugdunensis in the Crevillente area — Crevillente 2 (CR2), Crevillente 4B (CR4B), Crevillente 1, 2 and 3 by de Bruijn et al. (1975).

Measurements — See Tables 3-4 and Figs. 5, 16, 17.

Description of the material from Crevillente 4B

M_1 — The tma is always present and isolated. The anteroconid is symmetrical, with its cusps separated in little-worn specimens; its lingual lobe is connected to the metaconid in almost all cases. The labial cingulum is continuous and broad, with a big c1 (larger than the tma), connected to the hypoconid; there is always an accessory cuspid, next to the protoconid, and there may be another one between protoconid and anteroconid. The posterior heel is well developed, oval or blade-shaped. Among the specimens with preserved roots 40 % have two main roots, and the remaining 60 % have a vestigial third root.

M_2 — Anterior and posterior width are almost identical. The anterolabial cuspid is high and voluminous. The labial cingulum is continuous, with a well-developed c1, and another accessory cusp, attached to the protoconid. The posterior heel is oval or blade-shaped. There are two roots.

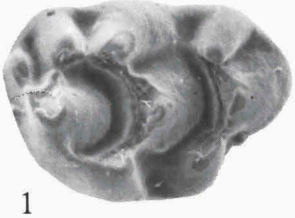
M_3 — The anterolabial cuspid is well developed. The hypoconid-entoconid complex is voluminous. The c1 is reduced to a mere enamel fold or absent. There are two roots.

Plate 2

Parapodemus lugdunensis Schaub, 1938 from Crevillente 4B
Fig. 1. M^1 dext., RGM 404 306.
Fig. 2. M^1 sin., RGM 404 288.
Fig. 3. M^2 sin., RGM 404 339.
Fig. 4. M^3 dext., RGM 404 348.
Fig. 5. M_1 dext., RGM 404 181.
Fig. 6. M_1 sin., RGM 404 168.
Fig. 7. M_2 dext., RGM 404 240.
Fig. 8. M_3 dext., RGM 404 282.

Parapodemus lugdunensis Schaub, 1938 from Crevillente 2
Fig. 9. M^3 dext., RGM 403 609.
Fig. 10. M^1 dext., RGM 402 502.
Fig. 11. M^1 sin., RGM 402 484.
Fig. 12. M_3 sin., RGM 413 583.
Fig. 13. M_1 dext., RGM 402 446.
Fig. 14. M_2 sin., RGM 402 451.

Parapodemus sp. from Crevillente 2
Fig. 15. M_1 dext., RGM 402 441.
Fig. 16. M^1 sin., RGM 402 495.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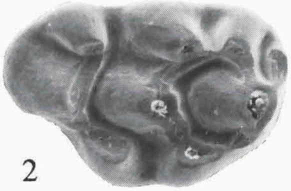
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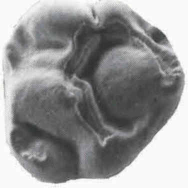
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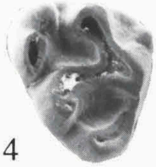
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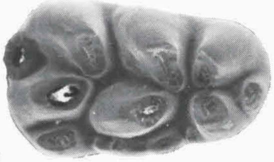
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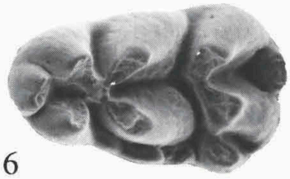
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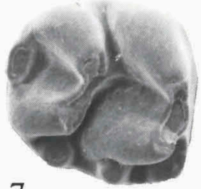
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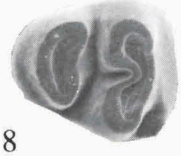
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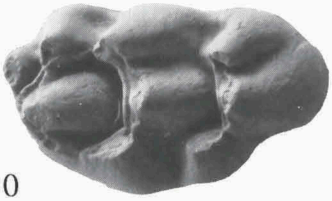
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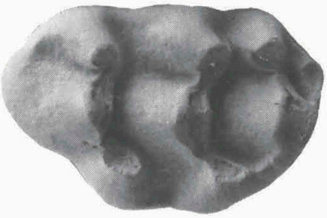
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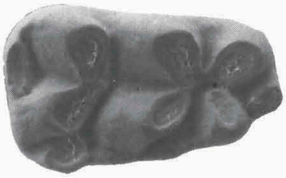
1 mm


12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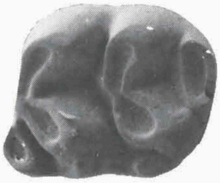
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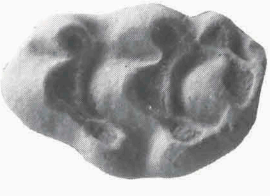
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M^1 — The t1 is close to the t2 and not connected to the t5. Only in one case (RGM 404 305) the t3 presents a small posterior spur. The t4 is connected to the t8 by a high and continuous crest. t6 and t9 are connected (except for the specimen RGM 404 312). t12 is oval-shaped, very voluminous and protuberant from the posterior wall of the tooth, forming a deep posterosinus. There are three main roots, plus a tiny one in the center of the tooth.

M^2 — The t1 is voluminous and t3 very reduced; both are isolated (90 %) or both are connected to the anterior wall of the t5 (10 %). In two specimens there is a t1bis. Cusp t4 is connected to t8 by a crest, which is lower than the homologous one in M^1. The t6 and t9 are convergently but weakly connected. In a few cases t9 is not connected to the t8. The t12 is big, but smaller than in M_1, and does not form a posterosinus. There are three roots.

M^3 — The t1 is large, oval-shaped, protruding lingually, and connected to the anterolingual wall of the t4; t3 is small, but present. In half the specimens the t9 is somewhat separated from the t8, and both cusps form a broad, constricted tubercle. Generally there are three roots, except for one specimen, that has two roots because the anterior ones are fused.

Description of the material from Crevillente 2

Although the locality CR2 is older than CR4B, we have given a full description of the population from CR4B because it is more numerous; we will now describe the differences encountered in the material from CR2.

M_1 — There are two specimens without tma. The only difference observed in comparison with CR4B is, that in the specimens from CR2 the connection between the anteroconid and the metaconid is somewhat weaker. In 50 % of the specimens there are two roots, in the other 50 % there is a very small third root, which occupies a centrolingual position.

M_2 — There are no differences in comparison with CR4B.

M_3 — There are no differences in comparison with CR4B. The anterolabial cuspid is big and high; c1 is linked to the hypoconid.

M^1 — The only difference observed is, that the stephanodonty is less-marked in the population from CR2, or, in other words, the connection t6-t9 is more complete in CR4B.

M^2 — Cusps t1 and t3 are generally isolated; t6 and t9 are convergent, but their tips are rarely connected. The t9 is sometimes separated from the t8.

M^3 — The t8 and t9 form one single tubercle; only in one case this tubercle is constricted. There are three roots.

Remarks — There are some small differences between the populations from CR2 and

---

Fig. 5. Length/width diagrams of the molars of *Parapodemus lugdunensis* from CR2 and CR4B, *Parapodemus* sp. from CR2, *P. barbarae* from CR15 and CR8, and *P. meini* from CR8 and CR7. For explanation of symbols see Fig. 8. CR2* represents *Parapodemus* sp. from Crevillente 2. CR8* with striped pattern represents *Parapodemus barbarae* and CR8 with discontinuous line represents *P. meini* from CR8.

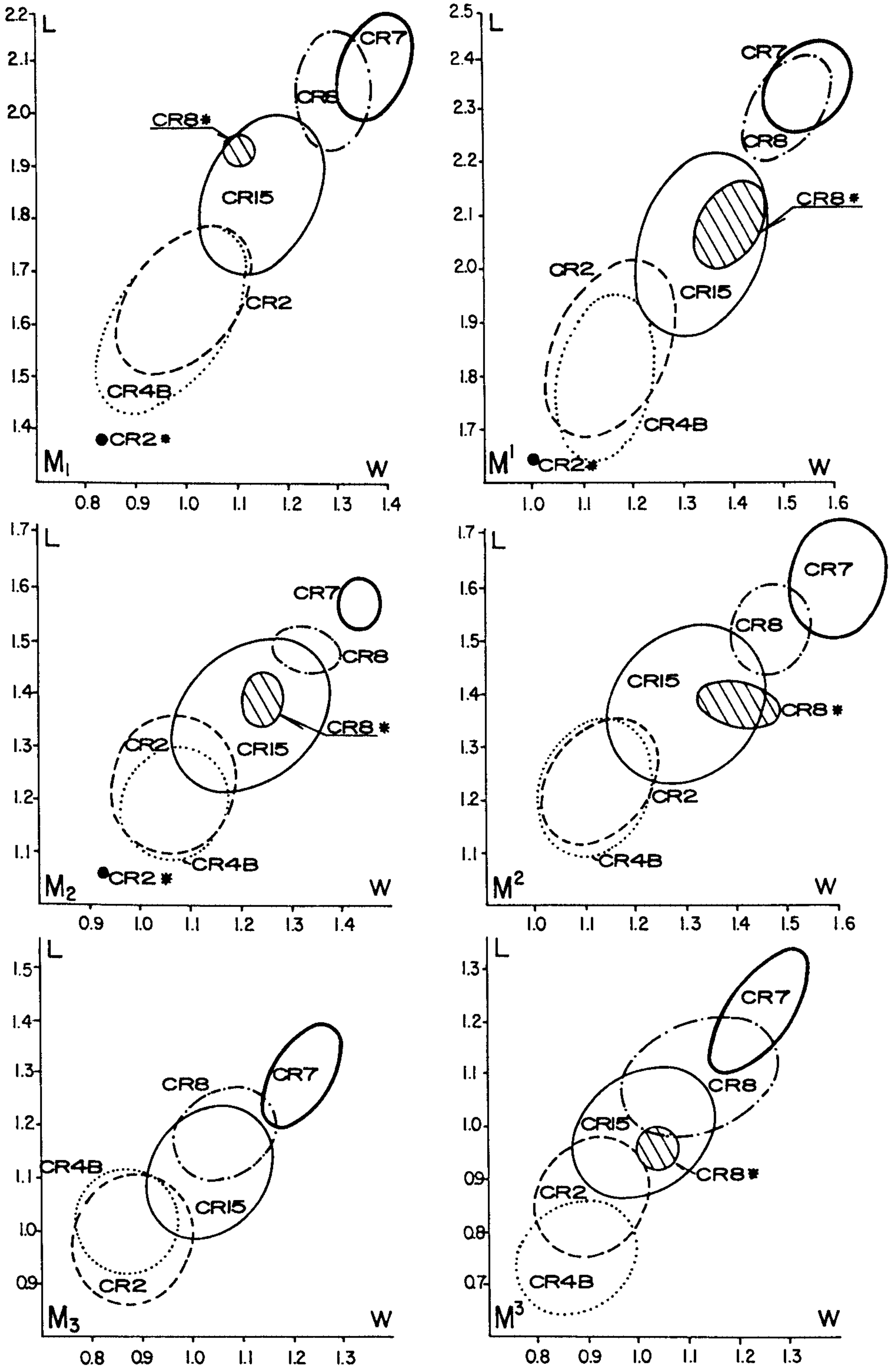
L
W
M1
CR7
CR8
CR8*
CR15
CR2
CR4B
CR2*
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
0.8
0.9
1.0
1.1
1.2
1.3
1.4
M1
2.5
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.0
1.1
1.2
1.3
1.4
1.5
1.6
M2
1.7
1.6
1.5
1.4
1.3
1.2
1.1
0.9
1.0
1.1
1.2
1.3
1.4
M2
M3
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.9
1.0
1.1
1.2
1.3
M3
1.3
1.2
1.1
1.0
0.9
0.8
0.7

Table 3. Measurements of the lower molars of *Parapodemus*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M_1													
CR7	5	1.99	2.062	2.14	7.26	0.061	7	1.32	1.357	1.42	7.30	0.036	1.52
CR8	12	1.94	2.003	2.13	9.34	0.064	12	1.25	1.293	1.33	6.20	0.028	1.55
CR8*	1		1.920				1		1.100				1.75
CR15	56	1.70	1.831	1.95	13.70	0.059	53	1.04	1.131	1.25	18.34	0.042	1.62
CR5A	5	1.71	1.756	1.82	6.23	0.042	5	1.08	1.112	1.18	8.85	0.041	1.58
CR4B	39	1.48	1.625	1.77	17.85	0.066	40	0.84	0.991	1.10	26.80	0.052	1.64
CR2	31	1.52	1.641	1.77	15.20	0.057	32	0.89	0.993	1.09	20.20	0.054	1.65
CR2*	1		1.380				1		0.830				1.66
M_2													
CR7	3	1.53	1.573	1.60			2	1.44	1.445	1.45			1.09
CR8	5	1.44	1.472	1.50	4.08	0.023	5	1.26	1.330	1.39	9.81	0.057	1.11
CR8*	3	1.35	1.393	1.43			3	1.24	1.247	1.25			1.12
CR15	79	1.23	1.342	1.48	18.45	0.047	81	1.09	1.210	1.33	19.83	0.054	1.11
CR5A	6	1.30	1.335	1.37	5.24	0.024	5	1.18	1.198	1.22	3.33	0.018	1.11
CR4B	56	1.10	1.204	1.27	14.35	0.037	58	0.98	1.068	1.16	16.82	0.036	1.13
CR2	34	1.12	1.216	1.30	14.88	0.049	34	0.96	1.049	1.16	18.87	0.040	1.16
CR2*	1		1.060				1		0.930				1.14
M_3													
CR7	6	1.21	1.308	1.36	11.67	0.058	6	1.17	1.233	1.29	9.76	0.040	1.06
CR8$	11	1.11	1.161	1.23	10.26	0.039	11	0.98	1.076	1.16	16.82	0.052	1.08
CR15	49	1.00	1.103	1.20	18.18	0.046	50	0.93	1.024	1.14	20.29	0.046	1.08
CR5A	2	1.08	1.095	1.11			2	0.91	0.960	1.01			1.14
CR4B	27	0.95	0.994	1.09	13.73	0.038	29	0.82	0.888	0.95	14.69	0.034	1.12
CR2	31	0.89	0.975	1.07	18.37	0.046	30	0.79	0.874	0.96	19.43	0.043	1.12

CR2* = Measurements of *P.* sp. from CR2.
CR2 = Measurements of *P. lugdunensis* from CR2.
CR8 = Measurements of *P. meini* from CR8.
CR8* = Measurements of *P. barbarae* from CR8.
CR8$ = Measurements of the M_3 of *P. meini* and *P. barbarae* from CR8.

CR4B. In the M_1 the connection of anteroconid and metaconid is weaker in CR2. The most important differences are found in the upper molars. In CR2 the molars are less stephanodont; t6 and t9 are more frequently connected, and the connection is higher in CR4B; in many specimens from CR2 the t9 is not connected to the t8, while, on the other hand, this morphology is an exception in CR4B.

There are no differences in the roots, neither in their number nor in their position.

The measurements don't present differences either, except for some isolated case (Fig. 5).

When these populations are compared with the ones from other European localities, it becomes evident, that the *Parapodemus lugdunensis* from CR2 and CR4B are among the smallest representatives of this species (Fig. 6), even smaller than the populations from Dorn-Dürkheim (Franzen & Storch, 1975) and Eichkogel (Daxner-Höck, 1977). The morphology does not differ substantially between the various populations. There are, however, some differences that are worthwhile mentioning:

Table 4. Measurements of the upper molars of *Parapodemus*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M^1													
CR7	8	2.28	2.334	2.40	5.13	0.044	8	1.48	1.551	1.61	8.41	0.046	1.50
CR8	8	2.24	2.302	2.38	6.06	0.056	10	1.43	1.512	1.58	9.97	0.048	1.52
CR8*	7	2.01	2.096	2.14	6.27	0.041	7	1.36	1.399	1.44	5.71	0.030	1.50
CR15	49	1.88	2.033	2.20	15.69	0.066	52	1.22	1.321	1.45	17.23	0.043	1.54
CR5A	2	1.93	1.995	2.06			7	1.20	1.267	1.35	11.76	0.050	1.57
CR4B	37	1.65	1.823	1.93	15.64	0.062	36	1.07	1.145	1.20	11.45	0.029	1.59
CR2	20	1.70	1.830	1.95	13.70	0.071	22	1.04	1.132	1.26	19.13	0.050	1.62
CR2*	1		1.640				1		1.000				1.64
M^2													
CR7	9	1.52	1.617	1.71	11.76	0.055	9	1.52	1.597	1.64	7.59	0.040	1.01
CR8	12	1.43	1.516	1.59	10.60	0.052	11	1.40	1.467	1.52	8.22	0.041	1.03
CR8*	2	1.37	1.380	1.39			2	1.35	1.400	1.45			0.99
CR15	66	1.28	1.388	1.51	16.49	0.049	66	1.18	1.322	1.42	18.46	0.056	1.05
CR5A	4	1.30	1.368	1.46			4	1.27	1.313	1.36			1.04
CR4B	56	1.11	1.210	1.34	18.78	0.049	56	1.02	1.122	1.21	17.04	0.036	1.08
CR2	27	1.14	1.227	1.32	14.63	0.051	26	1.03	1.124	1.23	17.70	0.049	1.09
M^3													
CR7	4	1.11	1.205	1.29			4	1.16	1.233	1.32			0.98
CR8	8	1.03	1.073	1.17	12.73	0.050	8	1.00	1.093	1.25	22.22	0.083	0.98
CR8*	3	0.93	0.957	0.98			3	1.03	1.040	1.06			0.92
CR15	51	0.90	0.986	1.10	20.00	0.043	51	0.89	1.007	1.10	21.11	0.055	0.98
CR5A	7	0.89	0.963	1.10	21.11	0.072	6	0.93	1.000	1.11	17.65	0.067	0.96
CR4B	29	0.79	0.848	0.93	16.28	0.040	29	0.77	0.880	0.97	22.99	0.051	0.96
CR2	21	0.77	0.862	0.95	20.93	0.045	21	0.82	0.905	1.00	19.78	0.047	0.95

CR2* = Measurements of *P.* sp. from CR2.
CR2 = Measurements of *P. lugdunensis* from CR2.
CR8 = Measurements of *P. meini* from CR8.
CR8* = Measurements of *P. barbarae* from CR8.

The M_1 from Dorn-Dürkheim have an extremely well-developed cingulum border, that forms a labial expansion of the tooth, and that is less high in front of the c1. Moreover, the upper molars are more stephanodont than in CR2 and CR4B

In nearly all the M_1 from CR2 and CR4B there is a well-developed tma, while on the other hand in the populations from Eichkogel (Daxner-Höck, 1977), Vivero de Pinos (Adrover, 1986), Alfambra, and Tortajada A (van de Weerd, 1976), the presence of tma is not that constant.

In the M^2 from CR4B and specially from CR2, t6 and t9 are frequently separated, while in the populations from other localities t6 and t9 are connected in almost all specimens.

The populations of *P. lugdunensis* from CR2 and CR4B are among the oldest ones known of this species. Their morphology is typical for *Parapodemus*: in M^2 t6 and t9 are often separated, though very close together and convergent; there tips never meet. In this respect they differ very much from *Progonomys*, where the t6 and t9 of the upper molars are distant and divergent.

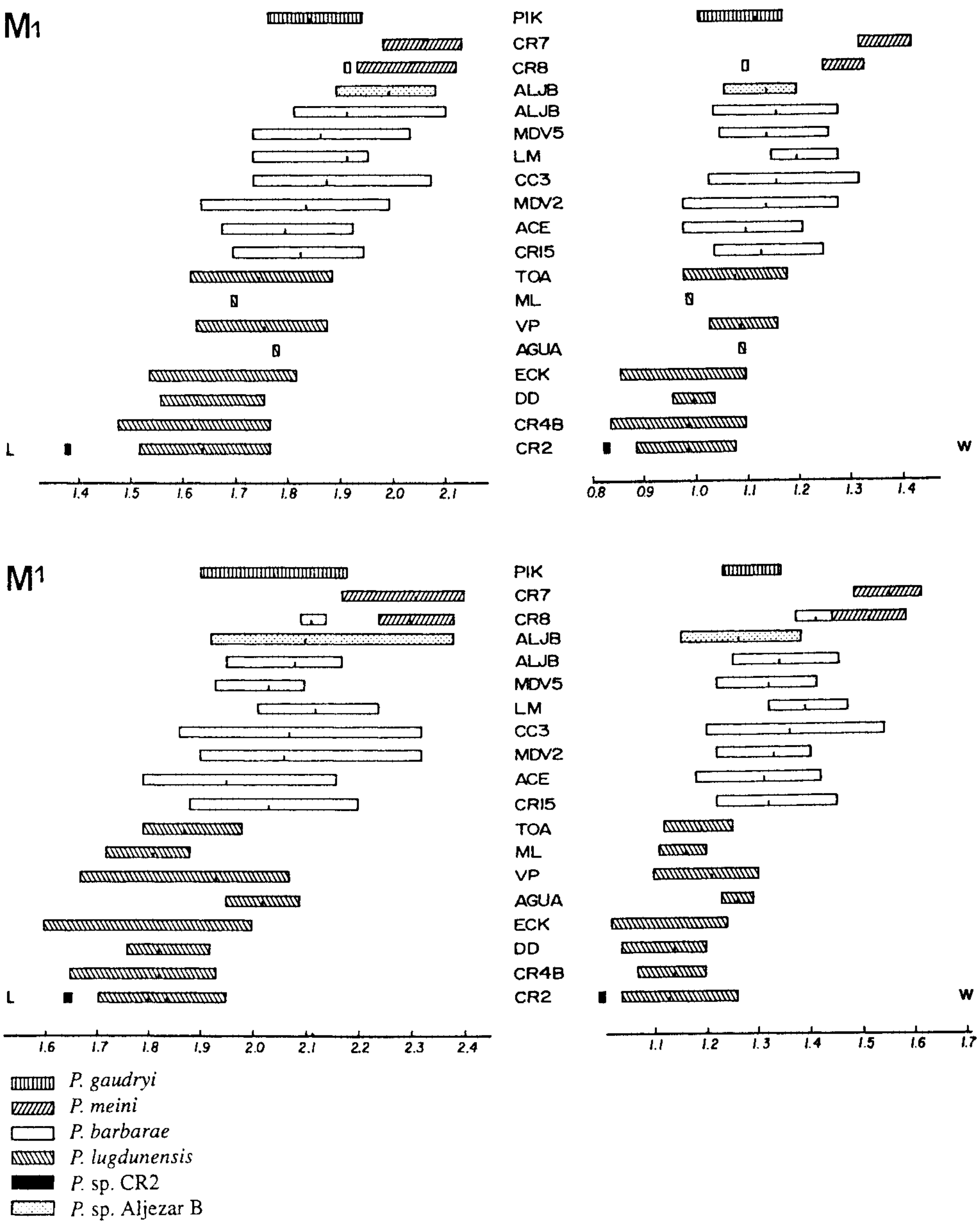

Fig. 6. Size ranges for length and width of the first molars of *Parapodemus* from several European localities.

Parapodemus sp.
Pl. 2, figs. 15-16.

Material — In CR2 we have found three specimens, that are clearly different from *Parapodemus lugdunensis* from the same locality (Figs. 5, 16).

Description — One very small M_1, RGM 402 441 (1.38 × 0.83 mm) has a labial lobe of the anteroconid that continues backwards as a high labial cingulum, connected with c1; there is a small c2 attached to the protoconid.

The M_2 RGM 413 632 is also very small (1.06 × 0.93). The anterolabial cuspid is big, the labial cingulum reduced to a minuscule c1.

The M^1 RGM 402 495 (1.64 × 1.00) has a high t4-t8 connection, t6 and t9 connected, and a voluminous t12.

Discussion — The degree of wear of these specimens proves that they are from different individuals. They probably represent a new species, but in view of the poor material we refrain from naming it formally.

Parapodemus barbarae van de Weerd, 1976
Pl. 3, figs. 1-12.

Original reference — *Parapodemus gaudryi barbarae* subsp. nov. in van de Weerd, 1976, pp. 79-84.

Holotype — An isolated M^1, LM 416, deposited in the 'Instituut voor Aardwetenschappen', University of Utrecht, The Netherlands.

Type-locality — Los Mansuetos (Teruel, Spain).

Localities with P. barbarae in the Crevillente area — Crevillente 5A (CR5A), Crevillente 15 (CR15), Crevillente 8 (CR8); Crevillente 4 (*P. gaudryi* in de Bruijn et al., 1975).

Measurements — See Tables 3-4 and Figs. 5, 18.

Description of the material from Crevillente 15

M_1 — The tma is always present, similar in size to c1. It may be isolated, or connected to one or both lobes of the anteroconid; in the latter case there is an anterior fossette (see Pl. 3, fig. 6). The anteroconid remains separated from the metaconid until in a very advanced state of wear. There are no longitudinal connections. The labial cingulum is continuous and wide, with a high and voluminous c1, similar in size to the tma and the terminal heel; there is always a second accessory tubercle at the base of the protoconid; there may be yet another one in front of the c1; moreover there are from one to three small tubercles between protoconid and anteroconid. The terminal heel is big and oval-shaped. There are two main roots.

M_2 — The anterolabial cuspid is big and high. Like in M_1 longitudinal connections are absent. The labial cingulum is continuous, c1 is always present, sometimes as big as the anterolabial cuspid; there may be up to three accessory tubercles more, in front of the c1, one of which is attached to the protoconid. The posterior heel is big and oval-shaped. There are two roots.

M_3 — The anterolabial cuspid is low but prominent in the anterior wall of the tooth. The c1 is generally absent. There are two roots.

M^1 — The t1 is weakly connected to the t2, and rarely presents a posterior spur; t3 is similar in size to t1. There frequently is a small t2bis, visible as a minuscule isolated cusp, close to the anterolabial border of the tooth. In a few cases there are accessory tubercles between t1 and t4 or between t3 and t6. The t4 is connected to t5 and t8 by high crests; 'morphotypes Apodemus' have not been encountered. Cusps t6 and t9 are equal in size, and in 90 % of the specimens these two cusps are connected. The t9 is always connected to t8. The t12 is of medium size or big, oval-shaped, and not integrated in the cingulum t9-t8. There are three roots.

M^2 — The t1 is big and isolated (in one case it is connected to the anterolingual wall of the t2); t3 is small and isolated too. The t4 is connected to t8 by a crest, which is lower than the equivalent one in M^1; 'morphotypes Apodemus' have not been encountered. The t9 is smaller than t6 and these cusps are connected in 90 % of the specimens; t9 is connected to t8. The t12 is small or of medium size, not integrated in the cingulum. There are three roots.

M^3 — The t1 is oval-shaped and isolated; t3 is very much reduced or absent. The posterior tubercle is generally formed by t8 and t9, and presents itself as wide cusp with a constriction; it may be connected either to t6 or to t4, in some cases it is isolated. There are three roots.

Description of the material from Crevillente 8

The collection of *Parapodemus barbarae* from CR8 is rather small. It is, however, important, because at this locality a second species of *Parapodemus* is found.

M_1 — There is only one – hardly worn – specimen, with an isolated tma, equal in size to the labial lobe of the anteroconid. The labial cingulum is reduced.

Plate 3

Parapodemus barbarae van de Weerd, 1976 from Crevillente 15

Fig. 1. M^1 sin., RGM 403 399.
Fig. 2. M^1 dext., RGM 403 440.
Fig. 3. M^2 sin., RGM 403 465.
Fig. 4. M^3 dext., RGM 403 578.
Fig. 5. M^2 dext., RGM 403 521.
Fig. 6. M_1 dext., RGM 403 262.
Fig. 7. M_1 sin., RGM 403 231.
Fig. 8. M_2 dext., RGM 403 311.
Fig. 9. M_3 dext., RGM 403 379.

Parapodemus barbarae van de Weerd, 1976 from Crevillente 8

Fig. 10. M_2 dext., RGM 403 027.
Fig. 11. M^3 dext., RGM 403 156.
Fig. 12. M^1 sin., RGM 403 132.


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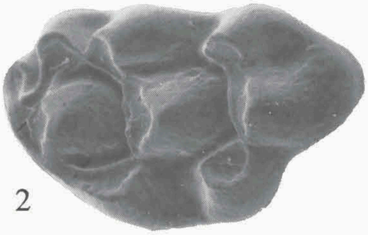
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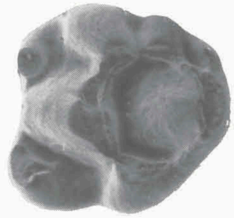
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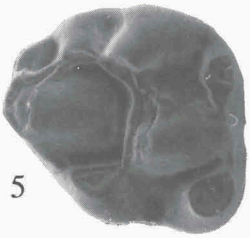
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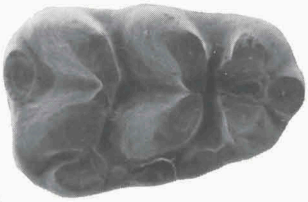
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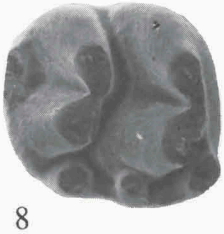
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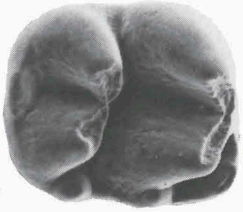
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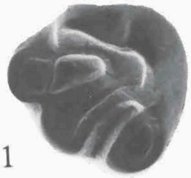
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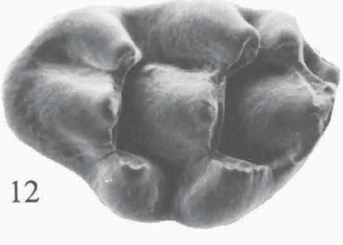
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1 mm

M_2 — The three available specimens are broad. They have a small anterolabial cuspid, a poorly developed labial cingulum, and much reduced accessory cuspids.

M_3 — We have not been able to separate the M_3 of this species from those of *P. meini* sp. nov. from the same locality. The molars have a small and very low, but ever present, anterolabial cuspid. There is no c1, but in some specimens one may observe a constriction in the labial part of the hypoconid-entoconid complex. There are two roots.

M^1 — The t1 is slightly larger than t3, and none of these two cusps develops a longitudinal spur. The t4 is united to the t8 by a rather low crest. No 'morphotypes Apodemus' have been found. Cusps t6 and t9 are connected. The t12 has a tubercular shape.

M^2 — Cusps t3 and t9 are reduced; t6 and t9 are united; t12 is tubercular, smaller than in M^1.

M^3 — These teeth are broad, with t1 united to the anterolabial wall of the t4. The posterior tubercle is simple, without constriction.

Crevillente 5A — This is a very poor locality, and has yielded only a few remains of *Parapodemus barbarae*, sufficient to prove its presence, but not important enough to be described.

Remarks — We have compared the material from CR15 and CR8 with the type-population from Los Mansuetos. The latter population is fairly homogeneous with the exception of one very small M_1, as may be observed in van de Weerd (1976, p. 78, fig. 14). This small specimen - LM 143 (1.74 × 1.15 mm) of the Utrecht collection - influences the size range M_1 considerably, but hardly influences the mean (Freudenthal & Martín Suárez, 1990).

The size ranges of the populations from CR15 and CR8 coincide fairly well with those of the type-population. There are no important morphological differences between the populations from Los Mansuetos and Crevillente. The trigonid of M_1 is similar in all of them: a well-developed tma, that delimits an anterior fossette by the way in which it is fused to the anteroconid; the latter has lobes, that remain separated until in a well-advanced state of wear. In M^1 and M^2 from CR15 the connecting crest between t4 and t8 is lower than it is in those from Los Mansuetos.

Parapodemus barbarae from Casa del Acero (CA) is the population with the smallest mean dimensions known in this species (Agustí et al., 1981), but there are several digested specimens among the measured material, that cause a considerable bias in the calculation of the means. The dimensions of the population from CR15 and CR8 are slightly larger than those of the population from Casa del Acero (Agustí et al., 1981); the morphology of the crown is very similar. In neither of these three localities 'morphotypes Apodemus' are found, although the connection t4-t8 is higher and broader in Casa del Acero (comparing specimens with a similar degree of wear). Cusps t6 and t9 are connected more frequently in CA than in CR15. In Casa del Acero half the M^1 have a vestigial fourth root, a feature that is absent in the population from CR15. These differences make us think that CA is younger than CR15, although the specimens from the latter locality are slightly larger.

There are some differences between the populations from Crevillente and Aljezar B. Equally long molars from Aljezar B are relatively narrower. The M_1 of *Parapodemus barbarae* from Aljezar B have a smaller tma than those from CR15 and CR8. In CR15 and CR8 there are no 'morphotypes Rhagapodemus', like those that Adrover (1986) describes as *Parapodemus* sp. from Aljezar B. On the other hand, these three populations share the separation of the anteroconid from the metaconid until in a well-advanced state of wear, and the presence of small accessory tubercles in various points of the M^1.

Parapodemus meini sp. nov.
Pl. 4, figs. 1-13.

Holotype — An isolated M^1 sin., RGM 402 720, Pl. 4, fig. 1, kept at the National Museum of Natural History, Leiden, The Netherlands.

Type-locality — Crevillente 7 (Alicante, Spain), UTM 30SXH396946.

Other localities with P. meini — Crevillente 8 (CR8).

Derivatio nominis — The species is dedicated to our friend and colleague P. Mein from Lyon, in appreciation of the many hours spent together, studying Muridae.

Stratigraphic distribution — Late Miocene, Turolian.

Measurements — See Tables 3-4 and Figs. 5, 7.

Diagnosis — Large-sized *Parapodemus*. The two lobes of the anteroconid of M_1 are frequently separated. M^1 and M^2 with t6 and t9 are convergent, but weakly connected. M^3 frequently with constricted posterior tubercle (t8 and t9).

Differential diagnosis — *Parapodemus meini* differs from all other species of *Parapodemus* by its big size. It differs from *P. lugdunensis* Schaub, 1938 by the absence of a connection between anteroconid and metaconid. It differs from *P. barbarae* van de Weerd, 1976 by the weak connection between t6 and t9. It differs from *P. gaudryi* (Dames, 1883) by the complete absence of t7.

Description of the material from the type-locality

M_1 — The tma is robust and isolated. The two lobes of the anteroconid remain separated from each other, and are also separated from the protoconid-metaconid pair, until in a very advanced state of wear. There are no longitudinal connections. The labial cingulum is continuous and well-developed. The c1 is voluminous, and bigger than the tma. There is a c2 at the base of the protoconid, and one or more cuspids between protoconid and anteroconid. There are two roots.

M_2 — The anterolabial cusp is isolated, high and prominent. The labial cingulum is continuous and large, with a c1 that is smaller than the anterolabial cuspid. There is a c2 at the base of the protoconid. The terminal heel is oval-shaped and big. There are two roots.

M_3 — The anterolabial cuspid is low and small; c1 is reduced or absent. There are two roots.

M^1 — Robust teeth. Cusps t1 and t3 are similar in size, and have no posterior connections (one single specimen shows a posterior spur on the t1). The t4 and t5 are connected at a low level. The connecting crest between t4 and t8 may be high or low. Cusps t6 and t9 become completely united in a very advanced state of wear; t9 is always connected to t8. The t12 is a small tubercle, not integrated in the t9-t8 cingulum. There are three main roots, and a vestigial one under the center of the tooth.

M^2 — The t1 is larger than t3, and both cusps are isolated. The t4 is connected to t5 and t8 by crests that are similar in height. Cusps t6 and t9 equal each other in size, and their apices may be separated or weakly connected. The t12 is a small tubercle. Only one root is preserved, the lingual one, which is large and undivided.

M^3 — The t1 is large and isolated, t3 is very much reduced. The posterior tubercle presents a constriction between t8 and t9. There are three roots.

Description of the material from Crevillente 8

M_1 — The tma is isolated and almost as large as the labial lobe of the anteroconid. The two lobes of the anteroconid are separated from each other until in a well-advanced state of wear. They are separated from the protoconid-metaconid pair too. The transversal connections between the tubercle pairs are very low. The labial cingulum is continuous, with a very voluminous c1, and a c2 at the base of the protoconid. Between protoconid and anteroconid there are one or two more cuspids. The terminal heel is oval-shaped, and is similar in size to c1. There are two roots.

M_2 — The anterolabial cuspid is not very big, and continues backwards in a continuous, but poorly developed, cingulum. Both c1 and c2 are always present. The terminal heel is oval-shaped and low. There are two roots.

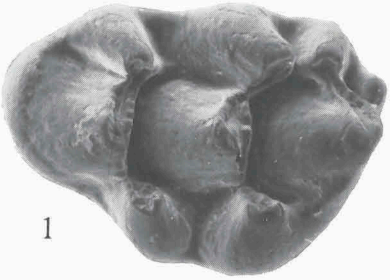
M_3 — It is not possible to separate the M_3 of *P. meini* from those of *P. barbarae* from the same locality. The M_3 have been described indiscriminately in the chapter on *P. barbarae*.

M^1 — The teeth are robust. The t1 is slightly larger than t3. In some case t3

Plate 4

Parapodemus meini sp. nov. from Crevillente 7
Fig. 1. M^1 sin., RGM 402 720, holotype.
Fig. 2. M^1 dext., RGM 402 726.
Fig. 3. M^2 dext., RGM 402 764.
Fig. 4. M^3 sin., RGM 402 739.
Fig. 5. M_1 dext., RGM 402 706.
Fig. 6. M_2 sin., RGM 402 709.
Fig. 7. M_3 dext., RGM 402 717.
Fig. 8. M_1 sin., RGM 402 702.

Parapodemus meini sp. nov. from Crevillente 8
Fig. 9. M^2 dext., RGM 403 091.
Fig. 10. M^3 sin., RGM 403 093.
Fig. 11. M^1 dext., RGM 403 073.
Fig. 12. M^1 sin., RGM 403 069.
Fig. 13. M_1 dext., RGM 403 038.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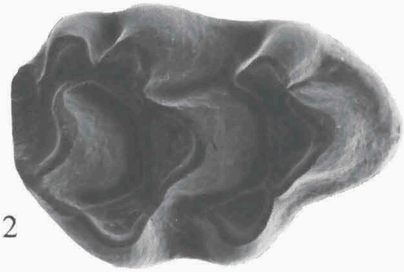
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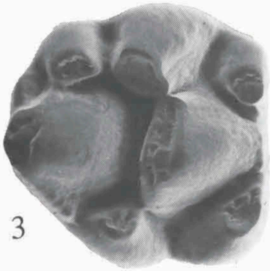
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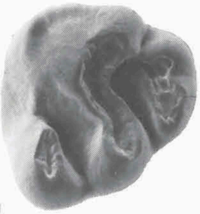
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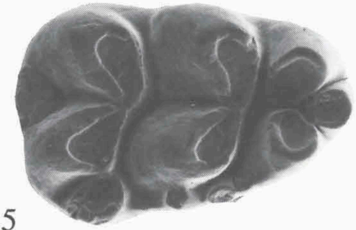
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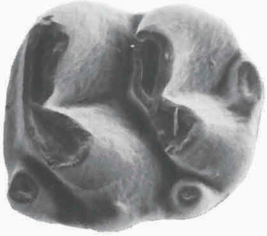
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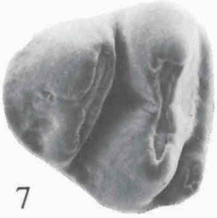
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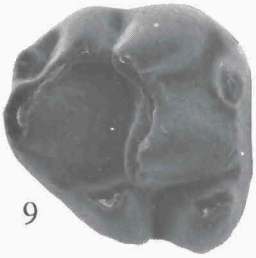
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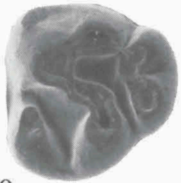
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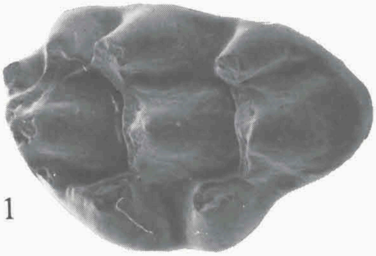
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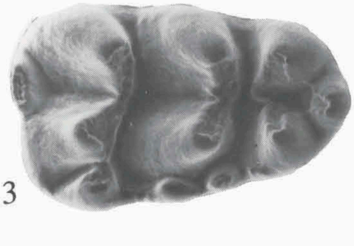
12

1 mm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bears a small longitudinal spur. The connection between t4 and t5 is slightly lower than the connection between t4 and t8; the latter cusp is somewhat inflated in one specimen. Cusps t6 and t9 may be weakly connected or their apices are separated. The t12 is tubercular and not integrated in the t9-t8 cingulum. There are three main roots, and a vestigial fourth one under the center of the tooth.

M^2 — The t1 is isolated, t3 is much reduced and isolated too. The connection t4-t8 is never widened. The t9 is larger than the t3, and may be united to the t6 or be separated at the top. The t12 is smaller than in M^1, but not integrated in the connection t9-t8. There are three roots.

M^3 — The t1 is isolated or connected to the anterolingual wall of t4. The t3 is reduced or absent. The posterior tubercle is formed by t8 and t9. There are no specimens with roots.

Remarks — *Parapodemus meini* from Crevillente 7 and 8 includes the largest specimens known among the representatives of the genus *Parapodemus* (Fig. 6) during the early Turolian.

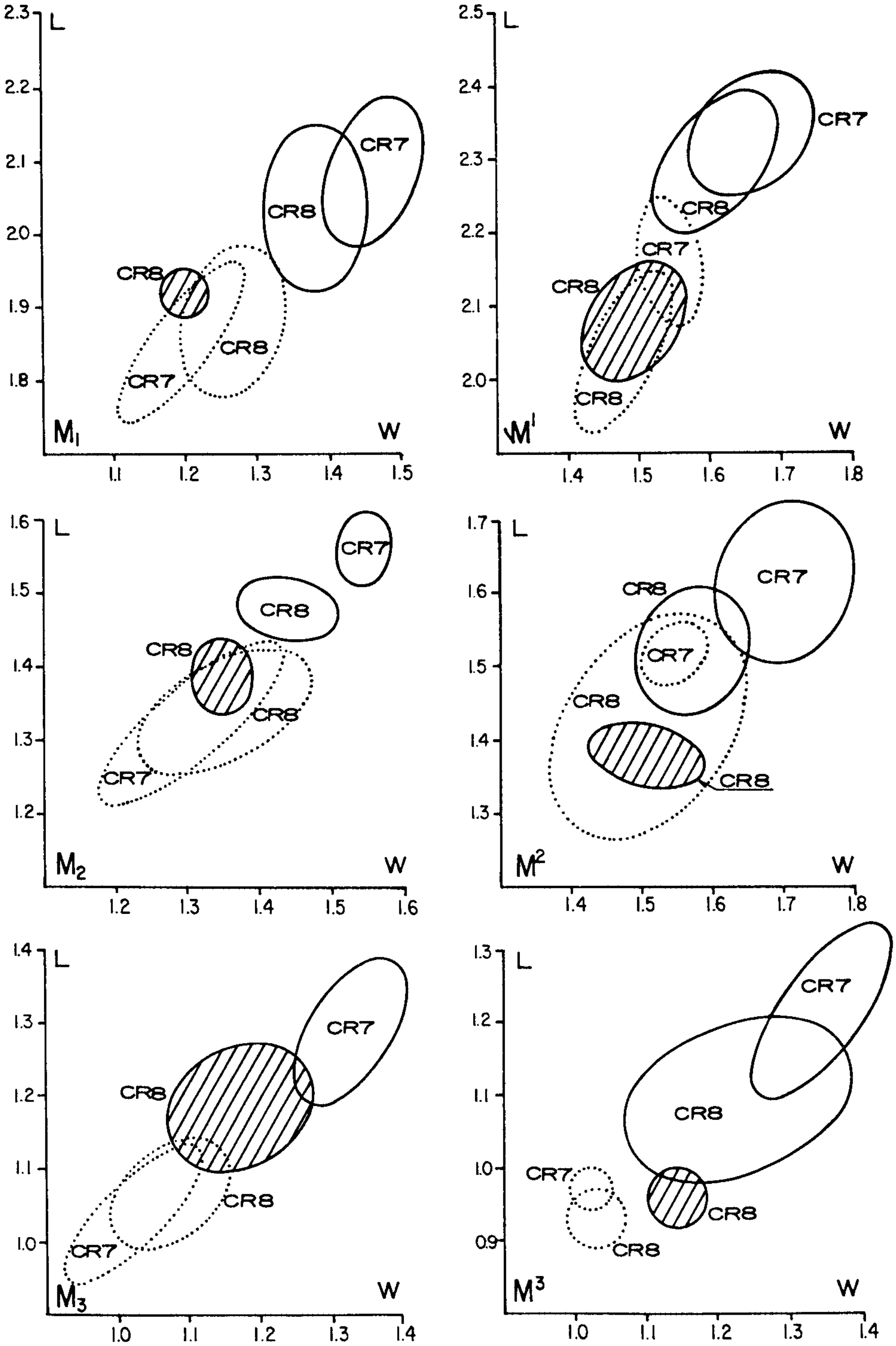
This big size is in contrast with its morphology, which shows no significant changes in comparison with the population from CR15, that is much older. In the M_1 from CR7 and CR8 the labial cingulum and the accessory cusps are somewhat less developed than in older populations.

In the upper molars of *P. barbarae* from CR15 one may observe small accessory tubercles in various points of the tooth, that are not present in those of *P. meini* from CR7 or CR8. The connection t4-t8, specially in M^1, is higher in CR7 and CR8 than in CR15, and in some cases appears to be slightly inflated (Pl. 4, fig. 2). On the other hand, the connection t6-t9 in M^1 and M^2 is lower than in CR15.

In a previous paper (Freudenthal et al., 1990) we have analyzed the coefficient of variability of c. 200 populations of Muridae. We found a high value for the *Parapodemus* from CR8, and mentioned the presence of two different morphotypes, specially in M^1 and M^2, but also in M^3. We have now come to the conclusion, that these two morphotypes represent in reality two species. On the one hand, the smaller specimens may be attributed to *Parapodemus barbarae*, and, on the other, the larger ones are specimens that by their morphology may be included in the new species *Parapodemus meini*. Once these species are separated the coefficient of variability of each of them takes a normal value.

The locality of CR8 is lithostratigraphically a few metres below CR7. The faunal data also indicate that CR8 is older. The collection of *Parapodemus meini* from CR7 is smaller than the one from CR8; however, we have chosen CR7 as the type-locality of the new species, because the large size (Fig. 7) and the morphological characters of the new species are more marked in CR7, and because *P. meini* is the only *Parapodemus* species in this locality. The population from CR8 may be considered a transitional one.

Fig. 7. Length/width scatter diagrams of the molars of *Parapodemus* and *Occitanomys* from CR7 and CR8. The discontinuous lines represent *O. adroveri*, the continuous lines represent *P. meini*, and the striped pattern represents *P. barbarae*.


M_1
L
W
2.3
2.2
2.1
2.0
1.9
1.8
1.1
1.2
1.3
1.4
1.5
CR7
CR8
CR8
CR8
CR7
M^1
L
W
2.5
2.4
2.3
2.2
2.1
2.0
1.4
1.5
1.6
1.7
1.8
CR7
CR8
CR7
CR8
CR8
M_2
L
W
1.6
1.5
1.4
1.3
1.2
1.2
1.3
1.4
1.5
1.6
CR7
CR8
CR8
CR8
CR7
M^2
L
W
1.7
1.6
1.5
1.4
1.3
1.4
1.5
1.6
1.7
1.8
CR7
CR8
CR7
CR8
CR8
M_3
L
W
1.4
1.3
1.2
1.1
1.0
1.0
1.1
1.2
1.3
1.4
CR7
CR8
CR8
CR7
M^3
L
W
1.3
1.2
1.1
1.0
0.9
1.0
1.1
1.2
1.3
1.4
CR7
CR8
CR7
CR8
CR8

A feature that calls the attention is the shape of the posterior tubercle of the M^3: it shows a constriction that clearly delimits t8 and t9. This feature is present in part of the population of *Parapodemus barbarae* from CR15 and in all the specimens of M^3 of *P. meini* from CR7 and CR8. It is also found in a population from Crevillente 17, to be described as a new genus and species (Martín Suárez & Freudenthal, in prep.), and it is shared with oriental Muridae like *Karnimata* and *Saidomys* (Jacobs, 1978).

Discussion

Schaub (1938) designated *Mus gaudryi* Dames, 1883 as type-species of the genus *Parapodemus* (see de Bruijn, 1976; Mein, 1978; Papp, 1947; van de Weerd, 1976; van de Weerd & de Bruijn, 1978), stating that 'Hügel 7 ist bei ihnen nicht entwickelt' (t7 is not developed).

Parapodemus gaudryi from Pikermi (Utrecht collection) frequently has a well-developed t7; in some cases t4 and t8 are connected by a very broad crest, that shows no sign of a tubercular widening (a disposition found in many specimens of the extant *Apodemus sylvaticus*). In the M_1 the lingual lobe of the anteroconid is connected to the metaconid.

In our opinion the generic name *Parapodemus* should be reserved for *Mus gaudryi* Dames, 1883. The determination of the Turolian species from Western Europe, now included in *Parapodemus*, has to be revised.

The oldest representatives of *Parapodemus* are contemporaneous with – and even older than – *Progonomys cathalai* (Mein et al., this volume). Therefore, *P. cathalai* from Montredon (type-locality) can hardly be the ancestor of *Parapodemus lugdunensis*. The origin of this species remains an open question.

The lineage *P. lugdunensis*, *P. barbarae* and *P. meini* shows evolutionary tendencies that differ from those found in other groups of Muridae: e.g. the loss of a longitudinal connection between anteroconid and metaconid; the loss of transversal connections in each pair of tubercles; a very broad and irregular labial cingulum in M_1. On the other hand the size increase from one population to the other may be very pronounced, specially in the case of *P. meini*. This tendency to a strong increase in size is also evidenced by the population of *Parapodemus* sp. from the latest Turolian of Lissieu.

Parapodemus meini may well be a descendant of *P. barbarae*. The morphological change is not excessive, but the size increase is important (Fig. 6). The presence of two species, ancestor and descendant, in one and the same locality has been proven more than once, and may be explained by means of the allopatric speciation model and subsequent sympatry, as laid out by Eldredge & Gould (1972).

Genus *Occitanomys* Michaux, 1969
Subgenus *Rhodomys* Martín Suárez & Mein, 1991

Occitanomys (Rhodomys) sondaari van de Weerd, 1976
Pl. 5, figs. 1-15.

Original reference — *Occitanomys sondaari* sp. nov. in van de Weerd, 1976, pp. 57-60.

Type locality — Tortajada A (Teruel, Spain).

Holotype — An isolated M^1 dext, TOA 492, kept at the 'Instituut voor Aardwetenschappen', University of Utrecht.

Localities with O. sondaari in the Crevillente area — Crevillente 2 (CR2), Crevillente 4B (CR4B), Crevillente 5A (CR5A); Crevillente 1, 2, and 3 in de Bruijn et al., 1975.

Measurements — See Tables 5-6 and Figs. 8, 16, 17.

Description of the material from Crevillente 2

M_1 — The anteroconid is almost symmetrical, with its lingual lobe connected to the metaconid in nearly all specimens. In 12 % of the cases there is a very small tma. The protoconid is not placed backwards with respect to the metaconid. In 33 % of the specimens there is a short longitudinal spur that tapers out at the base of the protoconid; in one case there is a very low longitudinal crest. The labial cingulum is continuous, with a small c1, and another accessory cuspid (c2) at the base of the protoconid; c2 is generally smaller than c1. There may be still another accessory cuspid between protoconid and anteroconid. The posterior heel is low, oval- to blade-shaped. There are two roots.

M_2 — The posterior part of the tooth is narrower than the anterior part. The anterolabial cuspid is well developed. A small longitudinal spur is found in 25 % of the specimens. The labial cingulum is continuous, with c1 vestigial or absent, and c2 well-developed and reclining on the labial wall of the protoconid. The posterior heel is oval-shaped and very low. There are two roots.

M_3 — The anterolabial cuspid is very reduced and low, and may be missing. The hypoconid-entoconid complex is small, and its lingual part converges towards the metaconid. The c1 is absent. There are two roots.

M^1 — The t1 is placed very much backwards, its anterior part may be united to t1bis or t2 (48 %), or not united (52 %); it may be separated from t5 (45 %) or connected to it. In the latter case the t1 is generally attached to the t5, and rarely the connection consists of a spur. In more than 60 % of the specimens t1bis is present, and connected to t2. t2 and t3 are close together and converging, very much separated from t5 and t6. The t4 is separated from t5 (34.5 %), or these cusps are connected by a very low crest. The t4 is separated from t8 by a deep valley. Cusps t6 and t9 are connected by a spur from t6 towards the base of t9 in 82 % of the specimens, in the remaining 18 % t6 and t9 are separated. The t9 is united with t8. The t12 is integrated in the cingulum t9-t8. There are three roots.

M^2 — The t1 is voluminous, its posterior part generally ends free; only in 24 % of the specimens it is united to t5; t1bis is very frequently present, and normally it is voluminous; t3 is small and isolated. The t4 is united with t5 by a higher connection than in M^1. Cusps t4 and t8 are separated. Cusps t6 and t9 are separated in 38 % of the specimens; in the remaining 62 % these two cusps are connected by means of a short spur like in M^1. The t12 is a widening of the t9-t8 connection. Of the 15 specimens with preserved roots, 12 specimens present three roots; the other 3 have four roots.

M^3 — The t1 is oval-shaped, not or hardly extending beyond the lingual wall of the tooth. The t3 is very much reduced or absent. Cusp t8 is small. There are three roots.

Description of the material from Crevillente 4B

In order not to repeat the descriptions, only the differences with respect to the population from CR2 are listed.

M_1 — In almost half the specimens there is a small bulging of enamel at the anterior border, not large enough, however, to form a tma. In general the c1 is big, which gives the tooth a greater width than in the material from CR2.

M_2 — One fourth of the populations has a larger c1 than in CR2.

M_3 — No differences with respect to CR2 have been observed.

M^1 — The t1 is attached to the lingual wall of t5 more frequently than in CR2 (75 %); the connection is not formed by a spur. The connection t6-t9 is slightly more frequent (87 %) and higher than in CR2, but the cusps are not completely united.

M^2 — The only difference with the population from CR2 is, like in M^1, that t6 and t9 are connected more frequently (79 %). The two specimens, in which the roots are preserved, have three roots.

M^3 — There are no differences in comparison with CR2.

Description of the material from Crevillente 5A

Crevillente 5A has yielded a small number of dental elements.

The M_1 are very similar to those from CR4B, with symmetrical anteroconid, and protoconid and metaconid placed almost opposite each other. The size distribution in both localities is identical.

M_2 and M_3 are similar to those from CR4B, though the size of the specimens from CR5A is slightly larger.

The M^1 from CR5A have their t1 separated from t1bis, like in the population from CR4B; the t6-t9 connection is slightly higher in the M^1 and M^2 from CR5A; the size is similar in both localities.

Plate 5

Occitanomys sondaari van de Weerd, 1976 from Crevillente 4B

Fig. 1. M^1 sin., RGM 404 459.

Fig. 2. M^1 dext., RGM 404 466.

Fig. 3. M^2 sin., RGM 404 476.

Fig. 4. M^3 dext., RGM 404 501.

Fig. 5. M_3 sin., RGM 404 447.

Fig. 6. M_1 dext., RGM 404 420.

Fig. 7. M_2 dext., RGM 404 441.

Occitanomys sondaari van de Weerd, 1976 from Crevillente 2

Fig. 8. M^1 sin., RGM 402 596.

Fig. 9. M^1 sin., RGM 402 598.

Fig. 10. M^2 sin., RGM 402 633.

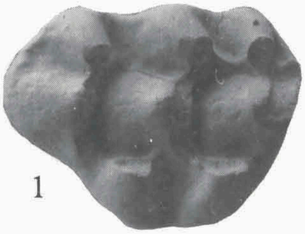
Fig. 11. M^3 sin., RGM 413 628.

Fig. 12. M^1 dext., RGM 402 616.

Fig. 13. M_1 sin., RGM 402 538.

Fig. 14. M_2 sin., RGM 402 564.

Fig. 15. M_3 dext., RGM 413 619.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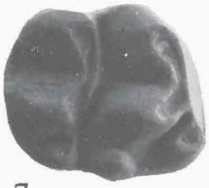
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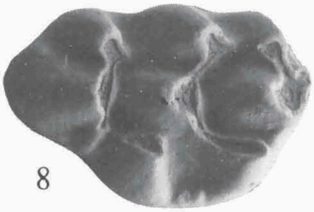
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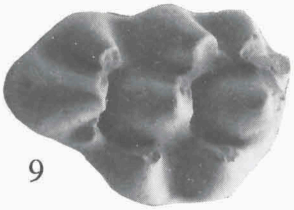
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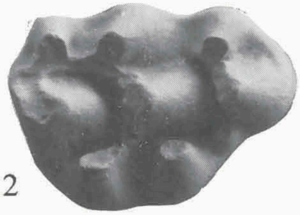
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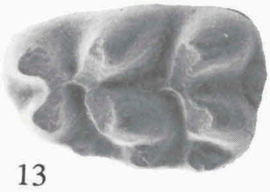
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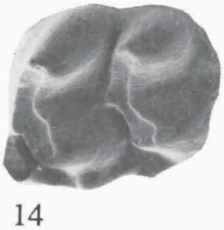
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15

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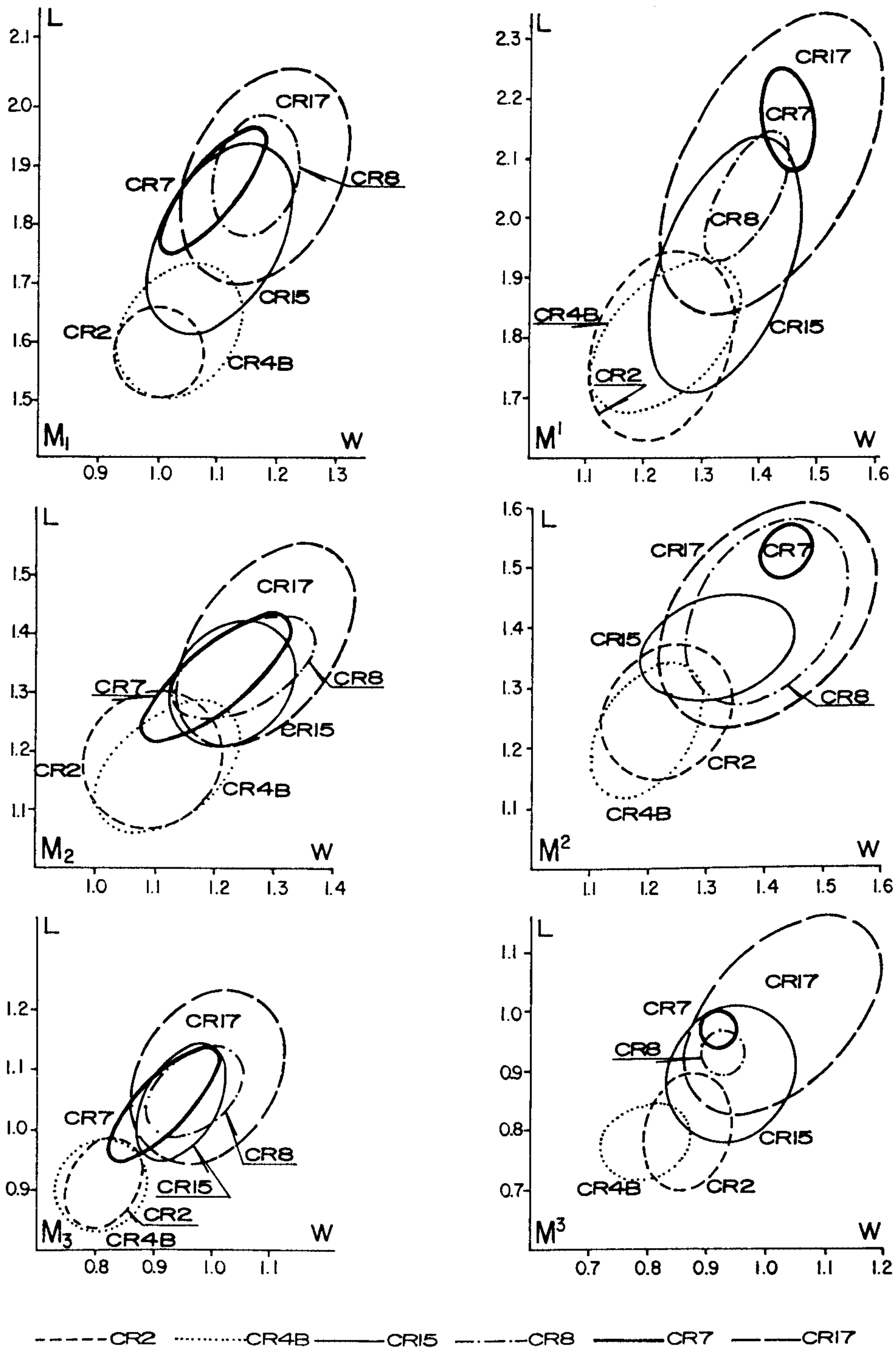


Fig.8. Length/width diagrams of the lower molars of *Occitanomys*.

Table 5. Measurements of the lower molars of *Occitanomys*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M_1													
CR17	35	1.73	1.889	2.04	16.45	0.070	38	1.05	1.186	1.28	19.74	0.049	1.59
CR7	2	1.78	1.850	1.92			2	1.04	1.095	1.15			1.69
CR8	5	1.80	1.866	1.97	9.02	0.068	5	1.12	1.168	1.21	7.73	0.037	1.60
CR15	17	1.62	1.755	1.91	16.43	0.068	17	1.02	1.102	1.17	13.70	0.045	1.59
CR5A	4	1.60	1.642	1.68			6	1.01	1.073	1.13	11.21	0.046	1.53
CR4B	18	1.51	1.609	1.70	11.84	0.058	19	0.94	1.019	1.12	17.48	0.049	1.58
CR2	14	1.53	1.577	1.64	6.94	0.033	15	0.95	1.003	1.06	10.95	0.035	1.57
M_2													
CR17	44	1.22	1.419	1.54	23.19	0.060	45	1.20	1.305	1.41	16.09	0.049	1.09
CR7	4	1.25	1.305	1.42			4	1.10	1.200	1.32			1.09
CR8	11	1.27	1.355	1.40	9.74	0.038	12	1.16	1.265	1.35	15.14	0.060	1.07
CR15	27	1.23	1.302	1.40	12.93	0.047	27	1.15	1.232	1.31	13.01	0.046	1.06
CR5A	8	1.22	1.275	1.33	8.63	0.039	6	1.06	1.160	1.24	15.65	0.061	1.10
CR4B	15	1.08	1.168	1.27	16.17	0.047	14	1.03	1.089	1.20	15.25	0.054	1.07
CR2	24	1.09	1.181	1.28	16.03	0.042	25	1.02	1.093	1.18	14.55	0.042	1.08
M_3													
CR17	57	0.97	1.103	1.21	22.02	0.055	57	0.88	1.025	1.11	23.12	0.046	1.08
CR7	2	0.98	1.040	1.10			2	0.86	0.920	0.98			1.13
CR8	6	1.02	1.052	1.12	9.35	0.035	6	0.90	0.962	1.02	12.50	0.044	1.09
CR15	16	0.99	1.042	1.12	12.32	0.048	16	0.88	0.950	1.00	12.77	0.033	1.10
CR5A	4	0.89	1.002	1.05			4	0.83	0.908	0.96			1.10
CR4B	11	0.87	0.912	0.96	9.84	0.028	11	0.76	0.822	0.88	14.63	0.031	1.11
CR2	14	0.85	0.905	0.96	12.15	0.038	14	0.77	0.821	0.86	11.04	0.028	1.10

Remarks — There are no important differences between the populations of *Occitanomys sondaari* from CR2, CR4B and CR5A. The size ranges are similar (Fig. 8). As far as the morphology is concerned, in the lower molars the cingulums are similar, and the c2 is slightly larger in CR4B; in the M_1 the connection of anteroconid and metaconid is higher in CR4B than in CR2; an emerging tma-structure is more frequent in CR4B. In the upper molars from CR4B and CR5A t6 and t9 are united more frequently than in CR2; in the M^1 from CR4B the t1bis is more developed than in CR2; in the M^2 this cusp is more frequent in CR2.

In both CR2 and CR4B the intrapopulational variability is very high. We have defined a number of character states, that are represented in the Figs 9-14. In all populations the distribution of the character states is independent of the size; or, in other words, there are no morphological patterns related to size. In the populations from CR2 and CR4B some specimens have a morphology like *Occitanomys hispanicus*, independently of the size of the specimen.

In comparison with the type-population (Tortajada A, van de Weerd, 1976), the labial cingulums of the M_1 and M_2 from CR2, CR4B and CR5A are more developed, and so are the accessory cuspids on this cingulum. The size of the specimens from CR2, CR4B and CR5A is slightly smaller than in TOA (Fig. 15).

In some M_1 of *O. sondaari* from Vivero de Pinos and Aguanaces (Adrover, 1986) the posterior heel is prolonged by crests, that surround the posterior part of

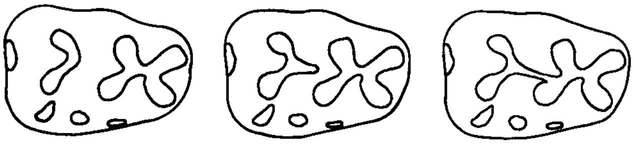
Table 6. Measurements of the upper molars of *Occitanomys*.

	Length						Width						L/W
	n	min.	mean	max.	V'	σ	n	min.	mean	max.	V'	σ	
M^1													
CR17	48	1.86	2.080	2.32	22.01	0.089	48	1.32	1.450	1.58	17.93	0.063	1.43
CR7	3	2.08	2.157	2.22			4	1.42	1.438	1.46			1.50
CR8	4	1.94	2.007	2.12			4	1.33	1.363	1.43			1.47
CR15	24	1.73	1.933	2.12	20.26	0.089	24	1.26	1.334	1.41	11.24	0.047	1.45
CR5A	4	1.79	1.823	1.85			7	1.25	1.281	1.34	6.95	0.031	1.42
CR4B	16	1.70	1.781	1.90	11.11	0.057	16	1.12	1.219	1.34	17.89	0.059	1.46
CR2	25	1.67	1.776	1.91	13.41	0.071	26	1.12	1.222	1.33	17.14	0.050	1.45
M^2													
CR17	55	1.26	1.437	1.58	22.54	0.066	54	1.27	1.429	1.56	20.49	0.067	1.01
CR7	2	1.50	1.520	1.54			2	1.42	1.440	1.46			1.06
CR8	14	1.28	1.419	1.54	18.44	0.074	13	1.30	1.373	1.51	14.95	0.065	1.03
CR15	19	1.30	1.367	1.42	8.82	0.031	21	1.13	1.327	1.44	24.12	0.062	1.03
CR5A	4	1.27	1.325	1.40			4	1.23	1.267	1.32			1.05
CR4B	10	1.14	1.217	1.32	14.63	0.071	11	1.09	1.199	1.28	16.03	0.056	1.01
CR2	32	1.12	1.258	1.34	17.89	0.051	32	1.13	1.219	1.31	14.75	0.050	1.03
M^3													
CR17	52	0.86	1.009	1.11	25.38	0.066	52	0.88	1.037	1.18	29.13	0.065	0.97
CR7	1		0.970				1		0.920				1.05
CR8	3	0.92	0.930	0.94			3	0.90	0.933	0.95			1.00
CR15	19	0.82	0.893	0.99	18.78	0.052	19	0.85	0.943	1.01	17.20	0.045	0.95
CR5A	3	0.74	0.827	0.91			4	0.80	0.893	0.95			0.93
CR4B	7	0.76	0.786	0.81	6.37	0.019	7	0.74	0.810	0.86	15.00	0.037	0.97
CR2	12	0.73	0.804	0.88	18.63	0.060	12	0.82	0.866	0.92	11.49	0.035	0.93

tooth (this phenomenon is also present in the M_1 from the type-locality). These crests are not present in the M_1 from CR2, CR4B and CR5A. In the upper molars of the populations from Crevillente the lingual longitudinal crests are not frequent (the t1 is rather more attached to the t5), and the labial longitudinal crests are absent. On the other hand, these connections are quite frequent in the specimens from Vivero de Pinos and Aguanaces.

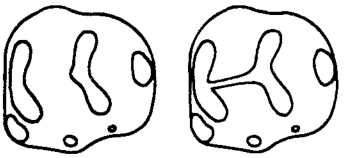
The specimens of *Occitanomys sondaari* from CR2 and CR4B are among the smallest of this species, together with some specimens from Puente Minero (Alcalá et al., 1991). The latter locality contains a faunal association similar to the one of CR2 and CR4B. The other Muridae and the Cricetidae from Puente Minero indicate, that this locality is older than CR2 and CR4B. The *Occitanomys* from Puente Minero is relatively large, but its morphology presents archaic characters: in the M^1 t1bis is absent in most specimens; in 78 % of the M^1 and in 66 % of the M^2 t6 and t9 are connected by a spur, but the tubercles are far apart, like in *O. hispanicus*. So, the *Occitanomys* from Puente Minero, combines large size with an archaic morphology, whereas the one from CR2 and CR4B, is characterized by a smaller size and derived morphology.

By its morphology and size the population from CR2 may be considered among the oldest known populations of the species. In many respects it reminds one of *Occitanomys hispanicus*, although the frequencies of the character states are different.



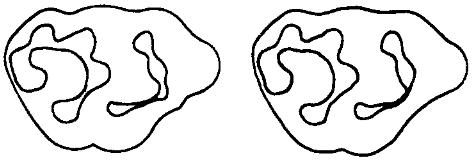
Locality	%	%	%	N
CR17	32.4	51.4	16.2	37
CR15	21.1	57.8	21.1	19
CR4B	70	30		20
CR2	66.7	33.3		18

Fig. 9. Percentages for the longitudinal connection in the M_1 of *Occitanomys*.



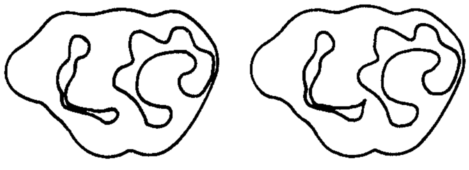
Locality	%	%	N
CR17	36.2	63.8	47
CR15	39.4	60.6	33
CR4B	81.2	18.8	16
CR2	75	25	24

Fig. 10. Percentages for the longitudinal connection in the M_2 of *Occitanomys*.



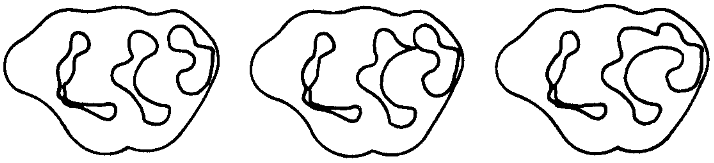
Locality	%	%	N
CR17	4.3	95.7	46
CR15	14.8	85.2	27
CR4B	12.5	87.5	16
CR2	37.9	62.1	29

Fig. 11. Percentages for the character states of t1bis in the M^1 of *Occitanomys*.



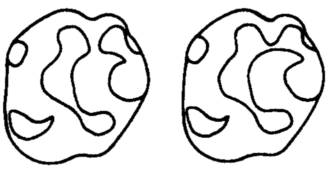
Locality	%	%	N
CR17	13	87	46
CR15	3.7	96.3	27
CR4B	25	75	16
CR2	44.8	55.2	29

Fig. 12. Percentages for the lingual longitudinal connection (t1-t5) in the M^1 of *Occitanomys*.



Locality	%	%	%	N
CR17		10.9	89.1	46
CR15		8.0	92.0	25
CR4B	13.3	86.7		15
CR2	17.9	82.1		28

Fig. 13. Percentages of the character states of the t6-t9 connection in the M^1 of *Occitanomys*.



Locality	%	%	N
CR17		100	54
CR15	20	80	20
CR4B	21.4	78.6	12
CR2	38.2	61.8	32

Fig. 14. Percentages of the character states of the t6-t9 connection in the M^2 of *Occitanomys*.

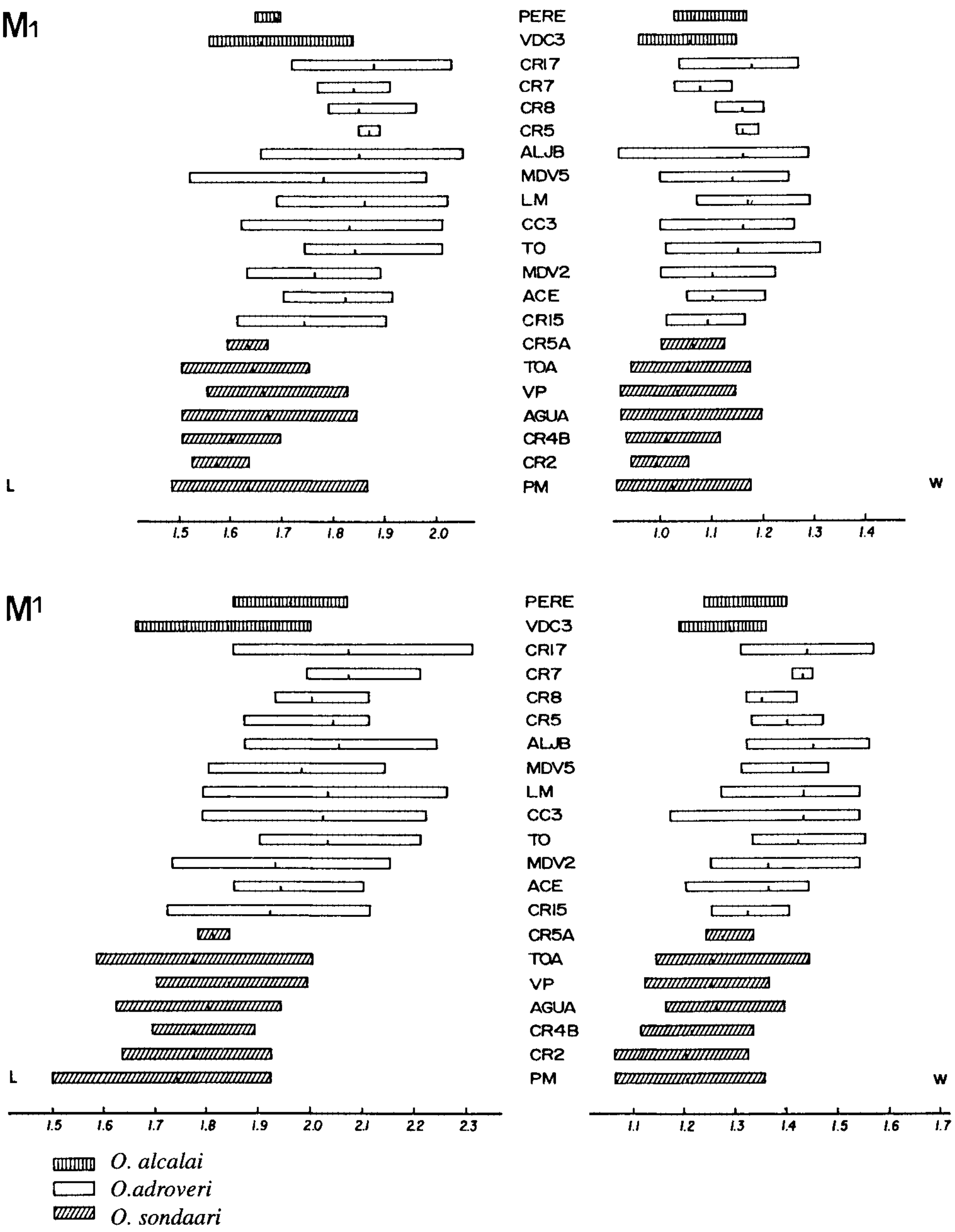


Fig. 15. Size ranges for length and width of the first molars of *Occitanomys* from several Spanish localities.

We attribute it to *O. sondaari*, because of the presence of a longitudinal spur in 33 % of the M_1 and in 25 % of the M_2; because t1bis is present in more than 60 % of the M^1 and in 80 % of the M^2; and, finally, because t6 and t9 are connected (not united) by a posterior spur of t6 in 82 % of the M^1 and in 62 % of the M^2.

Occitanomys (Rhodomys) adroveri (Thaler, 1966)
Pl. 6, figs. 1-16.

Original reference — *Parapodemus adroveri* sp. nov. in Thaler, 1966, pp. 127-129.

Type locality — Los Mansuetos (Teruel, Spain).

Holotype — M^{1-3}, M. 4029, deposited in the 'Institut de Paleontologia Miquel Crusafont', Sabadell (Spain).

Localities with O. adroveri in Crevillente — Crevillente 15 (CR15), Crevillente 8 (CR8), Crevillente 7 (CR7), Crevillente 17 (CR17), and some younger localities, that will be treated in a forthcoming paper.

Measurements — See Tables 5-6.

Description of the material from Crevillente 15

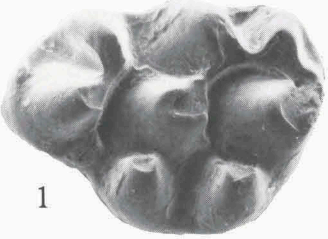
M_1 — The anteroconid is slightly asymmetrical, its lingual lobe is connected to the metaconid; a minuscule tma is present in half of the population. The protoconid is placed slightly backwards with respect to the metaconid. In nearly all specimens (79 %) there is a longitudinal spur from the posterior pair of cusps towards the base of the protoconid, rarely forming a low crest. The labial cingulum is continuous and broad, with a c1 of medium size. The c2 is larger than the c1, or equals it in size. The posterior cingulum is blade-shaped and low (in some cases it is triangular). There are two main roots and a trace of a third one.

M_2 — The posterior part of the tooth is narrower than the anterior part. The anterolabial cuspid is oval-shaped, united with its anterolingual face to the protoconid;

Plate 6

Occitanomys adroveri (Thaler, 1966) from Crevillente 17
Fig. 1. M^1 sin., RGM 413 345.
Fig. 2. M^1 dext., RGM 413 248.
Fig. 3. M^3 sin., RGM 413 428.
Fig. 4. M^2 sin., RGM 413 396.
Fig. 5. M^2 dext., RGM 413 403.
Fig. 6. M_1 sin., RGM 413 179.
Fig. 7. M_3 dext., RGM 413 296.
Fig. 8. M_2 dext., RGM 413 249.

Occitanomys adroveri (Thaler, 1966) from Crevillente 15
Fig. 9. M^1 dext., RGM 403 670.
Fig. 10. M^1 dext., RGM 403 679.
Fig. 11. M^2 dext., RGM 403 713.
Fig. 12. M^2 dext., RGM 403 701.
Fig. 13. M^3 dext., RGM 403 739.
Fig. 14. M_2 dext., RGM 403 600.
Fig. 15. M_1 dext., RGM 403 595.
Fig. 16. M_1 dext., RGM 403 586.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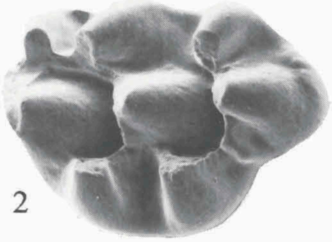
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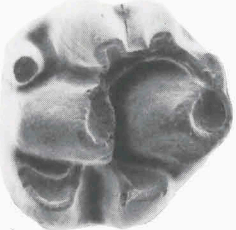
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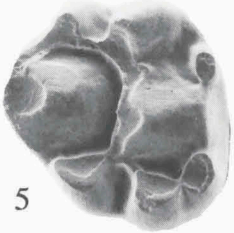
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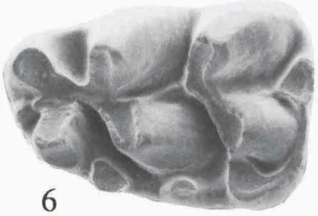
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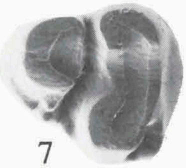
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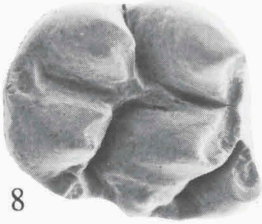
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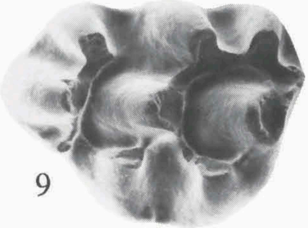
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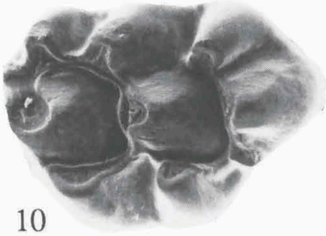
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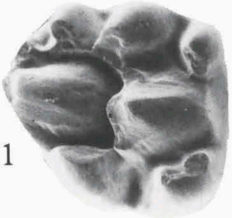
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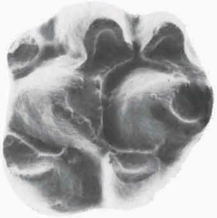
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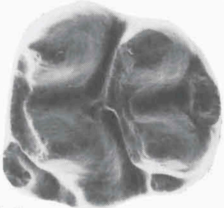
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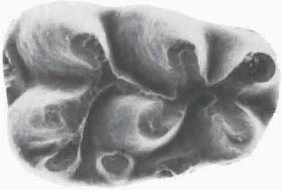
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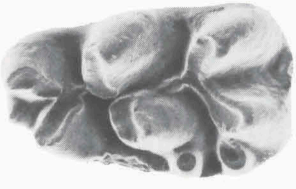
16

1 mm

its posterior part continues into a broad and continuous cingulum; there is a small c1 (absent in two cases) and a big c2. A longitudinal spur is present in nearly all the specimens; it never forms a crest. The posterior heel is low, oval- or blade-shaped, very broad, and it closes the posterior valley. There are two roots.

M_3 — The anterolabial cuspid is small and low. A c1 is present in one specimen only. The hypoconid-entoconid complex is small and very much inclined towards the lingual side of the tooth. There are two roots.

M^1 — The t1 is situated backwards; its anterior end may be free (46 %) or united to t1bis or to the t2 (54 %); t1bis is variable in size, absent in 4 cases only. The t1 is connected to the middle of the anterolingual wall of t5 by a short spur (this spur is never directed towards the connection t4-t5). In four specimens t3 has a short posterior spur. Cusp t4 is separated from t8 by a small valley. Cusps t6 and t9 are always connected. The t12 is always present, either as a small cusp (61.5 %) or as a widening of the cingulum t9-t8 (38.5 %). In two specimens there is a small bulging (t10?) in the posterolingual wall of the tooth. There are three main roots and a trace of fourth one.

M^2 — A t1bis is present in 60 % of the specimens, united to t1. In half the specimens the t1 or the t1-t1bis complex is completely isolated; in the other half it may have one or both of its ends, connected to the t5. The t3 is small and isolated. The t4 is separated from the t7 by a small valley. Cusps t6 and t9 are separated in two specimens. The t12 is a small swelling of the cingulum t9-t8. There are three roots.

M^3 — The t1 is isolated. The t3 is very much reduced or absent. The t8 is isolated. There are three roots.

Description of the material from Crevillente 8 and Crevillente 7

Crevillente 8 and Crevillente 7 have yielded a small number of specimens, of medium size, that are slightly larger than the material from CR15 (Figs. 8, 15). In the lower molars from CR8 the longitudinal spur is less constant than in CR15. In CR7 the labial cingulums of the lower molars are somewhat more reduced than in CR15. The upper molars present no differences with CR15.

Description of the material from Crevillente 17

M_1 — The anteroconid is slightly asymmetrical when there is a tma-like expansion of the enamel (38 %); when this expansion is absent, the anteroconid is symmetrical (62 %). The protoconid is situated backwards with respect to the metaconid. In most of the specimens there is a longitudinal connection (67.6 %), which forms a real crest in 16.2 % only (Fig. 9). The labial cingulum is continuous, with a voluminous c1; the c2 is smaller than the c1, and always present; in half the specimens there is one more accessory cuspid between protoconid and anteroconid; the cingulum continues behind the c1, and may surround the posterolabial wall of the hypoconid completely. The posterior heel is triangular, rarely blade-shaped, and absent in one specimen. There are two main roots and a very small third one in the center of the tooth.

M_2 — The tooth is a little narrower posteriorly than anteriorly. The anterolabial cuspid is high and oval-shaped, isolated or united to the anterior wall of the protoconid. In 64 % of the specimens there is a longitudinal connection (Fig. 10). The labial cingulum is continuous (completely absent in two specimens); c1 is small or absent; c2 is generally larger than c1. the posterior heel is low, oval- or blade-shaped, sometimes absent. There are two roots.

M_3 — The anterolabial cuspid is always present. The hypoconid-entoconid complex is small, inclined towards the lingual side. In some specimens there is an enamel ridge at the base of the posterolabial wall of the tooth. In two specimens there is a longitudinal spur. The c1 is present in 25 specimens, and absent in 32. There are two roots.

M^1 — The t1 is situated backwards; its anterior part may end free (47 %) or be united to the t1bis; the latter tubercle varies in size, and is absent in 4 % of the population only. Cusps t1 and t5 are generally connected. The labial longitudinal spur is present in four specimens only. Cusps t4 and t5 are generally united; t4 and t8 are separated by a valley. The t6 and the t9 equal each other in size, and are connected in nearly all cases. The t12 is generally reduced to a mere protuberance of the cingulum t9-t8. In some specimens there is a small enamel bulge at the crown base between t6 and t9. There are three main roots and a trace of a fourth one.

M^2 — The t1bis varies in size, and it is present in 80 % of the specimens. The t1 is connected to the lingual wall of the t5 in 37 % of the cases. The t3 doesn't have a posterior spur. Cusps t4 and t5 are generally united (96 %); t6 and t9 are always connected by the posterior spur of t6. The t12 may be absent, or be reduced to a small swelling of the cingulum t9-t8. There are three roots.

M^3 — The t1 may be isolated or united to the anterolingual wall of the t4. The t3 is generally reduced, sometimes absent. In some specimens the t8 is united to t4 or t6. There are three roots; the anterolingual one has a subdivided tip.

Remarks — The population of *Occitanomys adroveri* from CR15 has very wide ranges for length and width of the various dental elements (see Figs. 8, 15). The morphological variability is very broad too. Among the M_1, two specimens are short and broad, with a very wide labial cingulum, and a short longitudinal spur. These small specimens remind one of *Centralomys*.

The population from CR17 is, like the one from CR15, very variable in size and morphology. CR17 contains specimens of *Occitanomys adroveri* in which one may recognize some of the features that are found in *Stephanomys* from younger levels, like e.g.: presence of a longitudinal spur, which in 16 % of the population already forms a low crest; a labial cingulum, which is prolonged around the posterolabial wall of the hypoconid; c2 always present in the M_1; the anterior tip of t1, which is generally united to a well-developed t1bis; t4-t5 connected by a crest; and t12 vestigial in M^1 and M^2.

The specimens from CR17 are significantly larger than those from CR15, and there are a number of morphological differences: in the M_1 from CR15 the c2 may be missing, but if it is present, it is equal in size to c1, or even larger, while in the specimens from CR17 the c2 is always present, though smaller than c1. In M^1 the t1bis is more frequent in CR17 than in CR15. The most striking difference is found in t12, which is generally reduced to a mere protuberance of the cingulum t9-t8 in CR17, and forms a small cusp in the majority of the M^1 from CR15. In the M^2 from CR17 there are no significant differences in comparison with the population from CR15, except for the t4-t5 connection, which is higher in all the specimens from CR17.

Occitanomys adroveri from the type-locality Los Mansuetos (Utrecht collection) shows a great size variability. The major part of the population from CR15 lies within the size range of the population from Los Mansuetos, except for some small specimens from CR15 that fall outside this range. In the populations from CR17 the opposite happens: here the larger specimens fall outside the range of biometrical variability of the Los Mansuetos population. So, the population from Los Mansuetos is intermediate in size between CR15 and CR17. From a morphological point of view, it is difficult to make any separation between the populations from CR15, CR8, CR7, CR17 and Los Mansuetos. There are, however, some differences: the t1bis is absent in 15 % of the M^1 from CR15, in somewhat more than 7 % in those from LM, and in 4 % of the M^1 from CR17. The t6-t9 connection of the M^1 is complete in all three populations. The t6-t9 connection of the M^2 is absent in 20 % of the specimens from CR15, it is rarely absent in LM, and always present in CR17. The frequencies of the longitudinal spur in the lower molars are similar in the three populations. Morphologically the population from Los Mansuetos is intermediate between those from CR15 and CR17.

Occitanomys adroveri from Casa del Acero is on the average slightly larger than the population from CR15. The longitudinal connections are more frequent and higher in the molars from Casa del Acero than in CR15, specially the posterior spur of t3 in the M^1, that is present in nearly all the specimens from CA, only in 17 % of the specimens from CR15, and 8 % of the specimens from CR17. The t1bis is always present in CA and may be absent in CR15. By the size of the teeth, and by their morphology, *O. adroveri* seems to indicate that Casa del Acero is younger than CR15 and older than CR17.

Aljezar B (Adrover, 1986) contains a very heterogeneous population of *Occitanomys adroveri*, which does not present, however, 'morphotypes Centralomys' like in CR15. It is similar in size to the material from CR17, and the longitudinal connections are – like in Casa del Acero – more frequent and higher in Aljezar B.

Discussion — The subgenus *Rhodomys* groups various species of *Occitanomys*. *O. sondaari* and *O. adroveri* are considered to be ancestor and descendant respectively (van de Weerd, 1976; Adrover, 1986; and this paper).

We have carried out a morphological analysis of the populations (Figs. 9-14), studying several characters: presence/absence of a small tma in M_1; in M_1 and M_2 the number, relative size, and position of the accessory cuspids, the longitudinal connection, and the terminal heel; in M^1 and M^2 the presence/absence of t1bis, connections between the pairs t1-t5, t3-t5, t4-t5 and t6-t9, and the morphology of t12. in M^1 also the presence/absence of a connection between t1 and t1bis (if this cusp exists) or between t1 and t2 (if t1bis not exists).

As we mentioned in a previous paper (Freudenthal et al., 1991a) the localities in the area of Crevillente are located in stratigraphic superposition. Therefore, the analysis of the distribution of the character states allows us to trace the morphological changes between populations from localities whose relative stratigraphic position is beyond doubt (it is not deduced from biostratigraphic correlations). It is remarkable, that the distributions of the character states are independent of size; or, in other words, in any specific population, similar features are found in the smallest and in the largest specimens, and specimens with equal size may present distinct morphological states. Between the oldest and the youngest populations under study the following trends are observed:

M_1 — The presence of a small tma is rare in the oldest population and amounts a 40 % in the rest of the populations. The accessory tubercle c1 is present in all cases and its relative size augments in the course of time. On the other hand the relative size of c2 (in comparison with the c1) diminishes with time: the c2 is larger than the c1 in 40 % of the M_1 of *Occitanomys sondaari* from CR2, and only in 11 % in *O. adroveri* from CR17. The longitudinal connection between the two posterior tubercle pairs (Fig. 9) is absent in more than 65 % of the specimens of *O. sondaari* and is present in more than 65 % of those of *O. adroveri* (in some cases it even forms a crest). In the specimens of *O. sondaari* there are two roots and in those of *O. adroveri* there is a very small third one in the center of the tooth.

M_2 — The longitudinal connection (Fig. 10) is present in 25 % at the most in *O. sondaari*, and in more than 60 % in *O. adroveri*. The absence of c1 shows similar frequencies in all the populations; however, if present, its relative size is greater in the younger populations.

M^1 — The anterior tip of t1 may end free, or be united to t1bis (if present) or to t2; the frequencies are similar in all the populations studied. The t1bis (Fig. 11) is more frequent and larger in the more recent populations. The lingual (Fig. 12) and labial longitudinal connections, as well as the connection t4-t5 and the connection t6-t9 (Fig. 13) are more frequent and higher in the younger populations. The t12 may be integrated in the cingulum t9-t8, or it is tubercular; in *O. sondaari* the tubercular t12 is more frequent in the younger population; in *O. adroveri* on the other hand, the t12 is predominantly integrated in the cingulum in the younger populations. In the M^1 of *O. sondaari* there are three roots, and in those of *O. adroveri* there is an additional very small fourth one in the center of the tooth.

M^2 — The t1bis is present with similar frequencies and relative size in all the populations. The connection t1-t5 is similar in all the cases. On the other hand the connections t4-t5 and t6-t9 (Fig. 14) are more frequent and higher in the younger populations. Among the specimens of *O. adroveri* from CR2 with preserved roots 80 % have three roots, and 20 % have four. In the other populations, the M^2 have only three roots.

We may resume, that in the populations studied from the area of Crevillente we observe a size increase from the oldest to the youngest populations. In the course of time there is also an increase of connections between the tubercles, an increase of the relative size of c1 in the lower molars, and of t1bis in the M^1.

Associations of Muridae in the Crevillente area

Crevillente 2 contains four species of Muridae: *Huerzelerimys vireti*, *Occitanomys sondaari*, *Parapodemus lugdunensis*, and *Parapodemus* sp. In Fig. 16 the latter three are represented. *H. vireti* is much larger, and not included in the diagrams. The dental elements of *P. lugdunensis* are on the average somewhat larger than those of *O. sondaari*, but there is an important overlap.

Crevillente 4B contains three species of Muridae: *H. vireti* of large size, not included in Fig. 17, *O. sondaari*, and *P. lugdunensis*. Like in CR2 there is a large size overlap between the latter two.

In both localities, for the same length values of M^1 and M^2, the specimens of *Occitanomys* have a much greater width than those of *Parapodemus*.

Crevillente 15 also contains three species of Muridae: *Huerzelerimys turoliensis* (of large size), *Occitanomys adroveri*, and *Parapodemus barbarae* (none of these species occurs in CR2 and CR4B). Figure 18 shows the length/width diagrams for the teeth of *P. barbarae* and *O. adroveri*. The largest values invariably are those of *P. barbarae*, even for the widths of the upper molars. This means, that the size relations found in the previously mentioned – older – populations are not maintained.

Crevillente 8 has yielded four species of Muridae: *Huerzelerimys turoliensis* represented by one single M^3, *Occitanomys adroveri* and two species of *Parapodemus*: *P. barbarae* and *P. meini*.

Crevillente 7 contains two species: *Occitanomys adroveri* and *Parapodemus meini*. The diagrams in Fig. 7 give the measurements of the *Parapodemus* and *Occitanomys* material from both these localities.

Parapodemus barbarae from CR8 has a size overlap with *Occitanomys adroveri* from the same locality; the size relations found in CR15 are maintained.

On the other hand the specimens of *Parapodemus meini*, both from CR8 and from CR7, are considerably larger than the homologous teeth of *Occitanomys*.

The size increase among the species of *Parapodemus*, from the oldest levels to the youngest, is larger than the size increase within the genus *Occitanomys*.

Crevillente 17 contains *Occitanomys adroveri* and a Muridae gen. et sp. nov. (Martín Suárez & Freudenthal, in prep). This new murid is very large, much larger than *Occitanomys adroveri* from the same locality.

Biostratigraphy

Both the Muridae and the Cricetidae from Crevillente show close relationships with the Lower Turolian localities in the surroundings of Teruel. Though the numerical composition of the faunas is quite different from one area to the other, the faunal elements are identical, often at species level. Therefore, there can be little doubt, that the Crevillente faunas can be dated as Early Turolian.

The Muridae found in the Lower Turolian deposits of the area of Crevillente (Fig. 19) allow a refinement of the local biozonation established on the basis of the Cricetidae (Freudenthal et al., 1991b).

The first zone recognized coincides with the first zone for the Cricetidae (localities CR2 and CR4B). Between CR2 and CR4B exists a marine interval (Freudenthal et al., 1991a); however, the species of Muridae and Cricetidae (Freudenthal et al., 1991b) are the same at both localities (Fig. 19).

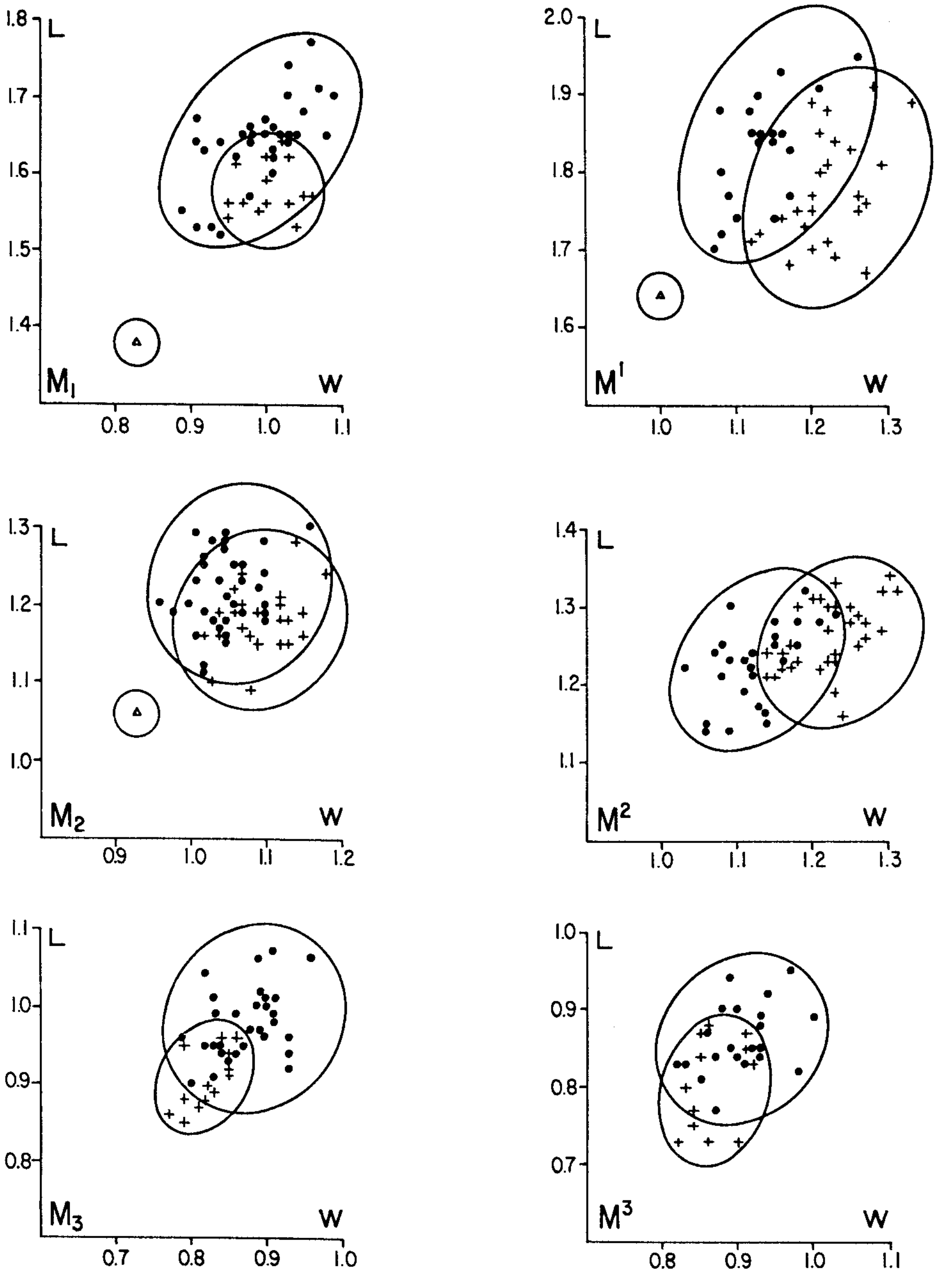

Fig. 16. Length/width diagrams of the molars of *Occitanomys sondaari* (+), *Parapodemus lugdunensis* (●) and *Parapodemus* sp. (Δ) from CR2.

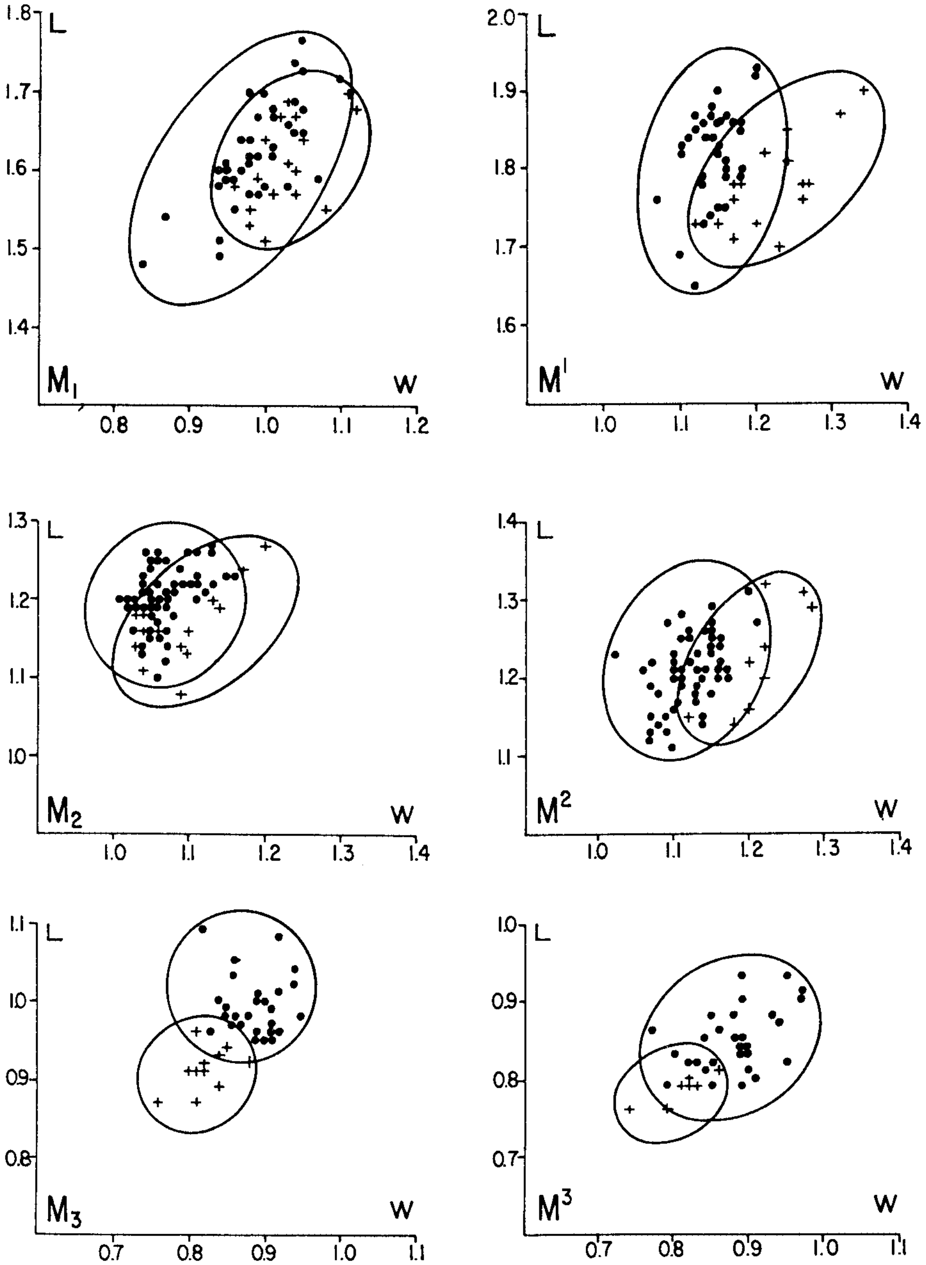

Fig. 17. Length/width diagrams of the molars of *Occitanomys sondaari* (+) and *Parapodemus lugdunensis* (●) from CR4B.

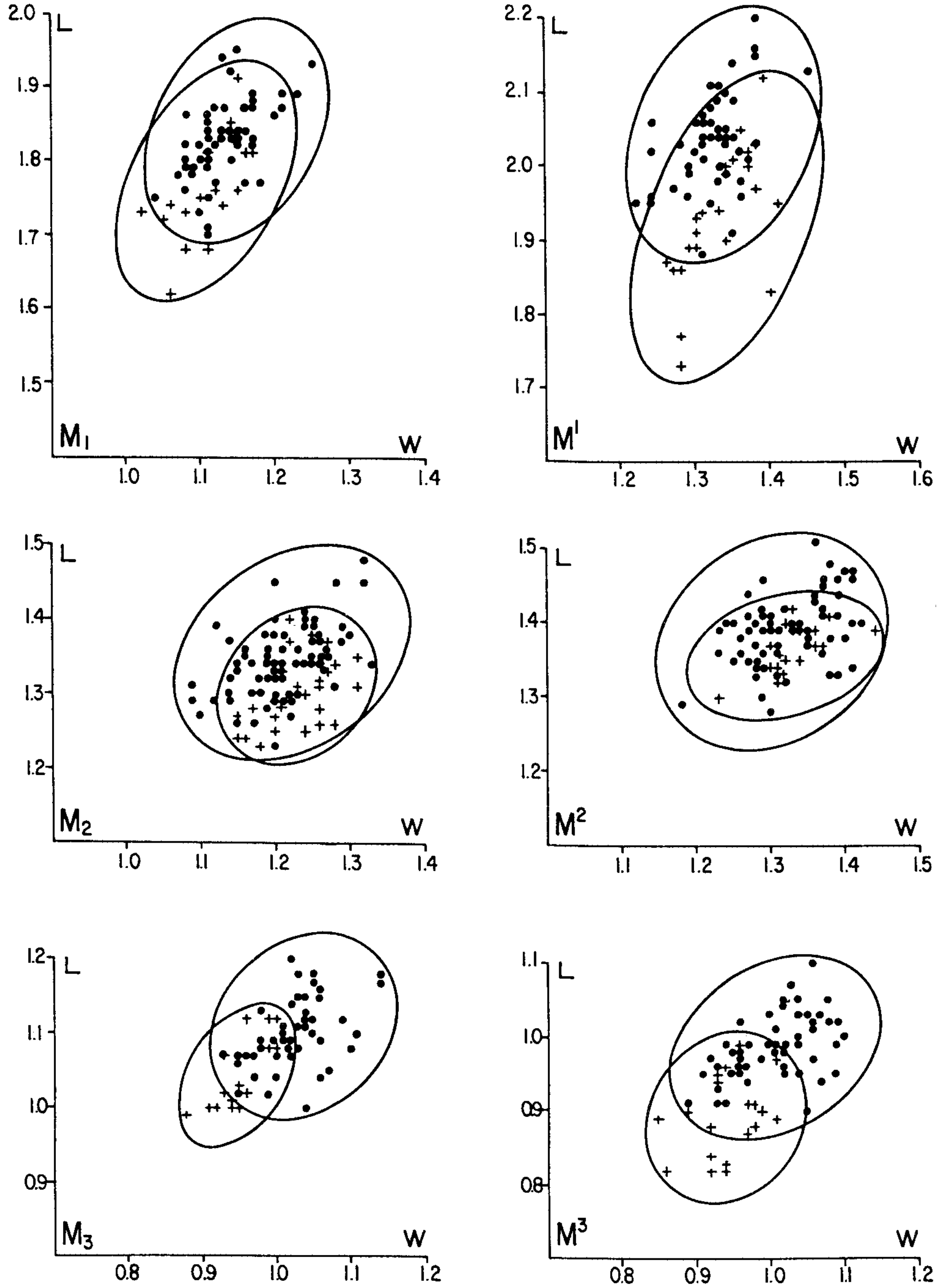

Fig. 18. Length/width diagrams of the molars of *Occitanomys adroveri* (+) and *Parapodemus barbarae* (●) from CR15.

CR 2	CR4B	CR15	CR 8	CR 7	CR17	
☒	☒					*Huerzelerimys vireti*
☒	☒					*Parapodemus lugdunensis*
☒	☒					*Occitanomys sondaari*
		☒	☒			*Huerzelerimys turoliensis*
		☒	☒			*Parapodemus barbarae*
		☒	☒	☒	☒	*Occitanomys adroveri*
			☒	☒		*Parapodemus meini*
					☒	Gen. nov., sp. nov.
☒	☒					*Neocricetodon occidentalis*
☒	☒					*Hispanomys peralensis*
		☒				*Neocricetodon plinii*
		☒				*Hispanomys adroveri*
		☒				*Hispanomys* sp.
			☒		☒	*Hispanomys* cf. *adroveri*
			☒		☒	*Neocricetodon lucentensis*

Fig. 19. Distribution of Muridae and Cricetidae in several fossiliferous levels in the Crevillente area.

Between CR4B and CR15 a complete renewal of the fauna of Cricetidae and Muridae takes place, which allows one to recognize a second zone, represented by the localities CR15 and CR5A. So, the cricetid zonation is confirmed by the Muridae, though CR5A is poor in Cricetidae, and was not studied in our previous paper.

The third zone based on the Cricetidae, contains the faunas from CR8, CR5, and CR17. On the basis of Muridae two faunal units are recognized in this zone: the first one comprises the faunas from CR8, CR5, and CR7 (the latter locality did not yield any Cricetidae); the second one is represented by CR17. The difference between these two is the disappearance of *Parapodemus* and the appearance of a Muridae gen. nov. sp. nov.; the faunal change is less drastic than the one between the first two zones.

The Muridae from the next two zones (based on the Cricetidae from CR14 and CR6 respectively) will be treated in a future paper.

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Errata
Pl. 5, fig. 11 should be turned about 150° clockwise.