Microdyromys (Gliridae, Rodentia, Mammalia) from the Early Oligocene of Montalbán (Prov. Teruel, Spain)

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Key words – Gliridae, Oligocene, Spain, new species.

A new species of *Microdyromys*, *M. puntarronensis*, is described from the Early Oligocene locality Montalbán 8 (Teruel, Spain). It is compared with the other Early Oligocene species of the genus, *M. misonnei*. The latter is known from Hoogbutsel (Belgium) and Montalbán 1D. Montalbán 8 is intermediate in age between Hoogbutsel and Montalbán 1D, and the dental pattern of its *Microdyromys* is more advanced than it is in Montalbán 1D. This leads to the conclusion that two lineages of *Microdyromys* existed in the Early Oligocene. An attempt is made to follow these lineages throughout the Late Oligocene and the Miocene.

Contents

Introduction

Freudenthal *et al*. (1990) described a new Early Oligocene fossiliferous section near Montalbán (Teruel, Spain). Faunal lists of the fossil mammal localities in this section were published by Freudenthal (1997), but the only exhaustive description of material from these very rich sites is in Freudenthal *et al*. (1992). The locality of Montalbán (MLB1D in our codification) has been the subject of several studies including those of Thaler (1969), Vianey-Liaud (1972a, b, 1976) and Freudenthal (1996, 2004). Vianey-Liaud (1994) described a new species of Gliridae, *Branssatoglis misonnei*, from the Early Oligocene of Hoogbutsel (Belgium) and Montalbán. Freudenthal (1997) transferred it to *Microdyromys* and mentioned its presence in all the Montalbán localities. Freudenthal & Martín-Suárez (2007) gave details on why this species is classified as a *Microdyromys*.

In this paper a new species of *Microdyromys* is described from Montalbán 8 and compared with the other Oligocene species of the genus. Montalbán 8 is intermediate in age between Hoogbutsel and Montalbán 1D (see Freudenthal *et al*., 1990), so one might expect the dental pattern of this species to be intermediate between that of the species from the other two localities. However, for several supposedly crucial features the situation is reversed; the material from Montalbán 8 is more advanced than that from Montalbán 1D and deserves a new species name. The material from Montalbán 1D is different from the Hoogbutsel population, but not enough to create yet another species and is kept in *M. misonnei*. These two species are compared with *M. praemurinus* (Freudenberg, 1941) from the Late Oligocene and *M. monspeliensis* Aguilar, 1977, from the Early Miocene, in an attempt to unravel their phylogenetic relationships.

Methods

Measurements were taken with a Wild M8 stereomicroscope, equipped with mechanical stage with electronic sensors, connected to a computer through a Sony Magnescale measuring unit. The photos were made on the ESEM FEI Quanta 400 in environmental mode at the 'Centro Andaluz de Medio Ambiente' in Granada (Spain).

Measurements are given in 0.1 mm units. The nomenclature of parts of the cheek teeth is as defined by Freudenthal & Martín-Suárez (2006).

Abbreviations of institutions in which specimens are deposited include IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium, and RGM, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

The locality codes used in this paper are listed in Table 1. The catalogue that begins with one of the locality codes refer to specimens, that will be deposited in the Departamento de las Ciencias de la Tierra, University of Zaragoza.

Table 1. Abbreviations of locality names.

AGT2D	Aguatón 2D	MLB3X	Montalbán 3X
ARM7	Armantes 7	MLB3Y	Montalbán 3Y
BU	Buñol	MLB8	Montalbán 8
GAIM	Gaimersheim	MLB9	Montalbán 9
GRB3	Gröben 3	MLB10	Montalbán 10
HB	Hoogbutsel	MLB11A	Montalbán 11A
LP4A	Las Planas 4A	MLB11B	Montalbán 11B
LP4B	Las Planas 4B	MLB13	Montalbán 13
LP5H	Las Planas 5H	NFM	Nouvelle Faculté Médecine
MA	Manchones	SS	Sansan
MIR1	Mirambueno 1	TOR	Toril
MIR2A	Mirambueno 2A	VA1A	Valdemoros 1A
MIR4B	Mirambueno 4B	VA3B	Valdemoros 3B
MIR4C	Mirambueno 4C	VICOST	St.-Victor-La-Coste
MIR13	Mirambueno 13	VIV	Vivel del Río
MLB1D	Montalbán 1D	VL2A	Villafeliche 2A
MLB3C	Montalbán 3C	VL4A	Villafeliche 4A
MLB3GG	Montalbán 3GG		

Morphology values (MV; see Freudenthal & Cuenca Bescós, 1984) have been calculated for the features mentioned in Table 2, where the supposedly most advanced character state appears on the right side. When only two states are distinguished they score 0 and 1 respectively; when five states are distinguished they score from 0 to 1, with increments of 0.25. Each specimen scores the value corresponding to its character state and the sum of the scores is divided by the number of specimens to obtain MV.

Systematic palaeontology

Genus *Microdyromys* de Bruijn, 1966

Type species – *Microdyromys koenigswaldi* de Bruijn, 1966.

Remarks – Apart from the type species, Daams & de Bruijn (1995) included the following species in *Microdyromys*: *Microdyromys complicatus* de Bruijn, 1966; *Microdyromys legidensis* Daams, 1981; *Microdyromys monspeliensis* Aguilar, 1977; *Microdyromys orientalis* Wu, 1986; *Microdyromys praemurinus* (Freudenberg, 1941); and *Microdyromys sinuosus* (Alvarez Sierra, 1986). All these species are Miocene, except for *M. praemurinus*, which is Late Oligocene. Freudenthal (1997) reported *Microdyromys* sp. from the Late Eocene of Aguatón 2D (prov. Teruel, Spain), which seems to be the oldest occurrence of the genus. So far, no data on Early Oligocene representatives are known. However, this is not a real absence, but a matter of taxonomic interpretation. Vianey-Liaud (1994) described a new species, *Branssatoglis misonnei*, from the Early Oligocene of Hoogbutsel (Belgium) and Montalbán, which we think is a *Microdyromys*. Uhlig (2001) described *Branssatoglis heissigi* from Gröben 3, which in our opinion is a *Microdyromys*, too.

Our interpretation changes considerably the contents of the genus *Microdyromys*. However, in this paper we refrain from arguing that change, because it is treated exhaustively in a paper on the subfamily *Branssatoglirinae* by Freudenthal & Martín Suárez (2007).

Table 2. Calculation of morphology values.

feature	increment	character states				
anterolophid/protoconid	1.00	free	connected			
anterotropid	0.25	absent	very small	small	medium	long
centrolophid length	0.33	absent	short	medium	long	
posterotropid	0.33	absent	small	medium	long	
endoloph	0.50	protocone	interrupted	complete		
postcentroloph length	0.33	absent	short	medium	long	
postcentroloph/metacone	1.00	connected	free			
prototrope	0.33	absent	short	medium	long	
lingual border	1.00	smooth	crenulated			

***Microdyromys misonnei* (Vianey-Liaud, 1994)**
Pl. 1.

Type locality – Hoogbutsel.

Holotype – M2 dext., IRSNB M1786. HOG 2548, as stated by Vianey-Liaud (1994), is a provisional number and should not be used. Vianey-Liaud gave the correct number in her figure 23k (information from Dr T. Smith, curator of fossil vertebrates, IRSNB).

Material – MLB1D 1160, 1280, 1405-1477, 1479-1495, 1497 - 1499, 1507, to be stored in the Departamento de las Ciencias de la Tierra, University of Zaragoza.

Localities in the Montalbán area – MLB1D, MLB3GG, MLB9, MLB10, MLB11A, MLB11B, MLB13, MIR13 .

Measurements – See Tables 3-6 and Figures 1, 2.

Remarks – Microdyromys misonnei was originally described as *Branssatoglis misonnei*. Apart from the type locality, its author attributed the material from Montalbán Sud to it, a locality that in our codification is MLB1D. In the following the MLB1D population will be described, in order to facilitate comparison with the new species from MLB8, to be described thereafter.

Description of M. misonnei from Montalbán 1D – d4 - Only one incomplete specimen has been found. The anterolophid is discontinuous. The anterotropid is absent. The metalophid is high connected to the metaconid. The centrolophid is absent. The mesoconid is placed on the labial border. The mesolophid is connected to the metalophid. The posterotropid is absent.

p4 - The shape is blunt. The anterolophid is continuous. The anterotropid is absent (3) or very small (1). The metalophid is high connected to the metaconid. The centrolophid is absent (1), short (1), of medium length (1) or long (2). The centrolophid-metaconid connection is absent (2) or low (2). The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is absent (2), very small (1), small (1) or long (1). The mesolophid is not connected to the mesoconid in two specimens (MLB1D 1407, 1408) and in one of these it forms a V with the posterotropid.

m1 - The anterolophid is labially free (12) or labially connected (2). The anterotropid is absent (1), small (2), of medium length (6) or long (6). The metalophid is free (5), low connected to the metaconid (2) or high connected (7). The centrolophid is of medium length (1) or long (14). The centrolophid-metaconid connection is absent (4), low (6) or high (5). The mesoconid is placed on the labial border (14) or connected to the hypoconid (1). The mesolophid is connected to the entoconid. The posterotropid is absent (2), very small (1), of medium length (2) or long (10). In one specimen (MLB1D 1416) the mesolophid is interrupted, and there is a longitudinal connection between metalophid and posterotropid.

m2 - The anterolophid is labially free (8) or connected (2). The anterotropid is very small (1), small (2), of medium length (5) or long (1). The metalophid is free (2), low connected to the metaconid (2) or high connected (6). The centrolophid is of medium length (2) or long (8). The centrolophid-metaconid connection is low (2) or high (8). The mesostylid is absent. The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is short (1) or long (9).

m3 - The anterolophid is labially free (5) or labially connected (4). The anterotropid is absent (4), small (2), of medium length (2) or long (1). The metalophid is free (2), low connected to the metaconid (3) or high connected (3). The centrolophid is short (2), of medium length (7) or long (1). The centrolophid-metaconid connection is absent (4), low (4) or high (1). The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is short (1), of medium length (5) or long (4).

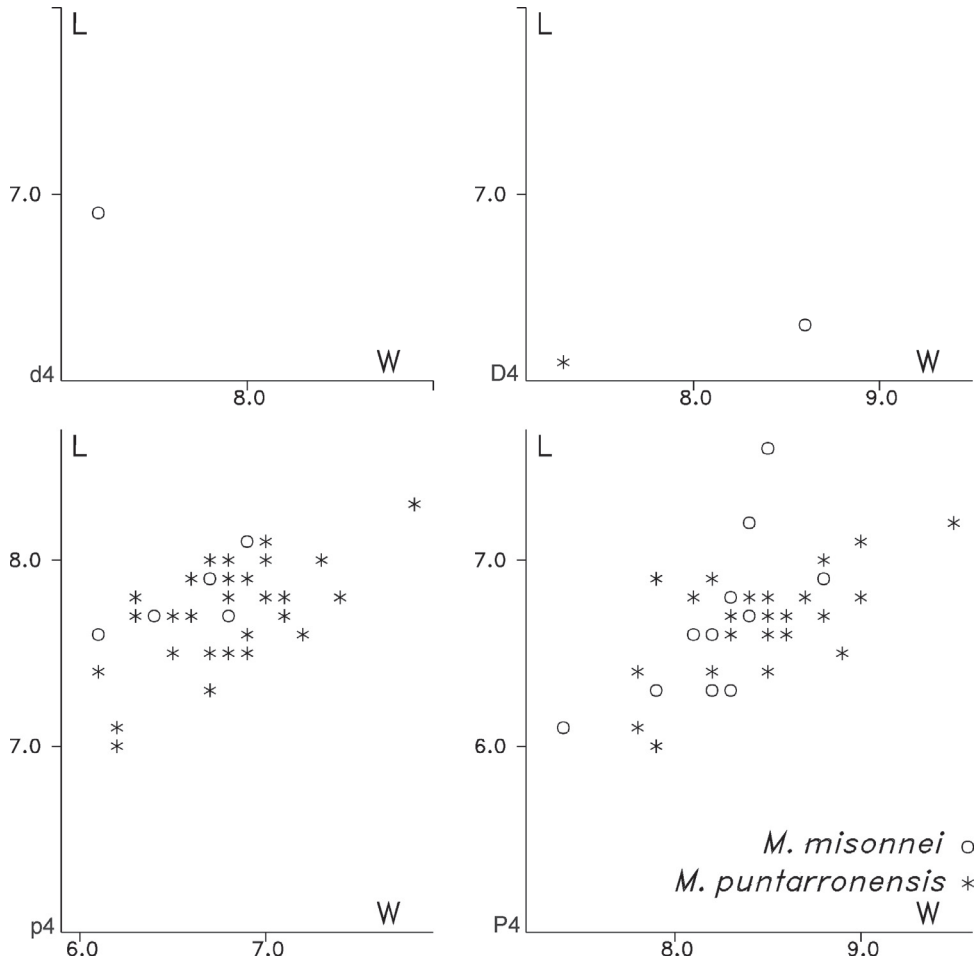

Fig. 1. Length/width diagrams of D4 and P4 of *M. misonnei* from MLB1D and *M. puntarronensis* from MLB8.

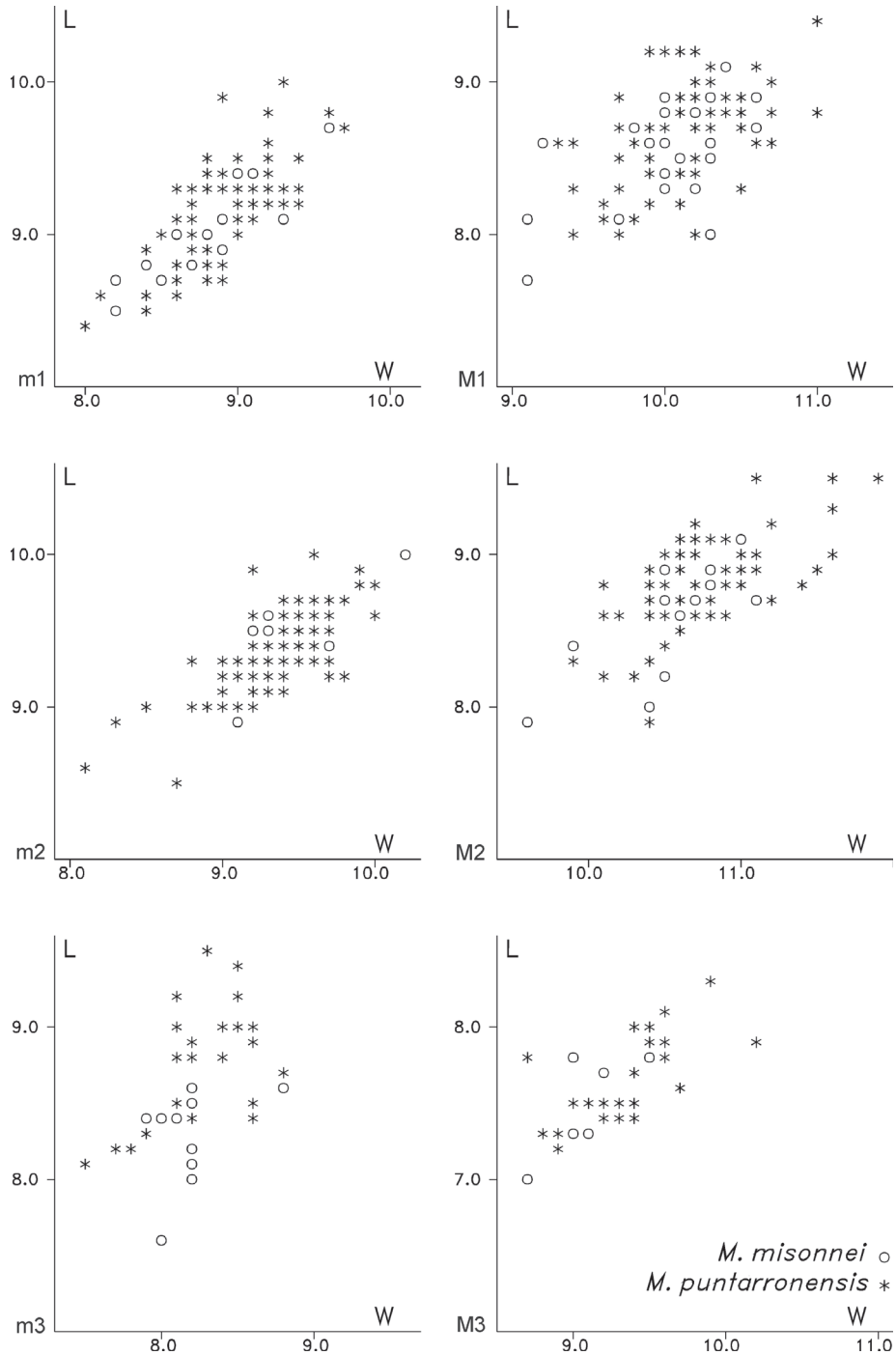

Fig. 2. Length/width diagrams of M1, M2, and M3 of *M. misonnei* from MLB1D and *M. puntarronensis* from MLB8.

D4 - The anteroloph is of medium length. The anterotrope is absent. The precentroloph is long, the postcentroloph is absent. Prototrope, metatrope and posterotrope are absent. The endoloph is formed by the protocone alone. The lingual border is smooth. In one specimen (MLB1D 1444) the metaloph is not connected to the protocone.

Table 3. Measurements of d4, p4 and m3 of *Microdyromys.*

	N	Min.	Mean	Max.	V′	σ	N	Min.	Mean	Max.	V′	σ
d4	Length						Width					
VICOST	2	7.1	7.40	7.8	9.4		2	6.1	6.30	6.6	7.9	
VIV	7	6.5	6.96	7.3	11.6	0.30	7	5.5	5.93	6.4	15.1	0.35
MIR1	4	7.1	7.63	8.3	15.6	0.50	4	6.1	6.50	6.8	10.9	0.36
GRB3	5	5.0	5.40	6.0	18.5	0.38	5	4.7	5.20	5.9	23.0	0.43
MLB1D	1		6.90				1		7.20			
MLB3C	2	6.6	7.15	7.7	15.4		2	5.9	6.00	6.1	3.3	
MLB3X	1		6.90				1		5.60			
p4	Length						Width					
NFM	5	5.1	5.50	6.0	16.3		5	5.4	5.70	5.9	8.8	
VICOST	5	7.3	7.80	8.1	10.4		5	6.3	7.00	7.8	21.3	
GAIM	2	4.9	5.10	5.3	7.84		2	4.5	4.80	5.1	12.5	
VIV	14	6.9	7.36	8.1	16.0	0.36	14	5.9	6.38	7.3	21.2	0.40
MIR2A	5	7.1	7.34	7.6	6.8	0.21	5	6.2	6.48	6.9	10.7	0.28
MIR1	3	7.8	7.93	8.2	5.0		3	6.6	6.97	7.2	8.7	
MIR4C	1		7.50				1		6.70			
MIR4B	1		7.20				1		6.00			
GRB3	6	6.2	6.50	6.7	7.69	0.22	5	5.4	5.70	6.0	10.5	0.26
MLB1D	5	7.6	7.80	8.1	6.4	0.20	5	6.1	6.58	6.9	12.3	0.33
MLB10	5	7.3	7.52	7.8	6.6	0.23	5	6.4	6.62	7.1	10.4	0.29
MLB3C	13	6.8	7.48	8.3	19.9	0.43	12	6.1	6.65	7.7	23.2	0.40
MLB8	28	7.0	7.71	8.3	17.0	0.29	28	6.1	6.79	7.8	24.5	0.39
MLB3Y	5	7.6	7.84	8.5	11.2	0.38	5	6.4	6.70	7.0	9.0	0.22
MLB3X	8	7.1	7.63	8.3	15.6	0.42	8	6.3	6.76	7.4	16.1	0.37
HB	3	7.2	7.50	8.0	10.5		3	6.6	6.93	7.2	8.7	
m3	Length						Width					
NFM	4	7.0	7.20	7.7	9.72		4	7.1	7.20	7.5	5.5	
VICOST	2	7.6	7.70	7.7	1.3		2	7.7	7.90	8.1	5.1	
VIV	17	7.5	8.07	8.7	14.8	0.37	16	6.8	7.79	8.6	23.4	0.49
MIR2A	2	8.0	8.25	8.5	6.1		2	7.3	7.70	8.1	10.4	
MIR1	12	7.4	8.18	9.0	19.5	0.44	12	7.4	8.03	8.5	13.8	0.36
MIR4C	1		8.90				1		8.00			
MIR4B	2	8.5	8.65	8.8	3.5		2	8.4	8.50	8.6	2.4	
GRB3	10	7.0	7.40	8.1	14.8	0.38	10	6.8	7.30	7.8	13.7	0.32
MLB11B	4	8.3	8.60	8.8	5.8	0.24	4	7.4	7.93	8.2	10.3	0.36
MLB1D	10	7.6	8.28	8.6	12.3	0.31	10	8.0	8.19	8.8	9.5	0.23
MLB10	1		7.80				1		7.10			
MLB3C	17	8.1	8.61	9.1	11.6	0.31	17	7.6	8.23	8.8	14.6	0.34
MLB8	22	8.1	8.76	9.5	15.9	0.40	23	7.5	8.23	8.8	16.0	0.34
MLB3Y	5	7.8	8.44	9.1	15.4	0.51	5	7.5	8.00	8.8	16.0	0.51
MLB3X	6	7.5	8.23	8.9	17.1	0.48	6	7.7	8.05	8.4	8.7	0.32
HB	3	8.6	9.37	9.8	13.0		3	8.4	9.10	9.6	13.3	

Table 4. Measurements of m1, m2 and m1,2 of *Microdyromys*.

	N	Min.	Mean	Max.	V′	σ	N	Min.	Mean	Max.	V′	σ
m1	Length						Width					
NFM	3	7.4	7.60	7.8	5.26		3	7.3	7.30	7.5	2.7	
GAIM	19	7.1	8.20	8.9	21.9		19	6.6	7.70	8.5	24.6	
VIV	18	8.4	9.14	9.8	15.4	0.39	18	8.2	8.87	9.7	16.8	0.39
MIR2A	7	8.6	9.31	9.8	13.0	0.38	7	8.0	8.96	9.5	17.1	0.47
MIR1	12	8.9	9.43	9.9	10.6	0.31	12	8.1	9.09	9.4	14.9	0.36
MIR4C	4	8.0	8.68	9.5	17.1	0.62	4	7.9	8.45	9.0	13.0	0.47
MIR4B	2	9.0	9.05	9.1	1.1		2	8.6	8.60	8.6	0.0	
GRB3	8	7.5	7.90	8.5	12.6	0.32	7	7.1	7.60	8.0	11.8	0.27
MLB11B	12	8.3	8.83	9.5	13.5	0.33	12	7.8	8.37	9.2	16.5	0.52
MLB1D	15	8.5	9.00	9.7	13.2	0.33	13	8.2	8.78	9.6	15.7	0.41
MLB10	7	7.7	8.61	9.2	17.8	0.53	7	7.9	8.41	9.6	19.4	0.57
MLB3C	29	7.9	9.07	10.3	26.4	0.49	29	7.5	8.76	9.6	24.6	0.49
MLB8	52	8.4	9.17	10.0	17.4	0.36	49	8.0	8.91	9.7	19.2	0.35
MLB3Y	3	8.4	9.13	9.9	16.4		3	8.6	8.90	9.1	5.6	
MLB3X	17	8.6	9.09	10.0	15.1	0.33	17	8.0	8.96	9.9	21.2	0.48
HB	7	8.7	9.03	9.5	8.8	0.26	7	8.6	8.94	9.4	8.9	0.30
AGT2D	1		7.90				1		7.60			
m2	Length						Width					
NFM	6	7.5	7.80	8.0	6.41		6	8.0	8.40	8.8	9.5	
GAIM	16	7.6	8.30	9.0	16.8		16	7.0	8.10	8.9	23.4	
VIV	28	8.4	9.31	10.1	18.4	0.40	27	8.5	9.27	10.0	16.2	0.39
MIR2A	6	8.8	9.35	10.0	12.8	0.45	4	8.8	9.40	10.1	13.8	0.55
MIR1	17	8.2	9.42	10.1	20.8	0.49	15	8.9	9.59	10.3	14.6	0.41
MIR4C	7	8.8	9.09	9.6	8.7	0.28	6	8.5	9.12	9.6	12.2	0.38
MIR4B	6	8.8	9.10	9.5	7.7	0.28	6	8.8	9.22	9.8	10.8	0.44
GRB3	5	7.0	7.40	8.1	14.8	0.38	6	6.8	7.30	7.8	13.7	0.32
MLB11B	4	9.1	9.23	9.5	4.3	0.19	5	8.9	9.48	10.1	12.6	0.48
MLB1D	8	8.9	9.41	10.0	11.6	0.33	6	9.1	9.47	10.2	11.4	0.41
MLB10	8	8.7	9.13	9.9	12.9	0.40	8	8.9	9.38	9.7	8.6	0.29
MLB3C	30	8.4	9.37	10.4	21.3	0.42	29	8.2	9.20	9.9	18.8	0.44
MLB8	55	8.5	9.34	10.0	16.2	0.30	54	8.1	9.32	10.0	21.0	0.39
MLB3Y	7	9.4	9.50	9.6	2.1	0.08	7	9.0	9.50	10.0	10.5	0.33
MLB3X	22	8.6	9.63	10.4	18.9	0.37	22	9.0	9.74	10.2	12.5	0.36
HB	4	8.9	9.28	9.5	6.5	0.29	5	8.3	9.28	9.9	17.6	0.64
m1,2	Length						Width					
NFM	9	7.4	7.73	8.0	7.8		9	7.3	8.03	8.8	18.6	
VICOST	26	8.6	9.20	10.1	16.0		26	8.3	9.30	10.1	19.6	
GAIM	35	7.1	8.25	9.0	23.0		35	6.6	7.88	8.9	29.7	
VIV	46	8.4	9.24	10.1	18.4	0.40	45	8.2	9.11	10.0	19.8	0.43
MIR2A	13	8.6	9.33	10.0	15.1	0.40	11	8.0	9.12	10.1	23.2	0.52
MIR1	29	8.2	9.42	10.1	20.8	0.42	27	8.1	9.37	10.3	23.9	0.46
MIR4C	11	8.0	8.94	9.6	18.2	0.45	10	7.9	8.85	9.6	19.4	0.52
MIR4B	8	8.8	9.09	9.5	7.7	0.24	8	8.6	9.06	9.8	13.0	0.47
GRB3	13	7.0	7.71	8.5	19.4		13	6.8	7.46	8.0	16.2	
MLB11B	16	8.3	8.93	9.5	13.5	0.34	17	7.8	8.70	10.1	25.7	0.72
MLB1D	23	8.5	9.14	10.0	16.2	0.38	19	8.2	9.00	10.2	21.7	0.52
MLB10	15	7.7	8.89	9.9	25.0	0.52	15	7.9	8.93	9.7	20.5	0.65
MLB3C	59	7.9	9.22	10.4	27.3	0.48	58	7.5	8.98	9.9	27.6	0.51
MLB8	107	8.4	9.26	10.0	17.4	0.34	103	8.0	9.13	10.0	22.2	0.42
MLB3Y	10	8.4	9.39	9.9	16.4	0.40	10	8.6	9.32	10.0	15.1	0.42
MLB3X	39	8.6	9.40	10.4	18.9	0.44	39	8.0	9.40	10.2	24.2	0.57
HB	11	8.7	9.12	9.5	8.8	0.29	12	8.3	9.08	9.9	17.6	0.48
AGT2D	1		7.90				1		7.60			

Table 5. Measurements of D4, P4 and M3 of *Microdyromys*.

	N	Min.	Mean	Max.	V′	σ	N	Min.	Mean	Max.	V′	σ
D4	Length						Width					
VICOST	3	5.7	6.20	6.6	14.6		3	6.6	7.00	7.3	10.1	
VIV	3	6.1	6.43	7.1	15.2		3	7.2	7.23	7.3	1.4	
MIR4C	1		9.20				1		9.70			
GRB3	2	5.5	5.60	5.7	3.57		2	6.0	6.10	6.2	3.28	
MLB1D	1		6.30				1		8.60			
MLB8	1		6.10				1		7.30			
HB	1		8.30				1		8.80			
P4	Length						Width					
NFM	2	5.1	5.20	5.3	3.85		2	6.5	6.50	6.5		
VICOST	12	5.9	6.60	7.2	19.8		12	7.1	7.90	8.4	16.8	
VIV	14	5.9	6.30	6.8	14.2	0.24	13	7.1	7.58	8.0	11.9	0.37
MIR2A	1		6.50				1		7.80			
MIR1	13	5.8	6.32	6.8	15.9	0.33	13	7.3	7.90	8.4	14.0	0.35
MIR4C	3	6.1	6.20	6.3	3.2		3	7.1	7.40	7.6	6.8	
GRB3	8	5.2	5.60	6.0	14.2	0.30	7	6.6	6.90	7.2	8.70	0.24
MLB1D	12	6.1	6.69	7.6	21.9	0.43	11	7.4	8.23	8.8	17.3	0.36
MLB10	1		6.60				1		7.90			
MLB3C	21	6.1	6.45	7.0	13.7	0.24	21	7.2	8.09	9.1	23.3	0.45
MLB8	23	6.0	6.67	7.2	18.2	0.29	24	7.8	8.46	9.5	19.7	0.42
MLB3Y	4	6.4	6.60	6.8	6.1	0.16	4	8.4	8.58	8.7	3.5	0.15
MLB3X	6	6.1	6.42	6.8	10.9	0.26	6	7.5	8.13	8.7	14.8	0.42
HB	3	6.2	6.60	7.0	12.1		4	7.9	8.40	8.9	11.9	0.44
M3	Length						Width					
NFM	1		6.10				1		7.30			
VICOST	4	7.6	7.90	8.1	6.4		4	9.1	9.40	10.0	9.4	
GAIM	2	6.4		7.4	14.5		2	7.5		8.9	17.1	
VIV	24	6.3	7.03	8.3	27.4	0.46	23	7.9	8.66	9.6	19.4	0.51
MIR2A	5	7.0	7.34	7.9	12.1	0.34	5	8.9	9.12	9.4	5.5	0.26
MIR1	9	6.9	7.39	8.0	14.8	0.37	11	8.4	9.15	9.8	15.4	0.43
GRB3	8	5.5	6.10	6.7	19.6	0.45	9	6.7	7.50	8.2	20.0	0.43
MLB11B	1		8.20				1		10.00			
MLB1D	6	7.0	7.48	7.8	10.8	0.33	6	8.7	9.07	9.5	8.8	0.27
MLB10	4	7.0	7.55	8.3	17.0	0.58	4	8.8	9.40	10.2	14.7	0.58
MLB3C	25	7.1	7.58	8.3	15.6	0.32	25	8.2	9.02	9.9	18.8	0.48
MLB8	22	7.2	7.66	8.3	14.2	0.30	23	8.7	9.33	10.2	15.9	0.35
MLB3Y	7	7.1	7.69	8.2	14.4	0.40	7	8.3	9.06	10.0	18.6	0.57
MLB3X	12	6.9	7.55	8.4	19.6	0.50	12	8.7	9.34	10.1	14.9	0.42
HB	4	7.2	7.48	7.9	9.3	0.31	4	9.2	9.70	10.0	8.3	0.38

Table 6. Measurements of M1, M2 and M1,2 of *Microdyromys*.

	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
M1	Length						Width					
NFM	6	6.7	7.20	7.6	12.5		6	8.6	8.80	9.3	7.8	
VIV	31	7.9	8.77	9.5	18.4	0.40	28	9.0	9.74	10.5	15.4	0.37
MIR2A	8	8.4	8.89	9.6	13.3	0.42	8	9.5	9.86	10.3	8.1	0.30
MIR1	7	8.6	9.10	9.7	12.0	0.45	6	9.6	10.23	10.8	11.8	0.42
MIR4C	6	8.0	8.80	9.3	15.0	0.45	6	8.7	9.75	10.4	17.8	0.61
MIR4B	5	8.1	8.46	8.9	9.4	0.36	5	9.3	9.64	9.9	6.2	0.26
GRB3	8	7.2	7.60	8.1	11.8	0.29	7	8.2	8.60	9.3	12.7	0.33
MLB11B	15	8.1	8.75	9.6	16.9	0.41	15	8.8	9.92	10.9	21.3	0.56
MLB1D	21	7.7	8.53	9.1	16.7	0.35	22	9.1	10.03	10.6	15.2	0.44
MLB10	7	8.2	8.83	9.9	18.8	0.63	7	9.2	9.70	10.1	9.3	0.31
MLB3C	34	8.1	8.67	9.3	13.8	0.26	36	9.3	9.99	11.2	18.5	0.35
MLB8	52	8.0	8.66	9.4	16.1	0.35	50	9.2	10.09	11.0	17.8	0.40
MLB3Y	8	7.9	8.61	9.3	16.3	0.49	8	9.0	9.90	10.7	17.3	0.56
MLB3X	15	7.7	8.56	9.4	19.9	0.42	15	9.5	10.15	11.0	14.6	0.43
HB	7	8.3	8.74	9.5	13.5	0.45	7	9.7	10.09	10.5	7.9	0.30
M2	Length						Width					
NFM	6	7.0	7.30	7.6	8.22		6	8.7	9.20	9.8	11.9	
VIV	35	7.9	8.82	9.7	20.5	0.40	35	9.8	10.38	11.2	13.3	0.38
MIR2A	7	8.5	9.00	9.5	11.1	0.36	6	10.0	10.47	10.8	7.7	0.29
MIR1	15	8.0	8.85	9.8	20.2	0.48	14	9.4	10.59	11.2	17.5	0.55
MIR4C	2	8.5	8.80	9.1	6.8		2	10.3	10.55	10.8	4.7	
MIR4B	1		8.30				1		10.10			
GRB3	5	7.3	7.60	8.0	9.21	0.28	5	8.5	8.80	9.4	10.2	0.35
MLB11B	12	7.8	8.67	9.8	22.7	0.52	11	9.8	10.45	11.4	15.1	0.52
MLB1D	12	7.9	8.58	9.1	14.1	0.37	12	9.6	10.53	11.1	14.5	0.43
MLB10	9	8.1	8.93	9.7	18.0	0.48	9	10.0	10.70	11.4	13.1	0.46
MLB3C	35	7.5	8.59	10.0	28.6	0.52	35	9.1	10.43	11.6	24.2	0.58
MLB8	49	7.9	8.81	9.5	18.4	0.33	47	9.9	10.76	11.9	18.3	0.44
MLB3Y	2	9.3	9.50	9.7	4.2		2	11.3	11.50	11.7	3.5	
MLB3X	21	8.3	8.89	9.8	16.6	0.31	21	9.7	10.67	11.5	17.0	0.44
HB	4	8.3	8.70	9.0	8.1	0.32	4	9.6	10.35	10.7	10.8	0.51
AGT2D	1		8.00				1		9.70			
M1,2	Length						Width					
NFM	12	6.7	7.25	7.6	12.6		12	8.6	9.00	9.8	13.0	
VICOST	21	7.9	8.80	9.3	16.3		21	9.6	10.50	11.1	14.5	
GAIM	20	7.4	7.90	8.8	17.7		20	7.5	8.90	9.9	27.6	
VIV	66	7.9	8.80	9.7	20.5	0.40	63	9.0	10.10	11.2	21.8	0.49
MIR2A	15	8.4	8.94	9.6	13.3	0.38	14	9.5	10.12	10.8	12.8	0.42
MIR1	22	8.0	8.93	9.8	20.2	0.48	20	9.4	10.48	11.2	17.5	0.53
MIR4C	8	8.0	8.80	9.3	15.0	0.41	8	8.7	9.95	10.8	21.5	0.65
MIR4B	6	8.1	8.43	8.9	9.4	0.33	6	9.3	9.72	10.1	8.2	0.30
GRB3	13	7.2	7.60	8.1	11.8		12	8.2	8.68	9.4	13.6	
MLB11B	27	7.8	8.71	9.8	22.7	0.46	26	8.8	10.15	11.4	25.7	0.60
MLB1D	33	7.7	8.55	9.1	16.7	0.35	34	9.1	10.21	11.1	19.8	0.49
MLB10	16	8.1	8.89	9.9	20.0	0.54	16	9.2	10.26	11.4	21.4	0.64
MLB3C	69	7.5	8.63	10.0	28.6	0.41	71	9.1	10.21	11.6	24.2	0.53
MLB8	101	7.9	8.73	9.5	18.4	0.35	97	9.2	10.41	11.9	25.6	0.54
MLB3Y	10	7.9	8.79	9.7	20.5	0.58	10	9.0	10.22	11.7	26.1	0.84
MLB3X	36	7.7	8.75	9.8	24.0	0.39	36	9.5	10.45	11.5	19.0	0.50
HB	11	8.3	8.73	9.5	13.5	0.39	11	9.6	10.18	10.7	10.8	0.38
AGT2D	1		8.00				1		9.70			

P4 - The anteroloph is short (1), of medium length (5) or long (4). The anterotrope is absent. The precentroloph is long. The postcentroloph is absent (8), short (2), of medium length (1) or long (1). The prototrope is absent (11) or long (1). The metatrope is absent. The centrolophs are not connected (11) or connected (1). The posterotrope is absent. The endoloph is formed by the protocone alone (2), anteriorly interrupted (3), posteriorly interrupted (1) or complete (2). The lingual border is smooth.

M1 - The anteroloph is lingually free (9), lingually low connected (7) or lingually high connected (2). The anterotrope is absent (20) or short (1). The precentroloph is long, connected to the paracone. The postcentroloph is of medium length (2) or long (20), connected to the metacone (21) or free from the metacone (1), always shorter than the precentroloph. The prototrope is absent (10), short (7), of medium length (3) or long (2). The metatrope is absent. The centrolophs are not connected (19) or connected midway (3). The posterotrope is absent. The endoloph is formed by the protocone alone (7), anteriorly interrupted (9) or complete (1). The lingual border is smooth (7) or crenulated (13).

M2 - The anteroloph is lingually free (4), lingually low connected (4) or lingually high connected (3). The anterotrope is absent. The precentroloph is long, connected to the paracone (12), free from the paracone (1) or connected to a mesostyl (1). The postcentroloph is long, connected to the metacone (8) or free from the metacone (5). The prototrope is absent (1), short (1), of medium length (5) or long (7). The metatrope is absent. The centrolophs are not connected (13) or connected lingually (1). The posterotrope is absent. The endoloph is anteriorly interrupted (7) or complete (4). The lingual border is smooth (3) or crenulated (9).

M3 - The anteroloph is lingually low connected (1) or lingually high connected (1). The anterotrope is absent. The centrolophs are not connected (2) or connected (4). Number of crests inside the trigone either two crests (1), three crests (4) or four crests (1). The mesostyl is absent (5) or present (1). The posterotrope is absent (4) or short (2). The endoloph is complete. The lingual border is smooth (2) or crenulated (1).

***Microdyromys puntarronensis* sp. nov.**

Pl. 2; Pl. 3, figs. 1-10.

Derivatio nominis – From the Barranco del Puntarrón, where the type locality is located.

Type locality – MLB8.

Holotype – M2 sin., MLB8 838.

Material - MLB8 601 - 806, 808-908, 929, 931, 1008, 1078, to be stored in the 'Departamento de Ciencias de la Tierra', University of Zaragoza.

Other localities – MLB3X, MLB3Y, MLB3C.

Measurements – See Tables 3-6 and Figures 1, 2.

Diagnosis – Complete endoloph very rare in M1, infrequent in M2, postcentroloph frequently detached from the metacone, prototrope well-developed. In m1,2 the anterotropid is well developed, the posterotropid is always long.

Differential diagnosis – *Microdyromys puntarronensis* differs from *M. praemurinus* and the Miocene species of *Microdyromys* by the low frequency of a complete endoloph. It differs from *M. misonnei* by the well-developed prototrope, the frequently detached postcentroloph, the less-developed endoloph and the well-developed anterotropid.

Description – p4 - The shape is blunt. The anterolophid is interrupted (4) or continuous (20). The anterotropid is absent (16), very small (9), small (1) or of medium length (1). The metalophid is free (7), low connected to the metaconid (1) or high connected (19). The centrolophid is absent (2), short (3), of medium length (3) or long (19). The centrolophid-metaconid connection is absent (10), low (3), high (12) or the centrolophid ends in a mesostylid (2). The mesoconid is placed on the labial border. The mesolophid is directed towards the metaconid (1), towards the entoconid (2) or connected to it (25). The posterotropid is absent (4), very small (2), small (3), of medium length (8) or long (11). The mesolophid may be connected to the posterotropid and the regular pattern of the crests may be interrupted.

m1 - The anterolophid is labially free (32) or labially connected (16). The anterotropid is very small (1), small (1), of medium length (10) or long (39). The metalophid is free (11), low connected to the metaconid (9) or high connected (30). The centrolophid is long. The centrolophid-metaconid connection is absent (10), low (7) or high (34). The mesoconid is placed on the labial border. The mesolophid is directed towards the entoconid (2) or connected to it (50). The posterotropid is long. In six specimens there is a small lingual crest between centrolophid and mesolophid, and in one case there is a small extra ridge between metalophid and centrolophid.

m2 - The anterolophid is labially free (45) or connected (10). The anterotropid is small (1), of medium length (2) or long (53). The metalophid is free (19), low connected to the metaconid (12) or high connected (24). The centrolophid is of medium length (1) or long (55). The centrolophid-metaconid connection is absent (4), low (10) or high (40). The mesoconid is placed on the labial border. The mesolophid is connected to the entoconid. The posterotropid is of medium length (1) or long (55). In four cases the metalophid forms a lingual U-shaped connection with the anterotropid.

m3 - The anterolophid is labially free (16) or connected (7). The anterotropid is very small (2), small (3), of medium length (11) or long (7). The metalophid is free (10), low connected to the metaconid (7) or high connected (6). The centrolophid is of medium length (11) or long (12). The centrolophid-metaconid connection is absent (3), low (3) or high (17). The mesoconid is placed on the labial border. The mesolophid is directed towards the entoconid (1) or connected to it (22). The posterotropid is very small (1), small (3), of medium length (6) or long (13). In three cases the mesoconid is separated from the mesolophid.

D4 - The anteroloph is of medium length. The precentroloph is of medium length, the postcentroloph is absent. Anterotrope, prototrope, metatrope and posterotrope are absent. The endoloph is anteriorly interrupted. The lingual border is smooth.

P4 - The anteroloph is short (4), of medium length (1) or long (19). The anterotrope is absent. The precentroloph is long, the postcentroloph is absent (6), short (8), of medium length (7) or long (3); when present the postcentroloph is very thin and low. The prototrope is absent (23) or short (1). The metatrope is absent. The centrolophs are not connected. The posterotrope is absent. The endoloph is posteriorly interrupted (11) or complete (10). The lingual border is smooth.

M1 - The anteroloph is lingually free (31), low connected (10) or high connected (5). A short anterotrope is present in one case only. The precentroloph is long, connected to the paracone (48) or connected to a mesostyl (2). The postcentroloph is of medium length (1) or long (51), constantly shorter than the precentroloph. It is connected to the metacone (22) or free from the metacone (26). The prototrope is short (1), of medium length (44) or long (6). The metatrope is absent (51) or of medium length (1). The centrolophs are not connected (41), connected lingually (4), connected midway (5) or there are two connections (1). The posterotrope is absent. The endoloph is formed by the protocone alone (31), anteriorly interrupted (13), posteriorly interrupted (1) or complete (1). The lingual border is smooth (18) or crenulated (26).

M2 - The anteroloph is lingually free (16), low connected (18) or high connected (10). The anterotrope is absent (38), short (9) or of medium length (3). The precentroloph is long, connected to the paracone (47), free from the paracone (1) or connected to a mesostyl (2). The postcentroloph is of medium length (2) or long (48), constantly shorter than the precentroloph. It is connected to the metacone (11), free from the metacone (10), placed centrally (14) or connected to a mesostyl (14). The prototrope is short (1), of medium length (26) or long (21). The metatrope is absent (47), short (1) or of medium length (2). The centrolophs are not connected (40), connected lingually (8), connected midway (1) or there are two connections (1). A short posterotrope is present in one case only. The endoloph is formed by the protocone alone (15), anteriorly interrupted (20), posteriorly interrupted (1) or complete (7). The lingual border is smooth (26) or crenulated (20). In MLB8 876 (Pl. 3, fig. 10), both centrolophs are connected to the paracone and there is an extra crest between them. In MLB8 879 the precentroloph is interrupted, and forms a mesostyl and an isolated central crest; the prototrope has taken the place of the precentroloph and is connected to the paracone.

M3 - The anteroloph is lingually free (4), low connected (3) or high connected (15). The anterotrope is absent (16), short (2), of medium length (4) or long (2). The centrolophs are not connected (16) or connected (8). Number of crests inside the trigone either two (1), three (21) or four crests (1). The mesostyl is absent (12), present (9) or multiple (2). The posterotrope is absent (18), short (1), of medium length (1) or long (2). The endoloph is formed by the protocone alone (2), anteriorly interrupted (3), posteriorly interrupted (2) or complete (14). The lingual border is smooth (16) or crenulated (7).

Microdyromys sp. from AGT2D

Pl. 3, figs. 11, 12.

Remarks – The Late Eocene locality Aguatón 2D in the Sierra Palomera (Teruel) has yielded a few specimens of *Microdyromys* that represent the oldest record of the genus so far. In the m1 (7.90 x 7.60), the anterolophid is not connected to the protoconid/metalophid; it is somewhat shorter than the metalophid and the furrow between them opens at the corner of the tooth. The anterotropid is short. The centrolophid is long, low connected to the ridge that descends longitudinally from the metaconid. The mesolophid is firmly connected to the entoconid. The posterotropid is of medium length. Anterotropid, centrolophid and posterotropid are very low.

In the M^2 (8.00 × 9.70), the anteroloph is lingually low connected to the protocone. There are two not interconnected centrolophs, connected to paracone and metacone, respectively; the precentroloph is very long and the postcentroloph is of medium length. Except for an almost non-existent prototrope, there are no tropes, neither inside nor outside the trigone. The endoloph is posteriorly complete, anteriorly interrupted. The lingual wall is not crenulated.

These specimens are much smaller than *Oligodyromys attenuatus* from the same localities. They are also smaller than *M. misonnei* and *M. puntarronensis*, and of the same size as or slightly larger than *M. heissigi* and *M. monspeliensis*.

The interruption between anterolophid and protoconid is situated in a forward position, like in Miocene *Microdyromys*. That may occur in the Lower Oligocene species, too, but there the separation is more frequently transverse, opening on the labial border.

Homology of the crests of M3

The elements of the lower dentition of the Gliridae are so similar that the same set of features may be studied in each of them. In the upper dentition the third molar presents a problem. M3 basically shows the same pattern as M1,2; however, when trying to homologize crest for crest the pattern of M3 with that of M1 and M2, doubts arise. Since part of our analysis focuses on trends from front to back within the dentition, a reliable interpretation of the pattern of M3 would be important.

Three specimens from HB and one from VIV may help to uncover the homologies (see Fig. 3). The specimen M1791 from HB is more or less easy to interpret: there is a long precentroloph, a long prototrope connected to the precentroloph and a long postcentroloph, which is shorter than the precentroloph, as is usual in M1,2.

In M1788 the same three crests are present and their connections have been lost. The central one is the precentroloph, which has moved far backwards.

M1789 seems to have a long precentroloph (crest 1) and an even longer postcentroloph (crest 2), a situation that does not occur in M1,2. Behind the postcentroloph there is a metatrope (crest 3), a crest that is never present in M1,2. In view of the differences with M1,2, and in analogy with M1791 and M1788, it is most probable that crest 1 is the prototrope that has come into contact with the paracone, crest 2 is the precentroloph that has moved backwards and come into contact with the metacone, and crest 3 is an isolated postcentroloph.

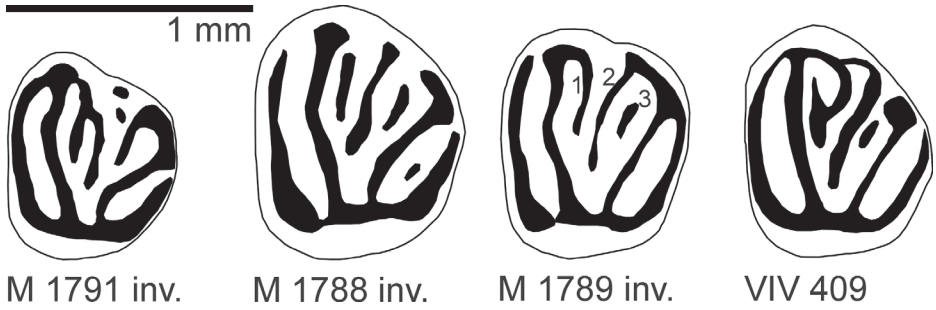

Fig. 3. Interpretation of the crests of M3. 1 = prototrope; 2 = precentroloph; 3 = postcentroloph.

The specimen VIV 409 confirms this interpretation; its basic configuration is very similar to the specimen M1791. Inside the trigone there are three crests, which can be interpreted as prototrope, precentroloph and postcentroloph without much doubt. In this case, however, the prototrope is firmly connected to the paracone, and the precentroloph is placed far backwards, and connected at a low level to the crest between prototrope and paracone. Apparently, this connection tends to get lost and it is highly probable that crest 2 in M1789 is the precentroloph that has established a connection with the metacone. This interpretation is supported to some extent by the M2 of *M. puntarronensis*, MLB8 876 (Pl. 3, fig. 10), where the same transformation has taken place, and where there is little doubt about the homology of the crests.

In order to test the development of the transformation through time, we drew all sufficiently well preserved M3 from HB, MLB1D, MLB8 and VIV schematically. In Figure 4 they are represented as left-hand specimens. The variability of the pattern of M3 is very high. In all populations the transformation of the crests as described above appears to take place: the prototrope gets in contact with the paracone; the precentroloph, which is the longest crest inside the trigone, looses contact with the paracone and shifts backwards; and it may get in contact with the metacone and look like a postcentroloph. However, conservative and advanced specimens are randomly distributed throughout the four populations and the degree of modernization is certainly not higher in VIV than in HB.

Our interpretation may be correct, but is not confirmed by a trend from the older towards the younger populations. Neither can the degree of development of the prototrope be used to discover a trend from M1 to M3.

Distinction of *M. puntarronensis* and *M. misonnei*

Comparing our morphological data for the *Microdyromys* populations from HB, MLB8, MLB1D, MIR and VIV, we found random distributions of frequencies for many features and a more or less continuous trend in others. However, for several features we found that the population from MLB8 was more advanced and the one from MLB1D less advanced than expected. Since this could be accidental, we added data from MLB3X (older than MLB8), MLB3C (younger than MLB8), and MLB11B and MLB10 (both about the same level as MLB1D). Thus, we have a sufficiently large

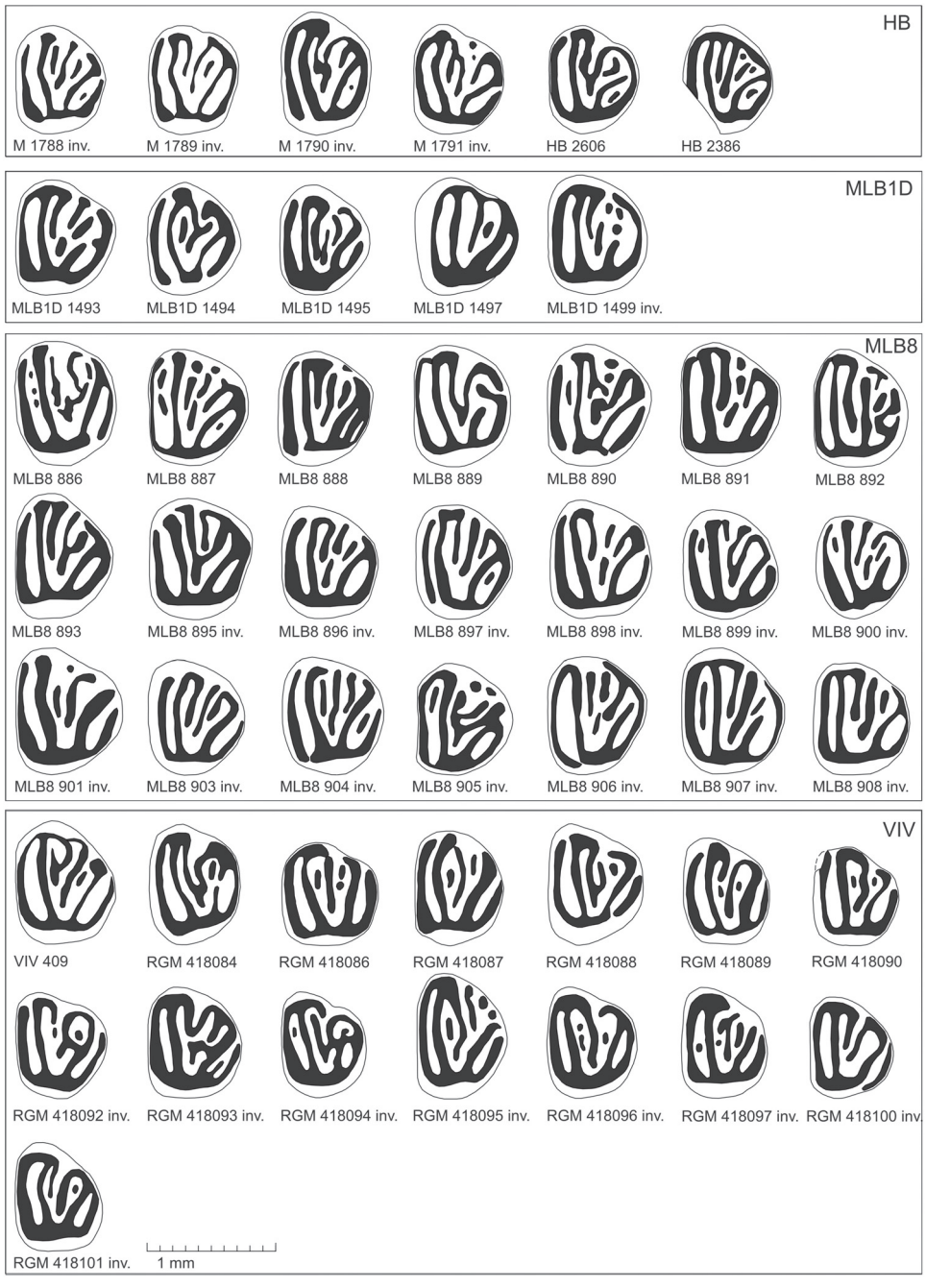

Fig. 4. The M3 of *Microdyromys* from HB, MLB1D, MLB8 and VIV.

number of specimens to discard chance and the observed differences were confirmed.

Table 7 shows that the anterotropid is fairly well-developed in *M. misonnei* from HB and seems to diminish in the other *M. misonnei* populations. On the other hand, it is clearly better developed in *M. puntarronensis* (on average longer = higher MV values).

The posterotropid is always long in the m1 and m2 of *M. misonnei* from HB, and on average shorter or even absent in the other *M. misonnei* populations (see Table 8). On the other hand, in *M. puntarronensis*, it maintains a degree of development similar to that of HB. In m3 the situation is more irregular, probably because the posterior part of that element is reduced with respect to m1 and m2.

The prototrope is always less developed in M1 than in M2 (see Table 9). As explained before, M3 has not been analyzed because it is frequently not clear which crest is the prototrope. In all populations of *M. misonnei*, the prototrope is on average less developed than in *M. puntarronensis*. In fact, the prototrope is always present in both M1 and M2 from MLB8, whereas it is absent in more the 60 % of the M1 from HB and MLB10, and in 45 % of the M1 from MLB1D.

The postcentroloph may be connected to the metacone (considered to be the original situation) or detached from it (the modernized situation). In this respect M2 is always more advanced than M1 and *M. puntarronensis* is more advanced than *M. misonnei*, at least in the M1 (Table 10).

Table 7. Frequency distribution (in percentages) and MV values for the anterotropid of the lower molars.

anterotropid	*M. misonnei*				*M. puntarronensis*		
m1	HB	MLB10	MLB1D	MB11B	MLB3X	MLB8	MLB3C
N	17	7	15	12	17	51	30
absent	5.9	42.9	6.7	33.3	0.0	0.0	0.0
very small	0.0	0.0	0.0	25.0	0.0	2.0	0.0
small	17.6	14.3	13.3	16.7	0.0	2.0	0.0
medium	29.4	42.9	40.0	16.7	17.6	19.6	23.3
long	47.1	0.0	40.0	8.3	82.4	76.5	76.7
m2							
N	25	8	9	5	23	56	25
absent	4.0	12.5	0.0	0.0	0.0	0.0	0.0
very small	0.0	0.0	11.1	20.0	0.0	0.0	0.0
small	20.0	12.5	22.2	0.0	0.0	1.8	4.0
medium	32.0	62.5	55.6	0.0	4.3	3.6	12.0
long	44.0	12.5	11.1	80.0	95.7	94.6	84.0
m3							
N	11	0	9	4	7	23	18
absent	9.1	0.0	44.4	25.0	0.0	0.0	33.3
very small	45.5	0.0	0.0	0.0	28.6	8.7	5.6
small	9.1	0.0	22.2	75.0	28.6	13.0	11.1
medium	9.1	0.0	22.2	0.0	28.6	47.8	16.7
long	27.3	0.0	11.1	0.0	14.3	30.4	33.3
MV m1	0.78	0.39	0.77	0.35	0.96	0.93	0.94
MV m2	0.78	0.66	0.67	0.85	0.99	0.98	0.95
MV m3	0.50		0.39	0.38	0.57	0.75	0.53

Table 8. Frequency distribution (in percentages) and MV values for the posterotropid of the lower molars.

posterotropid	*M. misonnei*				*M. puntarronensis*		
m1	HB	MLB10	MLB1D	MLB11B	MLB3X	MLB8	MLB3C
N	18	7	15	12	17	52	30
absent	0.0	0.0	13.3	0.0	0.0	0.0	0.0
small	0.0	14.3	6.7	16.7	0.0	0.0	0.0
medium	0.0	28.6	13.3	16.7	0.0	0.0	6.7
long	100.0	57.1	66.7	66.7	100.0	100.0	93.3
m2							
N	25	8	10	5	24	56	26
absent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
small	0.0	0.0	10.0	0.0	0.0	0.0	0.0
medium	8.0	25.0	0.0	20.0	0.0	1.8	3.8
long	92.0	75.0	90.0	80.0	100.0	98.2	96.2
m3							
N	11	0	10	4	7	23	18
absent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
small	9.1	0.0	10.0	0.0	28.6	17.3	0.0
medium	18.2	0.0	50.0	100.0	14.3	26.1	22.2
long	72.7	0.0	40.0	0.0	57.1	56.5	77.8
MV m1	1.00	0.81	0.78	0.83	1.00	1.00	0.98
MV m2	0.97	0.92	0.93	0.93	1.00	0.99	0.99
MV m3	0.88		0.77	0.67	0.76	0.80	0.93

Table 9. Frequency distribution (in percentages) and MV values for the prototrope of M1 and M2

prototrope	*M. misonnei*			*M. puntarronensis*			
M1	HB	MLB10	MLB1D	MB11B	MLB3X	MLB8	MLB3C
N	20	8	22	16	12	51	35
absent	65.0	62.5	45.5	37.5	16.7	0.0	17.1
short	15.0	25.0	31.8	31.3	8.3	2.0	8.6
medium	20.0	12.5	13.6	25.0	41.7	86.3	34.3
long	0.0	0.0	9.1	6.3	33.3	11.8	40.0
M2							
N	12	10	14	12	21	48	36
absent	25.0	20.0	7.1	25.0	0.0	0.0	0.0
short	33.3	20.0	7.1	8.3	0.0	2.1	2.8
medium	16.7	20.0	35.7	8.3	23.8	54.2	25.0
long	25.0	40.0	50.0	58.3	76.2	43.8	72.2
MV M1	0.18	0.17	0.29	0.33	0.64	0.70	0.66
MV M2	0.47	0.60	0.76	0.67	0.92	0.81	0.90

There are some features that show a difference between the two species, though hardly quantifiable, such as the length of the precentroloph. In both species this crest is always classified as long, but it is on average somewhat longer in *M. puntarronensis* than in *M. misonnei*.

Apparently we are dealing with two lineages. *Microdyromys puntarronensis* may be a descendant of *M. misonnei* from HB, and is clearly advanced in several features like anterotropid, posterotropid, prototrope and the posteroloph/metacone connection. *Micro-*

Table 10. Frequency distribution (in percentages) and MV values for the postcentroloph/metacone connection of M1 and M2.

	M. misonnei				*M. puntarronensis*		
M1	HB	MLB10	MLB1D	MB11B	MLB3X	MLB8	MLB3C
N	20	8	22	16	13	48	36
connected	95.0	100.0	95.5	100.0	76.9	45.8	75.0
free	5.0	0.0	4.5	0.0	23.1	54.2	25.0
M2							
N	12	9	13	11	20	49	34
connected	91.7	66.7	61.5	36.4	35.0	22.4	35.3
free	8.3	33.3	38.5	63.7	65.0	77.6	64.8
MV M1	0.05	0.00	0.05	0.00	0.23	0.54	0.25
MV M2	0.08	0.33	0.39	0.64	0.65	0.78	0.65

dyromys misonnei from the youngest levels of Montalbán maintains the degree of development of the population from HB or it even shows a simplification of the dental pattern.

Comparison with *M. praemurinus*

Remarks – The relation of the two lineages with the Late Oligocene species *M. praemurinus* will be analyzed. In the tables pertaining to this analysis (Tables 11-16) the three Spanish localities with *M. misonnei* (MLB1D, MLB10 and MLB11B) have been combined as MLB sup. The localities with *M. puntarronensis* are lumped together as MLB inf.

Anterolophid of m1,2 – See Table 11. In the m1,2 of *M. misonnei*, the anterolophid is predominantly separated from the protoconid (HB, MLB sup.); less frequently these crests are connected labially. Anterolophid and metalophid reach about equally far labially, and the separation opens on the labial wall of the tooth or at the anterolabial corner.

In the m1,2 of *M. puntarronensis* (MLB inf.), the anterolophid is predominantly separated from the protoconid. In the m1,2 of *M. praemurinus* (VIV, MIR), these two crests are always connected labially; this even helps to distinguish *M. praemurinus* from *Peridyromys murinus*, where the anterosinusid opens in the anterior wall of the tooth and the anterolophid gradually slopes down from the metaconid to its labial end. In *M. praemurinus* from Coderet, anterolophid and protoconid are transversely separated.

When anterolophid and metalophid are not connected in the Miocene species of *Microdyromys*, the labial end of the metalophid is curved forward and the anterolophid is shorter than the metalophid, the furrow between the two opening on the anterior wall of the tooth.

Anterolophid of m3 – With the m1,2 of *M. praemurinus* from VIV showing the advanced state of connected anterolophid, one would expect the same in m3, which usually is the most advanced of the lower molars. However, the situation is similar to that

Table 11. Character states and MV values of the anterolophid. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

anterolophid	*M. misonnei*		*M. puntarr.*	*M. praemurinus*		
m1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	15	33	87	4	13	18
lab. free	93.3	81.8	71.3	0.0	0.0	0.0
lab. connected	6.7	18.2	28.7	100.0	100.0	100.0
m2						
N	25	23	102	6	17	26
lab. free	100.0	87.0	82.4	16.7	0.0	0.0
lab. connected	0.0	13.0	17.6	83.3	100.0	100.0
m3						
N	9	13	43	1	10	16
lab. free	88.9	69.2	72.1	100.0	30.0	62.5
lab. connected	11.1	30.8	27.9	0.0	70.0	37.5
MV m1	0.07	0.18	0.29	1.00	1.00	1.00
MV m2	0.00	0.13	0.18	0.83	1.00	1.00
MV m3	0.11	0.31	0.28	0.00	0.70	0.38

Table 12. Character states and MV values of the anterotropid. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

anterotropid	*M. misonnei*		*M. puntarr.*	*M. praemurinus*		
m1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	17	34	98	4	12	18
absent	5.9	23.5	0.0	50.0	33.3	11.1
very small	0.0	8.8	1.0	0.0	25.0	11.1
small	17.6	14.7	1.0	0.0	0.0	11.1
medium	29.4	32.4	20.4	0.0	16.7	33.3
long	47.1	20.6	77.6	50.0	25.0	33.3
m2						
N	25	22	104	7	17	30
absent	4.0	4.5	0.0	57.1	23.5	13.3
very small	0.0	9.1	0.0	14.3	11.8	13.3
small	20.0	13.6	1.9	14.3	5.9	16.7
medium	32.0	45.5	5.8	0.0	52.9	33.3
long	44.0	27.3	92.3	14.3	5.9	23.3
m3						
N	11	13	48	1	12	17
absent	9.1	38.5	12.5	100.0	83.3	52.9
very small	45.5	0.0	10.4	0.0	0.0	23.5
small	9.1	38.5	14.6	0.0	16.7	17.6
medium	9.1	15.4	33.3	0.0	0.0	5.9
long	27.3	7.7	29.2	0.0	0.0	0.0
MV m1	0.78	0.54	0.94	0.50	0.44	0.67
MV m2	0.78	0.70	0.98	0.25	0.51	0.60
MV m3	0.50	0.38	0.64		0.08	0.19

in *M. misonnei*, with a separation between anterolophid and metalophid in the majority of the specimens. Nothing can be said about the m3 of *M. praemurinus* from Gaimersheim since only one specimen is known.

The labial end of the anterolophid in m1,2, when separated, is not much lower than

Table 13. Character states and MV values of the centrolophid. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

centrolophid	*M. misonnei*		*M. puntarr.*	*M. praemurinus*		
m1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	18	33	98	4	13	18
absent	0.0	0.0	0.0	0.0	0.0	0.0
short	5.6	0.0	0.0	0.0	0.0	0.0
medium	5.6	3.0	0.0	0.0	0.0	0.0
long	88.9	97.0	100.0	100.0	100.0	100.0
m2						
N	25	23	109	7	17	32
absent	0.0	0.0	0.0	0.0	0.0	0.0
short	0.0	0.0	0.0	0.0	0.0	0.0
medium	8.0	13.0	2.7	57.1	0.0	6.3
long	92.0	87.0	97.2	42.9	100.0	93.8
m3						
N	11	14	47	1	12	17
absent	9.1	0.0	2.1	0.0	0.0	0.0
short	0.0	14.3	0.0	0.0	0.0	0.0
medium	36.4	64.3	42.5	100.0	58.3	11.8
long	54.5	21.4	55.3	0.0	41.7	88.2
MV m1	0.95	0.99	1.00	1.00	1.00	1.00
MV m2	0.97	0.96	0.99	0.81	1.00	0.98
MV m3	0.79	0.69	0.84	0.67	0.81	0.96

the protoconid; the anterolophid descends from the metaconid until the axis of the molar and then rises again to somewhat below the level of the protoconid (e.g., in HB, MLB8 and MLB1D). But, in the m3 of the Oligocene species, the anterolophid, when separated from the protoconid, slopes down from the metaconid and it is very low at the anterolabial corner of the molar, like in the lower molars of *Peridyromys*.

Anterotropid – See Table 12. The anterotropid is well developed in HB and least developed in *M. praemurinus* from the Spanish localities, indicating a lineage *M. misonnei* - *M. praemurinus*, in which this crest shows a negative development. It is best developed in *M. puntarronensis*, which means that the latter species is not in the lineage *M. misonnei* - *M. praemurinus*.

Centrolophid – See Table 13. This crest does not show significant differences between the various populations. Nevertheless, the data are given here because there are differences with other species that will be discussed later. If one distinguishes between 'long' and 'very long', there is a difference between HB and VIV; in the m1,2 from VIV it is always very long, in HB only in 65 % of the specimens.

Endoloph – The degree of development of the endoloph is listed in Table 14. 'Protocone' means there is no endoloph; the protocone has no connection, neither with the anteroloph nor with the posteroloph. 'Interrupted' means there is one connection, either anteriorly or posteriorly. 'Complete' means both connections are present. The endoloph is less developed in M1 than in M2; it is most developed in M3. Its development

Table 14. Character states and MV values of the endoloph. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

endoloph	*M. misonnei*		*M. puntarr.*	*M. praemurinus*		
M1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	18	39	84	6	7	33
protocone	22.2	43.6	58.3	16.7	14.3	0.0
interrupted	77.8	35.9	38.1	50.0	0.0	51.5
complete	0.0	20.5	3.6	33.3	85.7	48.5
M2						
N	10	31	86	1	12	38
protocone	20.0	19.4	26.7	0.0	0.0	0.0
interrupted	50.0	48.4	43.1	100.0	16.7	7.9
complete	30.0	32.3	30.2		83.3	92.1
M3						
N	7	5	21	0	8	24
protocone	0.0	0.0	9.5	0.0	0.0	
interrupted	57.1	20.0	23.8		0.0	12.5
complete	42.9	80.0	66.7		100.0	87.5
MV M1	0.39	0.38	0.23	0.58	0.86	0.74
MV M2	0.55	0.57	0.52	0.50	0.92	0.96
MV M3	0.71	0.90	0.79		1.00	0.94

Table 15. Character states and MV values of the postcentroloph connection. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

postcentroloph	*M. misonnei*		*M. puntarronensis*	*M. praemurinus*.		
M1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	20	46	97	6	7	33
to metacone	95.0	97.8	60.8	33.3	85.7	66.7
free	5.0	2.2	39.2	66.7	14.3	33.3
M2						
N	12	33	103	2	14	37
to metacone	91.7	54.5	29.1	0.0	50.0	45.9
free	8.3	45.5	70.8	100.0	50.0	54.0
MV M1	0.05	0.02	0.39	0.67	0.14	0.33
MV M2	0.08	0.46	0.71	1.00	0.50	0.54

gradually increases through time and in MLB inf., especially in M1, it is less developed than one would expect. The situation is similar to that of the anterotropid of the lower molars (Table 12), though the trend is inverse. In the lineage *M. misonnei* - *M. praemurinus* the endoloph shows a trend towards increased development, whereas in *M. puntarronensis* the endoloph is less developed than in HB.

Postcentroloph connection – See Table 15. The postcentroloph is nearly always long. It may be attached to the metacone, which is thought to be the original situation. In advanced stages it first becomes detached from the metacone, then moves forward to a central position and may develop a mesostyl. As a rule for this feature, M1 is less developed than M2. In *M. misonnei* from HB this feature is least developed, followed by *M. misonnei* from MLB sup. It is more advanced in *M. praemurinus* from VIV, but it reaches

Table 16. Character states and MV values of the prototrope. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C.

prototrope	*M. misonnei*		*M. puntarronensis*	*M. praemurinus*.		
M1	HB	MLB sup.	MLB inf.	MIR4C	MIR1	VIV
N	20	46	98	6	7	36
absent	65.0	45.7	8.2	0.0	14.3	0.0
short	15.0	30.4	5.1	66.7	0.0	11.1
medium	20.0	17.4	62.2	33.3	28.6	47.2
long	0.0	6.5	24.5	0.0	57.1	41.7
M2						
N	12	36	105	2	14	39
absent	25.0	16.7	0.0	0.0	7.1	7.7
short	33.3	11.1	1.9	0.0	0.0	5.1
medium	16.7	22.2	38.1	0.0	35.7	35.9
long	25.0	50.0	60.0	100.0	57.1	51.3
MV M1	0.18	0.28	0.68	0.44	0.76	0.77
MV M2	0.47	0.69	0.86	1.00	0.81	0.77

its most advanced stage in MLB inf. The three populations of *M. praemurinus* vary greatly; the one from MIR4C is very much advanced and the one from MIR1 very little. The material is not abundant and the results may be unreliable.

Prototrope – See Table 16. The prototrope is better developed in M2 than in M1. Its length increases through time and the special position of *M. puntarronensis* is confirmed by the high degree of development, comparable to that of *M. praemurinus*.

Phylogeny

In Table 17 the MV values are given for M1+2 in order to incorporate data published by authors who did not distinguish between these elements. Of course, this obscures those cases where there is a considerable difference between these two elements. The last two lines of the table give the mean lengths of m1,2 and M1,2. The values for N (number of specimens) are an approximation, because not all the features could be observed in all the specimens due to wear and damage, so the actual number of specimens observed for each feature varies. The three Late Oligocene localities, MIR4C, MIR1 and VIV, treated separately in the preceding tables, are here lumped together.

The oldest record of *Microdyromys* is that of *Microdyromys* sp. from AGT2D; that material consists of an m1 and an M2 that do not allow any specification. The morphology of these specimens is certainly not more primitive that that of later species, but since the morphological variation is unknown nothing can be said about a relationship.

The next record may be that of cf. *Microdyromys praemurinus*, cited by Herb *et al*. (1984) from 'Synclinal du Charbon'; it might belong to *M. misonnei*.

Microdyromys misonnei from its type locality HB gives the lowest values of MV for nearly all features. The populations from MLB sup. are slightly more advanced than the one from HB, or at about the same level. *Microdyromys puntarronensis* from MLB inf. is in various features more advanced than *M. misonnei* and is at about the same level as *M.*

Table 17. MV values of various features. MLB sup. is a combination of MLB1D, MLB10 and MLB11B; MLB inf. is a combination of MLB3X, MLB8 and MLB3C; VIV/MIR is a combination of MIR4C, MIR1 and VIV.

	HB		MLB inf.		MLB sup.		VIV/MIR		GAIM		NFM	
	m1,2	m3	m1,2	m3	m1,2	m3	m1,2	m3	m1,2	m3	m1,2	m3
N	17	11	207	47	57	14	85	29	35	1	9	4
anterolophid/ protoconid	0.03	0.11	0.23	0.28	0.16	0.31	0.99	0.48	1.00			
anterotropid length	0.78	0.50	0.96	0.64	0.61	0.39	0.55	0.14	0.69			
centrolophid length	0.96	0.79	0.99	0.84	0.98	0.69	0.98	0.89	1.00	0.50	0.66	
	M1,2	M3	M1,2	M3	M1,2	M3	M1,2	M3	M1,2	M3	M1,2	M3
N	32	10	209	21	81	9	105	34	20		12	1
endoloph	0.45	0.71	0.38	0.79	0.46	0.90	0.85	0.95	0.98		1.00	
postcentrol. length	0.91		0.99		0.94		0.98		0.95		0.10	
postcentrol./ metacone	0.06		0.55		0.20		0.46		0.50		0.08	
prototrope length	0.29		0.77		0.46		0.76		0.60		0.05	
ling. border crenulated	0.38	0.70	0.49	0.30	0.50	0.33	0.87	0.63	0.60		0.00	
mean L. M1,2	8.73		8.70		8.68		8.98		7.90		7.25	
mean L. m1,2	9.12		9.28		9.01		9.26		8.25		7.73	

praemurinus from VIV/MIR; in some features it is even more developed than the latter. Probably, *M. misonnei* is the ancestor of *M. puntarronensis*.

Microdyromys misonnei is known from HB and from the upper levels of MLB; *M. puntarronensis* is found in the lower levels of MLB. This apparently discontinuous distribution of *M. misonnei* may be untrue; it cannot be excluded that the populations from the lower levels of MLB contain a mixture of the two species, with a majority of *M. puntarronensis*, and the younger populations of *M. misonnei* may contain some specimens of *M. puntarronensis*. The MLB8 population appears to be quite homogeneous, but the *M. puntarronensis* populations from MLB3X and MLB3C contain various specimens with a morphology that is more compatible with *M. misonnei*. In the Miocene there are many localities where two species of *Microdyromys* coexist and the situation in MLB may be similar. Such a mixture of species might explain why there are differences in the MV values of some features between MLB3X, MLB8 and MLB3C.

Microdyromys praemurinus from VIV/MIR is in nearly all features more advanced than *M. misonnei* from MLB1D. The data for *M. praemurinus* from GAIM, taken from the figures and the description of Kristkoiz (1992), show a high degree of coincidence with those of VIV/MIR; as said before, some of the features are highly variable among MIR4C, MIR1 and VIV, but the sum of these populations gives an acceptable result. *Microdyromys praemurinus* from GAIM is on average smaller than the same species from VIV/MIR (and also smaller than the two Early Oligocene species). *Microdyromys praemurinus* may be derived from *M. misonnei* and probably not from *M. puntarronensis*, which is more advanced in several features.

Microdyromys heissigi from Gröben 3 is very small. In the upper molars the postcentroloph is relatively short or even absent, the prototrope is very much reduced and the endoloph of M2 is always complete, contrary to all older species, where the postcentroloph is practically always long, the prototrope is better developed and the endoloph may be incomplete.

Microdyromys monspeliensis from NFM is clearly smaller than the two Early Oligocene species and of the same size as *M. heissigi*. The loss of the postcentroloph and prototrope is almost completely realized in this species. The endoloph is always complete.

Apparently, *M. heissigi* and *M. monspeliensis* form a lineage that is characterized by simplification of the dental pattern and very small size. It probably branches off from *M. misonnei* at the level of HB and not (much) later, because the later *misonnei* populations show a trend towards complication of some features, that are simple in GRB3.

Daams (1981, fig. 27) considered *M. monspeliensis* to be derived from *M. praemurinus* and (p. 64) said that the teeth of *M. monspeliensis* from the Spanish localities are somewhat smaller than those from NFM. However, comparison of the measurement tables by Aguilar (1977) and Daams (1981) shows that the Spanish teeth are considerably larger than those from NFM. In fact, those from NFM (and GRB3) are the smallest *Microdyromys* teeth known, even smaller than *M. praemurinus* from Gaimersheim, with which it has a size overlap, and there is not even a size overlap with the other species of the genus. Apparently, the material attributed by Daams to this species represents a different, as yet unnamed species.

Assuming the lineage *M. heissigi - M. monspeliensis* is correct, there is a clear reduction of the postcentroloph. In the populations from the Spanish Miocene attributed by Daams to *M. monspeliensis*, the postcentroloph is absent in a minority of the specimens only, another reason to reject their attribution to *M. monspeliensis* and also to reject their descendance from *M. monspeliensis*. On the other hand, the mixture of specimens with and without postcentroloph makes *M. heissigi* a good candidate for the ancestry of these supposed *monspeliensis* populations.

Daams (1981, fig. 27) considered *M. legidensis* to be derived from *M.* aff. *praemurinus* from Heimersheim. According to Uhlig (2001), the Heimersheim population is *M. heissigi*, but according to Uhlig (2002) it is *M.* cf. *misonnei*. The few available specimens seem to be larger than *M. heissigi*.

Microdyromys praemurinus may be the ancestor of *M. legidensis*, but in that case we see a gradual closing of the anterosinusid by the anterolophid/protoconid connection from *M. misonnei* to *M. praemurinus*, and a subsequent reopening of the anterosinusid by the loss of that connection. That is not logical, but, in the Miocene species anterolophid and metalophid are separated on the anterior wall of the tooth, the anterolophid ending lingually of the protoconid, whereas in the Oligocene species the anterosinusid opens more on the labial wall, and anterolophid and metalophid have frequently the same length. The morphology of the Miocene species may be interpreted as a new trend and not a reversal of the existing trend. Figure 5 gives the record of *Microdyromys* species in the Oligocene and in a selection of Miocene localities, and the possible phylogenetic relationships between these occurrences.

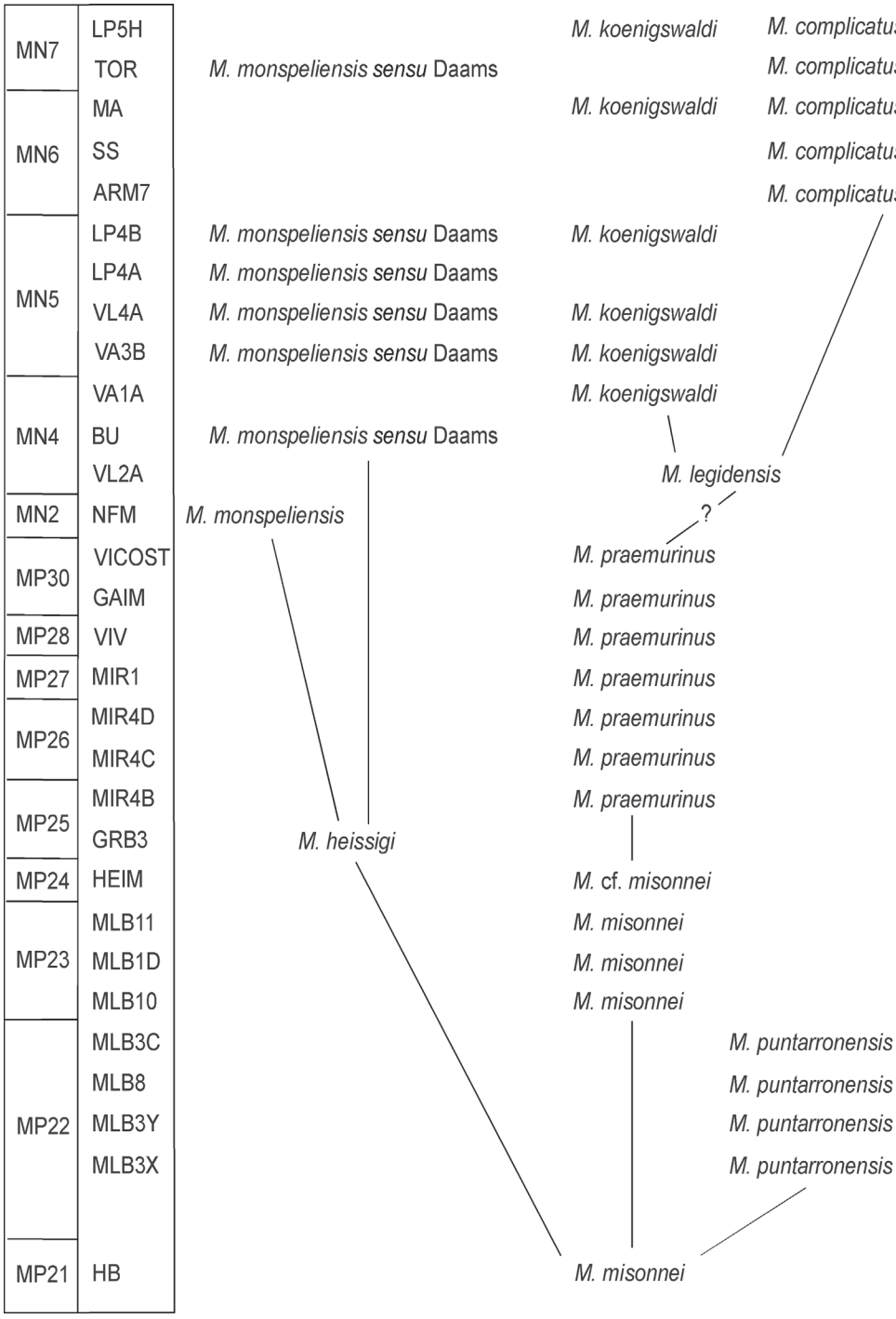

Fig. 5. Phylogeny of *Microdyromys*.

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Plate 1
Microdyromys misonnei from Montalbán 1D

Fig. 1. d4 sin., MLB1D 1405
Fig. 2. p4 sin., MLB1D 1406
Fig. 3. p4 dext., MLB1D 1410
Fig. 4. m1 sin., MLB1D 1414
Fig. 5. m1 sin., MLB1D 1416
Fig. 6. m1 dext., MLB1D 1419
Fig. 7. m2 sin., MLB1D 1425
Fig. 8. m2 dext., MLB1D 1433
Fig. 9. m3 sin., MLB1D 1435
Fig. 10. m3 dext., MLB1D 1441

Fig. 11. D4 sin., MLB1D 1444
Fig. 12. P4 sin., MLB1D 1446
Fig. 13. P4 dext., MLB1D 1450
Fig. 14. M1 sin., MLB1D 1457
Fig. 15. M1 dext., MLB1D 1474
Fig. 16. M2 sin., MLB1D 1482
Fig. 17. M2 dext., MLB1D 1486
Fig. 18. M3 sin., MLB1D 1495
Fig. 19. M3 dext., MLB1D 1499

Scale bar represents 1 mm.

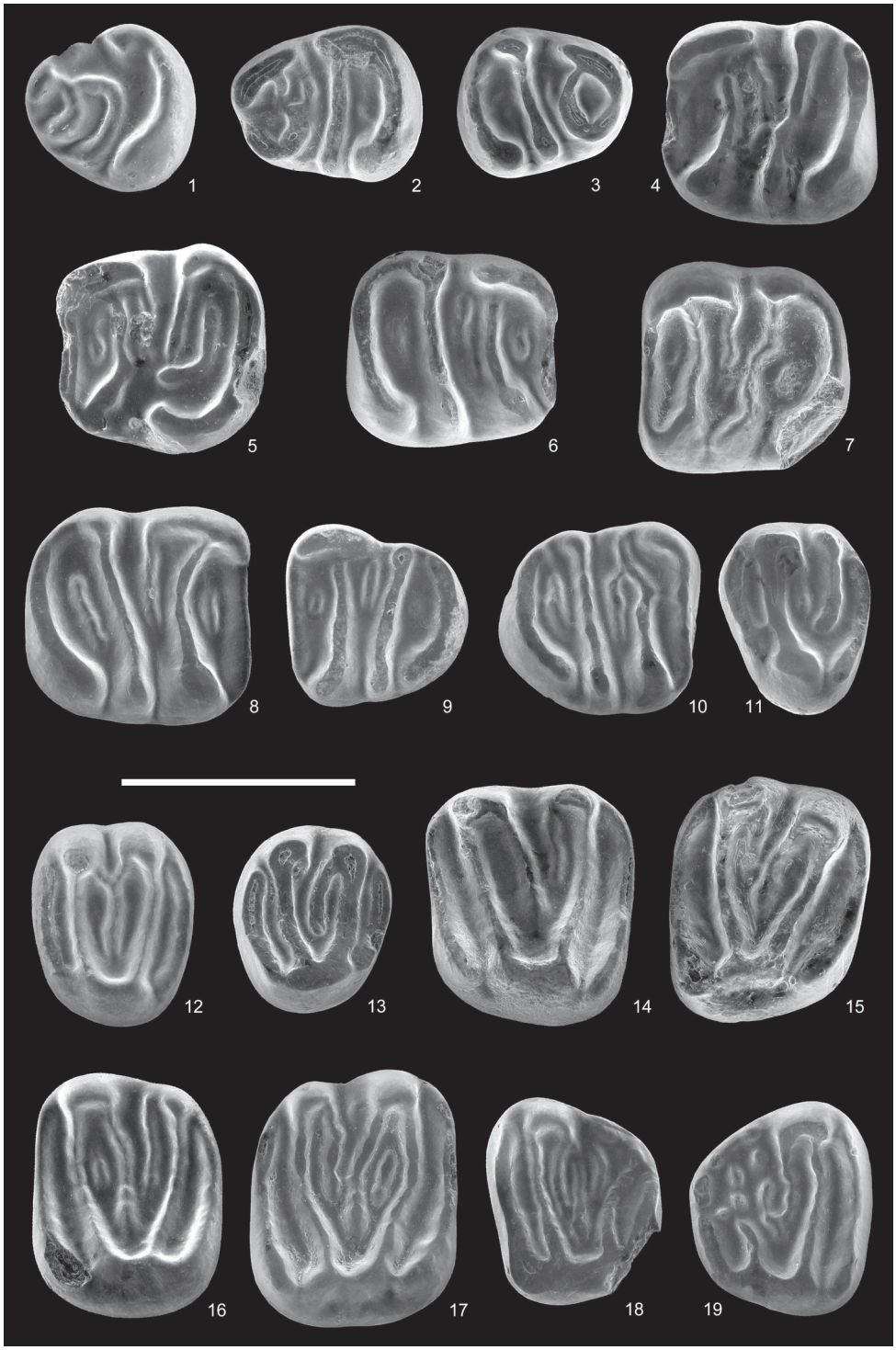
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Plate 2
Microdyromys puntarronensis sp. nov. from Montalbán 3C

Fig. 1. d4 sin., MLB3C 389430

Microdyromys puntarronensis sp. nov. from Montalbán 8

Fig. 2. p4 sin., MLB8 604
Fig. 3. p4 sin., MLB8 605
Fig. 4. p4 dext., MLB8 624
Fig. 5. m1 sin., MLB8 639
Fig. 6. m1 dext., MLB8 654
Fig. 7. m1 dext., MLB8 659
Fig. 8. m2 sin., MLB8 702
Fig. 9. m2 dext., MLB8 715
Fig. 10. m3 sin., MLB8 737
Fig. 11. m3 dext., MLB8 748

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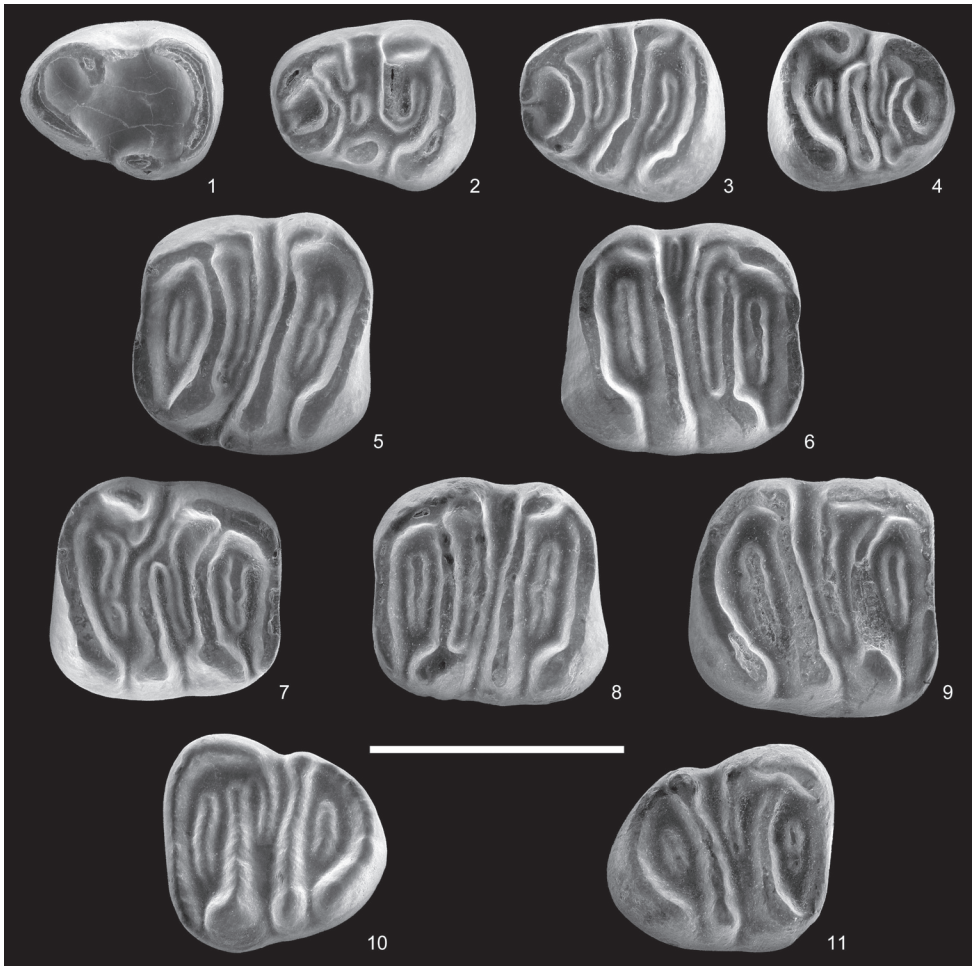
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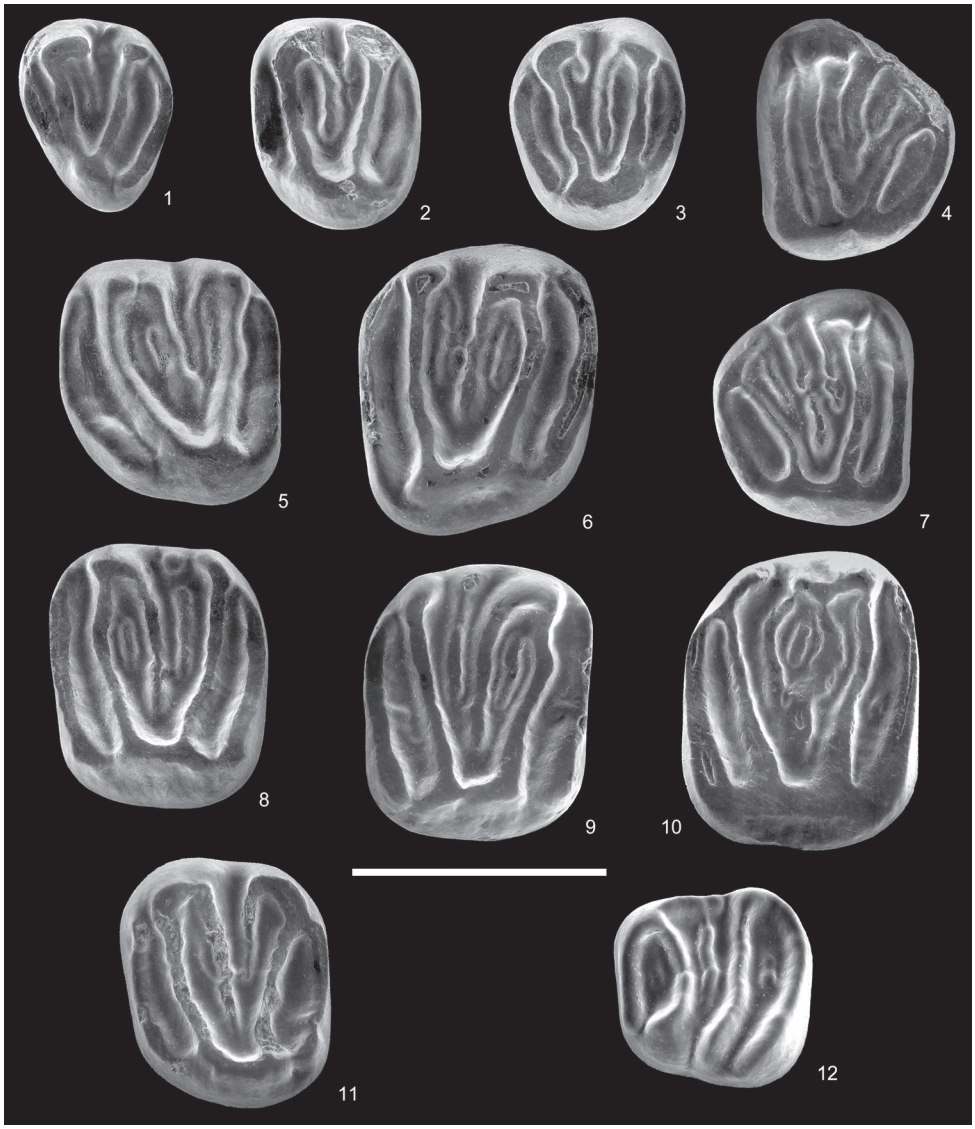
Plate 3
Microdyromys puntarronensis sp. nov. from Montalbán 8

Fig. 1. D4 sin., MLB8 757
Fig. 2. P4 sin., MLB8 764
Fig. 3. P4 dext., MLB8 773
Fig. 4. M3 sin., MLB8 893
Fig. 5. M1 sin., MLB8 784
Fig. 6. M1 dext., MLB8 819
Fig. 7. M3 dext., MLB8 896
Fig. 8. M2 sin., MLB8 838 (holotype)
Fig. 9. M2 dext., MLB8 871
Fig. 10. M2 dext., MLB8 876

Microdyromys sp. from Aguatón 2D

Fig. 11. M2 sin., RGM 417736
Fig. 12. m1 sin., AGT2D 885

Scale bar represents 1 mm.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