Castromys, a new genus of Muridae (Rodentia) from the Late Miocene of Spain

E. Martín Suárez & M. Freudenthal

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E. Martín Suárez, Departamento de Estratigrafía y Paleontología, Universidad de Granada, E-18071 Granada, Spain; M. Freudenthal, National Museum of Natural History, Postbus 9517, 2300 RA Leiden, The Netherlands, and Departamento de Estratigrafía y Paleontología, Universidad de Granada, E-18071 Granada, Spain.

In this paper a new genus of Muridae, *Castromys*, is described; type-species is *Castromys littoralis* sp. nov., from the Late Miocene of Crevillente (Alicante, Spain). Two previously described species, *Karnimata inflata* and *Valerymys juniensis* are assigned to this new genus. Its phylogeny and biostratigraphical implications are discussed.

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Introduction

Upper Miocene continental deposits are known from various Spanish basins, among which the Basin of Crevillente (Alicante) plays an important role. The first fossil micromammals from the Castro section in this basin were reported by Montenat in 1973, and published in 1977. De Bruijn et al. (1975) studied a number of superposed fossiliferous localities from the Castro section in detail. Recently various papers were published on faunas from the same section: a redescription of the section by Freudenthal et al. (1991b), the Cricetidae by Freudenthal et al. (1991a), and the Muridae by Martín Suárez & Freudenthal (1993). In the latter paper (op. cit., pp. 112, 116, fig. 19) the existence of a large 'Muridae gen. et sp. nov.' in the locality Crevillente 17 was mentioned. This murid will be the subject of the present paper.

Crevillente 17 is not the only locality in which this new genus is found. In the Crevillente area it is also represented in the localities Crevillente 14, 22 and 31. It has been found in the Granada Basin too (Víznar 1, Jun 2, and several other localities) and in the Teruel Basin (La Gloria 1 and 6, Arquillo 1, etc.).

Until now these populations were attributed either to the genus *Karnimata* or to *Valerymys*, like *Karnimata inflata* Mein, Moissenet & Adrover, 1990. The type-species

of *Karnimata, K. darwini*, was transferred to the genus *Progonomys* by Mein et al. (1993). *K. inflata*, however, is certainly not a *Progonomys*, and this means, that a new genus has to be created for a group of species that had previously been attributed to *Karnimata* or *Valerymys*.

Taxonomy

Family Muridae Gray, 1821
Subfamily Murinae Gray, 1821

Castromys gen. nov.

Type-species — *Castromys littoralis* sp. nov.

Derivatio nominis — After the hill 'Castro', E of the road Aspe-Crevillente (Alicante), where the type-locality of the type-species is located.

Species attributed to *Castromys*:
Valerymys juniensis Padial Ojeda & Ruiz Bustos, 1989
Karnimata inflata Mein, Moissenet & Adrover, 1990

Diagnosis — Muridae of about the same size as or bigger than the extant *Rattus rattus* (L., 1758). M^1 and M^2 with t6 and t9 frequently separated. Upper molars with broad central cusps. In the M^3 the two posterior cusps, t8 and t9, are differentiated. Lower molars with a well-developed labial cingulum; M_1 with the anteroconid generally separated from the protoconid-metaconid complex; tma voluminous.

Differential diagnosis — *Castromys* differs from *Progonomys* by its larger size, and by the presence of a tma in the M_1. It differs from *Occitanomys, Centralomys, Stephanomys*, and *Castillomys* by the absence of longitudinal connections between the cusps and by the forward position of t1 in the M^1. It differs from *Apodemus, Rhagapodemus* and *Parapodemus* by the absence of both a t7 and a high connection between t4 and t8; the anterior wall of the hypoconid-entoconid complex is almost straight in *Castromys*, whereas in the mentioned genera it is V-shaped. It differs from *Paraethomys* by having a well-developed t9 in the M^2. It differs from *Huerzelerimys* by the presence of a tma, and by the separation between the two anterior pairs of cusps in the M_1; in the upper molars t6 and t9 are generally separated. It differs from *Proceromys, Mus* and *Orientalomys* by the anterior position of t1 in the M^1.

Furthermore it differs from all these genera by the differentiation of hypocone and metacone in the M^3.

It differs from *Pelomys* and *Parapelomys* by the presence of a big tma in the M_1 and by having a well-developed t12 in the M^1 and M^2. It differs from *Saidomys* by its smaller size, by a better developed labial cingulum in the lower molars, and by the presence of t12 in the M^1 and M^2.

Castromys littoralis sp. nov.
Pl. 1, figs. 1-14; Pl. 2, figs. 1-12

Derivatio nominis — Latin littoralis is coastal, littoral; because the type-population was found in a sequence of lagoonal and coastal deposits.

Holotype — M^1 sin., RGM 413 092, deposited in the National Museum of Natural History, Leiden, The Netherlands.

Type-locality — Crevillente 17 (CR17), Province of Alicante, SE Spain, UTM 30SXH401949.

Measurements — See Table 1 and Figs. 1-3.

Diagnosis — *Castromys* of small size. M^1 and M^2 with t6 and t9 frequently separated, t12 always present. In the lower molars the anterior wall of the hypoconid-entoconid pair is almost straight, and only rarely there is a short longitudinal spur.

Differential diagnosis — *Castromys littoralis* differs from *Castromys inflatus* by its lesser size. In the upper molars the central cusps of *C. inflatus* are significantly broader than those of *C. littoralis*; the t6-t9 connections are present in some upper molars of *C. littoralis*, and they are always absent in *C. inflatus*. As far as the relative position of t8 and t9 of M^1 and M^2 is concerned, in *C. inflatus* these two cusps are much closer together, and the connection is broader than in *C. littoralis*. In the lower molars these two species can only be distinguished by their size.

C. littoralis differs from *C. juniensis* by its more voluminous tma in M_1, and by the presence of a t12 in M^2.

Populations attributed to this species:

Crevillente 22 (CR22), prov. Alicante, UTM 30SXH399951.

Jun 2B, Jun 2C (UTM 30SVG479199) and Víznar 1 (UTM 30SVG501199), prov. Granada.

Description of the material from the type-locality

M_1 — Posterior part of the molars broader than the anterior part. The tma is voluminous and generally isolated, situated in a central position or slightly shifted towards labial. The labial anteroconid cusp is slightly smaller than the lingual one, both cusps are isolated until an advanced degree of wear. The anteroconid is seldom united to the second pair of cusps. There is no longitudinal crest. The anterior wall of the hypoconid-entoconid pair is practically straight, only in some very worn specimens it takes the shape of a wide open 'V'. The labial cingulum is continuous and well-developed, with a c1 as big as the tma; c1 is protruding from the labial wall of the tooth and may be separated from or united to the hypoconid; there is a c2, attached to the base of the protoconid; the cingulum bears two or three more accessory cusps, in some specimens one of these small cusps is situated between c1 and c2. The terminal heel is big and oval-shaped. There are two roots, and in some cases a tiny beginning of a central root.

M_2 — Anterior and posterior widths almost equal. Like in M_1, the anterior wall of the hypoconid-entoconid pair is practically straight, only in two very worn specimens one may observe a longitudinal spur, which is short and low. The anterolabial cusp is big, and isolated at its top; posteriorly it is prolonged into a labial cingulum which bears a well-developed c1 (absent in one case), that is generally separated from the hypoconid; there is a c2, attached to the base of the protoconid; like in M_1 there may be a small cusp between c1 and c2. The posterior heel is oval-shaped and generally closes the talonid valley. There are two roots.

M_3 — The teeth are broad. The anterolabial cusp is small and very low, but well

discernable. In hardly worn specimens the protoconid-metaconid pair has a slightly trilobate occlusal surface. The hypoconid-entoconid complex is short and transversely widened; its labial part is compressed; in one specimen there is a small c1. The posterolabial wall of the tooth bears a cingulum ridge. There are two roots.

M^1 — Teeth very broad and voluminous, with steep bulbous cusps. The anterolabial wall of the tooth frequently presents an enamel ledge, that may be quite well-developed. The t1 is placed just slightly backwards, and in one case only there is a short posterior spur, directed towards the base of the t5. There is no t1bis. The t3 is equal in size to (or slightly smaller then) t1; in 5 specimens the t3 has a short posterior spur, that ends at the base of the t5. In one specimen there is a small cusp between t1 and t4. The t4 is united to t8 by a narrow and low crest. The t6 is larger than t9, and these two cusps are frequently separated. The t9 is united to t8 by a low crest, which is wider than the crest between t4 and t8. The t12 is oval-shaped, and so big that it encircles a posterosinus. There are three or four main roots, and an incipient central root.

M^2 — Rounded molars, with a big, completely isolated t1, and without t1bis. The t3 is small, similar in size to t9, and lingually united to the base of t2. Neither t1 nor t3 are provided with posterior spurs. The t4 is united to t8 by a narrow and very low crest; t5 and t8 are very broad. The t9 is smaller than t6, and generally these two cusps are separated. The connection between t9 and t8 is weaker than in M^1. The t12 is tubercular, and smaller than in M^1. There are three roots.

M^3 — This element is very much rounded, and has a voluminous and isolated t1. The t3 is very much reduced or absent. The posterior lobe is very broad, and shows a constriction that permits to distinguish hypocone and metacone (t8 and t9), the latter one being the smallest; t8 is separated from t4; t9 may be united to t6. In one specimen (Fig. 4a) there is a small posterior cusp, that might be interpreted as a t12. There are three roots.

Remarks — The enamel is quite rugose, especially on the posterior walls of the cusps of the lower molars, and the anterior walls of the cusps of the upper molars.

In the lower molars the cusps are strongly inclined forward. The anterior wall of the hypoconid-entoconid pair is almost straight or slightly curved, it never acquires the V-shape that is familiar in *Apodemus*. The connections within the pairs of cusps are very weak: in several specimens the lobes of the anteroconid do not meet. The other connections are slightly higher. In M_1 the anteroconid is generally separated

Plate 1.

Castromys littoralis gen. et sp. nov., from Crevillente 17.

Fig. 1. M^1 sin., RGM 413 092, holotype.
Fig. 2. M^2 sin., RGM 413 114.
Fig. 3. M^3 sin., RGM 413 153.
Fig. 4. M^3 dext., RGM 413 170.
Fig. 5. M^2 dext., RGM 413 142.
Fig. 6. M^1 dext., RGM 413 103.
Fig. 7. M^1 dext., RGM 413 101, labial view.
Fig. 8. M^3 sin., RGM 413 158.
Fig. 9. M_1 sin., RGM 413 001.
Fig. 10. M_2 sin., RGM 413 026.
Fig. 11. M_3 sin., RGM 413 055.
Fig. 12. M_3 dext., RGM 413 074.
Fig. 13. M_2 dext., RGM 413 053.
Fig. 14. M_1 dext., RGM 413 009.

Scale represents 1 mm.

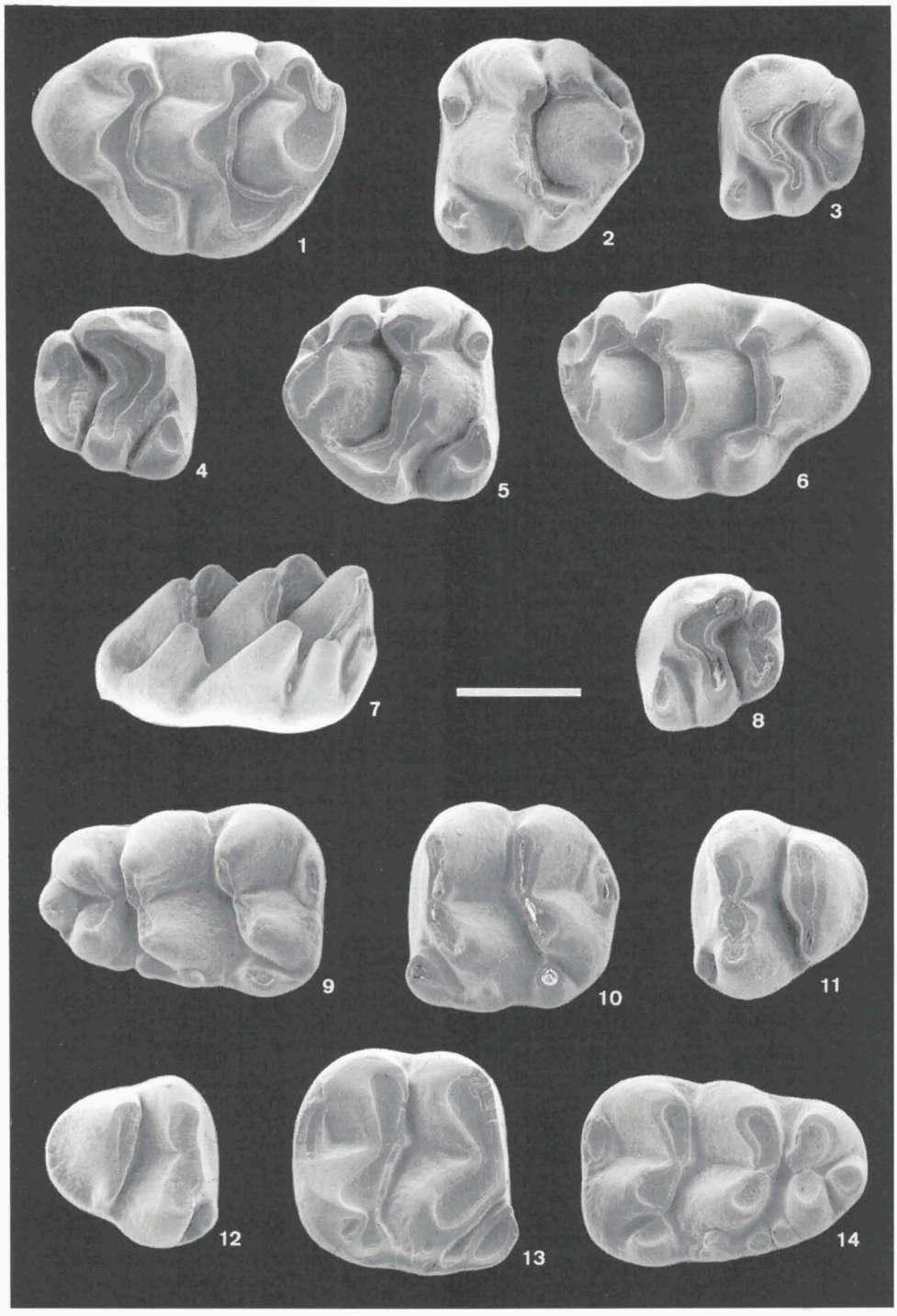
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Table 1. Measurements of molars of *Castromys*.

	length	min.	mean	max.	V'	σ	width	min.	mean	max.	V'	σ
M_1												
GLOR6	6	2.60	2.647	2.71	4.14	0.039	7	1.61	1.750	1.86	14.41	0.092
JUN2C	2	2.44	2.450	2.46	0.82	0.014	3	1.65	1.717	1.78	7.58	0.065
JUN2B	4	2.29	2.370	2.51	9.17	0.102	2	1.57	1.630	1.69	7.36	0.085
CR31	0						1		1.73			
CR22	3	2.35	2.377	2.41	2.52	0.031	4	1.56	1.610	1.64	5.00	0.035
CR17	14	2.16	2.278	2.40	10.53	0.078	16	1.38	1.500	1.61	15.38	0.067
M_2												
GLOR6	2	1.97	1.970	1.97			2	1.88	1.905	1.93	2.62	0.035
JUN2C	2	1.76	1.795	1.83	3.90	0.049	2	1.70	1.745	1.79	5.16	0.064
JUN2B	5	1.71	1.836	1.99	15.14	0.105	7	1.68	1.767	1.88	11.24	0.072
CR22	10	1.78	1.897	1.99	11.14	0.077	9	1.68	1.797	1.95	14.88	0.094
CR17	34	1.61	1.746	1.86	14.41	0.066	34	1.50	1.643	1.84	20.36	0.075
M_3												
GLOR6	1		1.77				1		1.65			
JUN2C	1		1.56				1		1.53			
JUN2B	3	1.49	1.570	1.63	8.97	0.072	2	1.42	1.430	1.44	1.40	0.014
CR31	2	1.71	1.710	1.71			2	1.57	1.575	1.58	0.63	7
CR22	7	1.50	1.553	1.74	14.81	0.085	6	1.35	1.427	1.48	9.19	0.047
CR17	28	1.30	1.423	1.56	18.18	0.076	29	1.27	1.379	1.52	17.92	0.074
M^1												
GLOR6	3	2.78	2.900	3.00	7.61	0.111	3	1.95	2.033	2.08	6.45	0.072
JUN2C	3	2.65	2.767	2.88	8.32	0.115	4	1.90	1.970	2.08	9.05	0.077
JUN2B	4	2.62	2.695	2.77	5.57	0.071	4	1.87	1.905	1.96	4.70	0.040
CR31	2	2.92	2.935	2.95	1.02	0.021	2	1.96	2.025	2.09	6.42	0.092
CR22	6	2.55	2.623	2.70	5.71	0.051	8	1.85	1.913	2.02	8.79	0.065
CR17	20	2.40	2.607	2.84	16.79	0.116	26	1.61	1.770	1.91	17.05	0.074
M^2												
GLOR6	3	2.04	2.083	2.11	3.37	0.038	3	2.00	2.097	2.17	8.15	0.087
JUN2C	2	1.81	1.845	1.88	3.79	0.049	3	1.95	2.007	2.10	7.41	0.081
JUN2B	3	1.83	1.873	1.93	5.32	0.051	3	1.85	1.893	1.96	5.77	0.059
CR31	2	2.02	2.035	2.05	1.47	0.021	2	2.06	2.095	2.13	3.34	0.049
CR22	12	1.72	1.864	2.04	17.02	0.110	13	1.75	1.882	2.02	14.32	0.080
CR17	34	1.57	1.741	1.89	18.50	0.081	37	1.59	1.774	1.95	20.34	0.072
M^3												
GLOR6	5	1.44	1.584	1.70	16.56	0.097	5	1.42	1.574	1.66	15.58	0.094
JUN2C	3	1.34	1.423	1.50	11.27	0.080	3	1.38	1.463	1.57	12.88	0.097
JUN2B	3	1.42	1.453	1.47	3.46	0.029	3	1.48	1.513	1.57	5.90	0.049
CR22	5	1.31	1.370	1.42	8.06	0.053	5	1.33	1.418	1.48	10.68	0.057
CR17	24	1.15	1.274	1.42	21.01	0.061	24	1.20	1.316	1.43	17.49	0.063

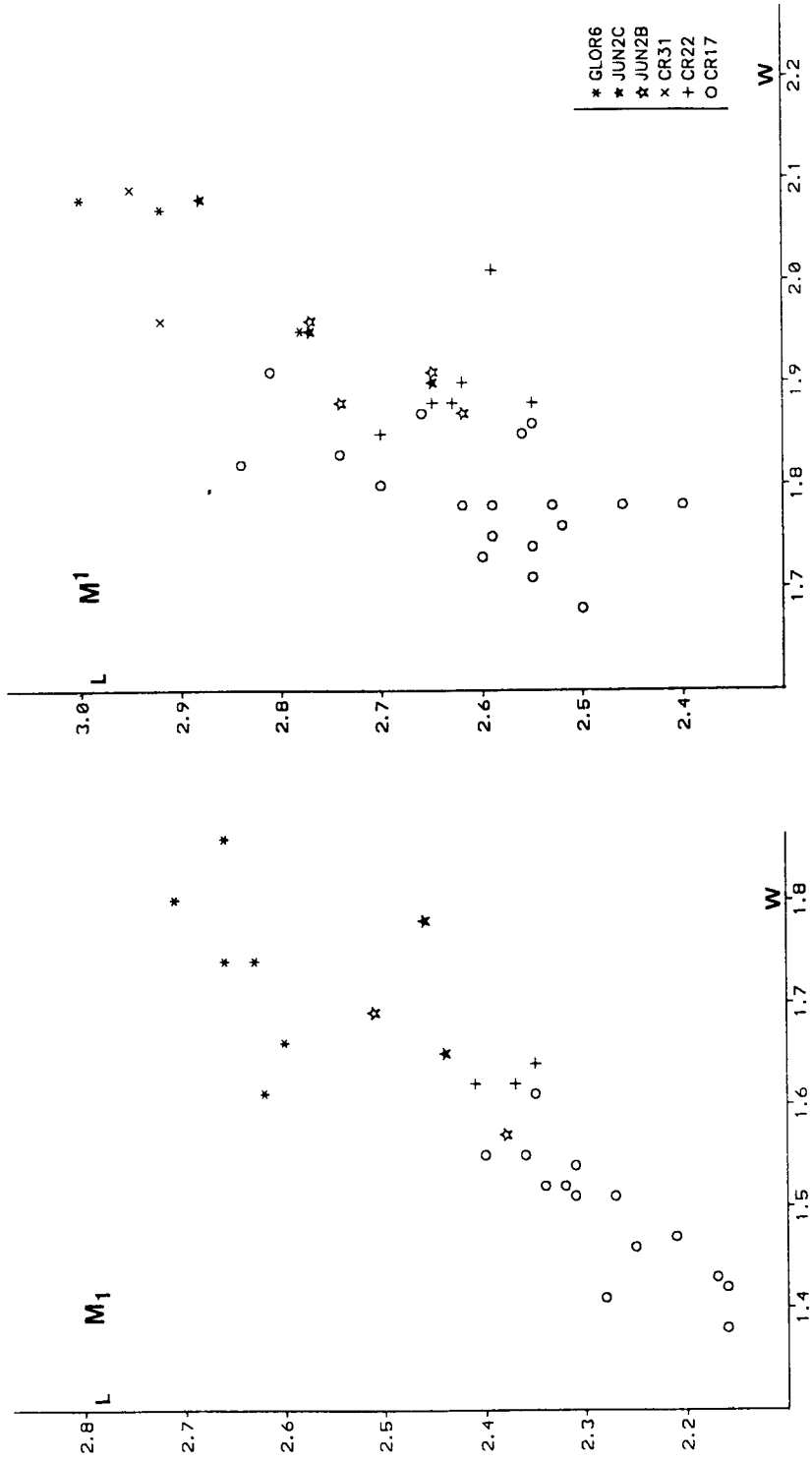


Fig. 1. Length/width diagrams of M_1 and M^1 of the species of *Castromys*.

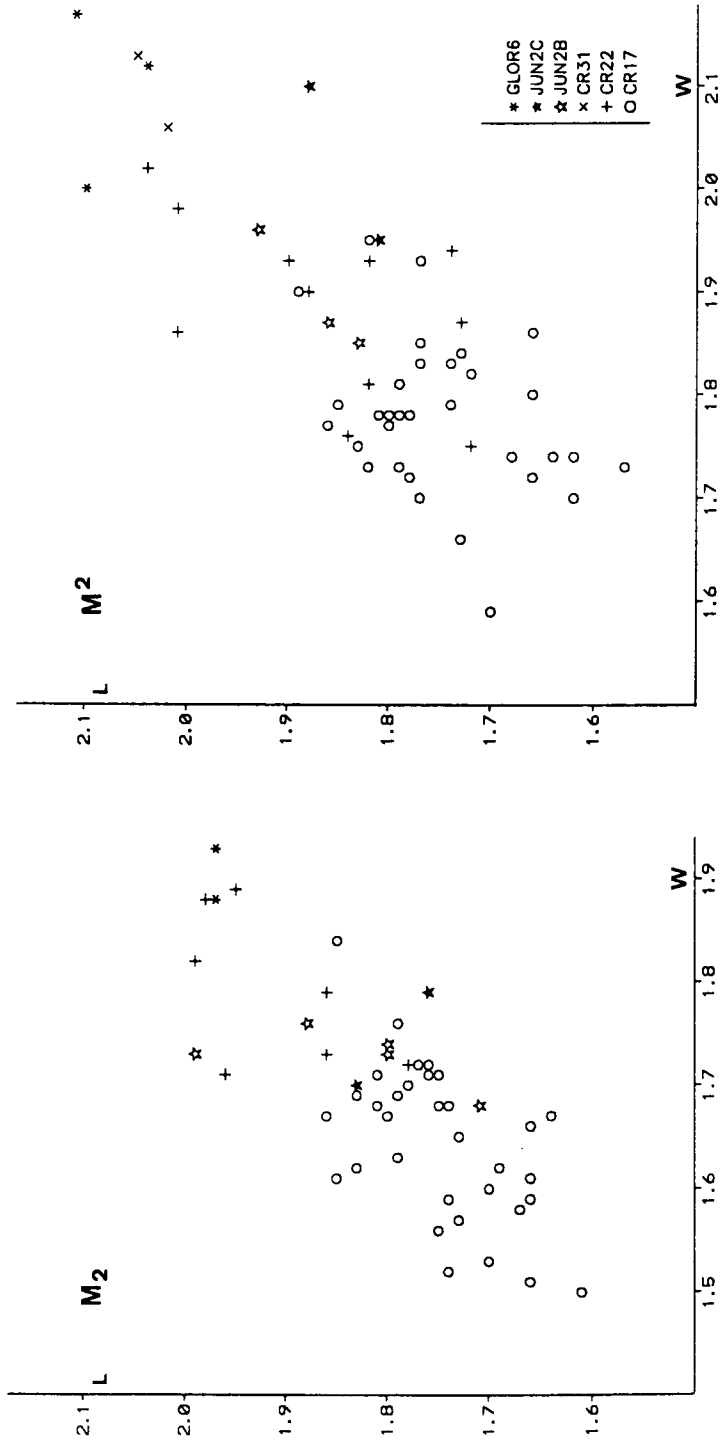


Fig. 2. Length/width diagrams of M_2 and M^2 of the species of *Castromys*.

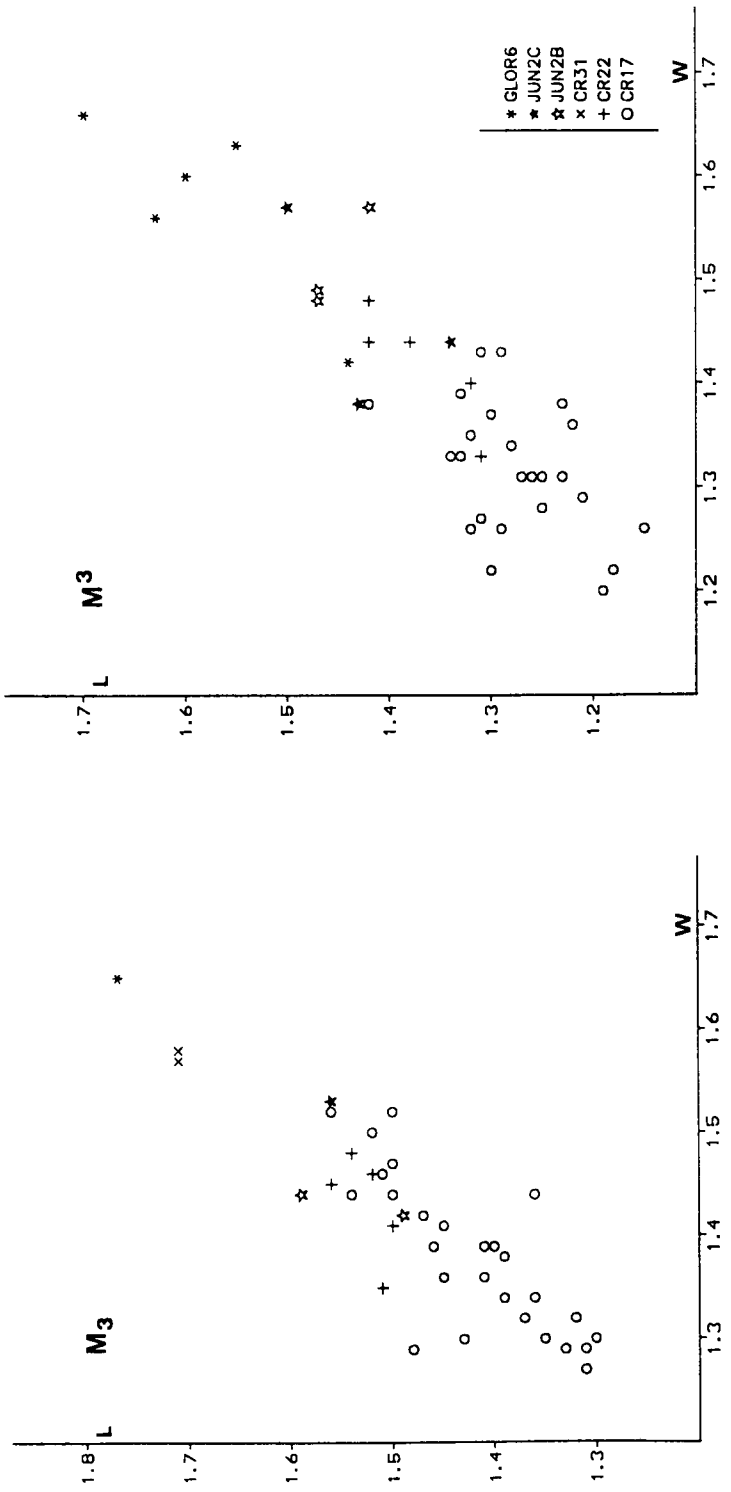


Fig. 3. Length/width diagrams of M_3 and M^3 of the species of *Castromys*.

from the second pair of cusps. In M_2 the anterolabial cusp is quite large and prominent, prolonged into the labial cingulum, which is broad. In M_3 the posterior cusp is very wide and prominent; in one case it shows a constriction which is possibly equivalent to the union of hypoconid and entoconid.

In the upper molars the central cusps are broader than the external ones. Since the transverse connections between the cusp pairs of the lower molars are very weak, wearing down of the upper molars begins not at the tops of the central cusps, but on their sides; therefore, in little-worn upper molars the wear facets of the central cusps (especially t5) are not continuous, but bilobated (Fig. 4b). In M^3 the posterior lobe is very wide (like in M_3); it is made up of t8 and t9 (the latter one being the smallest), separated by a constriction.

Description of the material from Crevillente 22

M_1 — Robust molars, in which the posterior part is clearly broader than the anterior part. A well-developed tma is united to both lobes of the anteroconid, which among each other are separated in juvenile specimens. The anteroconid is separated from the second pair of cusps in all specimens. The labial cingulum is low and continuous, bearing a voluminous c1, which is larger than the tma, and separated from the hypoconid by a small valley; c2 is attached to the protoconid, and there is one more cusp between protoconid and anteroconid. The posterior heel is low and wide, oval-shaped. There are two main roots, and an incipient central root.

M_2 — Teeth with a rounded outline, anterior width equal to posterior width or slightly larger. The anterolabial cusp is prominent and it is separated from the rest of the tooth by a deep and well-defined valley. In some specimens the c1 is voluminous and in others it is relatively small; there is one more small cusp at the base of the protoconid, that may be united or not to the anterolabial cusp. The posterior heel is low, wide, and oval-shaped. There are two roots.

M_3 — The anterolabial cusp is very small and low. There is no c1. A more or less prominent cingulum rounds the posterior border of the hypoconid-entoconid complex. There are two roots.

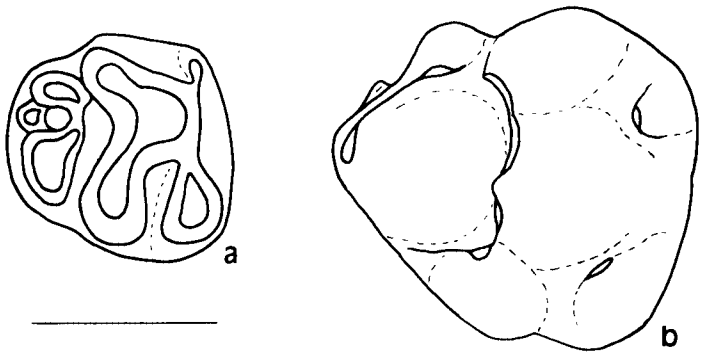


Fig. 4. *C. littoralis* from CR17. 4a: M^3 dext., RGM 413 171, showing the posterior complex formed by t8 and t9; this specimen has a small posterior cusp that may be interpreted as a t12. 4b: M^2 dext., RGM 413 178, hardly worn, which shows the bilobulated wear facet of the t5. Scale represents 1 mm.

M^1 — Oval-shaped teeth, with very broad central cusps. The unions of the central cusps with the lingual ones are lower and narrower than those with the labial ones. Along the anterior part of the tooth there may be a cingulum ridge. The t1 is placed slightly backwards in comparison with t2-t3, and it is larger than t3. The connection between t1 and t2 is very low. Neither t1 nor t3 are provided with a posterior spur. In one case there is an accessory cusp between t1 and t4. The t4 may be connected to t8 by a very low crest; t6 and t9 are separated. The t9 is united to t8 by a relatively broad crest. The t12 is of medium size, and low, not reaching the occlusal surface in little-worn specimens; it is always protruding from the posterior border of the tooth (and forms one of the points over which the length of the tooth is measured). There are three roots, and in some specimens there is an incipient central root.

M^2 — Teeth with a rounded outline. Like in M^1 the connections of the central cusps with the labial ones are higher than those with the lingual ones. The t1 is large and isolated, separated from t5. The t3 is small and isolated too. The t4 is weakly united to t5 and t8. The t6 and t9 are separated. The t9 is smaller than t6, and united to t8 by a relatively broad crest. The t12 is smaller than it is in M^1, and not protruding backwards (the length of the tooth is measured over t8). There are three roots; one specimen shows an incipient central root.

M^3 — Teeth with a rounded outline. The t1 is big and isolated, t3 is small. The M^3 is quite characteristic, because in the posterior lobe t8 and t9 are individualized; t8 is larger than t9. This posterior complex is separated from the rest of the tooth by a deep valley, that runs transversally through the tooth. In one specimen t6 and t9 are connected. There are three roots.

Remarks — In all elements the cusps are high, with steep walls.

In the anteroconid of M_1 the enamel of the anterior wall is thicker than in the rest of the anteroconid; on the contrary, in the other cusps of all three lower molars the enamel on the posterior walls is much thicker than on the anterior side. Furthermore, the enamel is rugose all over the tooth, especially on the posterior walls of the cusps. The anterior wall of the hypoconid-entoconid complex is almost straight, only in very worn specimens it may take the shape of a wide open 'V'.

In the upper molars the enamel is rugose throughout the tooth, especially on the anterior walls of the cusps. The connections t2-t3, t5-t6 and t8-t9 are quite high and very broad. In some specimens t4 is connected to t8 by a very low crest that never unites the apices of the cusps.

Description of the material from Jun 2B

M_1 — Robust teeth in which the metaconid is prominent and determines the width of the tooth. The tma is of medium size, placed in an anterolabial position, and united to the labial lobe of the anteroconid. The two lobes of the anteroconid are similar in size, separated among each other, and separated from the second pair of cusps. There are no longitudinal connections. The anterior wall of the hypoconid-entoconid pair is quite straight. The labial cingulum bears a c1, which is similar in size to the tma, and united to the hypoconid; the c2 is united to the protoconid, and there may be one or two more cusps in front of c2. The posterior heel is small and oval-shaped. There are two roots.

M_2 — The teeth are broader anteriorly than posteriorly. The anterolabial cusp is of medium size, with an isolated top, and it is prolonged into a labial cingulum. The c1 is similar in size to the anterolabial cusp, or smaller; c2 is attached to the base of the protoconid. The posterior heel is oval-shaped, and closes the talonid. There are two roots.

M_3 — The anterolabial cusp is very small. The protoconid-metaconid pair shows a trilobate wear surface. There is no c1, and there are two roots.

M^1 — There is a small cingulum ridge in front of t2. The t1 is weakly connected to the t2 by a low crest. The t3 is smaller than t1, and its connection with t2 is high. The t4 is united to t5 and to t8 by very low crests, the connection t5-t6 is higher. The top of t6 is inclined towards the t9 (the latter cusp is the smaller one); the apices of the cusps converge, but the connecting crest is very low. The connection t8-t9 is higher than the one between t5 and t6. The t12 is tubercular, small, but protruding from the posterior border of the tooth. There are four main roots (the lingual root is split), and a small central one.

M^2 — Rounded teeth, with isolated t1 and t3, of which the t3 is the smaller one. The connection t4-t5 is lower than the one between t5 and t6. The t9 is smaller than the t6, and these cusps are separated from each other. The t12 is small or absent. There are three or four roots.

M^3 — Rounded teeth with a big, isolated t1; t3 is absent in one specimen and very small in the other two. The posterior complex is formed by t8 and t9; t8 is separated from t4; t9 is united to t6 in one specimen. There are three or four roots.

Remarks — The teeth from Jun 2B have very steep cusps and rugose enamel. In the lower molars the transverse connections between the pairs of cusps are low; the anterior wall of the hypoconid-entoconid pair is straight, not 'V'-shaped. In M_1 the tma is well developed. In M_3 the posterior cingulum ridge is not very strong. In the upper molars the central cusps are broad, more so in M^2 than in M^1; the connections between the central cusps and the lingual ones are lower than those between central and labial cusps. t6 and t9 are quite close to each other in M^1 and more separated in M^2. In M^1 the cingulum ridge in front of t2 is clearly visible; t12 is present. The posterior complex of M^3 is split, with hypocone and metacone separated.

The populations from Jun 2C and Víznar 1

The material from JUN2C is poor; it consists of a right mandible and the two maxillaries of one single individual with the complete tooth rows, one right maxillary, and some isolated molars. The size of the teeth is slightly greater than in JUN2B, but there are no differences, neither in the morphology of the crown, nor in the number of roots. The teeth in the maxillaries and in the mandible are very much worn (Fig. 5).

In Víznar 1 we have found one very worn M^1 (2.80×1.91), one broken M^2, and one M_2 (1.82×1.74) that are very similar to the specimens from Jun 2.

Comparison of the populations from CR17, CR22 and JUN2

The collection from CR17 is the richest, and best preserved, of all populations

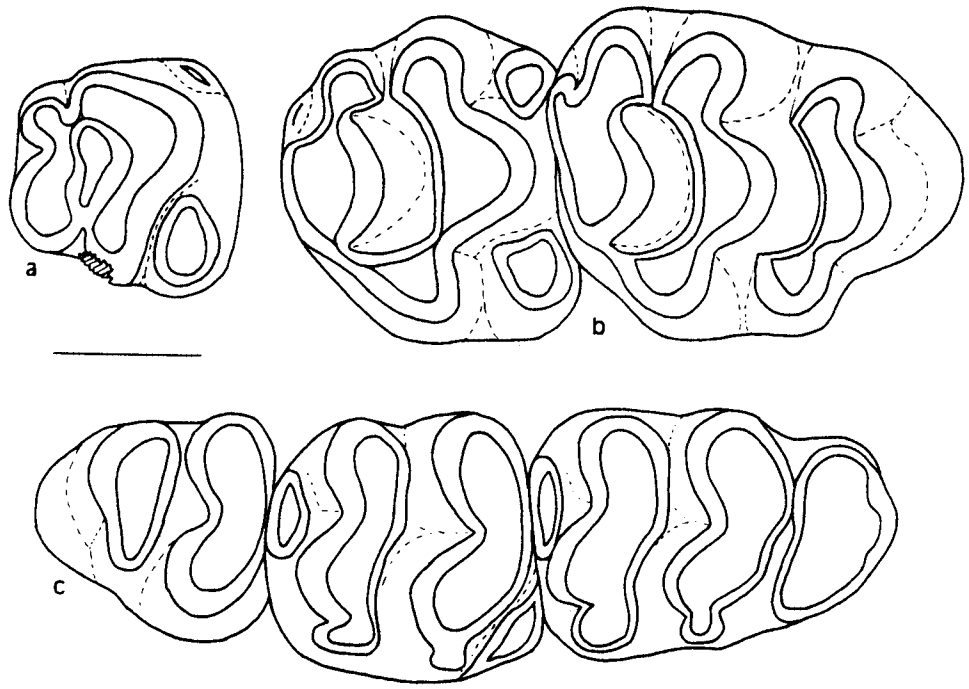


Fig. 5. *Castromys littoralis* from JUN2C; a: M^3 dext., JUN2C-14; b: M^2-M^3 dext., JUN2C-10. c: M_1-M_3 dext., JUN2C-1. Scale represents 1 mm.

studied in this paper. Therefore we have chosen CR17 as type-locality of the new species *C. littoralis*.

Comparing the populations from CR17, CR22 and JUN2B one may observe several differences. The general aspect of the material from JUN2B is more robust, though the measurements of these populations do not present any important differences. The largest specimens have been found in the population from JUN2B, CR22 is intermediate, and the smallest specimens have been found in CR17; but the ranges of measurements overlap largely (Fig. 6); the dimensions do not serve to distinguish these populations.

In all populations the enamel is rugose, especially on the posterior walls of the cusps of the lower molars, and on the anterior walls of the cusps of the upper molars. The rugosity of the enamel is more pronounced in the specimens from CR22 and JUN2B than in those from CR17. All molars have high cusps with steep walls, steeper in CR22 than in CR17 and JUN2B.

In the M_1 from CR22 the tma is united to both lobes of the anteroconid, in those from JUN2B it is united to the labial lobe of the anteroconid, while in the material from CR17 it is separated; in the collections from CR22 and JUN2B there is never an accessory cusp between c1 and c2. In the M_2 from CR17 and JUN2B the labial cingulum is wider than in those from CR22, since it originates from the anterolabial cusp which is larger too; the c1 in CR17 and JUN2B is large, in CR22 it is more variable, even though the material is more limited.

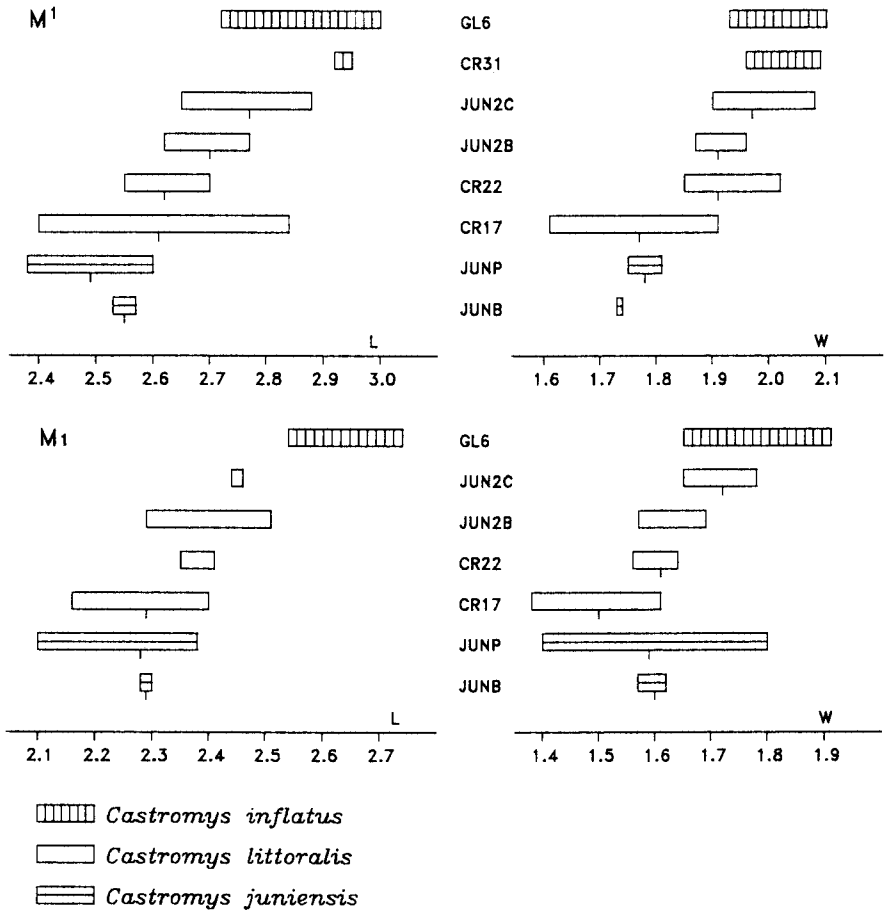


Fig. 6. Size ranges for length and width of the first molars of *Castromys*. GLOR6 = La Gloria 6, after Mein et al. (1990); JUNB = Canteras de Jun, after Brandy (1979); JUNP = Canteras de JUN, after Padial Ojeda & Ruiz Bustos (1989); other data from this paper.

In the upper molars from CR22 and JUN2B the central cusps are comparatively broader than in CR17, but in all these populations the variability is great. In CR22 and JUN2B the connections between the central and labial cusps are higher and broader than those between the central and lingual cusps; in the population from CR17 the labial and lingual connections are basically of the same importance (Fig. 7). In the upper molars from CR17 and JUN2B the connections t6-t9 are more frequent than in those from CR22. In the three populations the M^3 have a posterior lobe formed by hypocone and metacone (t8 and t9); in CR22 and JUN2B these are more individualized as cusps (and more separated) than in CR17.

The roots present more differences between these populations: some M_1 from CR17 and all M_1 from CR22 have two main roots and a small central one, in the specimens from JUN2B there is no central root. The M^1 from CR22 and JUN2C have three main roots, those from JUN2B have four roots, because the lingual one is split; in the

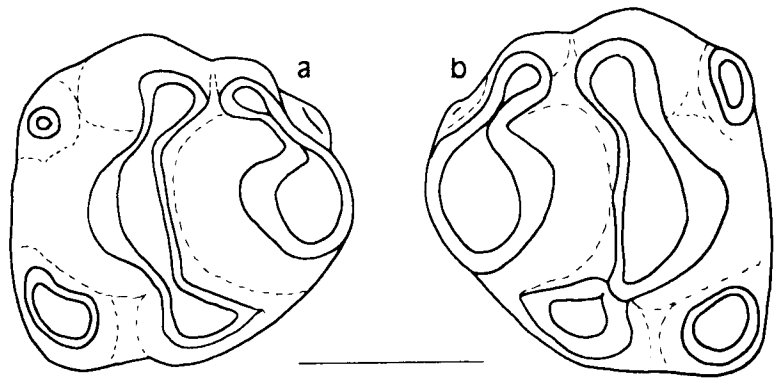


Fig. 7. a: M^2 sin. from CR17, RGM 413 115; b: M^2 dext. from CR22, CR22-40, which show, that the connections between t4 and t5 are broader in CR17 than in CR22. Scale represents 1 mm.

M^1 from CR17, the richest population, both morphologies are found. In the M^2 from CR17, CR22 and JUN2C there are three main roots, in those from JUN2B there are three or four. In the M^3 from CR17, CR22 and JUN2C there are three roots, in JUN2B there are three or four.

Discussion on the fossiliferous localities in the clay-pit of Jun.

The locality named 'Canteras de Jun' (CJ) was studied by Dabrio et al. (1978), Brandy (1979), Padial Ojeda (1986), and Padial Ojeda & Ruiz Bustos (1989). The authors of the latter paper state, that the fossiliferous level was sampled at least four times (beginning in 1974), until its disappearance in 1982, which was due to the quarrying activity. We have prospected, and sampled various fossiliferous levels in this clay-pit, and none of these coincides with the level described by the previously mentioned authors. But we have been confronted with the fact, that the quarrying activity causes rapid changes, and that it is not very probable that samples taken in different years come from the same bed (unless the sampling site be located in a remote and abandoned corner of the pit).

In fact the small population studied by Brandy (1979) seems to be homogeneous; on the other hand the fossils studied by Padial Ojeda & Ruiz Bustos (1989) must be attributed to two different species.

We sampled three different levels in the same clay-pit, labeled JUN1, JUN2 and JUN3. The only positive sample was JUN2. One month later we tried to take a large sample from JUN2, but the site had disappeared. We then took two samples of about 1000 Kg each, at a site that might be equivalent to JUN2. These samples were taken from two directly superposed beds, and labeled JUN2B and JUN2C.

In the localities JUN2B and JUN2C we have found *Occitanomys adroveri* and *Castromys littoralis*. The dimensions of the specimens of the latter species (see Table 1) are clearly larger than those of the large murid described from Canteras de Jun (CJ), both by Brandy (1979) and by Padial Ojeda & Ruiz Bustos (1989). Apparently our Jun localities (JUN2B and JUN2C) are different from the level sampled by the mentioned

authors.

The locality JUN2C is quite poor; we have found a small number of specimens of *Occitanomys adroveri, Castromys littoralis* and *Hispanomys* aff. *adroveri.*

The collection from JUN2B is richer, both in number of specimens and in number of species. Besides the species already mentioned for JUN2C, we have found two specimens of a Murinae indet., which for the moment is totally new; their morphology reminds one of *Occitanomys*, because of their brachyodonty, the development of the t1bis, their longitudinal connections, and the fully achieved stephanodonty. Furthermore they have a high number of roots, e.g. 5 roots in M^1. The specimens are very large for an *Occitanomys*, the length of M^1 is over 3 mm, which means that this Murinae is of the same size as *Castromys inflatus, Huerzelerimys turoliensis* and the *Stephanomys* of the Pliocene. The same Murinae indet. has been found in CR17, where it is represented by three upper molars and a lower molar, also of big size. In CR8 we have found one M^3, that we have attributed to *Huerzelerimys* in a previous paper (Martín Suárez & Freudenthal, 1993); this specimen might belong to the big Murinae indet. under question.

In our opinion this Murinae indet. may be represented in the locality CJ by the M^3, mentioned by Padial Ojeda (1986), which is characterized by having five roots, and a talon formed by one single cusp, contrary to the morphology in *Castromys*, where the talon consists of two cusps. The rest of the specimens from CJ belong to the species *V. juniensis*, which we transfer to the genus *Castromys*.

Castromys juniensis (Padial Ojeda & Ruiz Bustos, 1989)

Original reference — *Valerymys juniensis* Padial Ojeda & Ruiz Bustos, 1989.

Type-locality — Canteras de Jun (CJ).

Holotype — 'Ejemplar, JD/9 consistente en un M1 sup. izquierdo, depositado en la Cátedra de Ciencias Naturales I.B. de Getafe, y figurado en la Lámina 1 del trabajo' (op. cit., p. 14).

Original diagnosis — 'Las dimensiones en unos ejemplares coinciden y superan los mayores valores de *Valerymys vireti*, y en otros son inferiores o igualan los menores tamaños de *Valerymys turoliensis*. En el M1 inf. hay una pequeña raiz incipiente entre las dos principales. La raiz lingual del M2 sup. es bilobulada. El M3 sup. posee cuatro raíces y una pequeña protuberancia o raiz incipiente. El t12 en el M1 sup. es grande y variable o ausente en el M2 sup.' (op. cit., p. 14).

Emended diagnosis — *Castromys* of small size, M_1 with a small tma. M_2 with a reduced labial cingulum. M^2 with a vestigial t12, or without t12.

Remarks — Thanks to the kindness of Dr Ruiz Bustos we have been able to study part of the material from Canteras de Jun. We think that the specimens of the large murid from CJ, except for an M^3, belong to a species of the genus *Castromys*, because of the presence of a tma, the anterior wall of the hypoconid-entoconid pair being straight, because of the absence of longitudinal connections, and because the central cusps of the upper molars are very broad, especially in M^2.

Castromys juniensis is a murid of medium size, smaller than *Castromys inflatus*, and similar in size to *Castromys littoralis* from CR17 and CR22. Morphological diffe-

rences between *Castromys juniensis* and *Castromys littoralis* are: In the M_1 from CJ the tma is small, in *C. littoralis* it is large. The two lobes of the anteroconid are similar in size in the specimens from Crevillente, whereas in the two M_1 from CJ the lingual lobe is larger than the labial one. In one of the two M_1 from CJ the labial cingulum is narrow and very high, and in the M_2 from CJ the labial cingulum is weak or absent; on the other hand, in the specimens from CR17 and CR22 the labial cingulum is broad.

In some M^1 from CJ the t3 has a short posterior spur, which is absent in *C. littoralis*. In *C. juniensis* t9 and t6 are similar in size, while in *C. littoralis* t9 is smaller than t6; the connection of these two cusps is higher in the specimens from CJ than in those from CR17, or, in other words, the stephanodonty is more complete in *C. juniensis*. The transverse connections between the cusps are higher in the M^1 from CJ than in those from Crevillente. In the M^2 from CR17 and CR22 the t1 is isolated, in some specimen from CJ the t1 is united to t5 by a low posterior spur; furthermore the t12 is smaller in CJ than in CR17.

Castromys inflatus (Mein, Moissenet & Adrover, 1990)
Pl. 2, figs. 13-14

Original reference — *Karnimata inflata* Mein et al., 1990.
Synonymy —
Valerymys turoliensis from Barranco del Beiro, in Padial Ojeda, 1986
Valerymys turoliensis from Los Arcos, in Padial Ojeda, 1986
Valerymys turoliensis from Arquillo 1, in Mein et al., 1990
Mein et al. (1993) created the genus *Huerzelerimys* to accommodate *Valerymys turoliensis* and several other species, and transferred the above mentioned populations to *Karnimata inflata*.

Type-locality — Gloria 6, 'bord gauche de la piste Teruel-Masia la Gloria au Nord Est de la ville' (Mein et al., 1990, op. cit., p. 137).

Holotype — 'série dentaire supérieure gauche (Gloria 6 - 1)' (op. cit., fig. 6a).

Original diagnosis — 'Muridae de grande taille aux molaires très larges, molaires supérieures dépourvues de la liaison t6-t9, dépourvues d'éperon distal au t1, ayant conservé un t12, munies de trois racines; M3/ avec un t9 aligné distalement avec le t8 pour former une lame postérieure. Molaires inférieures avec une marge cingulaire large, des cuspides accessoires labiales bien développées; M/1 avec un fort tubercule impair médian, la première paire de cuspides isolée de la deuxième paire'.

Localities in the Crevillente area — CR31 (UTM 30SXH372939) and CR14 (UTM 30SXH371923).

Measurements — See Table 1.

Description of the type material from La Gloria 6

M_1 — Molars in which the posterior part is broader than the anterior part. The tma is voluminous, isolated and placed in a central position; the two lobes of the anteroconid remain separated from each other until in a well-advanced stage of wear. The anteroconid is separated from the second pair of cusps. The anterior wall of the hypoconid-entoconid pair is fairly straight. There are no longitudinal connections between the cusps. The labial cingulum is wide and continuous, with a c1, that

is similar in size to the tma, and separated from the hypoconid by a small valley; there is a c2, attached to the base of the protoconid, and there are one or two more cusps between protoconid and anteroconid. The posterior heel is oval-shaped and isolated; it does not close the talonid valley.

M_2 — The anterior and posterior widths are almost equal. The anterolabial cusp is isolated, and protrudes strongly forward; it is prolonged into a continuous labial cingulum, with a small c1 (smaller than the anterolabial cusp), and a c2 which is smaller than c1, and which is attached to the base of the protoconid; in one of the two available specimens there is a small cusp between the c2 and the anterolabial cusp. The posterior heel is oval-shaped, and united to hypoconid and entoconid; it closes the talonid valley.

M_3 — Molar with a small and low anterolabial cusp and a small c1. The hypoconid-entoconid complex is very broad, and surrounded by a very pronounced cingulum ridge.

M^1 — Very robust molars, with broad central cusps. The t1 is rounded and weakly united to the t2. In front of t2 there is cingulum ridge. The t3 is slightly smaller than t1, and its connection with t2 is very broad. Neither t1 nor t3 have posterior spurs. The t4 is weakly connected to t5, and separated from t8. The connection of the t5 with t6 is very broad. t6 and t9 are separated; t9 is similar in size to t3. The connection of t9 with t8 is high and broad, and through the effect of wear these two cusps seem to fuse. The t12 is medium-sized, and protrudes from the posterior border of the tooth.

M^2 — Rounded molars. The t1 is very voluminous, and weakly united to the anterolingual wall of t5. The t3 is small, rounded or oval-shaped, and, like t1, weakly connected to the anterolabial wall of t5. The t4 is united to t8 by a very low crest. The connection between t5 and t6 is very broad. The t9 is small (similar to t3), separated from t6 and broadly connected to t8. The t12 is tubercular in one specimen, and in the other two it is very reduced; it is never protruding.

M^3 — Teeth very rounded. The t1 is very large and united to the anterolingual wall of t5. The t3 is a small, but well-defined cusp. The posterior complex is formed by t8 and t9, which are weakly united among each other, or separated. In worn specimens the t8 is united to t4, but t9 remains separated from t6.

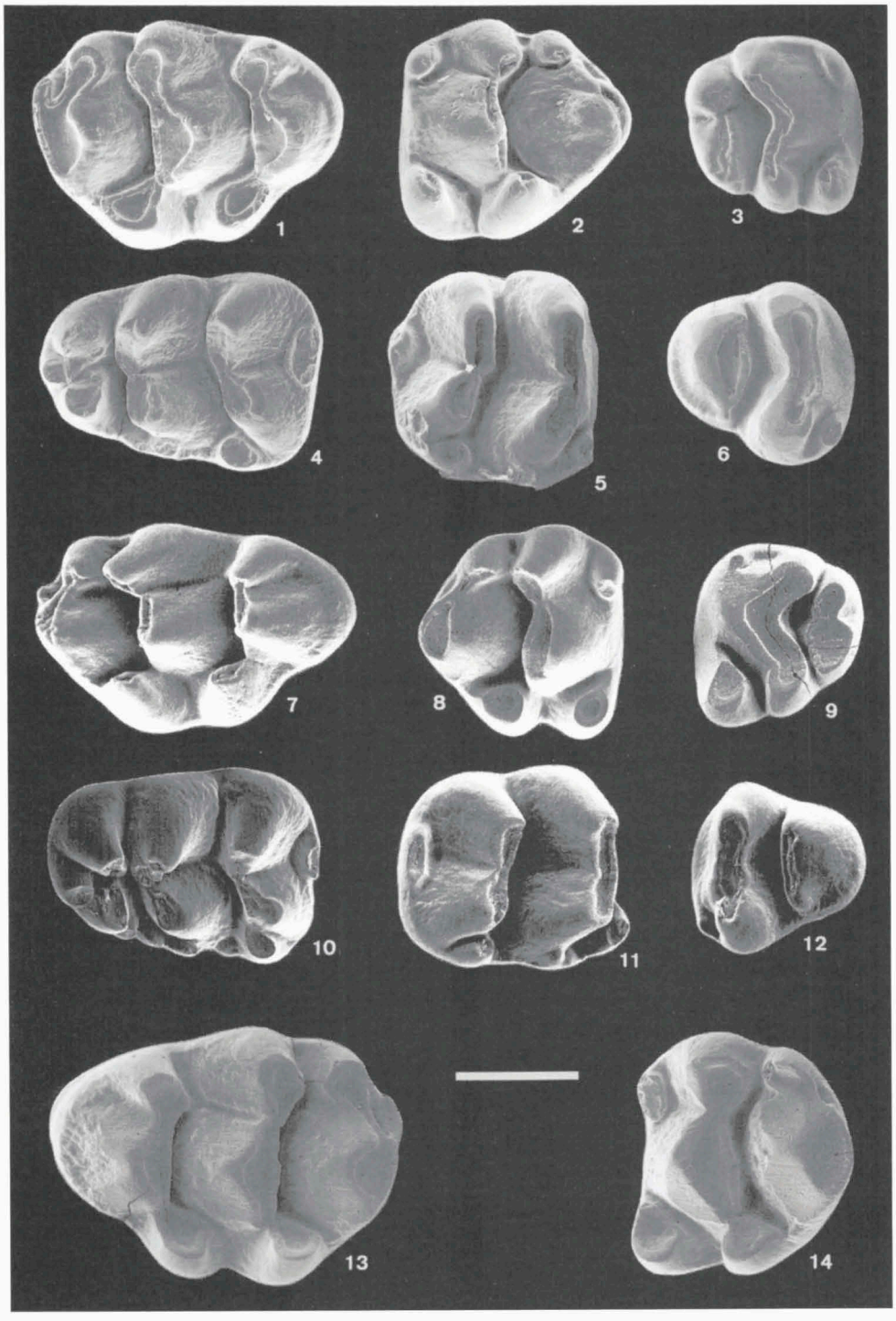
Plate 2.

Castromys littoralis gen. et sp. nov., from Crevillente 22.
Fig. 1. M^1 dext., CR22-24.
Fig. 2. M^2 sin., CR22-29.
Fig. 3. M^3 dext., CR22-45.
Fig. 4. M_1 sin., CR22-1.
Fig. 5. M_2 dext., RGM 413 646.
Fig. 6. M_3 dext., RGM 413 650.

Castromys littoralis gen. et sp. nov., from Jun 2B.
Fig. 7. M^1 dext., JUN2B-19.
Fig. 8. M^2 dext., JUN2B-23.
Fig. 9. M^3 sin., JUN2B-29.
Fig. 10. M_1 sin., JUN2B-1.
Fig. 11. M_2 dext., JUN2B-9.
Fig. 12. M_3 sin., JUN2B-12.

Castromys inflatus from Crevillente 31.
Fig. 13. M^1 sin., RGM 413 759.
Fig. 14. M^2 sin., RGM 413 761.

Scale represents 1 mm.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Remarks — Teeth with rugose enamel, relatively high-crowned, and with steep cusps.

In the lower molars the enamel on the posterior walls of the cusps is considerably thicker than on the anterior walls, except for the anteroconid of M_1, where the enamel on the anterior wall is slightly thicker than on the posterior wall. In the M_1 and M_2 the labial cingulum is higher between protoconid and anteroconid than between hypoconid and protoconid; in other words: there is a little depression in the cingulum between c1 and c2, while the cingulum is high in front of c2. In M_3 the protoconid-metaconid complex has a slightly trilobulate wear surface.

The upper molars have very broad central cusps and the connections of the central cusps with the labial ones are much higher and broader than those with the lingual cusps. The enamel on the anterior walls of the cusps is much thicker than on the posterior walls. In M^2 the connections between t4 and t8 and between t6 and t9 are somewhat higher than they are in M^1. In M^3 the t8 and t9 are two clearly individualized cusps.

The populations from CR31 and CR14

The population from CR31 is very poor; the measurements are given in Table 1. The morphology of the molars is similar to that of La Gloria 6, but the enamel is more rugose than in the type-population; in M_3 the posterior cingulum ridge is less developed. On the other hand, the cingulum in front of the t2 in M^1 is more developed than in La Gloria 6.

The material from CR14 is also very poor, and, unfortunately, badly preserved. Not a single specimen could be measured. The specimens are very similar to those of the type-population; longitudinal connections are totally absent; the upper molars have very broad central cusps, and the connections between t8 and t9 are very broad.

Discussion

The new genus *Castromys* includes three species: *C. juniensis*, *C. littoralis* and *C. inflatus*. *C. juniensis* is known only from the locality Canteras de Jun. This murid is similar in size to the oldest populations of *C. littoralis*, but some of its morphological features prove its position as a separate species.

The oldest locality with *C. littoralis* is CR17 (Fig. 8), where it is associated with *Occitanomys adroveri*, *Hispanomys* cf. *adroveri*, and *Neocricetodon lucentensis*; the latter species is only known in several levels of the Crevillente sequence (Freudenthal et al., 1991a). The next occurrence of *C. littoralis* is the locality CR22, in association with *Occitanomys adroveri*, *O. alcalai*, *Stephanomys stadii*, *Hispanomys* cf. *adroveri*, and *Neocricetodon* aff. *plinii*. In the Granada Basin it has been found in three localities: JUN2B, JUN2C and VIZ1. The largest specimens come from JUN2C.

Castromys inflatus is known from various localities in the Teruel Basin, later in age than the Crevillente localities: La Gloria 6, La Gloria 1, Velilla, and Tramacastiel. In La Gloria 6 it is associated with an *Apodemus*. *C. inflatus* has also been found in CR14 and CR31 (Crevillente, prov. Alicante) and in Barranco del Beiro and Los Arcos (Granada Basin; Padial Ojeda, 1986). It is a big murid, the smallest specimens are of the

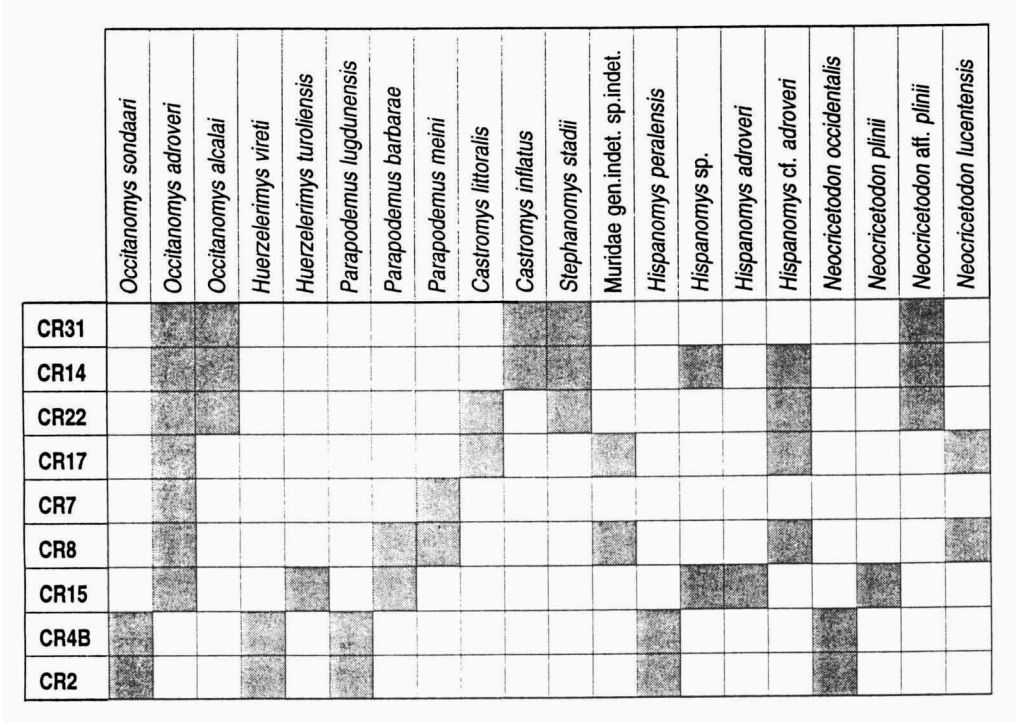

Fig. 8. Distribution of the Muridae and Cricetidae in the localities of the area of Crevillente.

same size as the largest ones of *C. littoralis*. The lower molars of *C. inflatus* are morphologically very similar to those of *C. littoralis*; the upper molars of *C. inflatus* have extremely broad central cusps, in comparison with the labial and lingual cusps. *C. inflatus* may be considered as a descendant of *C. littoralis*.

The Castro section in Crevillente is a good example of stratigraphically superposed fossil mammal localities: CR17 and CR22 are two superposed localities in this sequence, separated by some 10 m of sediments, which include a marine episode (sandstones with oysters). In the time span between the deposition of the two localities, an important immigration of Muridae takes place in the area: in CR22 appear for the first time *Occitanomys alcalai* and *Stephanomys stadii*; *Occitanomys adroveri* and *Castromys littoralis* are survivors from before this immigration moment.

CR14 and CR31 are localities in the same general area, but some distance away from the Castro Section. The lithostratigraphical correlations prove, that they belong to the same marly interval as CR22. These three localities have all Muridae in common, except for *Castromys*, since *C. littoralis* is found in CR22, and *C. inflatus* in CR14 and CR31.

The origin of *Castromys* is unknown. In our opinion it is not related to *Huerzelerimys*. The sequence of localities in the Castro Section is, from old to young: CR2, CR4B, CR15, CR8, CR7, CR17, CR22, CR31. In CR2 and CR4B we find *H. vireti*; in CR15 H. *turoliensis* is present, and in the younger levels *Huerzelerimys* has disappeared; it has not been found in CR7 and CR8. In CR17 we find a Muridae, which is intermediate in size between the murid from CR4B and the one from CR15, in other

words, intermediate in size between *H. vireti* and *H. turoliensis*, but undoubtedly more recent, because of its stratigraphical position. This murid, which we have called *Castromys littoralis* cannot be an intermediate form between *H. vireti* and *H. turoliensis*, not only because it appears later than *H. turoliensis*, but also because it is morphologically different from both *Huerzelerimys* species.

The M^3 of the *Castromys* species are characterized by a talon formed by two cusps, hypocone and metacone (t8 and t9 in the nomenclature of Miller, 1912). This bilobed structure of the talon is little frequent in Muridae; it is found in some species from the Pliocene of Afghanistan (Sen, 1983), like *Pelomys*, *Parapelomys* and *Saidomys*.

In CR7 and CR8 we have found the murid *Parapodemus meini*, which also has an M^3 with bilobed talon (Martín Suárez & Freudenthal, 1993). We suppose this *P. meini* to be a descendant of *Parapodemus barbarae*, present in the preceding levels of the Castro Section. The type-locality of *P. barbarae* is Los Mansuetos in Teruel (van de Weerd, 1976); the M^3 from this locality have not been figured, but the description reads: 'The t9 of some specimens is separated from the t8 by a small posterior furrow' (van de Weerd, 1976, p. 80). In *Parapodemus barbarae* from CR15 the M have a talon formed by two cusps (see Martín Suárez & Freudenthal, 1993, pl. 3).

We suppose, that *P. barbarae* evolved into *P. meini*, an evolution characterized by the loss of the posterior connection of the anteroconid, reduction of the transverse connections between the cusp pairs, separation of t6 and t9, and a strong size increase. If these tendencies are maintained, *Parapodemus meini* may have given rise to the first *Castromys*, *C. juniensis*. A thorough revision of the material from the type-locality and the numerous populations, that have been attributed to *P. barbarae* is necessary to decide whether there is a relationship between these two murids.

Biostratigraphical implications

As we have said in the introduction of this paper, some populations of Muridae that may be assigned to the genus *Castromys*, had previously been determined as *Huerzelerimys*, among these the one from Arquillo 1, reference locality of the subdivision MN13 (Mein, 1990).

The section of Castro Hill is a sequence in which marine and continental deposits alternate. The latter include numerous fossil mammal localities, ranging in age from the early Turolian to the Messinian (Montenat, 1977; de Bruijn et al., 1975; Freudenthal et al., 1991a, b; Martín Suárez & Freudenthal, 1993). It probably is the only sequence of continental deposits, known from this age, with such a wide time range. It has permitted us to separate chronologically the populations of *Huerzelerimys* and *Castromys*. This means that zone MN12 of Mein cannot be characterized entirely by the presence of *Huerzelerimys turoliensis*, but that it can be divided into a lower sub-unit characterized by the presence of *H. turoliensis*, and an upper sub-unit with *Castromys*, first associated with *Occitanomys adroveri*, and later with *Occitanomys alcalai* and *Stephanomys stadii*.

Accepting the three-partition of the Turolian as implied in Mein et al. (1990), the localities with a representant of the genus *Castromys* cover the upper part of the Middle Turolian and the lower part of the Upper Turolian. This is equivalent (according to the correlation proposal by Steininger et al., 1990) to Late Tortonian-Early Messinian in terms of marine chronostratigraphy.

Conclusions

Among the fossil Muridae from the Castro sequence in Crevillente several species have been found that are grouped in the new genus *Castromys*. Apart from the Crevillente area, this genus is known from the Granada and Teruel Basins.

The distinction between the species of *Huerzelerimys* and *Castromys* permits a detailed chronostratigraphy of the deposits, in which they are found: The species of *Huerzelerimys* may be used as indicators of an age comprised between the Late Vallesian, and the first part of the Middle Turolian (Late Tortonian), and the presence of the species of *Castromys* indicates an age of late Middle Turolian to early Late Turolian (latest Tortonian or Early Messinian).

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