Revision of the genus *Castillomys* (Muridae, Rodentia)

E. Martín Suárez & P. Mein

E. Martín Suárez & P. Mein. Revision of the genus *Castillomys* (Muridae, Rodentia). – Scripta Geol., 96: 47-81, 17 figs., 2 pls, Leiden, October 1991.

In this paper a revision of the genus *Castillomys* Michaux, 1969 is given. Previously described subspecies are elevated to species rank, and a new species, *Castillomys rivas*, is proposed. Several populations from Italy and Turkey are transferred to the genus *Centralomys* de Giuli, 1989. For a population from Maritsa the new subgenus *Rhodomys* is created within the genus *Occitanomys*.

E. Martín Suárez, Departamento de Estratigrafía y Paleontología e I.A.G.M. (C.S.I.C.). Universidad de Granada, E 18071 Granada, España; P. Mein, Département des Sciences de la Terre, Université Claude Bernard, 27-43 Bd. 11 Novembre, F 69622 Villeurbanne Cedex, France.

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Introduction

The genus *Castillomys*, with only one species, *C. crusafonti*, was created by Michaux (1969) for a group of Pliocene and Early Pleistocene Muridae from SW Europe with 'molaires brachidontes, forte stéphanodontie, *t*1 reculé, petite taille'. Since that date no general revision of the genus has been carried out. Van de Weerd (1976) created the subspecies *C. crusafonti gracilis* on the basis of material from Spanish localities older than Layna, the type-locality of *C. crusafonti*. Subsequently Mein et al. (1978) found at the locality of Valdeganga a *Castillomys*, which was larger than the known representatives, and considered it to be a new subspecies,

which was, however, not named. Recently Antunes & Mein (1989) described a new species, *Castillomys margaritae*, from the uppermost Miocene of Portugal. Coiffait et al. (1985) described a *C. crusafonti* aff. *crusafonti* from Argoub Kemellal (North Africa). From Italy only *Castillomys* (*Centralomys*) *benericettii* de Giuli, 1989 is known, found in the locality of Brisighella 1. For eastern Europe and Turkey we have the citations of *Castillomys magnus* Sen, 1977 from Çalta and *C. crusafonti* from Maritsa 1 (de Bruijn et al., 1970), which has later been called *C. debruijni* (Sen et al., 1989).

The taxonomy of the genus can be summarised as follows:

Genus	subgenus	species	subspecies	author
Castillomys		*crusafonti*		Michaux, 1969
		crusafonti	*gracilis*	van de Weerd, 1976
		magnus		Sen, 1977
		debruijni		Sen et al., 1989
		margaritae		Antunes & Mein, 1989
	Centralomys	*benericettii*		de Giuli, 1989

In this paper the following scheme is proposed:

Genus	subgenus	species	author
Castillomys		*margaritae*	Antunes & Mein, 1989
		gracilis	van de Weerd, 1976
		crusafonti	Michaux, 1969
		rivas	sp. nov.
Centralomys		*benericettii*	(de Giuli, 1989)
		magnus	(Sen, 1977)
Occitanomys	*Rhodomys*	*debruijni*	(Sen et al., 1989)

STUDIED MATERIAL

For the realization of this paper we could count with the population from Maritsa 1, put at our disposal by Dr H. de Bruijn (Utrecht); material from Çalta and Develi lent by Dr S. Sen; unpublished material from Casablanca 3 lent by Dr J. Agustí (Sabadell); material from several Moreda localities collected by Dr C. Castillo (Granada); the collections of the 'Département des Sciences de la Terre', (DST, Lyon) from Caravaca, Layna, Sète, Seynes, Mas Rambault (donated by Dr J. Michaux, Montpellier), Brisighella 25 (donated by Dr F. Massini, Florence); and material collected by the authors in the Betic and Teruel basins.

Acknowledgements – We wish to express our thanks to Drs Agustí, de Bruijn, Sen, and Castillo, who gave us permission to study their collections, including even un-

published material. We are grateful to Dr Rivas, who allowed us to give his name to a new species.

We thank Dr M. Freudenthal for his computer programs, that helped us process our data, for his scientific suggestions and for the correction of the English text.

The photographs have been made on the Zeiss 950 digital scan microscope of the University of Granada.

This study was realized within the framework of the research group 4076 'Paleogeografía de cuencas sedimentarias' of the Consejería de Educación y Ciencia de la Junta de Andalucía and within the research project PB 0582/86 of CICYT.

Morphological analysis, definition of character states

We have made a morphological and biometrical analysis of the previously mentioned populations. For each dental element a large number of characters has been studied; the characters considered to be diagnostic are listed hereafter. All definitions refer to little-worn specimens, unless otherwise stated.

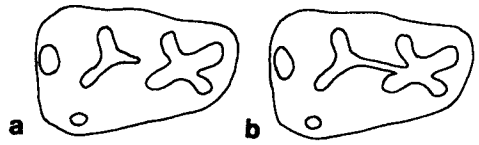
The nomenclature used in the descriptions is the one by van de Weerd (1976). Measurements were carried out on a Leitz Ortholux microscope with measuring clocks and/or on a Wild M7S binocular microscope with mechanical stage and Sony Magnescale LM12 digital measuring equipment.

M_1 and M_2

The characters considered to be diagnostic are: longitudinal connection between the two main pairs of cusps; shape and disposition of the labial cingulum; size of the posterior heel. Other characters that have been analyzed are: presence of tma; size, shape and disposition of accessory cuspids, etc.

Longitudinal connection – In the lower molars of *Castillomys* there may be a longitudinal structure that arises from the anteromedian part of the hypoconid-entoconid pair, and extends forward (Fig. 1). For this character two states are defined: When it reaches the posterior border of the enamel of the protoconid-metaconid at full height (i.c. when the two pairs are connected) we call it *longitudinal crest* (Figs. 1b and 4b). When, on the other hand, it tapers out in the valley between the two pairs of main cusps, without reaching the enamel border of the anterior pair, we call it *longitudinal spur.*

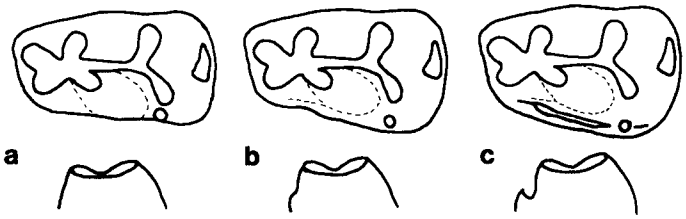
Labial cingulum – For the labial cingulum of M_1 and M_2 three states are defined: *absent* if there is no cingulum at the labial border of the protoconid (Figs. 2a and 5a). When a continuous cingulum connects hypoconid and anteroconid there are two possibilities: *narrow* when, at the level of the protoconid, it is a mere basal ledge (Figs. 2b and 5b); *wide* when it forms a lateral expansion of the tooth and is separated from the protoconid by a clearly distinguishable valley (Figs. 2c and 5c).



Locality	%	%	N
Casablanca 3	0	100	10
Loma Quemada 1	0	100	19
Mas Rambault	0	100	7
Valdeganga 7	0	100	22
Seynes	0	100	10
Moreda 1B	9	91	78
Belmez 1	12	88	26
Layna	20	80	25
Moreda 1A	9	91	88
Caravaca	91	9	11

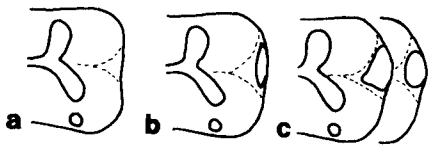
Fig. 1. Percentages for the longitudinal spur or crest in M_1.

Posterior heel – Three states are defined for this character (Figs. 3 and 6): *absent* when there is no cusp in the posterior valley (Figs. 3a and 6a). If such a cusp is present, it is considered *small* when it does not protrude beyond the posterior border of the tooth (Figs. 3b and 6b); or it is *large* when it overhangs the posterior border of the tooth, and this border is convex (Figs. 3c and 6c). The shape of the posterior heel is not important in this respect.



Locality	%	%	%	N
Casablanca 3	0	10	90	10
Loma Quemada 1	0	0	100	19
Mas Rambault	0	29	71	7
Valdeganga 7	0	4	96	23
Seynes	0	50	50	10
Moreda 1B	8	60	32	78
Belmez 1	13	74	13	23
Layna	12	44	44	25
Moreda 1A	7	52	41	87
Caravaca	8	75	17	12

Fig. 2. Percentages for the character states of the labial cingulum in M_1.



Locality	%	%	%	N
Casablanca 3	0	20	80	10
Loma Quemada 1	0	11	89	19
Mas Rambault	0	14	86	7
Valdeganga 7	0	13	87	23
Seynes	0	50	50	10
Moreda 1B	5	63	32	78
Belmez 1	13	65	22	23
Layna	4	64	32	25
Moreda 1A	3	54	43	37
Caravaca	0	75	25	12

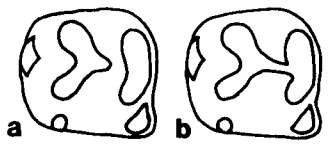
Fig. 3. Percentages for the character states of the posterior heel in M_1.

M_3

The only character considered to be diagnostic is the *longitudinal crest*, which may be *absent* or *present*. For definitions see the previous paragraph.

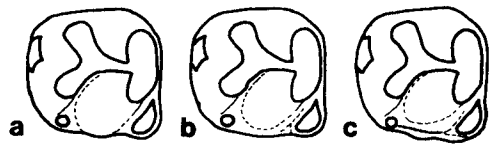
M^1

t1bis – Three character states are defined: *absent* when there is no cusp between t1 and t2 (Fig. 7a), usually there is a gap between t1 and t2. If present, it is considered *small* when it is no more than a slight widening of the crest between t1 and t2, or a ledge on the lingual base of t2 (Fig. 7b); it is defined as *large* when it is well-developed and affects the shape of the crown basis (Fig. 7c).



Locality	%	%	N
Casablanca 3	0	100	8
Loma Quemada 1	0	100	27
Mas Rambault	0	100	13
Valdeganga 7	0	100	22
Seynes	0	100	11
Moreda 1B	21	79	78
Belmez 1	41	59	17
Layna	23	77	22
Moreda 1A	21	79	73
Caravaca	100	0	16

Fig. 4. Percentages for the longitudinal spur or crest in M_2.

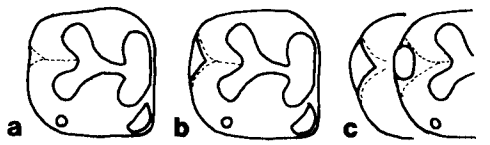


Locality	%	%	%	N
Casablanca 3	0	25	75	8
Loma Quemada 1	0	33	67	27
Mas Rambault	0	72	28	18
Valdeganga 7	0	42	58	19
Seynes	18	73	9	11
Moreda 1B	33	55	12	78
Belmez 1	18	64	18	17
Layna	21	54	25	24
Moreda 1A	9	79	12	75
Caravaca	37	63	0	16

Fig. 5. Percentages for the character states of the labial cingulum in M_2.

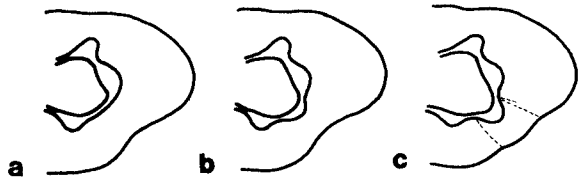
t2bis – Like in the previous case three states are defined: *absent* when there is no cusp between t2 and t3 (Fig. 8a). If present, it is considered *small* when it is nothing but a small notch on the crest between t2 and t3, or when it is just a minuscule isolated cusp in the anterolabial valley of the tooth between t2 and t3 (Fig. 8b); *large* when there is a well-developed crest throughout the length of the valley that separates t2 and t3 anteriorly (Fig. 8c).

Connection t1-t5 – The connection is present when there is a spur on the posterior wall of the t1, that reaches the anterior rim of the t4-t5 connection or the t5. We call this connection *lingual longitudinal crest* (Fig. 9b); it has nothing to do with the



Locality	%	%	%	N
Casablanca 3	0	37	63	8
Loma Quemada 1	0	31	69	26
Mas Rambault	0	54	46	13
Valdeganga 7	0	10	90	20
Seynes	0	100	0	11
Moreda 1B	24	52	24	78
Belmez 1	18	53	29	17
Layna	21	58	21	24
Moreda 1A	19	61	20	75
Caravaca	12	50	38	16

Fig. 6. Percentages for the character states of the posterior heel in M_2.

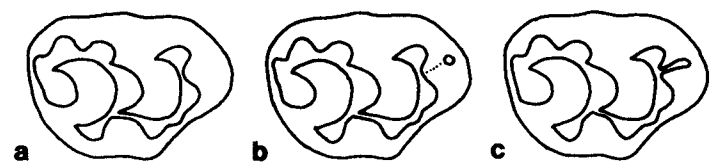


Locality	%	%	%	N
Casablanca 3	0	64	36	14
Loma Quemada 1	0	27	73	15
Mas Rambault	20	70	10	10
Valdeganga 7	21	54	25	24
Seynes	40	60	0	12
Moreda 1B	25	41	34	56
Belmez 1	40	43	17	35
Layna	37	63	0	27
Moreda 1A	36	48	16	112
Caravaca	0	86	14	14

Fig. 7. Percentages for the character states of the t1bis in M^1.

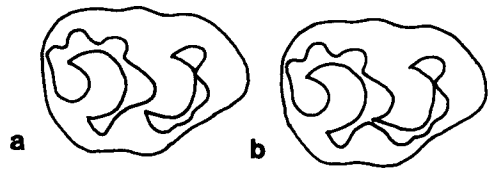
stephanodont crest. The other character state is *isolated t1*, which includes the cases where the spur is present, but does not reach the t4-t5 connection (Fig. 9a). In general there is a relation between the presence of t1bis and that of the lingual longitudinal crest.

Connection t3-t5 – The connection is present when there is a spur on the posterior wall of the t3, that reaches the anterior rim of the t5-t6 connection or the t5 (Fig. 10b). This is the *labial longitudinal crest*, which, like in the previous case, has



Locality	%	%	%	N
Casablanca 3	43	50	7	14
Loma Quemada 1	20	53	27	15
Mas Rambault	0	89	11	9
Valdeganga 7	17	75	8	24
Seynes	83	17	0	12
Moreda 1B	27	52	21	56
Belmez 1	53	38	9	34
Layna	63	37	0	27
Moreda 1A	53	35	12	109
Caravaca	100	0	0	14

Fig. 8. Percentages for the character states of the t2bis in M^1.

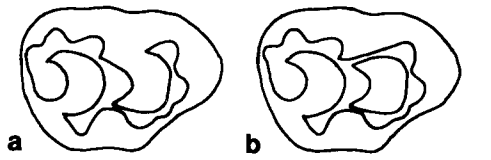


Locality	%	%	N
Casablanca 3	0	100	14
Loma Quemada 1	0	100	16
Mas Rambault	0	100	8
Valdeganga 7	21	79	24
Seynes	50	50	10
Moreda 1B	46	54	56
Belmez 1	39	61	33
Layna	36	64	25
Moreda 1A	43	57	110
Caravaca	93	7	14

Fig. 9. Percentages for the character-states of the lingual longitudinal crest (connection t1-t5) in M^1.

nothing to do with the stephanodont crest. The opposite case, when there is no connection, is called *isolated t3* (Fig. 10a).

Connection t4-t8 – For this character three states are distinguished: *absent* means that t4 and t8 are separated (Fig. 11a); *t4-t8 crest* means that there is a spur on the posterior wall of t4 that reaches the posterolingual border of t8; this connection, if present, has more or less the same height as the t4-t5 crest and its position is symmetrical with the t9-t8 crest (Fig. 11b). The third state, *inflated t4-t8 crest* means a thickening of the connection, which forms a small 't7' (Fig. 11c). In this case the connection t4-t8 is higher than the connection t4-t5-t6-t9.



Locality	%	%	N
Casablanca 3	0	100	14
Loma Quemada 1	0	100	16
Mas Rambault	0	100	10
Valdeganga 7	0	100	24
Seynes	0	100	12
Moreda 1B	27	73	51
Belmez 1	27	73	33
Layna	11	89	27
Moreda 1A	31	69	110
Caravaca	93	7	14

Fig. 10. Percentages for the character states of the labial longitudinal crest (connection t3-t5) in M^1.

Locality	%	%	%	N
Casablanca 3	7	57	36	14
Loma Quemada 1	12	38	50	16
Mas Rambault	10	80	10	10
Valdeganga 7	8	79	13	24
Seynes	58	42	0	12
Moreda 1B	75	25	0	56
Belmez 1	78	22	0	32
Layna	69	31	0	27
Moreda 1A	76	24	0	105
Caravaca	100	0	0	14

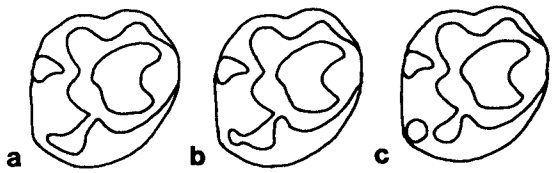
Fig. 11. Percentages for the character states of the t4-t7 connection in M^1.

M^2

t1bis – Three character states are defined: *absent* when there is no cusp between t1 and t2 (Fig. 12a). If present, it is considered *small* when it is an anterior constriction of t1 (Fig. 12b); it is defined as *large* when it is a well-developed cusp in front of t1 (Fig. 12c).

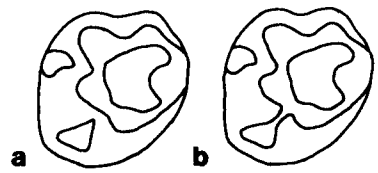
Connection t1-t5 – The definitions are identical to those given for M^1. So the states are *isolated t1* and *lingual longitudinal crest* (Fig. 13).

Connection t3-t5 – Like in M^1: *isolated t3* and *labial longitudinal crest* (Fig. 14).



Locality	%	%	%	N
Casablanca 3	0	33	67	6
Loma Quemada 1	0	32	68	19
Mas Rambault	0	0	100	2
Valdeganga 7	0	23	77	13
Seynes	9	82	9	11
Moreda 1B	27	58	15	55
Belmez 1	45	33	22	18
Layna	63	25	12	16
Moreda 1A	22	49	29	63
Caravaca	46	54	0	13

Fig. 12. Percentages for the character states of the t1bis in M^2.

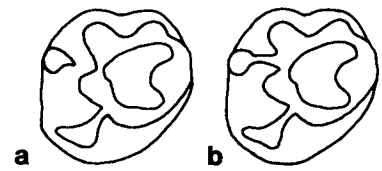


Locality	%	%	N
Casablanca 3	17	83	6
Loma Quemada 1	11	89	19
Mas Rambault	0	100	2
Valdeganga 7	11	89	18
Seynes	67	33	6
Moreda 1B	53	47	55
Belmez 1	61	39	18
Layna	57	43	14
Moreda 1A	56	44	63
Caravaca	100	0	13

Fig. 13. Percentages for the character states of the lingual longitudinal crest in M^2.

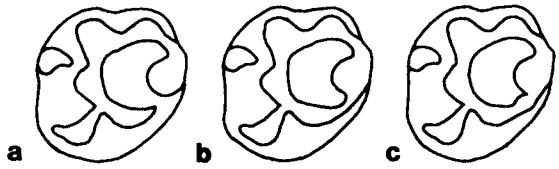
Connection t4-t8 – The character states are the same as in M^1: *absent*, *t4-t8 crest*, and *inflated t4-t8 crest* (Fig. 15).

The analysis of the mentioned characters has enabled us to quantify the distribution of the various character-states in the mentioned populations. A first observation is, that populations from stratified deposits are homogeneous. On the other hand the populations from karst fissures are more heterogeneous and present a mosaic distribution of character states.



Locality	%	%	N
Casablanca 3	17	83	6
Loma Quemada 1	11	89	19
Mas Rambault	0	100	2
Valdeganga 7	25	75	12
Seynes	73	27	11
Moreda 1B	84	16	55
Belmez 1	89	11	19
Layna	92	8	13
Moreda 1A	89	11	62
Caravaca	100	0	13

Fig. 14. Percentages for the character states of the labial longitudinal crest (connection t3-t5) in M^2.



Locality	%	%	%	N
Casablanca 3	0	50	50	6
Loma Quemada 1	0	21	79	19
Mas Rambault	0	100	0	2
Valdeganga 7	17	83	0	12
Seynes	63	37	0	8
Moreda 1B	73	27	0	55
Belmez 1	91	9	0	11
Layna	87	13	0	15
Moreda 1A	77	23	0	61
Caravaca	100	0	0	13

Fig. 15. Percentages for the character states of the t4-t7 connection in M^2.

The biometric data show the same pattern: populations from karst deposits show a higher variability; this feature has also been demonstrated by Freudenthal & Martín Suárez (1990).

Systematics

Genus *Castillomys* Michaux, 1969

Type-species – *Castillomys crusafonti* Michaux, 1969.

Original diagnosis – 'molaires brachiodontes, forte stéphanodontie, t1 reculé, petite taille'.

Emended diagnosis – Small murids with brachyodont molars; upper molars strongly stephanodont; t1 of M^1 placed backward with respect to t2, M^2 with 3 roots; upper and lower molars with longitudinal crests that gain importance in the course of evolution.

Castillomys rivas sp. nov.
Pl. 1, figs. 1-11.

Holotype – M^1 dext., LQ-1, 158; kept in the Department of Stratigraphy and Paleontology of the University of Granada.
Type-locality – Loma Quemada 1 (Granada, Spain), co-ordinates UTM 30SWG442811.

Other localities – Venta Micena 1, 2; Orce 1, 2, 3, 7; Cueva Victoria, Valdeganga 7, Bagur II, Mas Rambault.
Derivatio nominis – This species is dedicated to our friend and colleague Dr P. Rivas. This new *Castillomys* and Dr Rivas share a big size in comparison with their relatives.

Stratigraphic distribution – Latest Pliocene, Early Pleistocene.

Measurements – Table 1, Fig. 16.

Diagnosis – Large *Castillomys*. Lower molars with well-developed longitudinal crests, that connect the hypoconid-entoconid with the protoconid-metaconid. M_1 with a very broad labial cingulum, separated from the protoconid by a valley. M^1 and M^2 with lingual and labial longitudinal crests well-developed.The t4 and t8 are connected by a crest.

Differential diagnosis – *Castillomys rivas* differs from all other *Castillomys* species by its larger size.

It differs from *C. margaritae* by the presence of t1bis and t2bis.

It differs from *C. gracilis* by the presence of well-developed longitudinal crests in both the upper and the lower molars, and by the t4-t8 connection in M^1 and M^2.

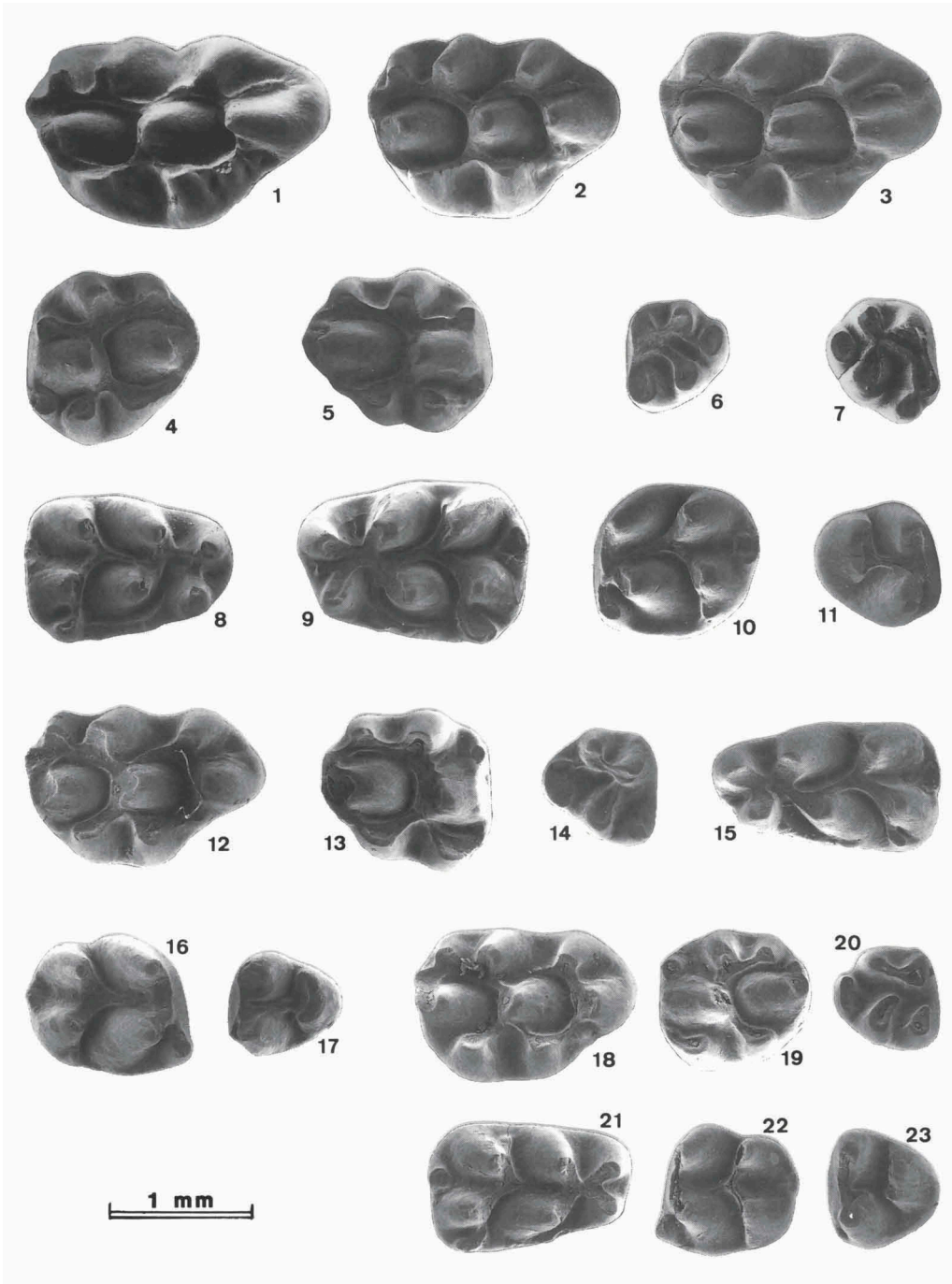
C. *rivas* differs from *C. crusafonti* by the presence of a longitudinal crest in all specimens of the lower molars and a very broad labial cingulum in M_1, that is separated from the protoconid by a valley. The M^1 and M^2 of *C. rivas* generally have t1bis, t2bis, and labial and lingual longitudinal crests; the stephanodont crown is completed by a connection t4-t8.

Plate 1

Castillomys rivas sp. nov.
From Loma Quemada 1; coll. University of Granada.
Fig. 1. M^1 dext., LQ-1 4.
Fig. 2. M^1 dext., LQ-1 160.
Fig. 3. M^1 dext., LQ-1 158, holotype.
Fig. 4. M^2 sin., LQ-1 164.
Fig. 5. M^2 dext., LQ-1 37.
Fig. 6. M^3 sin., LQ-1 180.
Fig. 7. M^3 dext., LQ-1 56.
Fig. 8. M_1 dext., LQ-1 64.
Fig. 9. M_1 sin., LQ-1 107.
Fig. 10. M_2 sin., LQ-1 117.
Fig. 11. M_3 dext., LQ-1 154.

Castillomys crusafonti Michaux, 1969
From Layna; coll. DST, Lyon.
Fig. 12. M^3 dext.
Fig. 13. M^2 dext.
Fig. 14. M^1 dext.
Fig. 15. M_1 sin.
Fig. 16. M_2 dext.
Fig. 17. M_3 sin.

Castillomys gracilis van de Weerd, 1976
From Caravaca; coll. DST, Lyon.
Fig. 18. M^1 dext.
Fig. 19. M^2 sin.
Fig. 20. M^3 dext.
Fig. 21. M_1 dext.
Fig. 22. M_2 sin.
Fig. 23. M_3 sin.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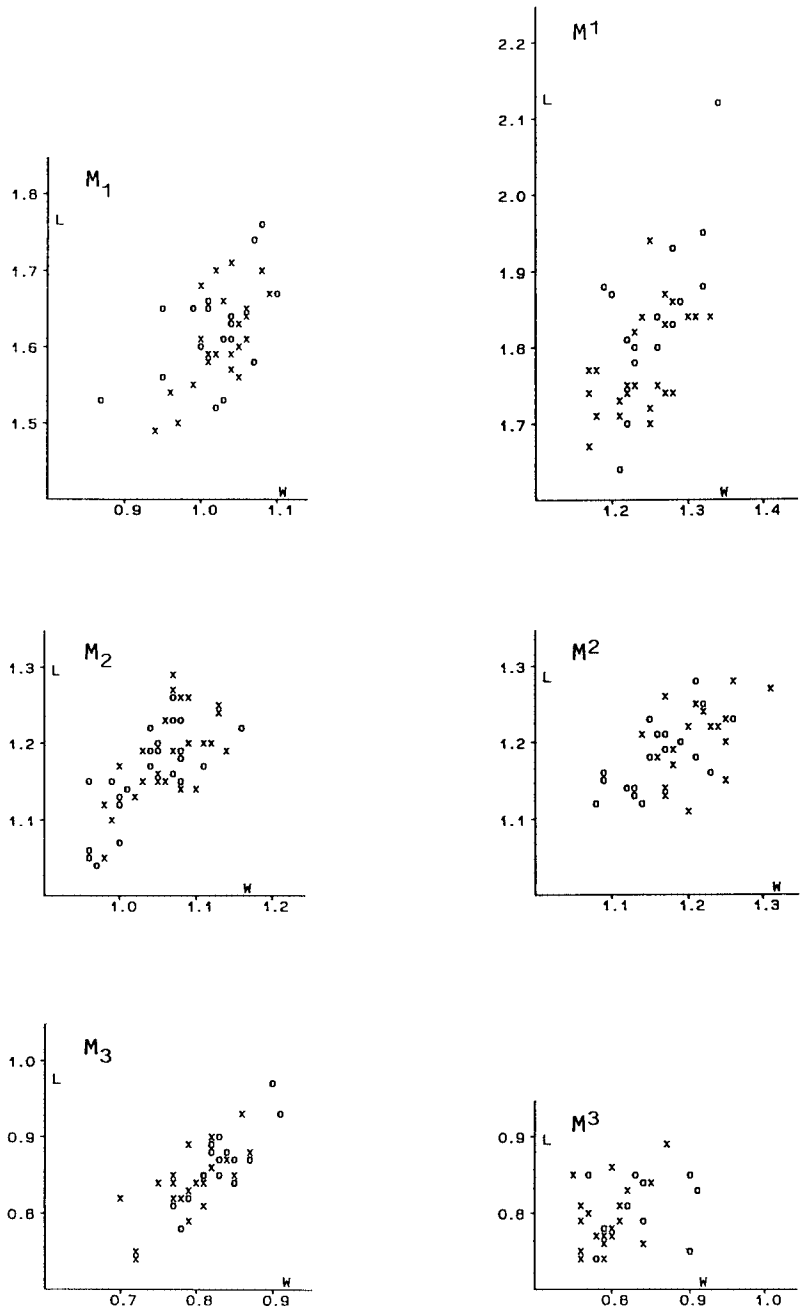


Fig. 16. Length/width diagrams of the molars of *Castillomys rivas* sp. nov.; o = Loma Quemada 1, × = Valdeganga 7.

Description of the type-material

M_1 – Teeth considerably much broader posteriorly than anteriorly. There is no tma. The anteroconid is asymmetrical; there is a very well-developed crest that connects the meeting point of the two anteroconid cusps with the labial part of the metaconid. The protoconid is situated well behind the metaconid. The longitudinal crest is high and diagonal, connecting the anterolabial wall of the entoconid with the posterolingual wall of the protoconid. The labial cingulum is separated from the protoconid by a deep valley, and forms a longitudinal crest along the labial border of the tooth. C1 is always present, and in half the specimens there is a second cuspid in the cingulum, situated between protoconid and anteroconid. The anterolingual border of the entoconid bears a small fold. The posterior heel is well-developed, oval or subtriangular, and extends beyond the posterior border of the tooth. There are two roots.

M_2 – Teeth with a subquadrate outline. The anterolabial cuspid is big and isolated. The longitudinal crest is high and diagonal. The labial cingulum is broad, though less than in M_1; c1 vestigial or absent; other cuspids on the cingulum are rarely present. The posterior heel is as large as the anterolabial cusp (*alc*), its shape is round or oval, and it extends beyond the posterior wall of the tooth. There are two roots.

M_3 – Anterolabial cusp well-developed, though it is not as high as the other cusps. The longitudinal crest is high and always present. The hypoconid-entoconid complex is completely shifted towards the lingual side of the tooth. In some specimens there is a minuscule c1, that is never isolated. There are two roots.

M^1 – The t1 lies so far backwards, that in some cases it has even lost contact with the t2. A t1bis is present; it is reduced to a small bulge on the wall of t2, or well-developed on the t1-t2 crest. A t2bis is absent in 20 % of the specimens, small in 53 %, or a well-developed fold that extends far into the valley between t2 and t3 (27 %); see Fig. 8. The lingual and labial longitudinal crests are high and well-marked. Generally the connection t4-t8 is higher than the connections t4-t5-t6-t9; in 50 % of the entire population (57 % of the specimens with crest) it widens and forms a t7. The t12 is a thickening of the t9-t8 crest. There are three main roots, and a very small one in the centre of the molar. One of the specimens (Pl. 1, fig. 1; LQ-1 4) is considerably larger than the rest, especially in its length (Fig. 16); its morphology is identical to the other specimens.

M^2 – This element has a rounded shape. t1bis is always present: reduced to a widening of the anterolabial end of t1, or tubercular and either connected to, or separated from t1. The lingual longitudinal crest is present in 90 % of the specimens; when this connection is absent, t1 is isolated. In 90 % of the specimens the labial longitudinal crest connects t3 and t5, in the other cases there is an anterior spur on the t5 or on the t5-t6 crest, that does not reach the t3. In one case there is no t3. The connection t4-t8 is thickened like in M^1. The t12 is a mere protuberance of the t9-t8 crest. There are three roots.

M^3 – The t1 is connected to t5; t1 is double in 30 % of the specimens. A t3 is absent. The t4 is very massive and united to t5. The t8 is isolated. There are two or three roots.

Remarks – Within the genus *Castillomys*, *C. rivas* includes the youngest populations with the largest dimensions. These are all found in the Iberian Peninsula and Southern France. No record is known from outside this biogeographic province.

In its oldest occurrence (the Upper Pliocene of Valdeganga 7, Albacete) it is associated with *Mimomys* aff. *medasensis* (Mein et al., 1978). In the Guadix-Baza Basin this species of *Mimomys* is associated with *Castillomys crusafonti*, and *C. rivas* is restricted to Pleistocene levels. In the oldest Guadix-Baza occurrence (Orce 2) *C. rivas* is associated with *Mimomys ostramosensis* and *M. pusillus* (Martín Suárez, 1988); in its type-locality the Arvicolidae are represented by *Mimomys savini*, *Allophaiomys nutiensis*, and *Allophaiomys burgondiae*. The youngest record known is from Cúllar de Baza B, where it is associated with *Pitymys* (Agustí, 1985).

The dental morphology of *C. rivas* shows several characters that can be considered apomorphic within the context of the evolution of the genus. E.g. in all the three lower molars the longitudinal crests are very well-developed; in M_1 the labial cingulum is so strongly developed, that it might be called a labial longitudinal crest. In M^1 and M^2 there is a connnection t4-t8, which, in quite some cases, is thickened, forming a beginning of a t7; or, in other words, the stephanodonty is as complete as in many *Apodemus*.

Castillomys crusafonti Michaux, 1969.
Pl. 1, figs. 12-17.

1969 *Castillomys crusafonti sp.* nov. – Michaux, pp. 6-8; pl. 1, figs. 1-3.

Holotype – A left maxillary with M^1-M^3, Ly-1311, kept in the Instituto de Paleontología, Sabadell.

Localities – Layna (Soria; type),Moreda 1A, 1B; Rambla Seca, Belmez, Gorafe 2, 3, 5; Cañada del Castaño 1, 2; Galera 2, Alquería, Villalba Alta 1, 2, 3; Villalba Alta Río 2, 3; Lomas de Casares 1, Escorihuela, Sarrión 2, La Gloria 2, Orrios III, Arquillo III, Sète, Seynes, Balaruc II, 6; Mont-Hélène, Lo Fournas 4, Pla de la Ville, Serrat d'en Vacquer.

Stratigraphic distribution – Middle Pliocene: latest Alfambrian, earliest 'Villanian or Villafranchian'; zones MN 15, 16 and 17 of Mein (1975, 1990).

Measurements – See Table 1. The measurements indicated by LAY* are those of M_1 and M^1 taken from the original description (Michaux, 1969); those indicated by LAY are the measurements of all specimens of a collection of *Castillomys* from Layna, kept in the DST.

Original diagnosis – 'voir celle du genre' (Michaux, 1969, p. 6).

Emended diagnosis – *Castillomys* of medium size. M_1 and M_2 with a longitudinal spur, which forms a crest in 50 % to 90 % of the specimens. M_2 generally without

posterior heel or with a reduced one. In the upper molars t1 develops a lingual longitudinal crest in more than half the M^1 and in somewhat less than half the M^2. The majority of the M^1 have a labial longitudinal crest (t3-t5). In M^2 the t3 is generally isolated.

Differential diagnosis – *C. crusafonti* differs from *C. margaritae* by its larger size and by the presence of a labial longitudinal crest in the majority of the M^1.

The lower molars of *C. crusafonti* have a longitudinal spur, which in the majority of the specimens forms a crest; in *C. gracilis*, on the other hand, this spur never forms a complete crest. In *C. crusafonti* the spur of the t3 forms a labial longitudinal crest in more than 70 % of the M^1, whereas in *C. gracilis* it doesn't form a crest. The t1 of M^2 is usually isolated in *C. gracilis*.

Description – See Michaux (1969, pp. 6-8).

Remarks – The population from Layna is extremely heterogeneous in size and morphology, as was proven already by Freudenthal & Martín Suárez (1990). It is an abundant material, in which two morphotypes may be distinguished:
An 'archaic' morphotype (*gracilis* type), in which M_1 has a symmetrical anteroconid and a very low longitudinal spur; M^1 without t2bis and with very poorly developed crests; and a 'derived' morphotype (*crusafonti* type), in which M_1 has an asymmetrical anteroconid and well-developed longitudinal crests; M^1 with a small t2bis and very high crests.

The populations from Moreda 1A, Moreda 1B and Belmez are very similar to the type population from Layna (see Figs. 1-15, and 17). So, all these populations are highly heterogeneous, a fact that led Castillo (1990) to the conclusion that in these localities associations of *Castillomys gracilis* and *C. crusafonti* are found.

Of all the character-states defined in this paper only the degrees of development of t1bis and of the lingual longitudinal crest (connection t1-t5) show a positive correlation (never 100 %). The rest of the character-states is independent, nor is there a correlation with size. This means that within *Castillomys crusafonti* the attribution of the morphotypes 'archaic' and 'derived' to two separate groups (*gracilis* and *crusafonti*) is impossible. Firstly, because the independent distribution of the character-states resides in a mosaic morphology. Secondly, one would expect a correlation between 'archaic' morphotypes and small size, and 'derived' morphotypes and large size. Though this is frequently true, there are numerous small specimens with characters that can be considered apomorphic within the context of the genus, e.g. well-developed t1bis. Many large specimens show plesiomorph characters like longitudinal spurs that don't form crests.

Aguilar et al. (1986) attribute the population from Mont-Hélène to *C. gracilis*, though they state that morphologically it is identical to the population from Sète (attributed to *C. crusafonti*). On the basis of size and morphology we include this population in *C. crusafonti*.

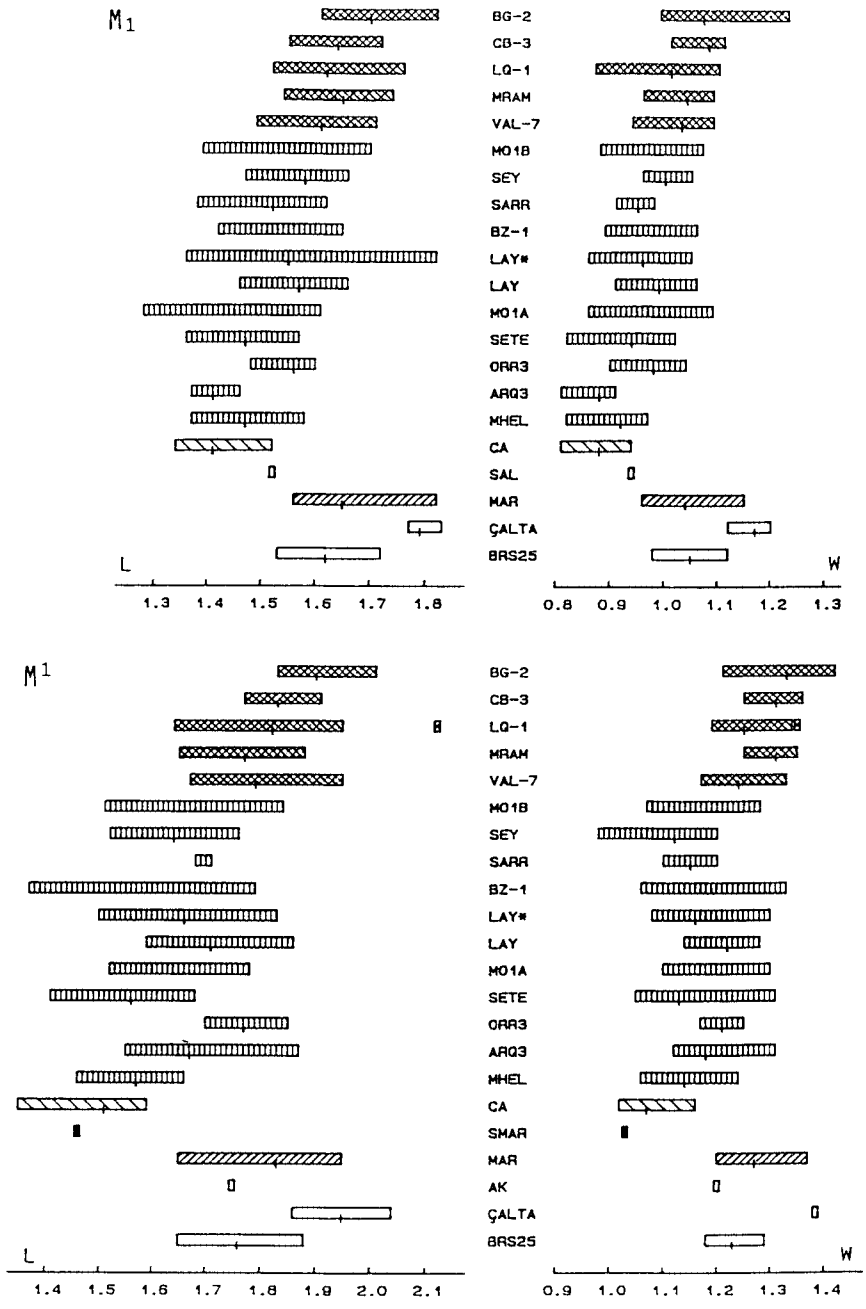


Fig. 17. Size ranges for length and width of the first molars of *Centralomys*, *Rhodomys* and *Castillomys*. The population from Argoub Kemellal has been tentatively placed in *Centralomys* (see paragraph on *Castillomys* from Argoub Kemellal). For an explanation of the locality codes see Table 1 (p. 78).

= *Centralomys*; = *Rhodomys*; = *Castillomys margaritae*; = *C. gracilis*; = *C. crusafonti*; = *C. rivas*.

Castillomys gracilis van de Weerd, 1976.
Pl. 1, figs. 18-23.

1976 *Castillomys crusafonti gracilis* sp. nov. – van de Weerd,pp. 73-76, pl. 8, figs. 1-5.

Holotype – Isolated M^1, CA no. 1801, kept in the Instituto de Paleontología, Sabadell.
N. B. Van de Weerd's choice of no. CA 1081 as holotype is quite unfortunate. It is the only specimen showing a connection between t3 and t5/t6. All other M^1 in the collections of Utrecht and DST have an isolated t3.

Localities – Caravaca (Murcia; type), Botardo C, D; Gorafe 1, 4; La Gloria 4, Orrios 1, Celadas 6, Aldehuela, La Alberca 1, Alcoy, Salobreña (?).

Stratigraphic distribution – Latest Miocene (?), Early Pliocene: latest Turolian (?), Early Alfambrian; zones MN 13 (?) and 14 of Mein (1990).

Measurements – The measurements in Table 1 are taken from van de Weerd (1976).

Original diagnosis – 'The teeth of *C. crusafonti gracilis* are very small and low. Some M^1 show a connection between t3 and t5/t6'.

Emended diagnosis – *Castillomys* of small size. In M_1 and M_2 the longitudinal spur rarely forms a crest. In M^1 t1 and t3 develop posterior spurs that rarely form longitudinal crests. M^2 with t1 and t3 isolated. In both M^1 and M^2, t4 and t8 are isolated. M^3 with t1, t4 and t8 generally isolated, not connected to the t5-t6 complex.

Differential diagnosis – See under *C. rivas* and *C. crusafonti*. *C. gracilis* differs from *C. margaritae* by the presence of t1bis and t12.

Description – See van de Weerd (1976, pp. 73-76).

Remarks – This is the smallest *Castillomys* species, even smaller than *C. margaritae*. It is known solely from the Iberian Peninsula. There are few localities with an abundant material of *C. gracilis*. In the Teruel Basin *Castillomys* is very rare, as well as in the Granada Basin, where none of the thirty-odd Lower Pliocene localities have yielded any *Castillomys* material. In the Guadix-Baza Basin, where *Castillomys* is abundant, there are hardly any Lower Pliocene localities.

Castillomys margaritae Antunes & Mein, 1989

1989 *Castillomys margaritae* sp. nov. – Antunes & Mein, p. 165, pl. 1, fig. 13.

Holotype – M^1 dext., 1.46 x 1.03.

Type-locality – Santa Margarida (Alvalade Basin, Portugal).

Diagnosis and differential diagnosis – See Antunes & Mein, 1989.

Original description – 'cette dent vraiment très petite correspond aux valeurs minimales observées dans la population de *C. crusafonti gracilis*. On note également le grand développement du t3 aussi important que le t2. La corne du t3 dirigée vers la base du t5 est épaisse; chez *C. crusafonti gracilis* le t3 est plus petit que le t2, la corne du t3 est grêle. La forme et la disposition des racines ne diffère pas de celle des autres espèces du genre *Castillomys*: il y a trois racines principales inclinées vers l'avant dont l'antérieure est la plus grosse; on trouve en outre une minuscule racine centrale.

La très petite taille laisserait supposer une forme très (ou la plus) primitive au sein de la lignée. Le très grand recul du t1, au contraire, semble un caractère apomorphe plaçant cette forme en dehors de la lignée *C. crusafonti gracilis*-C. *crusafonti crusafonti*.' (Antunes & Mein, 1989, p. 165).

'*Castillomys* sp.'

1985 *Castillomys crusafonti* aff. *crusafonti* Michaux – Coiffait et al., p. 173, pl. 1, fig.8.

Locality – Argoub Kemellal.

Material – Unknown number of M^1, average measurements: L = 1.75 mm, W = 1.20 mm.

Remarks – The study of this *Castillomys* is part of the doctoral thesis of Mrs B. Coiffait, who considers this population close to the Brisighella material (Mrs Coiffait, personal communication). This would mean that it should be included in the genus *Centralomys*, though the M^2 from Argoub Kemellal have three roots, and those from Brisighella have four roots.

Discussion on the genus *Castillomys*

The origin of this group remains uncertain. Various authors suggest an Asian origin, though there is no record of similar fossils outside the Ibero-Occitanian faunal province and North Africa.

The oldest representative, *C. margaritae*, does not clarify much, since its relationship with the *Castillomys* from the Pliocene and Pleistocene is unclear. The same goes for the *Castillomys* from Salobreña.

One might construe the evolutionary lineage *C. gracilis* - *C. crusafonti* - *C. rivas*. As shown in the descriptions of the character-states there is a clear difference between the older and the younger populations. For almost all characters that are

considered diagnostic *C. gracilis* and *C. rivas* are located at opposite points of the variability. *C. crusafonti*, on the other hand shows a mosaic distribution intermediate between the former two, to such a degree, that the differential diagnosis has to rely on frequency percentages.

Within the supposed lineage *gracilis-crusafonti-rivas*, a number of morphological changes may be noted, that seem to point towards an anagenetical evolution:

M_1 – The longitudinal spur is a long and high crest and the labial cingulum is wider in the youngest populations, and, consequently, the teeth are relatively broader. The number of accessory cuspids increases with the width of the cingulum, but the relative size of c1 remains almost constant. The posterior heel is more developed in the youngest populations.

M_2 – Like in M_1, the longitudinal crest is more evident and the labial cingulum broader in the youngest populations. The labial cingulum is always narrower than in M_1. The number of accessory cusps and the relative size of c1 decrease in the course of time.

M_3 – The longitudinal crest is present in the youngest populations only. The hypoconid-entoconid complex is relatively smaller and shifted towards lingual in the youngest populations; this leaves a wide valley in the labial part of the talonid.

M^1 – The lingual (t1-t5) and labial (t3-t5) longitudinal connections gain importance in the course of time; they form crests in the youngest populations. Solely in the youngest populations there may be a crest between t4 and t8, that completes the stephanodont crest. In none of the populations it is present in 100% of the specimens. E.g. in 50% of the specimens of the type-population of *C. rivas* the t4-t8 crest is inflated and forms a small t7, that may be even more developed than in many *Parapodemus* specimens. The degree of development of t1bis is variable through time: present in *C. gracilis*, absent in a considerable part of the *C. crusafonti* material, present again in *C. rivas*, where it may even be quite large. The degree of development of t2bis, on the other hand, increases through time.

M^2 – The longitudinal connections t1-t5 and t3-t5 are more developed in the youngest populations. The connection t4-t8 increases too, and, like in M^1, a little t7 may arise. Strangely enough, t1bis does not show the same pattern as in M^1, since in M^2 its size increases and it becomes more isolated in the course of time.

M^3 – In the type-material of *C. gracilis* t1, t4 and t8 are isolated. In *C. crusafonti* t1 and t8 are isolated and t4 and t5 may be isolated or connected. In *C. rivas* t4 and t5 are always connected; t1 is isolated in some specimens from Valdeganga III and connected to t5 in all specimens from Loma Quemada 1; in the latter population t8 is connected to t6 by a weak longitudinal crest.

Size increases from the oldest towards the youngest populations, but this increase is not the same in the various dental elements. We have calculated the degree of size increase on the basis of the mean values of length and width of the populations from Caravaca and Loma Quemada. The size of M_1 increases equally for the length (14.08 %) and the width (14.77 %). In M_2 the length increases more than the width (18.37 % and 14.28 respectively), so the width/length relation decreases from the oldest population (0.928 in Caravaca) towards the youngest one (0.896 in Loma

Quemada); this relation is subject to oscillations, fundamentally due to population size: the most unexpected values are found in the less numerous populations. In M_3 the length (11.54 %) increases less than the width (18.75 %).

The increase of the width of the upper molars is larger than in the lower molars: 17.76 % for M^1, 17.17 % for M^2, and 31.25 % for M^3. The increase of the length is largest in M^1 (21.19 %), less in M^3 (20.89 %), and least in M^2 (11.32 %).

Genus *Centralomys* de Giuli, 1989

Type-species – *Centralomys benericettii* (de Giuli, 1989).

Original diagnosis – 'degree of stephanodonty somewhat intermediate between *Castillomys* and *Occitanomys*. Tubercula bent backwards as in Orientalomys. M^2 with 4 roots. Both M^1 and M^2 with t1-t5 and t4-t8 connection; isolated t3 and well developed t1-bis'.

Emended diagnosis – Medium-sized Muridae. Teeth with voluminous cusps. Anteroconid of M_1 symmetrical. Lower molars with very broad labial cingulums and reduced longitudinal spurs. Upper molars with weak longitudinal connections. M^2 with four roots.

Centralomys benericettii (de Giuli, 1989)
Pl. 2, figs. 12-17.

1989 *Castillomys* (*Centralomys*) *benericettii* sp. nov. – de Giuli, pp. 206-208, pl. 3, figs. 1-10.

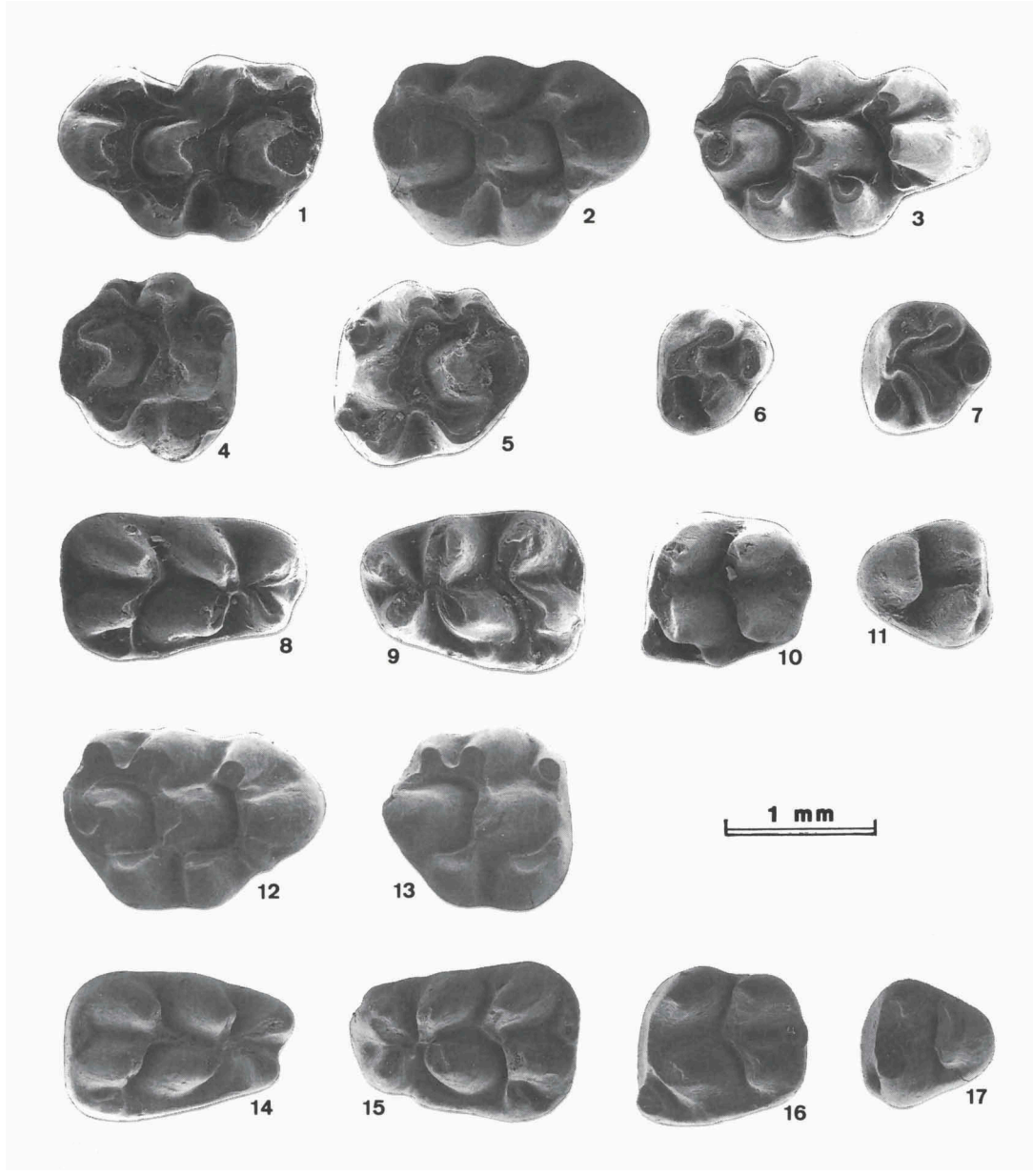
Holotype – M^1 sin., BRS 1 (op. cit., pl. 3, fig. 1), kept at the Dipartamento di Scienze della Terra, Università di Firenze.

Type-locality – Brisighella 1, Monticino quarry, Brisighella (Faenza, Italia).

Plate 2

Occitanomys (Rhodomys) debruijni (Sen et al., 1989)
From Maritsa; coll. Instituut voor Aardwetenschappen, Utrecht.
Fig. 1. M^1 sin., MA 461.
Fig. 2. M^1 dext., MA 471, holotype.
Fig. 3. M^1 dext., MA 472.
Fig. 4. M^2 dext., MA 483.
Fig. 5. M^2 sin., MA 494.
Fig. 6. M^3 sin., MA 503.
Fig. 7. M^3 sin., MA 505.
Fig. 8. M_1 dext., MA 404.
Fig. 9. M_1 sin., MA 415.
Fig. 10. M_2 sin., MA 434.
Fig. 11. M_3 dext., MA 443.

Centralomys benericettii (de Giuli, 1989)
From Brisighella 25. Coll. DST, Lyon.
Fig. 12. M^1 dext.
Fig. 13. M^2 dext.
Fig. 14. M_1 dext.
Fig. 15. M_1 sin.
Fig. 16. M_2 sin.
Fig. 17. M_3 sin.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Stratigraphic distribution – Late Miocene or Early Pliocene.

Measurements – In the original description no measurements are given, and only M^1 and M^2 are described. We were able to study a collection of *Centralomys* from the locality Brisighela 25 (BRS 25), donated to the DST by Dr F. Massini (Firenze). The measurements are given in Table 1.

Original diagnosis – 'Small sized murid, occurring with few specimens in many of the Brisighella sites. The comparative description of the new subgenus accounts for the new species'.

Emended diagnosis – Small-sized *Centralomys*. M_1 may have a small tma. Upper molars with t3 isolated, and the connections t1-t5 and t4-t8 very low, without forming crests. t12 very much reduced. M^1 with a very large t1bis.

Description of the material from BRS 25

M_1 – Teeth with 'inflated' cusps. A minuscule tma is visible in 19 % of the specimens. Anteroconid almost symmetrical; the connection between the anteroconid and the second pair of cuspids varies considerably: in some specimens the lingual cusps are connected, in others the labial cusps; in other cases there is an anterior spur on the metaconid, that may or may not be in contact with the labial lobe of the anteroconid. There is no spur or longitudinal crest between the second and the third pair of cusps. The labial cingulum is very broad, and forms a continuous crest, separated from the protoconid by a valley. The c1 is well developed; there may be a second accessory cusp on the cingulum, either at the level of the protoconid, or between protoconid and anteroconid. The posterior cingulum is big and protuberant, rounded, or triangular. There are two roots.

M_2 – Anterolabial cuspid very well developed, with a rounded shape (also in worn teeth). In some specimens there is a weak longitudinal spur, that starts from the hypoconid-entoconid complex and is directed forward towards the protoconid, without ever forming a crest. The labial cingulum is broad, but (contrary to M_1) stuck to the protoconid. The c1 varies between absent and well-developed, but in each specimen it is smaller than the posterior heel. In 7 % of the specimens a thickening of the cingulum at the level of the protoconid forms a second accessory labial cuspid. The posterior heel is absent (7 %) or of medium size (93 %), oval-shaped, never subtriangular. There are two roots.

M_3 – Anterolabial cuspid reduced or absent. There is no trace of a longitudinal spur or crest. A small ledge, labially of the hypoconid, forms the c1 (in one specimen the c1 is separated). The hypoconid-entoconid complex is slightly shifted lingually. There are two roots.

M^1 – The cusps are higher than in the M^1 of *Castillomys*. The t1 is situated backwards and t1bis is always present, situated in the t1-t2 connection, slightly closer to t2 than to t1. In worn specimens t1 and t5 are connected. In fresh specimens one can observe, that the incipient connection does not start as a posterior spur of t1, but as a lingual spur of t5, that is directed anteriorly towards t1. The t3

develops a posterior spur, that is directed towards the base of t5, but the cusp t3 remains isolated. The t4 sends a basal spur in the direction of t8, but these cusps remain isolated until an advanced degree of wear. The t12 is reduced to a slight swelling of the crest t9-t8. There are three roots.

M^2 – The t1 is voluminous and isolated (not connected to t5); in its anterior part it forms a t1bis, which is isolated in 8 % of the cases. The t3 is isolated. The crest t4-t5 is very low and appears only in well-worn specimens. The t4 is isolated in fresh specimens. The stephanodonty is very incomplete. The t12 is absent (84 %) or reduced to a widening of the crest t9-t8 (16 %). There are four roots.

M^3 – The t1 is connected to t5. The t3 is very reduced or absent. The t4 is connected to t5. The t8 is isolated. There is a valley between t4 and t6, that, with increasing wear, forms a completely isolated mesosinus. There are three roots.

Centralomys magnus (Sen, 1977)

1977 *Castillomys magnus* sp. nov. – Sen, pp. 95-99, pl. 1, figs. 1-14; pl. 2, figs. 1-3.

Holotype – M^1 dext., (ACA, 824).

Type-locality – Çalta (Ankara, Turkey).

Stratigraphic distribution – Middle Pliocene, latest Alfambrian.

Measurements – In Table 1 the measurements by Sen (1977) are given.

Original diagnosis – 'M^1 avec t1 et t3 reculés par rapport au t2 et reliés à la couronne par des cornes postérieures; cingulum postérieur réduit, stéphanodontie très développée. M_1, contrairement à celle de *C. crusafonti*, dépourvue de tma et possédant une marge cingulaire plus forte et une crête médiane plus faible. Dimensions des molaires plus grandes que celles de *C. crusafonti*'.

Description – See Sen (1977).

Discussion on the genus *Centralomys*

We include two species in this genus: *Centralomys benericettii*, which was found in uppermost Miocene or lowermost Pliocene deposits in central Italy (de Giuli, 1989); and *C. magnus*, from the Middle Pliocene of the Isle of Rhodes and Anatolia. They have dental morphologies with characters of both *Occitanomys* and *Castillomys*. The teeth are larger than those of *Castillomys*, and smaller than those of *Occitanomys*, found in western European localities of similar age. The dental morphology of *Centralomys* is archaic in comparison with that of *Castillomys*: the development of the longitudinal crests, in both the lower and the upper molars, is poor to nil. The stephanodonty is considerably less advanced than in *Castillomys*; at least in *C.*

benericettii t6 and t9 remain separated until in a well-advanced state of wear. *Centralomys* differs from *Occitanomys* by the better development of the longitudinal crests, by the backward position of t1 in the M^1, and by the large labial cingulum in M_1 and M_2. The presence of four roots in the M^2 of *Centralomys* is a character that distinguishes it from *Castillomys* and *Occitanomys*. However, in a sample of 100 M^2 of *Castillomys* from Mont-Hélène, 5 specimens have a lingual root with two canals and a bifid tip, and in 2 specimens the lingual root is completely subdivided. *Centralomys* is more closely related to *Castillomys* then to *Occitanomys*.

Genus *Occitanomys* Michaux, 1969.

Type species – *Occitanomys brailloni* Michaux, 1969.

Original diagnosis – 'Stéphanodontie moins accusée que celle de *Stephanomys* et *Castillomys*, mais plus forte que celle du genre *Apodemus*, t1 reculé, taille moyenne'.
N.B. For some comments on this diagnosis see the discussion on the genus *Occitanomys*.

Remarks – The importance of *Occitanomys* for this study is the fact, that it includes several populations, that were initially described as *Castillomys*. We are dealing with one specimen found by Adrover (1986) in Arquillo 3, with the population from Develi (Sen et al., 1989), and the population from Maritsa.

Occitanomys alcalai Adrover, Mein & Moissenet, in press

1986 *Castillomys* sp. – Adrover, p. 219, fig. 46, no. 16.

Locality – Arquillo 3.

Material – 1 M_1 (1.71 x 1.13).

Remarks – According to Adrover (1986, p. 219), this M_1 is intermediate in size between *Castillomys* and *Occitanomys*; it is supposed to have an aberrant morphology in comparison with both these genera. In our opinion this is not a *Castillomys*, but we are dealing with *Occitanomys alcalai* (Adrover, Mein & Moissenet, in press), which is characterized by its symmetrical anteroconid.

Occitanomys sp.

1989 *Castillomys* debruini sp. nov. – Sen et al., pp. 1731, 1734, figs. b-e (pro parte).

Locality – Develi (Anatolia, Turkey).

Material – 1 M^1, 1 M^3, 3 M_2, and 1 M_3.

Description – See Sen et al., 1989.

Remarks – Sen et al. (1989) attribute this population to *C. debruijni*. Their fig. b represents an M^1, in which the t1 is connected to t2 and t5. In the Maritsa population, however, the t1 is separated from the t2, and the prelobe is formed exclusively by t2 and t3. Dr Sen kindly allowed us to study the material; we think it is a species of *Occitanomys*, different from the population from Maritsa, and not even belonging to the subgenus *Rhodomys* subgen. nov. A specific determination is not possible in view of the limited material available.

Subgenus *Rhodomys* subgen. nov.

Type-species – *Castillomys debruijni* Sen et al., 1989.

Derivatio nominis – The genus is named after the Isle of Rhodes, where the type-species was found, and after the Greek word for mouse.

Diagnosis – Small-sized *Occitanomys*; M^1 with t1 placed very far backwards, often isolated from t2, and sometimes connected to t5 by a longitudinal crest. M_1 without tma and with a poorly developed longitudinal spur (or crest) between entoconid and protoconid; M_2 reduced posteriorly, and sometimes possessing a c2.

Attributed species – *Occitanomys sondaari* van de Weerd, 1976.

Occitanomys (*Rhodomys*) *debruijni* (Sen et al., 1989)
Pl. 2, figs. 1-11.

1970 *Castillomys crusafonti* Michaux – de Bruijn et al., pp. 546-547; pl. 2, figs. 1-3, 5-6.
1989 *Castillomys debruijni* sp. nov. – Sen et al. (pro parte: only the population from Maritsa 1, not the one from Develi).

Holotype – M^1 dext., MAR-471, kept in the Instituut voor Aardwetenschappen, University of Utrecht, figured in de Bruijn et al., 1970, pl. 2, fig. 3.

Type-locality – Maritsa 1 (Isle of Rhodes, Greece).

Stratigraphic distribution – Early Pliocene, zone MN14 of Mein (1975, 1990).

Measurements – See Table 1.

Original diagnosis – 'Crête longitudinale faible sur les molaires inférieures, connection absente ou imparfaite entre le t3 et le t5-t6 sur la M^1. Tubercule postérieur

isolé sur la M^3. Taille intermédiaire entre *C. crusafonti* et *C. magnus*.' (Sen et al., 1989, p. 1734).

Emended diagnosis – Large-sized *Rhodomys*; M^1 with a big, sometimes isolated, t1bis; labial longitudinal spur (connection t3-t5) reduced or absent. The t8 in M^3 is generally isolated. Lower molars with a longitudinal spur that seldom forms a crest. M_2 without c1.

Description

M_1 – Morphology highly variable. There are specimens with asymmetrical and others with symmetrical anteroconid. The tma is absent. In three specimens there is a longitudinal spur, which in only one case forms a crest. The labial cingulum varies between reduced and very broad. In the latter case it bears one or two accessory cuspids (apart from c1). The posterior heel is low and oval-shaped.

M_2 – The anterior part of the tooth is much broader than the posterior part. The anterolabial cusp is isolated and high. Half the specimens have a longitudinal spur, which never forms a crest. The labial cingulum is reduced or broad; in the latter case it bears an accessory cuspid at the level of the protoconid. There is no c1. The posterior heel is oval-shaped and very low, almost absent.

M_3 – The anterolabial cusp is reduced (66.6 %) or well developed (33.3 %). There is no c1. The hypoconid-entoconid complex is shifted lingually.

M^1 – The material is very heterogeneous, both in size and morphology. The t1 is placed extremely far backwards, and separated from t2; it may be isolated (fresh specimens) or connected to the lingual wall of t5. A t1bis is always present. The prelobe is made up of t2 and t3 only. The t3 bears a short posterior spur. The t4-t5-t6-t9-t8 are connected by very low crests; in one specimen t4 and t5 are separated. The t4 and t8 are connected at their bases only; their tops are separated by a valley; in 22.2 % of the cases there is a minuscule cusplet in the external part of this valley. The t12 is a swelling of the connection t9-t8.

M^2 – The t1 is isolated or weakly connected to t5. The t1bis equals t3 in size in 81.25 % of the cases. The t4-t5-t6-t9-t8 connected by a stephanodont crest, which is higher than in M^1. The t4 is connected to t8; there is no trace of an enamel protuberance on the external side of the connection t4-t8. A t12 is absent.

M^3 – The t1 is voluminous and generally connected to t5. There is no t3. The t8 is isolated, except for one specimen.

Remarks – Thanks to the kindness of Dr H. de Bruijn we have been able to study the material from Maritsa. It is a very heterogeneous population, both in size and morphology. Among the M^1 more than 41 % have a t1 completely separated from the t2. This feature estranges this population from *Castillomys* and *Centralomys*, and is shared with *Orientalomys* and ancient populations of *Occitanomys*. A difference with *Orientalomys* is the absence of tma in the M_1 from Maritsa 1.

The population from Maritsa 1 was first attributed to *Castillomys crusafonti* (de Bruijn et al., 1970). It was restudied by van de Weerd (1976), who called it *Castillomys* sp., and supposed it to be part of an evolutionary lineage different from

crusafonti-gracilis because of the combination of larger size and very primitive morphology. In later papers this *Castillomys* is not even mentioned in the faunal lists of Maritsa 1 (de Bruijn et al., 1979). Sümengen et al. (1990) recognize it to be an *Occitanomys* and report it from Igdeli.

Sen et al. (1989) studied the material from Develi (Anatolia, Turkey), which in their opinion is very similar to that from Maritsa, and defined a new species for the Maritsa material, which they called *Castillomys debruijni*, similar to *C. magnus*, but smaller and with a 'degré évolutif moindre'.

We find little in common between this population and those of *Castillomys* from western Europa. Apart from a significantly larger size, the population from Maritsa shows a number of characters, e.g. the total absence of longitudinal crests, that separate it clearly from *Castillomys* sensu stricto.

It differs from *Centralomys*, which has four roots in M^2, while *O.* (*Rhodomys*) *debruijni* has only three.

Discussion on the genus *Occitanomys*

The original diagnosis of this genus is very wide; in order to give a more restricted diagnosis a complete revision of the genus is necessary, but this falls outside the scope of this paper. We are sure, however, that it contains a number of species, that should be transferred to other genera or at least subgenera.

One of the species to be excluded from *Occitanomys* is *O. provocator* de Bruijn, 1976, in which the t1 is not placed very far backward, and in which the t6 and t9 are separated. This species should be included in the genus *Karnimata*.

O. pusillus (Schaub, 1938) and *O. neutrum* de Bruijn, 1976 form a separate subgenus, characterized by the presence of t12 and tma, and a poorly developed t1bis; it combines these plesiomorphic characters with well-developed longitudinal crests, and the tendency to form 4 roots in M^2.

Small forms of *Occitanomys* have been found in several localities in the Eastern Mediterranean, like Dorkovo (Thomas et al., 1986), Develi (Sen et al., 1989) and Igdeli (Sümengen et al., 1990). Either they have not been described, or the material is so poor, that its relation with *O.* (*Rhodomys*) *debruijni* from Maritsa cannot be established.

TABLE 1: MEASUREMENTS

	Length				Width			
	N	min.	mean	max.	N	min.	mean	max.
M_1								
BG-2	7	1.61	1.70	1.82	7	0.99	1.07	1.23
CB-3	11	1.55	1.64	1.72	11	1.01	1.08	1.11
LQ-1	17	1.52	1.62	1.76	19	0.87	1.01	1.10
MRAM	8	1.54	1.60	1.74	8	0.96	1.04	1.09
VAL-7	22	1.49	1.61	1.71	22	0.94	1.03	1.09
Mo1B	87	1.39	1.51	1.70	87	0.88	0.96	1.07

	Length				Width			
	N	min.	mean	max.	N	min.	mean	max.
SEY	31	1.47	1.58	1.66	31	0.96	1.00	1.05
SARR	4	1.38	1.52	1.62	4	0.91	0.95	0.98
Bz-1	25	1.42	1.51	1.65	26	0.89	0.95	1.06
LAY*	25	1.36	1.55	1.82	25	0.99	1.09	1.22
LAY	27	1.46	1.57	1.66	27	0.91	0.99	1.06
Mo1A	90	1.28	1.50	1.61	88	0.86	0.95	1.09
SETE	19	1.36	1.47	1.57	19	0.82	0.94	1.02
ORR3	9	1.48	1.56	1.60	9	0.90	0.98	1.04
ARQ3	4	1.37	1.41	1.46	4	0.80	0.88	0.91
MHEL	20	1.37	1.47	1.58	20	0.82	0.92	0.97
CA	10	1.34	1.42	1.52	10	0.80	0.88	0.94
SAL	1	–	1.52	–	1	–	0.94	–
MAR	15	1.56	1.65	1.82	15	0.96	1.04	11.5
AK	?	–	1.75	–	?	–	1.20	–
ÇALTA	4	1.77	1.79	1.83	4	1.12	1.17	1.20
BRS25	19	1.53	1.62	1.72	20	0.98	1.05	1.12
M_2								
CB-3	8	1.17	1.22	1.26	8	1.04	1.11	1.17
LQ-1	24	1.04	1.16	1.26	27	0.96	1.06	1.16
VAL-7	22	1.05	1.18	1.29	22	0.98	1.06	1.14
Mo1B	92	1.02	1.10	1.22	94	0.91	1.00	1.19
SARR	2	1.10	1.13	1.16	2	0.91	0.95	0.98
Bz-1	14	1.01	1.11	1.18	14	0.93	1.01	1.11
LAY	28	1.03	1.14	1.20	28	0.94	1.01	1.08
Mo1A	73	0.95	1.09	1.22	73	0.84	0.99	1.12
ORR3	4	1.00	1.13	1.22	4	0.86	0.94	1.01
ARQ3	2	1.02	1.06	1.10	2	0.91	0.94	0.96
MHEL	14	0.98	1.08	1.18	14	0.92	1.00	1.04
CA	10	0.94	0.98	1.02	10	0.86	0.91	0.96
DEV	3	–	1.27	–	3	–	1.14	–
MAR	17	1.09	1.20	1.28	16	1.03	1.10	1.18
ÇALTA	5	1.25	1.30	1.36	5	1.15	1.19	1.24
BRS25	28	1.16	1.23	1.32	28	1.03	1.11	1.28
M_3								
LQ-1	16	0.78	0.87	0.97	16	0.77	0.83	0.91
VAL-7	20	0.78	0.84	0.93	20	0.70	0.79	0.87
Mo1B	32	0.75	0.82	0.91	32	0.69	0.77	0.84
LAY	15	0.77	0.83	0.87	15	0.70	0.76	0.82
Mo1A	14	0.71	0.82	0.88	14	0.70	0.79	0.89
ORR3	1	–	0.77	–	1	–	0.76	–
ARQ3	1	–	0.85	–	1	–	0.77	–
MHEL	3	0.76	0.77	0.80	3	0.75	0.76	0.77
CA	1	–	0.78	–	1	–	0.70	–

	Length				Width			
	N	min.	mean	max.	N	min.	mean	max.
DEV	1	–	0.86	–	1	–	0.82	–
MAR	10	0.85	0.90	0.95	10	0.79	0.85	0.91
ÇALTA	2	0.97	1.00	1.03	2	0.92	0.94	0.97
BRS25	6	0.94	0.96	0.99	6	0.82	0.87	0.91
M^1								
BG-2	10	1.83	1.90	2.01	10	1.21	1.33	1.42
CB-3	14	1.75	1.83	1.91	14	1.25	1.31	1.36
LQ-1	16	1.64	1.84	2.12	16	1.19	1.26	1.35
MRAM	9	1.65	1.77	1.88	9	1.17	1.26	1.36
VAL-7	24	1.67	1.79	1.95	24	1.17	1.24	1.33
Mo1B	67	1.51	1.67	1.84	72	1.07	1.19	1.28
SEY	20	1.52	1.64	1.76	20	0.98	1.12	1.20
SARR	2	1.68	1.70	1.71	2	1.10	1.15	1.20
Bz-1	40	1.37	1.61	1.79	40	1.06	1.20	1.33
LAY*	63	1.50	1.66	1.83	63	1.08	1.16	1.30
LAY	29	1.59	1.71	1.86	29	1.13	1.21	1.28
Mo1A	91	1.52	1.65	1.78	91	1.10	1.19	1.30
SETE	24	1.41	1.56	1.68	24	1.05	1.13	1.31
ORR3	3	1.70	1.77	1.85	3	1.17	1.21	1.25
ARQ3	9	1.55	1.67	1.87	9	1.12	1.18	1.31
MHEL	19	1.46	1.57	1.66	19	1.06	1.14	1.24
CA	10	1.35	1.51	1.59	10	1.02	1.07	1.16
SMAR	1	–	1.46	–	1	–	1.03	–
DEV	1	–	1.88	–	1	–	1.32	–
MAR	17	1.65	1.83	1.95	18	1.20	1.27	1.37
ÇALTA	4	1.86	1.95	2.04	4	1.38	1.39	1.39
BRS25	4	1.65	1.76	1.88	4	1.18	1.23	1.29
M^2								
CB-3	6	1.20	1.24	1.28	6	1.20	1.24	1.31
LQ-1	18	1.12	1.18	1.28	19	1.08	1.16	1.25
VAL-7	18	1.11	1.20	1.28	18	1.14	1.21	1.31
Mo1B	62	1.05	1.15	1.24	62	1.04	1.13	1.24
SARR	1	–	1.06	–	1	–	1.16	–
Bz-1	17	1.05	1.16	1.33	17	1.10	1.17	1.36
LAY	18	1.05	1.17	1.28	18	1.07	1.15	1.26
Mo1A	68	1.02	1.14	1.33	68	1.02	1.14	1.45
ORR3	3	1.15	1.17	1.20	3	1.08	1.11	1.13
ARQ3	5	1.10	1.18	1.30	5	1.03	1.11	1.26
MHEL	14	0.99	1.09	1.15	14	0.99	1.09	1.15
CA	10	1.00	1.06	1.10	10	0.96	0.99	1.03
SAL	1	–	1.12	–	1	–	1.11	–
MAR	16	1.15	1.23	1.35	16	1.17	1.23	1.32

	Length				Width			
	N	min.	mean	max.	N	min.	mean	max.
ÇALTA	2	1.24	1.31	1.38	3	1.12	1.23	1.33
BRS25	12	1.16	1.23	1.31	12	1.17	1.22	1.29
M^3								
LQ-1	10	0.74	0.81	0.85	10	0.77	0.84	0.91
VAL-7	19	0.74	0.80	0.89	10	0.75	0.80	0.85
Mo1B	14	0.71	0.79	0.91	14	0.64	0.72	0.82
LAY	10	0.68	0.78	0.90	10	0.71	0.80	0.93
Mo1A	13	0.70	0.81	0.92	13	0.69	0.77	0.89
ORR3	1	–	0.80	–	1	–	0.75	–
MHEL	1	–	0.79	–	1	–	0.73	–
CA	2	0.65	0.67	0.70	2	0.62	0.64	0.67
DEV	1	–	0.98	–	1	–	0.88	–
MAR	17	0.79	0.87	0.96	16	0.75	0.89	1.00
ÇALTA	1	–	1.00	–	1	–	0.99	–
BRS25	4	0.82	0.88	0.95	4	0.91	0.93	0.94

Explanation of locality codes for Table 1 and Fig. 17:
AK = Argoub Kemellal data by Coiffait et al. (1985)
ARQ3= Arquillo 3, Adrover (1986)
BG-2 = Bagur 2, López et al. (1976)
BRS25 = Brisighella 25, collection DST, Lyon
Bz-1 = Belmez 1, Castillo (1990)
CA = Caravaca, van de Weerd (1976)
CB-3 = Casablanca 3, unpublished data Dr J. Agustí
ÇALTA = data by Sen (1977)
DEV = Develi, Sen et al. (1989)
LAY* = Layna, Michaux (1969)
LAY = Layna, collection DST, Lyon
LQ-1 = Loma Quemada 1, Martín Suárez (1988) and new data in this paper
MAR = Maritsa, de Bruijn et al. (1970)
MHEL = Mont-Hélène, Aguilar et al. (1986)
Mo1A = Moreda 1A, Castillo (1990)
Mo1B = Moreda 1B, Castillo (1990)
MRAM = Mas Rambault, Michaux (1969)
ORR3 = Orrios, Adrover (1986)
SAL = Salobreña, Aguilar et al. (1983)
SARR = Sarrión, Adrover (1986)
SETE = data by Michaux (1969)
SEY = data by Michaux (1969)
SMAR = Santa Margarida, Antunes & Mein (1989)
VAL-7 = Valdeganga 7 = Valdeganga III in Mein et al. (1978)

Conclusions

Various lineages of small Muridae without t7 and tma exist in Europe during the Early Pliocene and possibly Late Miocene. Many of these murids had been included in the genus *Castillomys*. Our revision of many populations has shown, that we are dealing with different groups, that probably belong to the same stock.

We have divided this complex into three genera. One of these, *Centralomys*, groups the populations known from Italy and Turkey. It is characterized by large teeth with characters considered to be plesiomorph in the context of the evolution of European Muridae (e.g. the poor development of the longitudinal crests). The population from Maritsa is attributed to the new subgenus *Rhodomys*.

The species belonging to the genera *Castillomys*, *Centralomys* and *Occitanomys* share a number of characters: teeth with a tendency to develop the stephanodont crest (t4-t5-t6-t9-t8); labial and lingual longitudinal crests in the upper molars; the longitudinal connection in the lower molars. Contrary to *Stephanomys* the teeth are very brachyodont. Differences are: The position of t6 in relation with t3 and t9, and the shape of t6 in labial view. In *Castillomys* and *Centralomys* t6 is almost vertical, its top lies halfway between t3 and t9; in *Occitanomys* t6 is inclined, and its top lies closer to t9 than to t3. The connection t3-t5. In *Castillomys* this crest ends at the level of the connection t5-t6; in *Occitanomys* it ends at half height of t5 (if it exists); in *Centralomys* it is directed towards the base of t5. The shape of the anterior palatine foramen. It is long and wide in *Castillomys* and *Centralomys*; long and narrow in *Occitanomys* (unknown in the population from Maritsa). The shape of the labial cingulum in the lower molars. In *Occitanomys* and *Centralomys* there is a continuous crest that connects c1 with the labial anteroconid, and which generally bears various accessory cusps; in *Castillomys* this crest ususally is discontinuous at the base of the protoconid or before the protoconid; the accessory cusps are less developed, and only in the youngest populations the crest is continuous. The shape of M_2. Clearly more reduced posteriorly in the teeth of species belonging to *Occitanomys*.

The genus *Castillomys* remains restricted to southern France, the Iberian Peninsula, and maybe North Africa. It seems difficult to accept an Asiatic origin for this genus, since no record is known from outside of these three areas. The persistence of *Castillomys* during a long period of time in an area with strong climatic oscillations may indicate that we are dealing with a group capable of living in a wide scale of climatic conditions, and that it cannot be used as a palaeoclimatological marker.

The development of longitudinal crests is a parallel evolution in *Castillomys*, *Stephanomys* and, at a lesser scale, in *Occitanomys* and *Centralomys*. These four genera share the circumstance that no extant representatives are known. Why did only the Muridae survive that never developed longitudinal crests?

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Manuscript received 30 May 1991.