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Gliridae from the late Oligocene of the province of Teruel (Spain)

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ABSTRACT

The Calatayud-Teruel Basin is one of the richest areas of Spain, when fossil mammals are concerned. Around the village of Montalbán many lower Oligocene fossil mammal localities are known and several upper Oligocene localities with rich micromammal faunas are present between the villages of Vivel del Río Martín and Martín del Río. Previous papers on these upper Oligocene localities were dedicated to the Cricetidae and to the zapodid *Plesiosminthus*, in this work we describe the fauna of Gliridae, composed of the genera *Gliravus*, *Butseloglis*, *Peridyromys*, *Microdyromys,* and *Paraglis*. Among these the latter genus is very poorly represented. *Microdyromys* is of special importance because its presence in our material permits a new concept of the phylogeny of the genus.

Keywords: Gliridae, Mammalia, Oligocene, Teruel.

RESUMEN

La depresión de Calatayud-Teruel es una de las zonas más ricas de España en mamíferos fósiles. Alrededor del pueblo de Montalbán se conocen muchos yacimientos del Oligoceno inferior y varios yacimientos del Oligoceno superior se encuentran entre los pueblos de Vivel del Río Martín y Martín del Río. Trabajos anteriores sobre estos yacimientos tratan de los cricétidos y del zapódido *Plesiosminthus*. En el presente trabajo describimos la fauna de Gliridae, compuesta por los géneros *Gliravus*, *Butseloglis*, *Peridyromys*, *Microdyromys* y *Paraglis*. Entre ellos, el material de *Paraglis* es muy escaso. *Microdyromys* es especialmente importante porque su presencia en nuestro material permite establecer una nueva filogenia del género.

Palabras clave: Gliridae, Mammalia, Oligoceno, Teruel.

1. INTRODUCTION

The Calatayud-Teruel Basin is one of the richest areas of Spain, when fossil mammals are concerned. The easternmost part of this Basin, the depression of Montalbán, is formed by lower Oligocene deposits that have yielded rich vertebrate faunas. Farther to the west important deposits of late Oligocene age are present which, in the area of Mirambueno, between the villages of Martín del Río and Vivel del Río Martín, contain several important localities of fossil mammals. The first one of these, Vivel, was discovered by E. Moissenet in 1978; the other ones denominated Mirambueno 1-4D were discovered by our team during the years 1986-1991.

Previous papers on the localities studied here are Freudenthal *et al*. (1994) on *Pseudocricetodon*, Freudenthal (1994) on the other Cricetidae, Freudenthal (1997) providing faunal lists, and Freudenthal & Martín-Suárez (2017) on the Dipodidae *Plesiosminthus*.

The aim of this paper is the contribution to the knowledge of the fossil Gliridae from the upper Oligocene sites of the Mirambueno area. Gliridae are an important part of the faunas and Hugueney *et al*. (1985) published the new species *Gliravus bravoi* from Vivel (now placed in the genus *Butseloglis* Vianey-Liaud, 2004). Here we will describe the entire glirid fauna from Mirambueno and Vivel, containing the genera *Gliravus*, *Butseloglis* (with a discussion on the original diagnosis of this genus), *Peridyromys*, *Microdyromys* (with a new diagnosis of this genus), and *Paraglis*.

2. MATERIAL AND METHODS

The localities studied are situated near the eastern border of the Calatayud-Teruel Basin, topographical map of Spain 1:50,000 Segura de los Baños 27-19 (492), between the villages of Martín del Río and Vivel del Río Martín, on the southwestern bank of the river Vivel (Fig. 1).

UTM coordinates of the fossiliferous localities were taken in the field and checked on the topographic map, which uses the ED50 datum point. Since the standard today is ETRS89 we converted our data (Table 1). However, we use ED50 data, since they are compatible with the printed map.

The fossil material will be stored, partly in the Museo de Geología of the University of Zaragoza (Spain) and partly in the Netherlands Centre for Biodiversity Naturalis, Leiden (The Netherlands).

The terminology of parts of the cheek teeth (Fig. 2) follows Freudenthal (2004). The taxonomy follows Freudenthal & Martín-Suárez (2013). V' is the variability coefficient as defined by Freudenthal & Cuenca (1984).

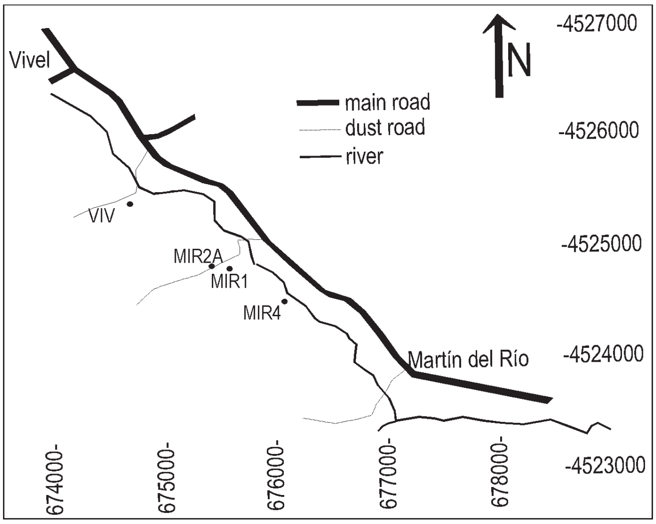


Figure 1. Map of the area of Mirambueno.

Table 1. UTM co-ordinates.

	FIELD ED50	ETRS89
MIR1	0675545 / 4524770	0675436 / 4524560
MIR2A	0675404 / 4524803	0675295 / 4524593
MIR4	0676048 / 4524496	0675939 / 4524286
VIV	0674649 / 4525328	0674540 / 4525118

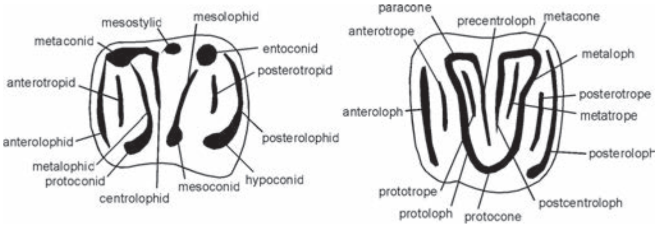


Figure 2. Nomenclature of parts of cheek teeth, adapted after Freudenthal (2004). When there is only one centroloph, and its homology cannot be decided, it is called midcentroloph. The figures are drawn as left-hand molars with the anterior side facing to the left.

Abbreviations used are explained in Table 2. In the taxonomic descriptions of the following section, numbers in parentheses indicate number of specimens that show the referred feature.

Measurements were taken with a Wild M8 binocular microscope, equipped with a mechanical stage with electronic sensors, connected to a computer through a Sony Magnescale measuring unit. Measurements are given in mm. The orientation of the specimens for measuring was as described by Freudenthal (2004). Photographs were taken on the electron microscope FEI ESEM QUANTA 400 of the Centro de Instrumentación Científica of the University of Granada.

Table 2. Abbreviations used.

Code	Locality	Country	MP/MN zone
ARM7	Armantes 7	Spain	MN6
ATE3	Ateca 3	Spain	MN3
BOUZ	Bouzigues	France	MN2A
BU	Buñol	Spain	MN4
CARRAS	Carrascosa del Campo	Spain	MP26
COD	Coderet	France	MP30
GAIM	Gaimersheim	Germany	MP28
GRB3	Gröben 3	Germany	MP24
HB	Hoogbutsel	Belgium	MP21
HEIM	Heimersheim	Germany	MP24
LP4A	Las Planas 4A	Spain	MN5
LP4B	Las Planas 4B	Spain	MN5
LP4C	Las Planas 4C	Spain	MN5
LP5H	Las Planas 5H	Spain	MN7/8
MA	Manchones	Spain	MN6
MIR1	Mirambueno 1	Spain	MP27
MIR2A	Mirambueno 2A	Spain	MP27
MIR4B	Mirambueno 4B	Spain	MP25
MIR4C	Mirambueno 4C	Spain	MP26
MIR4D	Mirambueno 4D	Spain	MP26
MLB10	Montalbán 10	Spain	MP23
MLB11B	Montalbán 11B	Spain	MP23
MLB11B+	Montalbán 11B + 10 +1D	Spain	MP23
MLB1D	Montalbán 1D	Spain	MP23
MLB3C	Montalbán 3C	Spain	MP22
MLB3C+	Montalbán 3C + 3X + 8	Spain	MP22
MLB3X	Montalbán 3X	Spain	MP22
MLB3Y	Montalbán 3Y	Spain	MP22
MLB8	Montalbán 8	Spain	MP22
NFM	Nouvelle Faculté de Médecine	France	MN1
PAREJ	Pareja	Spain	MP26
OBERL	Oberleichtersbach	Germany	MP30
SS	Sansan	France	MN6
TOR	Toril	Spain	MN7/8
ULMW	Ulm-Westtangente	Germany	MN2A
VA1A	Valdemoros 1A	Spain	MN5
VA3B	Valdemoros 3B	Spain	MN5
VICOST	St.Victor-la-Coste	France	MP29
VIV	Vivel del Río	Spain	MP28
VL2A	Villafeliche 2A	Spain	MN4
VL4A	Villafeliche 4A	Spain	MN5
VR7	Vargas 7	Spain	MN5
p4, m1, m2, m3	lower cheek teeth		
P4, M1, M2, M3	upper cheek teeth		
mA	million years		
mcd	metaconid		
ecd	entoconid		
pac	paracone		
MN	MN zone		
MP	MP zone		

3. SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order RODENTIA Bowdich, 1821

Family **Gliridae** Muirhead, 1819

Subfamily Gliravinae Schaub, 1958

Genus Gliravus Stehlin & Schaub, 1951

Type species *Gliravus majori* Stehlin & Schaub, 1951

Original diagnosis. (Translated from German): “Brachyodont, with two premolars in the maxilla. Upper molars trigonodont with simple and small mesostyl. Trigone crests without intermediate cusps. Lower molars with four cusps and isolated mesoconid. Mesolophid not yet developed. Paraconid separated from protoconid, like in *Sciurus vulgaris*”.

Remarks. Daams & de Bruijn (1995) recognized 15 species of *Gliravus* and since then two new species have been described (Table 3). Daams & de Bruijn included the genus *Glamys* Vianey-Liaud, 1989 in *Gliravus*. Vianey-Liaud (2004) created the genus *Butseloglis*, which contains about half the species originally placed in *Gliravus*.

In our concept, *Gliravus* is restricted to three upper Oligocene species (MP25-26): *G. majori* Stehlin & Schaub, 1951, *G. alvarezae* Lacomba & Morales, 1987, and *G. caracensis* Daams, Freudenthal, Lacomba & Alvarez, 1989. These species share the tendency towards a connection between anteroloph and posteroloph, lingually of the protocone (see Stehlin & Schaub, 1951; fig. 198), and we think this character should form part of the diagnosis of the genus *Gliravus*. Consequently, the material attributed to *Gliravus* cf. *majori* by Vianey-Liaud (1969) is not a *Gliravus*, and the only certain specimen of *G. majori* is the holotype.

Freudenthal (2004) placed *G. garouillensis* Vianey-Liaud, 1994 with doubt in *Schizogliravus* (= *Butseloglis*). Peigné *et al*. (2014) noted that some specimens of that species show the same tendency to form a ridge lingually of the protocone. Therefore *G. garouillensis* may well belong to *Gliravus*.

The attribution of the following species is doubtful: *G. meridionalis* Hartenberger, 1971, *G. minor* Bosma & de Bruijn, 1982, *G. pyrenaicus* Agustí & Arcas, 1997, and *G. robiacensis* Hartenberger, 1965. They are from the late Eocene (MP17) and seem to represent an as yet undescribed genus, since there is no record in the interval MP18-MP24.

The g*enus Butseloglis* Vianey-Liaud, 2004 contains *B. bravoi* (Hugueney, Adrover & Moissenet, 1985), *B. bruijni* (Hugueney, 1967), *B. daamsi* (Bosma & de Bruijn, 1982), *B. hispanicus* (van Dam, 1998), *B. itardiensis* (Vianey-

Liaud, 1989), *B. micio* (Misonne, 1957), *B. montisalbani* (Freudenthal, 2004), and *B. tenuis* (Bahlo, 1975).

The genus *Glamys* Vianey-Liaud, 1989 contains *G. priscus* (Stehlin & Schaub, 1951), *G. olallensis* Freudenthal, 1996, *G. umbriae* Freudenthal, 2004, and possibly *G. devoogdi* (Bosma & de Bruijn, 1979), *G. fordi* (Bosma & de Bruijn, 1979), and *G. minor* (Bosma & de Bruijn, 1982).

Gliravus majori Stehlin & Schaub, 1951

Type-locality. Quercy.

Holotype. Skull with P3-M3 dext., Q.P.625, Basel.

Original diagnosis. (Translated from German and adapted): “The anteroloph occupies the entire width of the crown, and in M3 it forms, together with the posteroloph, a continuous internal cingulum”.

Table 3. Species originally described as *Gliravus* and our taxonomic interpretation.

species	genus	type locality	age
alvarezae Lacomba & Morales, 1987	*Gliravus*	Carrascosa del Campo	MP25
bravoi Hugueney, Adrover & Moissenet, 1985	*Butseloglis*	Vivel del Río	MP28
bruijni Hugueney, 1967	*Butseloglis*	Coderet	MP30
caracensis Daams, Freudenthal, Lacomba & Alvarez, 1989	*Gliravus*	Pareja	MP25
daamsi Bosma & de Bruijn, 1982	*Butseloglis*	Headon Hill 2	MP17
devoogdi Bosma & de Bruijn, 1979	*Glamys*	Headon Hill 7	MP19
fordi Bosma & de Bruijn, 1979	*Glamys*	Bouldnor Cliff	MP21
hispanicus van Dam, 1998	*Butseloglis*	Sossís 2B	MP17
itardiensis Vianey-Liaud, 1989	*Butseloglis*	Itardies	MP23
majori Stehlin & Schaub, 1951	*Gliravus*	Quercy	?
meridionalis Hartenberger, 1971	?	Fons 4	MP17
micio (Misonne, 1957)	*Butseloglis*	Hoogbutsel	MP21
minor Bosma & de Bruijn, 1982	?	Headon Hill 2	MP17
priscus Stehlin & Schaub, 1951	*Glamys*	La Débruge	MP18
pyrenaicus Agustí & Arcas, 1997	?	Sossís 1	MP17
robiacensis Hartenberger, 1965	?	Robiac Sud	MP16
tenuis Bahlo, 1975	*Butseloglis*	Heimersheim	MP23

Description of *Gliravus majori* from Mirambueno 4B. (Fig. 3, Table 4).

p4. Shape blunt. Anterolophid interrupted. Anterotropid absent (9) or small (1). Metalophid free (2) or high connected to the metaconid (8). Centrolophid absent (5), short (4), or of medium length (1). Centrolophid-metaconid connection absent (9) or low (1). Mesostylid absent. Mesoconid placed on the labial border (2) or more centrally (8). Mesolophid short (3), directed towards the metaconid (3), connected to the metaconid (2), directed towards the entoconid (1), or connected to the entoconid (1). Posterotropid absent (8) or very small (2).

m1. Anterolophid labially free. Anterotropid absent. Metalophid free (1), low connected to the metaconid (7), or high connected to the metaconid (6). Centrolophid absent (13) or of medium length (2). Centrolophid-metaconid connection absent (14) or high (1). Mesostylid absent. Mesoconid placed on the labial border (9) or more centrally (6). Mesolophid of medium length (2), directed towards the metaconid (7), connected to the metaconid (5), or to lingual border (1). Posterotropid absent (11), very small (1), or of medium length (3).

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (4), low connected to the metaconid (9), or high connected to the metaconid (4). Centrolophid absent (14) or short (3). Centrolophid-metaconid connection absent (14) or high (3). Mesostylid absent. Mesoconid placed on the labial border (6) or more centrally (10). Mesolophid directed towards the metaconid (6), connected to the metaconid (9), or directed towards the entoconid (2). Posterotropid absent (15) or very small (2).

m3. Anterolophid labially free. Anterotropid absent. Metalophid free (3), low connected to the metaconid (2), or high connected to the metaconid (9). Centrolophid absent (10), short (3), or of medium length (3). Centrolophid-metaconid connection absent (13), low (1), or high (1). Mesostylid absent (11) or crest (1). Mesoconid placed on the labial border (4) or more centrally (14). Mesolophid short (1), directed towards the metaconid (3), connected to the metaconid (4), directed towards the entoconid (3), or connected to the entoconid (6). Posterotropid absent.

P4. Anteroloph short (2) or long (5). Anterotrope absent. Precentroloph absent (4) or long (2). Midcentroloph absent (4), short (2), or long (1). Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (4), anteriorly interrupted (1), or posteriorly interrupted (2). Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (13), short (2), or long (1). Precentroloph absent (14) or connected to the paracone (2). Midcentroloph absent (14), short (1), or long (1). Postcentroloph absent (2) or long (14). Postcentroloph absent (3), connected to the metacone (4), or free from the metacone (9). Prototrope absent. Metatrope absent.

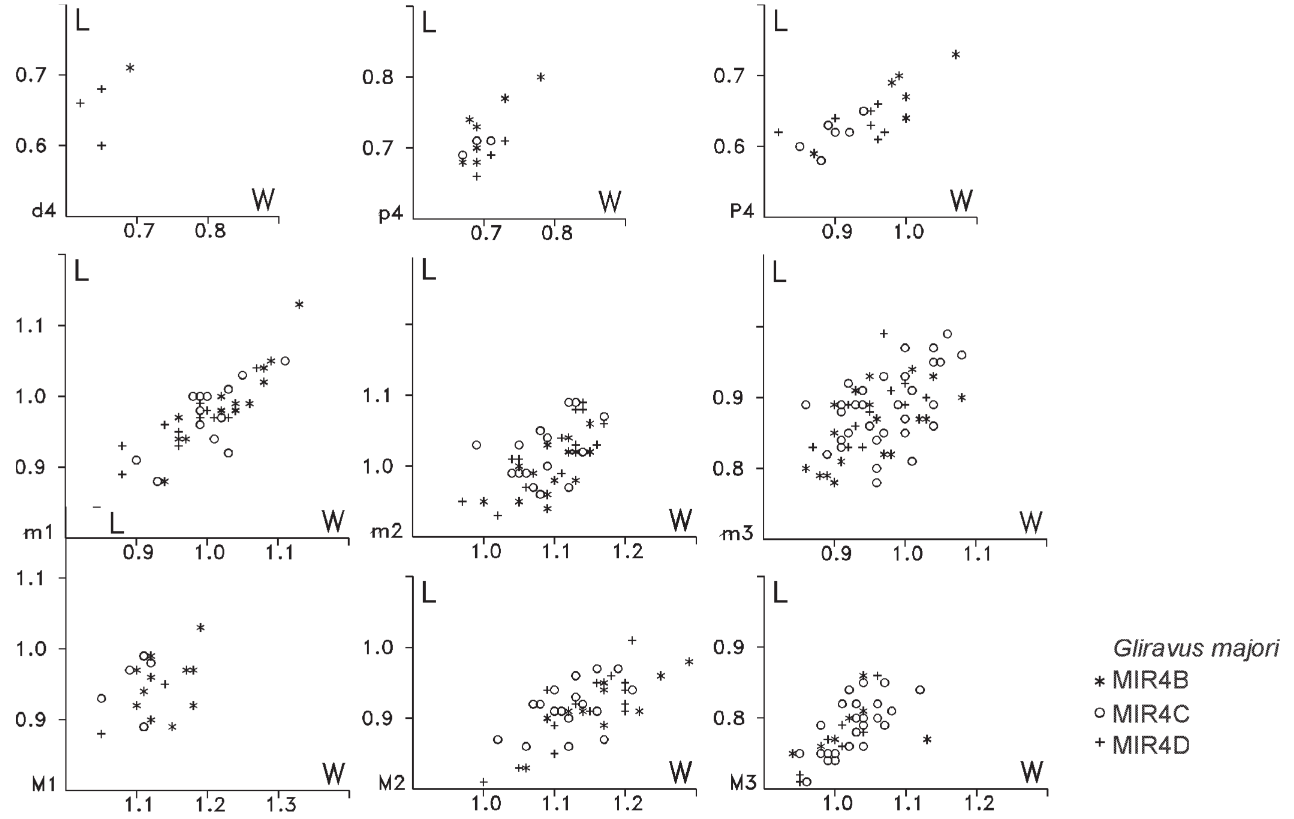


Figure 3. Length/width diagrams of *Gliravus majori* from Mirambueno.

Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (10), partially around protocone (2), or all around protocone (1).

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (9), short (1), or long (1). Precentroloph absent (9) or connected to the paracone (2). Midcentroloph absent (6) or long (6). Postcentroloph absent (7) or long (5). Postcentroloph absent (6), connected to the metacone (1), or free from the metacone (4). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (3), partially around protocone (4), or all around protocone (3).

M3. Anteroloph lingually free (4) or lingually high connected (1). Anterotrope absent. Prototrope absent. Metatrope absent. Crests inside the trigone: 1 crest (6) or two crests (1). Mesostyl absent (4) or present (3). Posterotrope absent. Endoloph formed by the protocone alone (1), partially around protocone (2), or all around protocone (2). Lingual border smooth.

Description of *Gliravus majori* from Mirambueno 4C. (Fig. 3, Figs. 4.1-4.4, Table 4).

p4. Shape blunt. Anterolophid interrupted (1) or continuous (2). Anterotropid absent. Metalophid free (2) or high connected to the metaconid (1). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid absent. Mesolophid absent. Posterotropid absent.

m1. Anterolophid labially free. Anterotropid absent (13), very small (1), or small (1). Metalophid free (7), low connected to the metaconid (4), or high connected to the metaconid (3). Centrolophid absent (14) or short (1). Centrolophid-metaconid connection absent (14) or low (1). Mesostylid absent. Mesoconid placed on the labial border (10) or more centrally (5). Mesolophid directed towards the metaconid (10) or connected to the metaconid (5). Posterotropid absent (7), very small (6) or small (2).

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (4), low connected to the metaconid (9), or high connected to the metaconid (2). Centrolophid absent (13), short (2), or of medium length (1). Centrolophid-metaconid connection absent (15) or low (1). Mesoconid placed on the labial border (1) or more centrally (15). Mesolophid curved forward (1), directed towards the metaconid (8), connected to the metaconid (6), or directed towards the entoconid (1). Posterotropid absent (12), very small (2), or small (2).

m3. Anterolophid labially free (31) or labially connected (1). Anterotropid absent (31) or very small (1).

Table 4. Measurements of *Gliravus majori*, *G. alvarezae* (CARRAS), and *G. caracensis* (PAREJ).

	Length						Width					
d4	N	Min.	Mean	Max.	V’	σ	N	Min.	Mean	Max.	V’	σ
MIR4D	3	0.60	0.647	0.68	12.5		3	0.62	0.640	0.65	4.7	
MIR4B	1		0.710				1		0.690			
p4												
CARRAS	15	0.74	0.85	1.02	31.8		15	0.73	0.81	0.92	23.0	
PAREJ	1		0.73				1		0.69			
MIR4D	3	0.66	0.687	0.71	7.3		3	0.69	0.710	0.73	5.6	
MIR4C	3	0.69	0.703	0.71	2.9		3	0.67	0.690	0.71	5.8	
MIR4B	7	0.68	0.729	0.80	16.2	0.046	9	0.63	0.701	0.78	21.3	0.045
m1												
CARRAS	34	0.89	1.01	1.17	27.2		34	0.95	1.05	1.24	26.5	
PAREJ	21	0.91	0.95	0.99	8.4		21	0.92	0.99	1.10	17.8	
MIR4D	11	0.89	0.962	1.04	15.5	0.038	11	0.88	0.974	1.07	19.5	0.058
MIR4C	14	0.88	0.968	1.05	17.6	0.051	14	0.90	1.009	1.11	20.9	0.058
MIR4B	14	0.88	0.988	1.13	24.9	0.062	13	0.93	1.029	1.13	19.4	0.060
m2												
CARRAS	36	0.87	1.11	1.17	29.4		36	0.95	1.13	1.25	27.3	
PAREJ	21	0.90	0.95	1.03	13.5		21	0.93	1.06	1.16	22.0	
MIR4D	13	0.93	1.021	1.09	15.8	0.051	13	0.97	1.094	1.17	18.7	0.060
MIR4C	15	0.96	1.019	1.09	12.7	0.043	16	0.99	1.084	1.17	16.7	0.046
MIR4B	14	0.94	0.996	1.06	12.0	0.037	15	0.97	1.085	1.15	17.0	0.051
m1,2												
CARRAS	70	0.87	1.061	1.17	29.4		70	0.95	1.091	1.25	27.3	
PAREJ	42	0.90	0.950	1.03	13.5		42	0.92	1.025	1.16	23.1	
MIR4D	24	0.89	0.994	1.09	20.2	0.054	24	0.88	1.039	1.17	28.3	0.084
MIR4C	29	0.88	0.994	1.09	21.3	0.053	30	0.90	1.049	1.17	26.1	0.063
MIR4B	28	0.88	0.992	1.13	24.9	0.050	28	0.93	1.059	1.15	21.2	0.061
m3												
CARRAS	12	0.85	0.92	1.00	16.2		12	0.94	0.99	1.04	10.1	
PAREJ	9	0.84	0.88	0.90	6.9		9	0.89	0.95	1.01	12.6	
MIR4D	11	0.83	0.885	0.99	17.6	0.048	11	0.87	0.955	1.03	16.8	0.046
MIR4C	32	0.78	0.888	0.99	23.7	0.053	31	0.86	0.973	1.08	22.7	0.056
MIR4B	18	0.78	0.859	0.94	18.6	0.053	18	0.86	0.953	1.08	22.7	0.064
P4												
CARRAS	18	0.78	0.88	0.89	13.2		18	0.89	1.08	1.25	33.6	
PAREJ	5	0.60	0.69	0.75	22.2		5	0.92	0.99	1.08	16.0	
MIR4D	8	0.61	0.643	0.71	15.2	0.032	8	0.82	0.931	0.97	16.8	0.050
MIR4C	7	0.58	0.626	0.68	15.9	0.033	6	0.85	0.897	0.94	10.1	0.031
MIR4B	7	0.59	0.669	0.73	21.2	0.045	6	0.87	0.985	1.07	20.6	0.065
M1												
MIR4D	3	0.88	0.930	0.96	8.7		2	1.05	1.095	1.14	8.2	
MIR4C	5	0.89	0.952	0.99	10.6	0.041	5	1.05	1.096	1.12	6.5	0.028
MIR4B	12	0.89	0.955	1.03	14.6	0.042	13	1.06	1.130	1.19	11.6	0.040
M2												
MIR4D	14	0.81	0.914	1.01	22.0	0.054	14	1.00	1.141	1.21	19.0	0.065
MIR4C	17	0.86	0.915	0.97	12.0	0.035	17	1.02	1.121	1.20	16.2	0.048
MIR4B	10	0.83	0.918	0.98	16.6	0.042	10	1.06	1.168	1.29	19.6	0.071
M1,2												
CARRAS	66	0.92	1.03	1.16	23.1		66	1.09	1.24	1.45	28.3	
PAREJ	58	0.82	0.92	1.02	21.7		58	0.98	1.12	1.27	25.8	
MIR4D	17	0.81	0.916	1.01	22.0	0.051	16	1.00	1.135	1.21	19.0	0.065
MIR4C	22	0.86	0.924	0.99	14.1	0.039	22	1.02	1.115	1.20	16.2	0.045
MIR4B	22	0.83	0.938	1.03	21.5	0.045	23	1.06	1.147	1.29	19.6	0.057
M3												
CARRAS	17	0.84	0.95	1.07	24.1		17	0.86	1.00	1.10	24.5	
MIR4D	7	0.71	0.770	0.86	19.1	0.050	7	0.95	1.001	1.06	10.9	0.042
MIR4C	25	0.71	0.787	0.85	17.9	0.039	24	0.95	1.024	1.12	16.4	0.042
MIR4B	7	0.75	0.789	0.86	13.7	0.038	7	0.94	1.021	1.13	18.4	0.060

Metalophid free (5), low connected to the metaconid (6), or high connected to the metaconid (18). Centrolophid absent (14), short (12), or of medium length (4). Centrolophid-metaconid connection absent (15), low (3), or high (12). Mesostylid absent (15), present (5), or crest (5). Mesoconid placed on the labial border (9) or more centrally (23). Mesolophid directed towards the metaconid (1), connected to the metaconid (1), directed towards the entoconid (15), or connected to the entoconid (14). Posterotropid absent (31) or very small (1).

P4. Anteroloph absent (3), short (2), of medium length (1), or long (1). Anterotrope absent. Precentroloph absent (6) or long (1). Midcentroloph absent (4), short (1), or of medium length (2). Postcentroloph absent (6) or long (1). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (5) or long (1). Precentroloph absent (5) or connected to the paracone (1). Midcentroloph absent. Postcentroloph absent (1), short (1), or long (5). Postcentroloph absent (1), connected to the metacone (2), or free from the metacone (4). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (5), partially around protocone (1), or all around protocone (1). Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (17) or long (1). Precentroloph absent (17) or connected to the paracone (1). Midcentroloph absent (5), of medium length (2), or long (10). Postcentroloph absent (13) or long (4). Postcentroloph absent (13), connected to the metacone (2), or free from the metacone (2). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (13), partially around protocone (4), or all around protocone (1). Lingual border smooth.

M3. Anteroloph lingually free (21), lingually low connected (2), or lingually high connected (1). Anterotrope absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Crests inside the trigone: 1 crest (23) or two crests (2). Mesostyl absent. Posterotrope absent. Endoloph formed by the protocone alone (10), partially around protocone (8), or all around protocone (6).

Description of *Gliravus majori* from Mirambueno 4D. (Fig. 3, Table 4).

d4. Anterolophid interrupted. Anterotropid absent. Centrolophid absent (1) or long (1). Centrolophid-metaconid connection absent (1) or low (1). Mesostylid absent. Mesoconid placed centrally. Mesolophid absent. Posterotropid absent.

p4. Shape blunt. Anterolophid continuous. Anterotropid absent. Metalophid high connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed centrally. Mesolophid absent. Posterotropid absent.

m1. Anterolophid labially free. Anterotropid absent. Metalophid free (5), low connected to the metaconid (4), or high connected to the metaconid (2). Centrolophid absent (9) or short (2). Centrolophid-metaconid connection absent (10) or low (1). Mesostylid absent. Mesoconid placed on the labial border (10) or more centrally (1). Mesolophid directed towards the metaconid (7), connected to the metaconid (3), or directed towards the entoconid (1). Posterotropid absent (7) or small (4).

In two specimens there is a longitudinal connection (ectolophid) between metalophid, mesolophid and posterolophid

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (6), low connected to the metaconid (5), or high connected to the metaconid (2). Centrolophid absent (12) or short (1). Centrolophid-metaconid connection absent. Mesostylid absent (11), present (1), or crest (1). Mesoconid placed on the labial border (6) or more centrally (7). Mesolophid of medium length (1), directed towards the metaconid (8), or connected to the metaconid (4). Posterotropid absent (8), very small (2), or small (3).

In one specimen there is a longitudinal connection (ectolophid) between metalophid, mesolophid and posterolophid

m3. Anterolophid labially free. Anterotropid absent. Metalophid free (1) or high connected to the metaconid (9). Centrolophid absent (4), short (1), or of medium length (4). Centrolophid-metaconid connection absent (5) or low (5). Mesostylid absent. Mesoconid placed on the labial border (4) or more centrally (7). Mesolophid directed towards the entoconid. Posterotropid absent.

P4. Anteroloph absent (1), short (4), or long (3). Anterotrope absent. Precentroloph absent. Midcentroloph absent (5), short (2), of medium length (1), or long (1). Postcentroloph absent (6), of medium length (1), or long (2). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (5) or posteriorly interrupted (4). Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent. Precentroloph absent. Midcentroloph absent (1) or long (2). Postcentroloph absent (2) or long (1). Postcentroloph absent (2) or free from the metacone (1). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (1) or partially around protocone (2).

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (12) or long (1). Precentroloph absent (12) or connected to the paracone (1). Midcentroloph absent (5) or long (8). Postcentroloph absent (9) or long (4). Postcentroloph absent (9) or connected to the metacone (4). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (8), partially around protocone (3), or all around protocone (2).

M3. Anteroloph lingually free (6) or lingually low connected (1). Anterotrope absent. Crests inside the trigone: 1 crest (6) or two crests (1). Mesostyl absent. Posterotrope absent. Endoloph complete (1), partially around protocone (2), or all around protocone (4).

Remarks. In MIR4D, the three specimens of p4 are extremely reduced, and consist of only two crests: the posterolophid, and an anterior crest for which we cannot say whether it is the anterolophid or the metalophid. MIR4B 86, MIR4C1025 and MIR4C1026 show this feature too.

Discussion on the *Gliravus* species. *G. alvarezae* is characterized by a continuous cingulum, lingually of the protocone, in all upper molars. In *G. caracensis*, this feature is present but not frequent (8 out of 61 M1,2) and in 26 specimens such a cingulum is present but incomplete. In *G. majori*, this character is only present in the M3 and incomplete in M2, but *G. majori* is only known by its type specimen, a skull fragment from the Quercy, and cannot be evaluated statistically. Therefore, we may assume that *G. alvarezae* and *G. majori* are different species, but the comparison of *G. majori* and *G. caracensis* is not possible.

The three species are roughly of the same size, but there are some problems. In MIR4B there is one large m1 (MIR4B 94, 1.13 x 1.13), well outside the range of the rest of the material (Fig. 3), and consequently the variability coefficient V' is very high (24.9), and suggests the presence of a second species (Table 4). Comparing the measurements of our material with the published data of *G. alvarezae* we found the latter species to present a very wide size range in all elements, certainly not common within a single species (Table 4). Only the size limits of m1 are comparable to our material, for all other elements the maximum is considerably larger, and precisely in m1 we suspect the presence of a second species. An additional problem is the scale in the figure of Lacomba & Morales (1987; pl. 2, fig. 13): according to the scale the holotype of *G. alvarezae* would have a length of 1.21, outside the limits of the measurements table in the same paper.

Genus Butseloglis Vianey-Liaud, 2004

Synonymy. *Schizogliravus* Freudenthal, 2004

Though the publication of the paper by Vianey-Liaud is marked as 2003, it appeared in 2004. Freudenthal (2004) created the genus *Schizogliravus* in a paper that appeared several months later.

Type species. *Butseloglis micio* (Misonne, 1957) from Hoogbutsel (Belgium), lectotype: m2 dext., Ct.M. 1143 (Natural Science Institute, Brussels).

Diagnosis. The original diagnosis of this genus is based on skull characters, in spite of the fact that no such material is found in Hoogbutsel, the type-locality of the type-species. Probably *Gliravus itardiensis* Vianey-Liaud, 1989, type-locality Itardies, is the basis for the skull characters in the diagnosis of *Butseloglis.*

Freudenthal (1996) considered the difference beweeen *B. itardiensis* and *B. micio* to be the presence/absence of an anterotropid in m1,2. In fact, Vianey-Liaud (1989) reported all 24 m1,2 from Itardies to lack the anterotropid and the anterotropid of m1,2 in *B. itardiensis* from OLA4A is absent, except for one case of a very small anterotropid among 143 m1,2. On the other hand, Vianey-Liaud (1994) said that 101 m1,2 of *B. micio* from Hoogbutsel present all variations of the anterotropid between absent and well-developed. In our opinion such a different morphology of m1,2 justifies the distinction of two species.

However, the homogenity of the material attributed to *Butseloglis micio* by Vianey-Liaud (1994) is questionable; maybe (most of) the m1,2 with anterotropid belong to another species, probably a *Bransatoglis*. If that is true *B. itardiensis* indeed may be a synonym of *B. micio*.

The lectotype of *B. micio* lacks the anterotropid and its general aspect is fully compatible with the diagnosis of *Butseloglis*, as given hereafter.

In view of the fact that skull characters are hardly ever known for fossil glirid species, we prefer the diagnosis of *Schizogliravus* Freudenthal, 2004, to characterize *Butseloglis*: P4 triangular like in *Glamys* with a fairly well developed anteroloph. Upper molars with two centrolophs that are frequently connected lingually, or with one single centroloph, which may be the precentroloph or the postcentroloph; extra crests practically absent. In the lower molars, the anterotropid is absent to rare, the centrolophid varies between absent and frequent, but is not very well developed, the posterotropid may be frequent. The postero-lingual corner of M3 is strongly reduced.

Butseloglis bruijni (Hugueney, 1967)

Type locality. Coderet, France (MP30).

Holotype. m2 sin., 96182, Lyon.

Original diagnosis. (Translated from French). "About the size of *Gliravus majori* Stehlin and Schaub, *Gliravus bruijni* differs from all the currently known species of the genus by the absence of a mesoconid in the lower molars; the mesolophid, more or less reduced has a tendency to fuse with the hypoconid; the anterolophid, displaced by the forward position of the protoconid, is short; there are no accessory crests in the posterosinusid; the lower molars have three roots. In the upper molars, generally asymmetrical, the protocone has a tendency to split, the cingulums do not or hardly reach beyond the point of the trigone; the anterior one may be in contact with the protocone; presence of one or two centrolophs of variable direction. P4 very molariform".

Description of *Butseloglis bruijni* from Mirambueno 1. (Figs. 4.5-4.8, Fig. 5, Table 5).

p4. Shape blunt (1) or pointed (1). Anterolophid interrupted. Anterotropid absent. Metalophid low connected to the metaconid (1) or high connected to the metaconid (1). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid on the hypoconid. Mesolophid short. Posterotropid absent.

m1. Anterolophid labially free. Anterotropid absent. Metalophid low connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed centrally. Mesolophid of medium length (1) or directed towards the metaconid (1). Posterotropid absent.

m2. Anterolophid labially free. Anterotropid absent. Metalophid low connected to the metaconid (5) or high connected to the metaconid (2). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border (1), placed centrally (2), or on the hypoconid (4). Mesolophid of medium length (2), curved forward (1), directed towards the entoconid (3), or long and straight (1). Posterotropid absent (6) or very small (1).

m3. Anterolophid labially free. Anterotropid absent. Metalophid low connected to the metaconid (1) or high connected to the metaconid (1). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed centrally. Mesolophid directed towards the entoconid. Posterotropid absent.

P4. Anteroloph absent (1), short (1), of medium length (3), or long (6). Anterotrope absent (10) or short (1). Precentroloph absent (5), short (4), or of medium length (2). Midcentroloph absent. Postcentroloph absent (10) or short (1). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (2) or of medium length (2). Precentroloph absent (2) or connected to the paracone (1). Midcentroloph absent. Postcentroloph absent (2), short (1), or of medium length (1). Postcentroloph absent (2) or connected to the metacone (1). Prototrope absent. Metatrope absent. The centrolophs are not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (5), short (1), or long (2). Precentroloph absent (5), connected to the paracone (2), or free from the paracone (1), generally vague. Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M3. Anteroloph lingually free (6) or lingually high connected (1). Anterotrope absent. Precentroloph absent (4) or long (2). Postcentroloph absent (4) or long (2). Prototrope absent. Metatrope absent. Centrolophs not connected. Crests inside the trigone: absent (1), one crest (5), or four crests (1). Mesostyl absent (6) or present (1). Posterotrope absent. Endoloph formed by the protocone alone (6) or complete (1). Lingual border smooth.

Description of *Butseloglis bruijni* from Mirambueno 2A. (Fig. 5, Table 5).

d4. Anterolophid continuous. Anterotropid absent. Metalophid high connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed centrally. Mesolophid of medium length. Posterotropid absent.

p4. Shape blunt. Anterolophid interrupted (1) or continuous (1). Anterotropid absent. Metalophid high connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed centrally (1) or on the hypoconid (1). Mesolophid absent. Posterotropid absent.

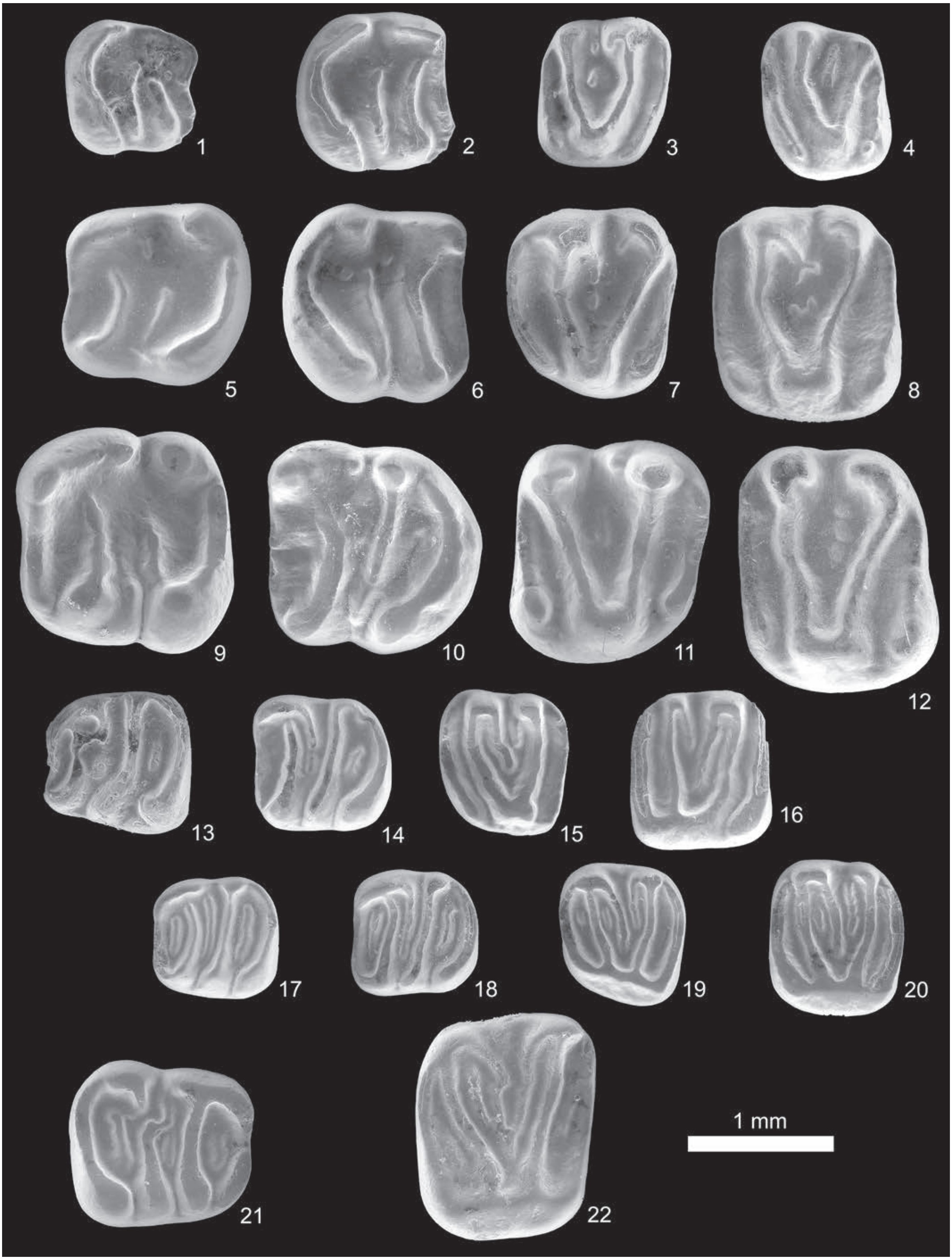
m1. Anterolophid labially free. Anterotropid absent. Metalophid high connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid on the hypoconid. Mesolophid directed towards the metaconid. Posterotropid absent.

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (1) or low connected to the metaconid (4). Centrolophid absent (3), short (1), or short central (1). Centrolophid-metaconid connection absent (4) or low (1). Mesostylid absent. Mesoconid placed on the labial border (2), placed centrally (1), or on the hypoconid (2). Mesolophid directed towards the metaconid (2), directed towards the entoconid (2), or connected to the entoconid (1). Posterotropid absent (2) or very small (3).

m3. Anterolophid labially free. Anterotropid absent. Metalophid low connected to the metaconid (2) or high connected to the metaconid (1). Centrolophid absent (2) or short (1). Centrolophid-metaconid connection absent (2) or high (1). Mesostylid absent. Mesoconid placed centrally (2) or on the hypoconid (1). Mesolophid directed towards the entoconid (1) or connected to the entoconid (2). Posterotropid absent.

D4. Anteroloph long. Anterotrope absent. Precentroloph long. Postcentroloph short. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

P4. Anteroloph long. Anterotrope absent. Precentroloph of medium length. Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs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1 mm

not connected. Posterotrope absent. Endoloph posteriorly interrupted. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent. Precentroloph absent. Midcentroloph absent. Postcentroloph long. Postcentroloph free from the metacone. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (1), of medium length (2), or long (1). Precentroloph absent (1), connected to the paracone (2), or free from the paracone (1). Midcentroloph absent. Postcentroloph absent (3) or short (1). Postcentroloph absent (3) or connected to the metacone (1). Prototrope absent (3) or short (1). Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (3) or all around protocone (1). Lingual border smooth.

Description of *Butseloglis bruijni* from Mirambueno 4C and 4D. (Fig. 5, Table 5).

p4. Shape blunt (12) or pointed (2). Anterolophid interrupted (9) or continuous (1). Anterotropid absent. Metalophid free (4), low connected to the metaconid (3), or high connected to the metaconid (5). Centrolophid absent (10) or of medium length (3). Centrolophid-metaconid connection absent (11) or low (3). Mesostylid absent. Mesoconid placed centrally (3) or on the hypoconid (11). Mesolophid short (2), curved forward (1), directed towards the metaconid (4), or directed towards the entoconid (7). Posterotropid absent (11) or very small (1).

In some specimens there are several structures between metalophid and mesolophid for which the homologies uncertain.

m1. Anterolophid labially free. Anterotropid absent. Metalophid free (3) or low connected to the metaconid (2). Centrolophid absent (3) or short (1). Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border (2), placed centrally (2), or on the hypoconid (1). Mesolophid of medium length (1), curved forward (2), directed towards the metaconid (1), or directed towards the entoconid (1). Posterotropid absent.

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (6) or low connected to the metaconid (2). Centrolophid absent (4), short (3), or of medium length (1). Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border (5) or more centrally (3). Mesolophid of medium length (2), directed towards the metaconid (2), directed towards the entoconid (4), or connected to the entoconid (1). Posterotropid absent (4), very small (1), small (2), or long (1).

m3. Anterolophid labially free (20) or labially connected (1). Anterotropid absent (20) or very small (1). Metalophid free (9) or low connected to the metaconid (10). Centrolophid absent (12), short (6), or of medium length (2). Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border (19) or more centrally (2). Mesolophid directed towards the metaconid (2), directed towards the entoconid (5), or connected to the entoconid (14). Posterotropid absent (16), very small (3), or small (2).

P4. Anteroloph of medium length (6) or long (7). Anterotrope absent. Precentroloph absent (2), short (2), of medium length (5), or long (4); in two cases double. Midcentroloph absent (13) or of medium length (1). Postcentroloph absent (4), short (2), of medium length (5), or long (3). Prototrope absent (12) or short (1). Metatrope absent. Centrolophs not connected (13) or connected (1). Posterotrope absent. Endoloph formed by the protocone alone.

M1. Anteroloph lingually free. Anterotrope absent (12), short (3), or of medium length (1). Precentroloph absent (4), short (6), or long (4); in two cases the long precentroloph is interrupted. Precentroloph absent (4), connected to the paracone (9), or free from the paracone (1). Midcentroloph absent (16) or long (1). Postcentroloph absent (1), of medium length (1), or long (13). Postcentroloph absent (1), connected to the metacone (11), or free from the metacone (2). Prototrope absent. Metatrope absent. Centrolophs not connected (11) or connected lingually (4). Posterotrope absent. Endoloph formed by the protocone alone.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (1) or of medium length (3). Precentroloph absent (1), connected to the paracone (2), or free from the paracone (1). Midcentroloph absent. Postcentroloph of medium length (2) or long (2). Postcentroloph connected to the metacone (2) or free from the metacone (1). Prototrope absent. Metatrope absent. Centrolophs not connected (2) or connected lingually (1). Posterotrope absent. Endoloph formed by the protocone alone.

Figure 4. (1-4) *Gliravus majori* from Mirambueno 4C; **1)** m1 dext. MIR4C 1035. **2)** m2 dext. MIR4C 1052. **3)** M1 dext. MIR4C 1103. **4)** M2 sin. MIR4C 1105. **(5-8)** *Butseloglis bruijni* from Mirambueno1. **5)** m1 sin. RGM 417560. **6)** m2 dext. RGM 417567. **7)** M1 sin. RGM 417579. **8)** M2 sin. RGM 417584. **(9-12)** *Butseloglis bravoi* from Vivel del Río. **9)** m1 sin. VIV 445. **10)** m2 sin. VIV 455. **11)** M1 dext. VIV 480. **12)** M2 sin. VIV 488. **(13-16)** *Peridyromys murinus* from Vivel del Río. **13)** m1 sin. RGM 417950. **14)** m2 sin. RGM 417955. **15)** M1 sin. RGM 417972. **16)** M2 dext. RGM 417978. **(17-20)** *Microdyromys* cf. *legidensis* from Vivel del Río. **17)** m1 sin. VIV 334. **18)** m2 sin. VIV 343. **19)** M1 sin. VIV 368. **20)** M2 sin. VIV 390. **(21-22)** *Paraglis* cf. *fugax*, MIR2A from Mirambueno 2A. **21)** m1 dext. MIR2A 154. **22)** M2 dext. MIR2A RGM 418411.

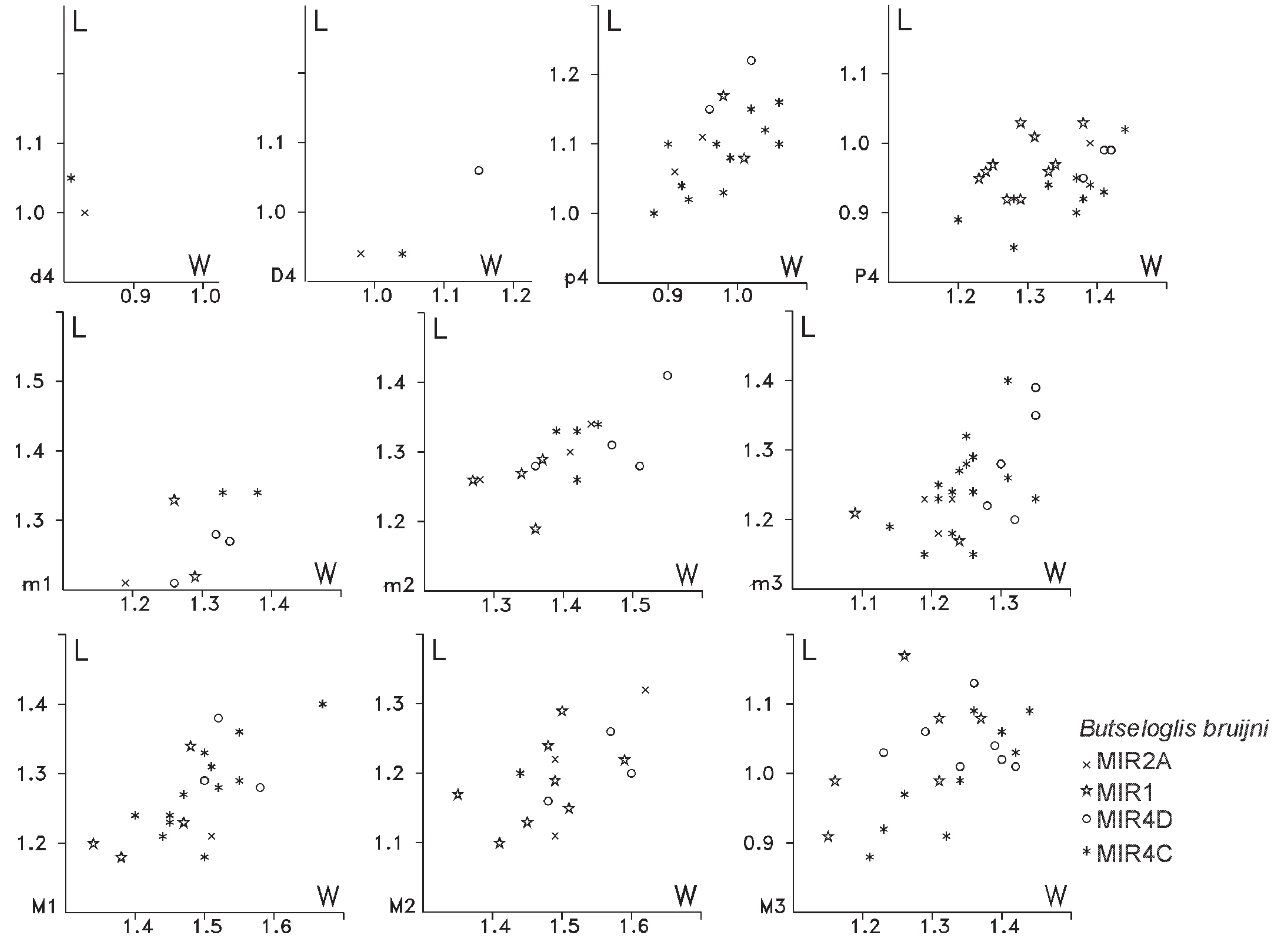

Figure 5. Length/width diagrams of *Butseloglis bruijni* from Mirambueno.

M3. Anteroloph lingually free. Anterotrope absent (15) or short (1). The centrolophs are not connected (15) or connected (1). Crests inside the trigone: 1 crest (11) or two crests (5). Mesostyl absent (12) or present (3). Posterotrope absent. Endoloph formed by the protocone alone. In various specimens there are longitudinal connections.

Remarks. The available material is quite poor. Nevertheless, some tendencies may be noticed in the development of several features in the sequence MIR4B - MIR1 - MIR2A.

From MIR4 to MIR1 the dental pattern becomes more simple: tropes are lost, centroloph(id)s are lost. The mesoconid leaves the lingual border and may connect to the hypoconid. The metalophid-metaconid connection becomes more frequent.

Vianey-Liaud (1994) supposed that the mesoconid of the lower molars disappeared at some time between MP20 and MP25, and that the morphotype *bruijni* is established in MP25 without subsequent important changes. Vianey-Liaud *et al.* (1995) saw a progressive shift of the base of the mesolophid towards the hypoconid from MP25 to MP30. This was based on very few data, and by now much more information is available, which basically confirms the ideas expressed by that author.

In Table 6 we compare frequency data for the position of the mesoconid/mesolophid of p4 and m2 of *B. itardiensis* from OLA4A (MP21), *B. montisalbani* from MLB8 (MP22) and MLB1D (MP23) and *B. bruijni* from Mirambueno, without implying an evolutionary relationship between these species. We call the base of the mesolophid mesoconid, even if it is not inflated to form a cusp.

From MP21 to MP23 the base of the mesolophid begins to shift from the labial border towards a more central position, and from MP26 onwards it may fuse with the hypoconid. In our material from Mirambueno there may be a mesoconid on the labial border, in other specimens the base of the mesolophid is placed more centrally, or the mesolophid arises from the hypoconid. In the younger localities Coderet and Pech Desse (Vianey-Liaud, 1994) the mesolophid of *B. bruijni* is always placed on the hypoconid and there is no mesoconid. Our interpretation is that the mesoconid gradually shifts from the border to a more central position and then fuses with the hyponid.

Table 5. Measurements of *Butseloglis bruijni*.

	Length						**Width**					
d4	N	Min.	Mean	Max.	V’	σ	N	Min.	Mean	Max.	V’	σ
MIR2A	1		1.000				1		0.830			
MIR4C	1		1.050				1		0.810			
p4												
MIR2A	2	1.06	1.085	1.11	4.6		2	0.91	0.930	0.95	4.3	
MIR1	2	1.08	1.125	1.17	8.0		2	0.98	0.995	1.01	3.0	
MIR4D	3	1.05	1.140	1.22	15.0		2	0.96	0.990	1.02	6.1	
MIR4C	11	1.00	1.082	1.16	14.8	0.053	11	0.88	0.977	1.06	18.6	0.064
m1												
MIR2A	1		1.210				1		1.190			
MIR1	2	1.22	1.275	1.33	8.6		2	1.26	1.275	1.29	2.4	
MIR4D	3	1.21	1.253	1.28	5.6		3	1.26	1.307	1.34	6.2	
MIR4C	2	1.34	1.340	1.34	0.0		2	1.33	1.355	1.38	3.7	
m2												
MIR2A	4	1.26	1.290	1.34	6.2	0.038	4	1.27	1.355	1.44	12.5	0.083
MIR1	5	1.19	1.252	1.29	8.1	0.038	6	1.18	1.325	1.43	19.2	0.088
MIR4D	4	1.28	1.320	1.41	9.7	0.062	4	1.36	1.473	1.55	13.1	0.082
MIR4C	5	1.20	1.292	1.34	11.0	0.061	4	1.39	1.420	1.45	4.2	0.024
m1,2												
MIR2A	5	1.21	1.274	1.34	10.2	0.049	5	1.19	1.322	1.44	19.0	0.103
MIR1	7	1.19	1.259	1.33	11.1	0.046	8	1.18	1.313	1.43	19.2	0.078
MIR4D	7	1.21	1.291	1.41	15.3	0.060	7	1.26	1.401	1.55	20.6	0.109
MIR4C	7	1.20	1.306	1.34	11.0	0.055	6	1.33	1.398	1.45	8.6	0.042
m3												
MIR2A	3	1.18	1.213	1.23	4.1		3	1.19	1.210	1.23	3.3	
MIR1	2	1.17	1.190	1.21	3.4		2	1.09	1.165	1.24	12.9	
MIR4D	5	1.20	1.288	1.39	14.7	0.082	5	1.28	1.320	1.35	5.3	0.031
MIR4C	16	1.12	1.238	1.40	22.2	0.070	15	1.14	1.247	1.35	16.9	0.051
D4												
MIR2A	1		0.940				1		0.980			
MIR4D	1		1.060				1		1.150			
MIR4C	1		0.940				1		1.040			
P4												
MIR2A	1		1.000				1		1.390			
MIR1	10	0.92	0.972	1.03	11.3	0.040	10	1.23	1.293	1.38	11.5	0.048
MIR4D	3	0.95	0.977	0.99	4.1		3	1.38	1.403	1.42	2.9	
MIR4C	11	0.85	0.931	1.02	18.2	0.045	10	1.20	1.345	1.44	18.2	0.073
M1												
MIR2A	1		1.210				1		1.510			
MIR1	5	1.18	1.246	1.34	12.7	0.065	4	1.34	1.418	1.48	9.9	0.068
MIR4D	3	1.28	1.317	1.38	7.5		4	1.50	1.533	1.58	5.2	0.034
MIR4C	12	1.18	1.278	1.40	17.1	0.064	12	1.40	1.501	1.67	17.6	0.070
M2												
MIR2A	4	1.11	1.218	1.32	17.3	0.086	3	1.49	1.533	1.62	8.4	
MIR1	8	1.10	1.186	1.29	15.9	0.062	8	1.35	1.473	1.59	16.3	0.071
MIR4D	3	1.16	1.207	1.26	8.3		3	1.48	1.550	1.60	7.8	
MIR4C	1		1.200				1		1.440			
M1,2												
MIR2A	5	1.11	1.216	1.32	17.3	0.074	4	1.49	1.528	1.62	8.4	0.062
MIR1	13	1.10	1.209	1.34	19.7	0.068	12	1.34	1.454	1.59	17.1	0.073
MIR4D	6	1.16	1.262	1.38	17.3	0.077	7	1.48	1.540	1.60	7.8	0.044
MIR4C	13	1.18	1.272	1.40	17.1	0.065	13	1.40	1.496	1.67	17.6	0.069
M3												
MIR1	8	0.91	1.030	1.17	25.0	0.079	7	1.15	1.253	1.37	17.5	0.083
MIR4D	7	1.01	1.043	1.13	11.2	0.042	7	1.23	1.347	1.42	14.3	0.067
MIR4C	9	0.88	0.993	1.09	21.3	0.079	9	1.21	1.331	1.44	17.4	0.083

Table 6. Characters of the mesoconid in *Butseloglis itardiensis* (OLA4A), *B. montisalbani* (MLB8 and MLB1D) and *B. bruijni* (MIR).

	MP21	MP22	MP23	MP26	MP27	MP27
mesoconid	OLA4A	MLB8	MLB1D	MIR4	MIR1	MIR2A
p4	N	N	N	N	N	N
labial border	70	17	24			
absent	0	0	0	0	0	
centrally	1	3	8	3	0	1
on hypoconid	0	0	0	11	2	1
m1						
labial border	56	28	40	2	0	0
centrally	0	0	2	2	2	0
on hypoconid	0	0	0	1	0	1
m2						
labial border	81	39	51	5	1	2
centrally	0	1	3	3	2	1
on hypoconid	0	0	0	0	4	2
m3						
labial border	81	15	58	19	0	0
centrally	1	0	1	2	2	2
on hypoconid	1	0	0	0	0	1

The entire process is most advanced in p4 and gradually decreases from p4 to m3. In Mirambueno, the *bruijni*-morphology is not yet fully established; our material is insufficient to decide whether it permits to distinguish it as a different species.

Butseloglis bravoi (Hugueney, Adrover & Moissenet, 1985)

Type locality. Vivel del Río.

Holotype. m2 sin., VRA 4, Zaragoza.

Original diagnosis. (Translated from French). "The largest species of the genus (*Gliravus*), similar to G. *bruijni* because of the connection metalophid-hypoconid, but different -apart from its size- by the presence of a mesoconid".

Description of *Butseloglis bravoi* from VIV1. (Figs. 4.9-4.12, Fig. 6, Table 7). The lower molars may present little longitudinal connections. The mesolophid is placed on the hypoconid; there may be an additional mesoconid.

d4. Anterolophid interrupted (2) or continuous (1). Anterotropid absent. Metalophid low connected to the metaconid (2) or high connected to the metaconid (3). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid absent. Mesolophid absent (1), short (1), of medium length (2), or directed towards the entoconid (1). Posterotropid absent.

p4. Shape blunt. Anterolophid interrupted. Anterotropid absent. Metalophid free (1), low connected to the metaconid (1), or high connected to the metaconid (1). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid absent. Mesolophid short (2) or directed towards the metaconid (1). Posterotropid absent.

m1. Anterolophid labially free. Anterotropid absent. Metalophid free (4), low connected to the metaconid (8), or high connected to the metaconid (2). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent (12), present (1), or crest (1). Mesoconid placed on the labial border (5) or on the hypoconid (9). Mesolophid of medium length (5), directed towards the metaconid (1), directed towards the entoconid (7), or to lingual border (1). Posterotropid absent (8) or very small (5).

m2. Anterolophid labially free. Anterotropid absent. Metalophid free (5), low connected to the metaconid (9), or high connected to the metaconid (1). Centrolophid absent (14) or short (1). Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border (2) or on the hypoconid (13). Mesolophid short (1), of medium length (2), directed towards the metaconid (1), directed towards the entoconid (8), connected to the entoconid (2), or long and straight (1). Posterotropid absent (11), very small (3), or small (1).

m3. Anterolophid labially free. Anterotropid absent. Metalophid free (2) or low connected to the metaconid (15). Centrolophid absent (13), short (3), or medium central (1). Centrolophid-metaconid connection absent. Mesostylid absent (15) or present (2). Mesoconid placed centrally (8) or on the hypoconid (9). Mesolophid directed towards the entoconid (4) or connected to the entoconid (13). Posterotropid absent (9) or very small (8).

D4. Anteroloph of medium length. Anterotrope absent. Precentroloph of medium length (1) or long (3). Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

P4. Anteroloph of medium length (2) or long (5). Anterotrope absent. Precentroloph short (1), of medium length (2), or long (5). Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (7) or posteriorly interrupted (1). Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (7), short (1), of medium length (2), or long (6). Precentroloph absent (7), connected to the paracone (1), or free from the paracone (8). Midcentroloph absent (13), short (1), of medium length (1), or long (1). Postcentroloph absent (12), of medium length (1), or long (3). Postcentroloph absent (12) or free from the metacone (4). Prototrope absent. Metatrope absent (15) or short (1).

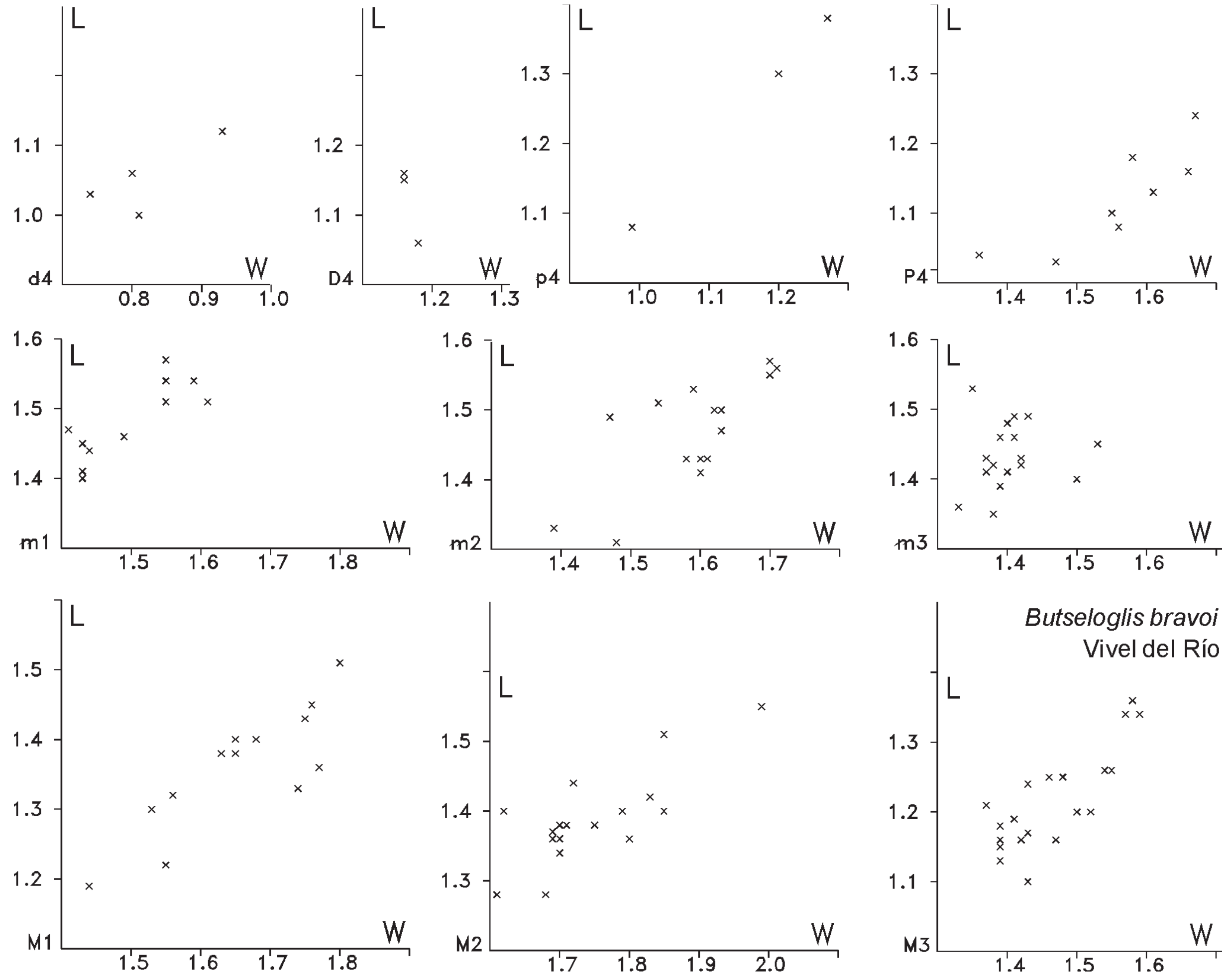

Figure 6. Length/width diagrams of *Butseloglis bravoi* from Vivel del Río.

Centrolophs not connected (15) or connected midway (1). Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (8), short (2), of medium length (3), or long (6). Precentroloph absent (8) or free from the paracone (11). Midcentroloph absent (17), of medium length (1), or long (1). Postcentroloph absent (6), short (4), of medium length (5), or long (3). Postcentroloph absent (5) or free from the metacone (13). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth. In a few specimens there are some small cusps inside trigone.

M3. Anteroloph lingually free. Anterotrope absent. Precentroloph absent (7), short (2), of medium length (2), or long (4). Postcentroloph absent (4), short (2), of medium length (6), or long (2). Crests inside the trigone: 1 crest (9), two crests (9), or three crests (2). Mesostyl absent (9) or present (11). Posterotrope absent. Endoloph formed by the protocone alone (17) or anteriorly interrupted (1). Lingual border smooth.

Subfamily *Peridyromyinae* Freudenthal & Martín-Suárez, 2013

Diagnosis. Daams (1981) gave the following diagnosis for the Myomiminae: "Concave occlusal surface, main cusps fairly well developed, extra ridges narrower than main ridges, relatively high-crowned molars in some genera, generally no endoloph in the M1,2 and a simple dental pattern." Freudenthal & Martín-Suárez (2013) made this the diagnosis of Peridyromyinae and excluded *Myomimus*.

Genera included. *Peridyromys*; *Altomiramys* Díaz-Molina & López-Martínez, 1979; *Armantomys*; *Miodyromys* Kretzoi, 1943; *Praearmantomys* de Bruijn, 1966a; *Pseudodryomys* de Bruijn, 1966a; *Simplomys* García-Paredes *et al.*, 2009; *Tempestia* van de Weerd, 1976; *Ramys* García Moreno & López Martínez, 1986 and *Vasseuromys* Baudelot & de Bonis, 1966.

Genus *Peridyromys* Stehlin & Schaub, 1951

Table 7. Measurements of *Butseloglis bravoi* (* = publ. Hugueney *et al*., 1985).

	Length						Width					
d4	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
VIV*	4	1.00	1.053	1.12	11.3	0.051	5	0.73	0.802	0.93	24.1	0.080
p4												
VIV	6	1.14	1.20	1.25	9.2		6	1.06	1.13	1.19	11.6	
VIV*	3	1.08	1.253	1.38	24.4		3	0.99	1.153	1.27	24.8	
m1												
VIV	19	1.37	1.49	1.57	13.6		19	1.29	1.47	1.59	20.8	
VIV*	14	1.40	1.481	1.57	11.4	0.055	11	1.41	1.498	1.61	13.2	0.074
m2												
VIV	19	1.33	1.49	1.58	17.2		19	1.43	1.62	1.81	23.5	
VIV*	15	1.31	1.468	1.57	18.1	0.078	15	1.39	1.589	1.71	20.6	0.089
m1,2												
VIV	38	1.33	1.490	1.58	17.2		38	1.29	1.545	1.81	33.5	
VIV*	29	1.31	1.474	1.57	18.1	0.067	26	1.39	1.551	1.71	20.6	0.094
m3												
VIV	17	1.31	1.42	1.53	15.5		17	1.36	1.44	1.59	15.6	
VIV*	17	1.35	1.434	1.53	12.5	0.048	17	1.33	1.405	1.53	14.0	0.049
D4												
VIV*	3	1.06	1.123	1.16	9.0		4	1.16	1.190	1.26	8.3	0.048
P4												
VIV	13	0.96	1.10	1.20	22.2		13	1.44	1.52	1.65	13.6	
VIV*	8	1.03	1.120	1.24	18.5	0.072	8	1.36	1.558	1.67	20.5	0.102
M1												
VIV*	14	1.19	1.362	1.51	23.7	0.086	14	1.44	1.666	1.81	22.8	0.113
M2												
VIV*	17	1.28	1.389	1.55	19.1	0.068	19	1.54	1.735	1.99	25.5	0.102
M1,2												
VIV	30	1.25	1.37	1.46	15.5		30	1.44	1.70	1.87	26.0	
VIV*	31	1.19	1.377	1.55	26.3	0.076	33	1.44	1.705	1.99	32.1	0.111
M3												
VIV	22	1.15	1.24	1.39	18.9		22	1.38	1.49	1.62	16.0	
VIV*	20	1.10	1.216	1.36	21.1	0.072	21	1.37	1.471	1.59	14.9	0.074

Original diagnosis. (Translated from German and adapted): The anterior side of the trigone of M1 and M2 points obliquely backward. Lingual cusps and lingual end of the posteroloph fused. In the trigone there are two small, accessory ridges (centrolophs), of which the anterior one joins the paracone. Lower molars with well-developed mesoconid-entoconid ridge (=mesolophid). The protoconid ridge (=metalophid) does not reach the metaconid. Paraconid (=anteroconid), metaconid and mesolophid (=centrolophid) form a continuous ridge, which curves twice at right angles.

Type species *Peridyromys murinus* (Pomel, 1853)

Peridyromys murinus (Pomel, 1853)

Type locality and neotype. The original material of Pomel, from Langy, France, is lost. Stehlin & Schaub coined the name to material from Montaigu-le-Blin. De Bruijn (1966) designated as neotype a maxilla with M1-M2, MA 3215, kept at the Basel Museum.

Description of *Peridyromys murinus* from Mirambueno 1. (Fig. 7, Table 8).

d4. Anterolophid interrupted. Anterotropid absent. Metalophid free. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent.

p4. Shape blunt. Anterolophid continuous. Anterotropid absent. Metalophid free. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent.

m1. Anterolophid labially free (5) or labially connected (6). Anterotropid absent (9), small (1), or of medium length (1). Metalophid free (1), low connected to the metaconid (7), or high connected to the metaconid

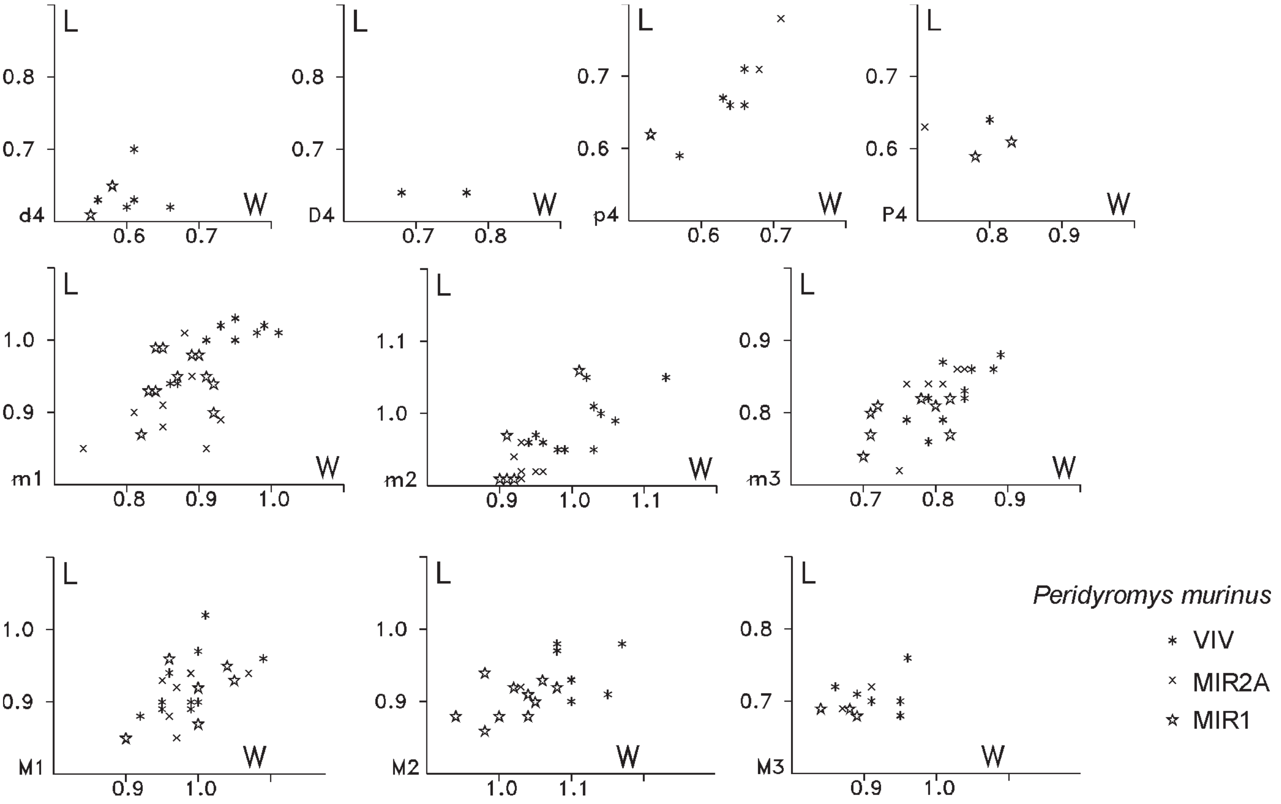

Figure 7. Length/width diagrams of *Peridyromys murinus* from Mirambueno and Vivel del Río.

(3). Centrolophid of medium length (2) or long (9). Centrolophid-metaconid connection low (1) or high (10). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (5), very small (1), small (1), of medium length (3), or long (1).

m2. Anterolophid labially free (3) or labially connected (2). Anterotropid absent. Metalophid low connected to the metaconid (3) or high connected to the metaconid (2). Centrolophid of medium length (1) or long (4). Centrolophid-metaconid connection low (1) or high (4). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (2), very small (1), or of medium length (2).

m3. Anterolophid labially free. Anterotropid absent. Metalophid free (1), low connected to the metaconid (5), or high connected to the metaconid (1). Centrolophid short (5), short central (1), or of medium length (1). Centrolophid-metaconid connection absent (1), low (3), or high (3). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (1) or connected to the entoconid (6). Posterotropid absent (6) or very small (1).

P4. Anteroloph of medium length (1) or long (1). Anterotrope absent. Precentroloph absent (1) or short (1). Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (2), of medium length (3), or long (1). Postcentroloph connected to the metacone. Prototrope absent. Metatrope absent. Centrolophs not connected (3), connected lingually (1), or connected midway (2). Posterotrope absent. Endoloph formed by the protocone alone (2) or anteriorly interrupted (4). Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (4), of medium length (5), or long (1). Postcentroloph connected to the metacone. Prototrope absent. Metatrope absent. Centrolophs not connected (9) or connected midway (1). Posterotrope absent. Endoloph formed by the protocone alone (2) or anteriorly interrupted (7). Lingual border smooth.

M3. Anteroloph lingually high connected. Anterotrope absent (2) or short (1). Precentroloph absent (1) or long (1). Postcentroloph absent (1) or long (1). Prototrope absent. Metatrope absent. Centrolophs not connected. Crests inside the trigone: 1 crest. Mesostyl absent (2) or present (1). Posterotrope absent. Endoloph complete. Lingual border smooth.

Table 8. Measurements of *Peridyromys murinus*.

	Length						Width					
d4	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
VIV	5	0.62	0.640	0.70	12.1	0.034	5	0.56	0.608	0.66	16.4	0.036
MIR1	2	0.61	0.630	0.65	6.3		2	0.55	0.565	0.58	5.3	
p4												
VIV	5	0.59	0.658	0.71	18.5	0.043	5	0.57	0.632	0.66	14.6	0.037
MIR2A	2	0.71	0.745	0.78	9.4		2	0.68	0.695	0.71	4.3	
MIR1	1		0.620				1		0.530			
m1												
VIV	9	0.94	0.997	1.03	9.1	0.034	9	0.86	0.939	1.01	16.0	0.052
MIR2A	8	0.85	0.905	1.01	17.2	0.053	8	0.74	0.858	0.93	22.8	0.061
MIR1	11	0.87	0.946	0.99	12.9	0.038	11	0.82	0.870	0.92	11.5	0.038
m2												
VIV	11	0.95	0.985	1.05	10.0	0.038	11	0.94	1.011	1.13	18.4	0.056
MIR2A	6	0.91	0.928	0.96	5.3	0.018	6	0.92	0.935	0.96	4.3	0.016
MIR1	5	0.91	0.952	1.06	15.2	0.066	5	0.91	0.932	1.01	10.4	0.044
m1,2												
VIV	20	0.94	0.991	1.05	11.1	0.036	20	0.86	0.979	1.13	27.1	0.064
MIR2A	14	0.85	0.915	1.01	17.2	0.043	14	0.74	0.891	0.96	25.9	0.061
MIR1	16	0.87	0.948	1.06	19.7	0.046	16	0.82	0.889	1.01	20.8	0.049
m3												
VIV	10	0.76	0.828	0.88	14.6	0.040	10	0.76	0.826	0.89	15.8	0.041
MIR2A	6	0.72	0.827	0.86	17.7	0.053	6	0.75	0.798	0.84	11.3	0.039
MIR1	8	0.74	0.793	0.82	10.3	0.029	8	0.70	0.758	0.82	15.8	0.053
D4												
VIV	2	0.64	0.640	0.64	0.0		2	0.68	0.725	0.77	12.4	
P4												
VIV	2	0.64	0.655	0.67	4.6		1		0.800			
MIR2A	1		0.630				1		0.710			
MIR1	2	0.59	0.600	0.61	3.3		2	0.78	0.805	0.83	6.2	
M1												
VIV	12	0.88	0.930	1.02	14.7	0.043	10	0.92	0.986	1.09	16.9	0.046
MIR2A	6	0.85	0.910	0.94	10.1	0.037	6	0.95	0.985	1.07	11.9	0.044
MIR1	6	0.85	0.913	0.96	12.2	0.044	6	0.90	0.992	1.05	15.4	0.055
M2												
VIV	7	0.90	0.941	0.98	8.5	0.034	6	1.08	1.113	1.17	8.0	0.038
MIR2A	1		0.920				1		1.030			
MIR1	11	0.86	0.902	0.94	8.9	0.025	10	0.94	1.019	1.08	13.9	0.043
M1,2												
VIV	19	0.88	0.934	1.02	14.7	0.039	16	0.92	1.034	1.17	23.9	0.076
MIR2A	7	0.85	0.911	0.94	10.1	0.034	7	0.95	0.991	1.07	11.9	0.043
MIR1	17	0.85	0.906	0.96	12.2	0.032	16	0.90	1.009	1.08	18.2	0.048
M3												
VIV	6	0.68	0.712	0.76	11.1	0.027	6	0.86	0.920	0.96	11.0	0.040
MIR2A	2	0.69	0.705	0.72	4.3		2	0.87	0.890	0.91	4.5	
MIR1	3	0.68	0.687	0.69	1.5		3	0.84	0.870	0.89	5.8	

Description of *Peridyromys murinus* from Mirambueno 2A. (Fig. 7, Table 8).

p4. Shape blunt. Anterolophid continuous. Anterotropid absent. Metalophid free. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (1) or of medium length (1).

m1. Anterolophid labially free (3) or labially connected (5). Anterotropid absent (7) or very small (1). Metalophid free (4), low connected to the metaconid (3), or high connected to the metaconid (1). Centrolophid short (1), of medium length (1), or long (6). Centrolophid-metaconid connection low (3) or high (5). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the metaconid (1) or connected to the entoconid (7). Posterotropid absent (1), small (2), or of medium length (5).

m2. Anterolophid labially free (2) or labially connected (4). Anterotropid absent (5) or very small (1). Metalophid free (1) or low connected to the metaconid (5). Centrolophid of medium length (1) or long (5). Centrolophid-metaconid connection low (1) or high (5). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (2), of medium length (3), or long (1).

m3. Anterolophid labially free (1) or labially connected (5). Anterotropid absent. Metalophid free (2), low connected to the metaconid (3), or high connected to the metaconid (1). Centrolophid absent (1), short (2), medium central (1), or of medium length (2). Centrolophid-metaconid connection absent (5) or low (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (4) or of medium length (2).

P4. Anteroloph long. Anterotrope absent. Precentroloph long. Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (2), of medium length (3), or long (1). Postcentroloph connected to the metacone. Prototrope absent. Metatrope absent. Centrolophs not connected (4), connected lingually (1), or connected midway (1). Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short. Postcentroloph connected to the metacone. Prototrope absent. Metatrope absent. Centrolophs connected midway. Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

M3. Anteroloph lingually free (1) or lingually high connected (1). Anterotrope absent. Precentroloph absent (1) or long (1). Postcentroloph short (1) or long (1). Prototrope absent. Metatrope absent. The centrolophs are not connected. Crests inside the trigone: 1 crest (1) or two crests (1). Mesostyl absent (1) or present (1). Posterotrope absent. Endoloph anteriorly interrupted (1) or complete (1). Lingual border smooth.

Description of *Peridyromys murinus* from Vivel Del Río. (Figs. 4.13-4.16, Fig. 7, Table 8).

d4. Anterolophid continuous. Anterotropid absent (3) or small (1). Metalophid free (3) or high connected to the metaconid (1). Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid short (2), of medium length (1), or connected to the entoconid (1). Posterotropid absent (3) or small (1).

p4. Shape blunt. Anterolophid interrupted (1) or continuous (4). Anterotropid absent. Metalophid free (3) or high connected to the metaconid (2). Centrolophid absent (4) or of medium length (1). Centrolophid-metaconid connection absent (4) or high (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (2) or connected to the entoconid (3). Posterotropid absent.

m1. Anterolophid labially free (4) or labially connected (5). Anterotropid absent (8) or small (1). Metalophid free (1), low connected to the metaconid (1), or high connected to the metaconid (7). Centrolophid short central (1), of medium length (1), or long (7). Centrolophid-metaconid connection absent (2), low (3), or high (4). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (2), of medium length (1), or long (6).

m2. Anterolophid labially free (11) or labially connected (1). Anterotropid absent. Metalophid free (5), low connected to the metaconid (4), or high connected to the metaconid (3). Centrolophid short (1), of medium length (3), or long (8). Centrolophid-metaconid connection low (1) or high (11). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (3), very small (2), small (2), of medium length (3), or long (2).

m3. Anterolophid labially free. Anterotropid absent. Metalophid free (2), low connected to the metaconid (5), or high connected to the metaconid (3). Centrolophid short (5), of medium length (3), or long (1). Centrolophid-metaconid connection absent (1), low (2), or high (5). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (8) or small (2).

D4. Anteroloph long. Anterotrope absent. Precentroloph absent. Postcentroloph long. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

P4. Anteroloph of medium length (1) or long (1). Anterotrope absent. Precentroloph absent. Midcentroloph absent. Postcentroloph long. Prototrope absent. Metatrope absent. centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone. Lingual border smooth.

M1. Anteroloph lingually free. Anterotrope absent. Precentroloph of medium length (1) or long (11). Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (5) or of medium length (7). Postcentroloph connected to the metacone. Prototrope absent. Metatrope absent. Centrolophs not connected (6), connected lingually (3), or connected midway (3). Posterotrope absent. Endoloph formed by the protocone alone (3) or anteriorly interrupted (8). Lingual border smooth.

M2. Anteroloph lingually free. Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (1), of medium length (5), or long (1). Postcentroloph connected to the metacone. Prototrope absent (6) or short (1). Metatrope absent (6) or of medium length (1). Centrolophs not connected (4), connected lingually (1), or connected midway (2). Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

M3. Anteroloph lingually free (1), lingually low connected (1), or lingually high connected (4). Anterotrope absent. Precentroloph absent (3) or short (2). Postcentroloph long. Prototrope absent. Metatrope absent (5) or short (1). The centrolophs are not connected. Crests inside the trigone: 1 crest (3) or two crests (3). Mesostyl absent. Posterotrope absent. Endoloph formed by the protocone alone (1) or complete (5). Lingual border smooth.

Discussion. *Peridyromys murinus* has a long stratigraphic record of 12.2 Ma. The oldest populations are from MIR1 and MIR2A (MP27), here described. The youngest record is from Buñol (MN4; Daams, 1981). This seems to be a very long range for a species.

The posterotropid of m1,2 is more frequently present in our Oligocene populations than it is in Miocene populations (Table 9). As a general rule we may assume that old glirids have less crests than younger ones, or, in other words, increased number of crests is an advanced character. If we assume that to be true for *Peridyromys* the frequent presence of a posterotropid in m1,2 of Oligocene *P. murinus* and its predominant absence in younger populations may mean that the Oligocene and Miocene representatives are not directly related, and that we are dealing with two different lineages.

Table 9. Absence/presence of posterotropid in m1,2 of *Peridyromys* (in %). Data from Alvarez Sierra *et al.* (1990) and this work.

posterotropid m1,2	absent	present	n
Agreda	99.5	0.5	209
La Galocha 5	95	5	19
San Juan	100	0	17
Bouzigues	70	30	316
Cetina	93	7	55
Santa Cilia	94	6	32
Vivel del Río	23.8	76.2	21
Mirambueno 2A	21.4	78.6	14
Mirambueno 1	43.7	56.3	16

Subfamily *Bransatoglirinae* Daams & de Bruijn, 1995

Genus *Microdyromys* de Bruijn, 1966

Type species *Microdyromys koenigswaldi* de Bruijn, 1966

Diagnosis of the genus. (Modified after Freudenthal & Martín-Suárez, 2007b). Small Gliridae with a slightly or moderately concave occlusal surface and regular, parallel crests. Lingual wall of upper molars often crenulated. Tendency to form a complete endoloph in the older species, complete endoloph present in the younger ones. Both centrolophs long, the precentroloph being longer than the postcentroloph. Centrolophs generally not interconnected. In the upper molars extra crests (tropes) outside the trigone are rare, except for the youngest species. In the lower molars (m1,2) the anterotropid is frequent and the posterotropid is almost constantly present.

Microdyromys koenigswaldi de Bruijn, 1966

Holotype. M2 dext., VA3B 1516, Museo de Paleontología, Sabadell.

Type locality. Valdemoros 3B (MN4, Calatayud-Teruel Basin, Spain). According to de Bruijn (1966, 1967) only one species of *Microdyromys* is present in VA3B. Daams (1981) recognized *M. koenigswaldi* together with what he erroneously called *M. monspeliensis*. But the two were treated together, except for M1,2, and comparison with *M. legidensis* is not possible. For a discussion on the erroneous classification of *M. monspeliensis* see Freudenthal & Martín-Suárez (2007a).

De Bruijn (1967) reported 28 M1,2 of *M. koenigswaldi* from VA3B, all of which have two centrolophs and a prototrope (morphotype H of Daams, 1981). On the other hand, Daams (1981) reported 31 M1,2, two of which lacked a prototrope (for *M. koenigswaldi* and *M. monspeliensis* sensu Daams, 1981 together). The length of the smallest specimen of de Bruijn (1967) is 9.1, that of Daams (1981) is 7.4. In a list kindly provided to us by Dr García Paredes (Madrid) appears a M1 dext. with catalogue number 1548, measurements 7.5 x ± 8.7, which apparently is the specimen Daams attributed to *M. monspeliensis.* Its catalogue number is not in the list of material from VA3B, given by de Bruijn (1967), and its provenance is doubtful. Thanks to Dr de Bruijn we have the complete catalogue lists of the *Microdyromys* material from VA3B; they are mostly typewritten and ordered by dental element. However, the numbers 1546 - 1560 are handwritten and form a random mixture of dental elements. Apparently they were added later and do not form part of the original collection.

Freudenthal (1963; p.78) said in the description of *Megacricetodon collongensis* from VA3B: “This material comes from a bed of only a few centimeters thick, and therefore is very homogeneous”. In fact this bed was a small lens that was only accessible during a very short time and all material that does not form part of the original collection, almost certainly is from another level, close to - but different from - VA3B. See also Freudenthal & Martín-Suárez (2018).

The other specimens attributed to *M. monspeliensis* by Daams (1981) morphologically and metrically fit in the distribution of *M. koenigswaldi*, and the presence of *M. monspeliensis* sensu Daams (1981) in VA3B is not sustained. The only exception is nr 1473, LxW 0.87 x 0.81, classified as m3 in the doctoral thesis of de Bruijn, classified as m2 by de Bruijn (pers. comm., 2018), and considered to be a m1 of which the length cannot be measured reliably by García Paredes (pers. comm., 2018).

Another problem is the presence of *M. remmerti* García-Paredes, Peláez Campomanes & Alvarez Sierra, 2010 in VA3B. It is based on four specimens (one p4, one m3 and two M3), all of them belonging to the original (Utrecht) collection, but, in the absence of first and second molars, the available material is an insufficient basis. García-Paredes *et al*. (2010) considered *M. remmerti* to be a descendant of *M. koenigswaldi*, and its presence in VA3B would mean the co-occurrence of ancestor and descendant in the same locality, which we think is improbable. In our opinion only one species of *Microdyromys* is present in VA3B: *M. koenigswaldi.* Figure 8 shows the LxW diagrams of the material from VA3B, as obtained from the measurement lists of de Bruijn. In the graphs the conflicting numbers mentioned above are indicated.

Microdyromys legidensis Daams, 1981

Holotype. M2 sin., VL2A 1116, currently still in the Utrecht collections. Daams (1981) said: “The holotype will be stored in a collection to be designated by the Comisión Nacional de Geología (Spain)”.

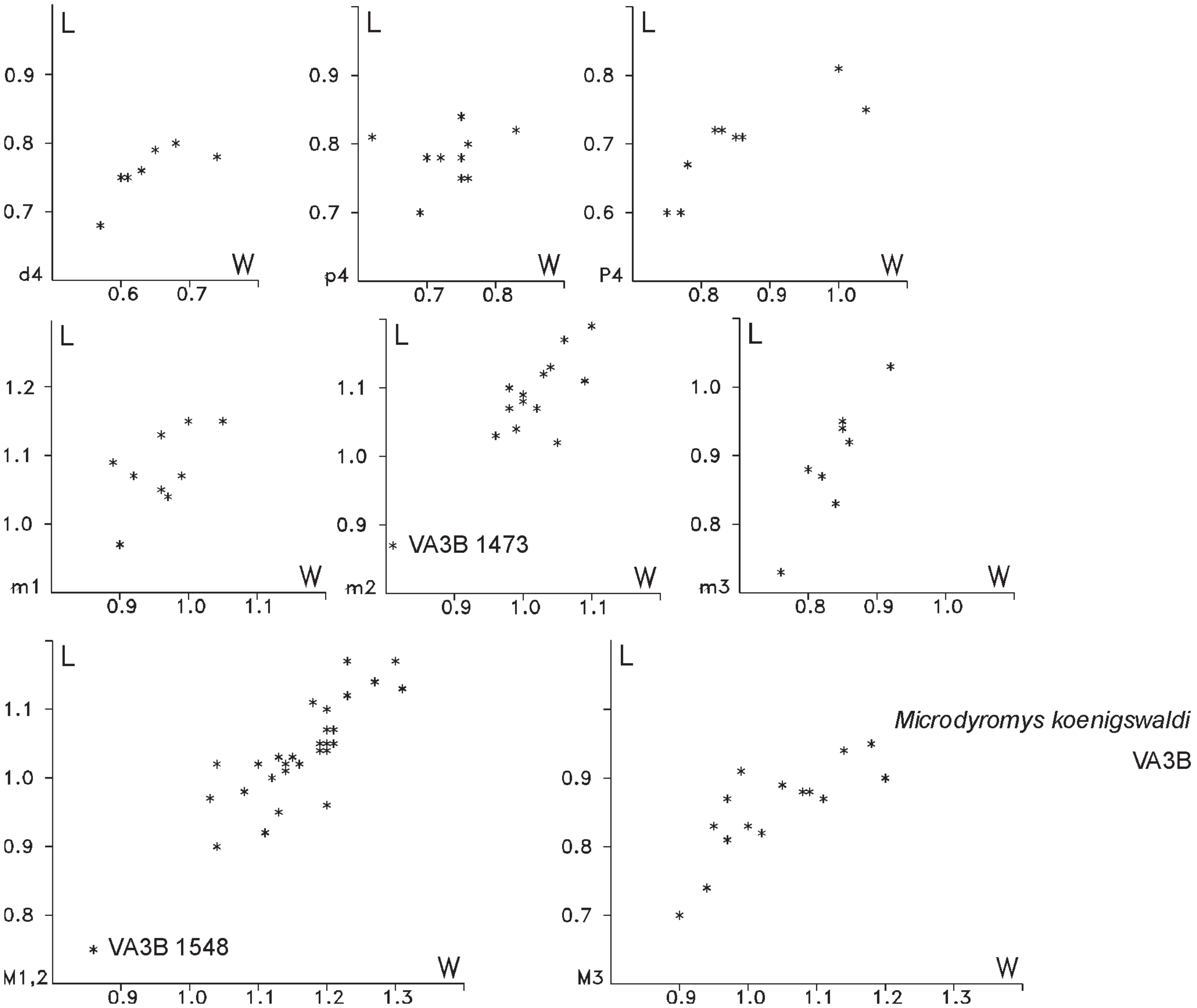

Figure 8. Length/width diagrams of *Microdyromys koenigswaldi* from Valdemoros 3B.

Type locality. Villafeliche 2A (MN4, Calatayud-Teruel Basin, Spain).

Original diagnosis. Relatively small teeth with the intermediate morphotype H of M1,2 dominating.

N.B. Morphotype H of Daams (1981) refers to M1,2 having both precentroloph and postcentroloph, plus a prototrope.

Distribution. According to Daams (1981): St.-Victor-la-Coste (MP29), Coderet (MP30), Bouzigues (MN2), Ateca 3 (MN4).

According to the differential diagnosis by Daams (1981) the only difference between *M. legidensis* (type-locality VL2A) and *M. koenigswaldi* (type-locality VA3B) is size, but, unfortunately, in VL2A he recognized (but not distinguished) *M. legidensis* and *Peridyromys murinus*; his morphological and measurement data lump these two species; only M1,2 was treated separately and can be used to compare size.

Not only is the M1,2 of *M. koenigswaldi* larger than that of *M. legidensis*; all *Microdyromys* populations younger than VL2A have a larger mean value for length and width of M1,2 than all older populations (Figs. 9-10). Therefore we consider *M. legidensis* from VL2A to be a valid species. However, the lack of detail for most of the dental elements makes it impossible to classify other populations unambiguously. Consequently, we classify our material from the upper Oligocene as *Microdyromys* cf. *legidensis*.

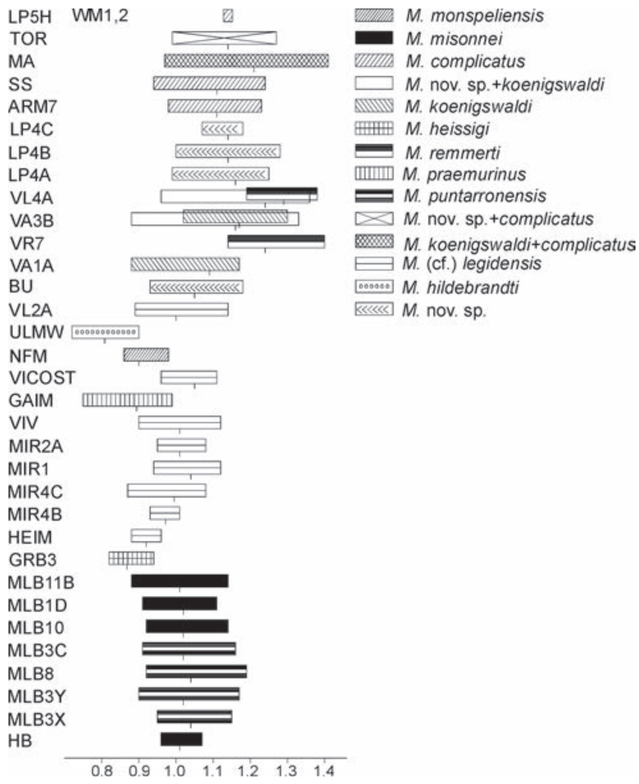

Figure 10. Distribution of the width of *Microdyromys.*

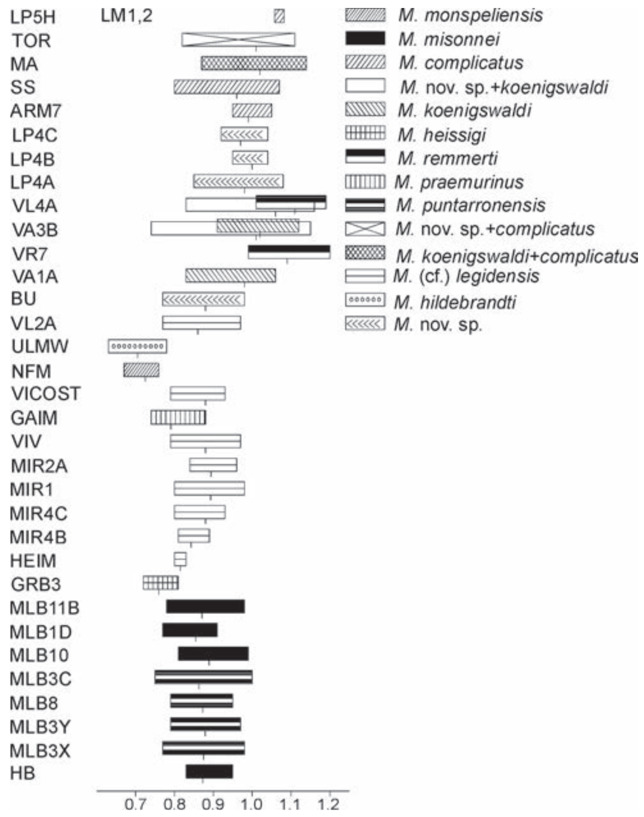

Figure 9. Distribution of the length of *Microdyromys*.

Microdyromys cf. *legidensis* Daams, 1981

Synonymy.

1987 *Microdyromys praemurinus*, Hugueney *et al*. (1987).

1997 *Microdyromys* sp., Freudenthal (1997).

2007 *Microdyromys praemurinus* pro parte, Freudenthal & Martín-Suárez (2007a).

Distribution. Mirambueno 1, 2A, 4B, 4C, 4D, Vivel del Río.

Description of *Microdyromys* cf. *legidensis* from Mirambueno 4B. (Fig. 11, Table 10).

p4. Shape blunt. Anterolophid continuous. Anterotropid very small. Mesostylid absent. Mesolophid connected to the entoconid. Posterotropid long.

m1. Anterolophid labially connected. Anterotropid of medium length (1) or long (1). Metalophid free (1) or low connected to the metaconid (1). Centrolophid of medium length (1) or long (1). Centrolophid-metaconid connection absent (1) or low (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid of medium length (1) or long (1).

m2. Anterolophid labially free (1) or labially connected (5). Anterotropid absent (5) or very small (1). Metalophid free (1), low connected to the metaconid (4), or high connected to the metaconid (1). Centrolophid absent (1), of medium length (3), or long (2). Centrolophid-metaconid connection low (4) or high (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (1), of medium length (3), or long (2).

m3. Anterolophid labially connected. Anterotropid absent. Metalophid low connected to the metaconid. Centrolophid of medium length. Centrolophid-metaconid connection low (1) or high (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (1) or long (1).

M1. Anteroloph lingually free (4) or lingually low connected (1). Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph of medium length (2) or long (3). Postcentroloph connected to the metacone (4) or free from the metacone (1). Prototrope absent (1), short (3), or of medium length (1). Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted . Lingual border smooth (1) or crenulated (4).

Description of *Microdyromys* cf. *legidensis* from Mirambueno 4C. (Fig. 11, Table 10).

p4. Shape blunt. Anterolophid continuous. Anterotropid absent. Metalophid high connected to the metaconid. Centrolophid absent. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid long and straight. Posterotropid long.

m1. Anterolophid labially connected. Anterotropid absent (2) or long (2). Metalophid low connected to the metaconid (1) or high connected to the metaconid (3). Centrolophid long. Centrolophid-metaconid connection low (2) or high (2). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid of medium length (1) or long (3).

m2. Anterolophid labially free (1) or labially connected (5). Anterotropid absent (4), very small (1), small (1), or long (1). Metalophid free (6) or low connected to the metaconid (1). Centrolophid of medium length (4) or long (3). Centrolophid-metaconid connection absent (2), low (1), or high (4). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the metaconid (1), directed towards the entoconid (2), or connected to the entoconid (4). Posterotropid of medium length (1) or long (6).

m3. Anterolophid labially free. Anterotropid absent. Metalophid free. Centrolophid of medium length. Centrolophid-metaconid connection low. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid of medium length.

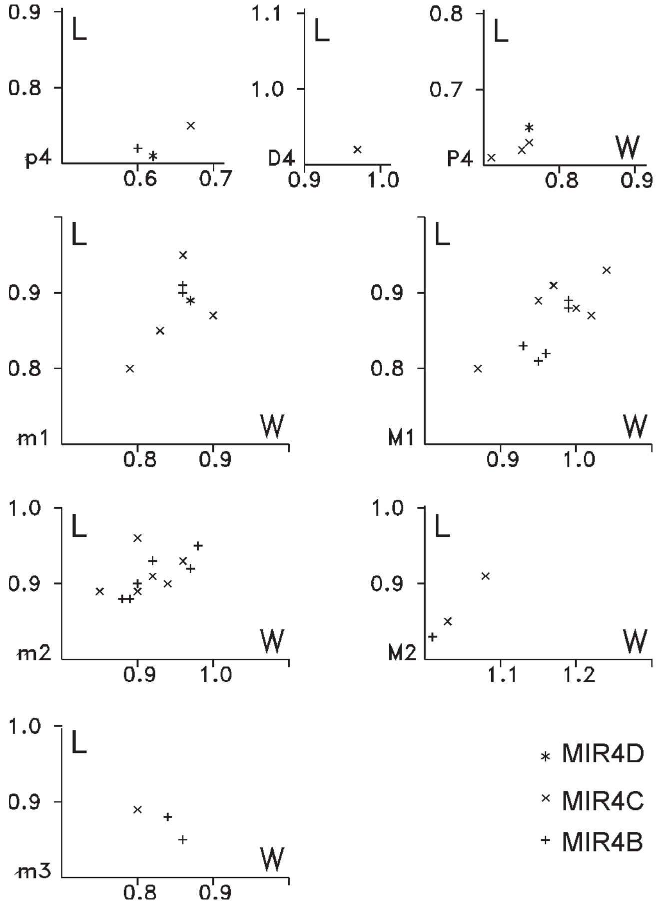

Figure 11. Length/width diagrams of *Microdyromys* cf. *legidensis* from Mirambueno 4.

D4. Anteroloph long. Anterotrope of medium length. Precentroloph long. Postcentroloph absent. Prototrope long. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph complete. Lingual border smooth.

P4. Anteroloph short (1) or of medium length (2). Anterotrope absent. Precentroloph of medium length (1) or long (2). Midcentroloph absent. Postcentroloph absent (1), of medium length (1), or long (1). Prototrope absent. Metatrope absent. Centrolophs not connected (1) or connected (2). Posterotrope absent. Endoloph complete. Lingual border smooth.

M1. Anteroloph lingually free (4) or lingually high connected (2). Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph long, but always shorter than precentroloph. Postcentroloph connected to the metacone (2), free from the metacone (1), or placed centrally (3). Prototrope short (4) or of medium length (2). Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (1), anteriorly

Table 10. Measurements of *Microdyromys* cf. *legidensis*.

	Length						Width					
d4	N	Min.	Mean	Max.	V’	σ	N	Min.	Mean	Max.	V’	σ
VIV	7	0.65	0.696	0.73	11.6	0.030	7	0.55	0.593	0.64	15.1	0.035
MIR1	4	0.71	0.763	0.83	15.6	0.050	4	0.61	0.650	0.68	10.9	0.036
p4												
VIV	14	0.69	0.736	0.81	16.0	0.036	14	0.59	0.638	0.73	21.2	0.040
MIR2A	5	0.71	0.734	0.76	6.8	0.021	5	0.62	0.648	0.69	10.7	0.028
MIR1	3	0.78	0.793	0.82	5.0		3	0.66	0.697	0.72	8.7	
MIR4D	1		0.710				1		0.620			
MIR4C	1		0.750				1		0.670			
MIR4B	1		0.720				1		0.600			
m1												
VIV	18	0.84	0.914	0.98	15.4	0.039	18	0.82	0.887	0.97	16.8	0.039
MIR2A	7	0.86	0.931	0.98	13.0	0.038	7	0.80	0.896	0.95	17.1	0.047
MIR1	12	0.89	0.943	0.99	10.6	0.031	12	0.81	0.909	0.94	14.9	0.036
MIR4D	1		0.890				1		0.870			
MIR4C	4	0.80	0.868	0.95	17.1	0.062	4	0.79	0.845	0.90	13.0	0.047
MIR4B	2	0.90	0.905	0.91	1.1		2	0.86	0.860	0.86	0.0	
m2												
VIV	28	0.84	0.931	1.01	18.4	0.040	27	0.85	0.927	1.00	16.2	0.039
MIR2A	6	0.88	0.935	1.00	12.8	0.045	4	0.88	0.940	1.01	13.8	0.055
MIR1	17	0.82	0.942	1.01	20.8	0.049	15	0.89	0.959	1.03	14.6	0.041
MIR4C	7	0.88	0.909	0.96	8.7	0.028	6	0.85	0.912	0.96	12.2	0.038
MIR4B	6	0.88	0.910	0.95	7.7	0.028	6	0.88	0.922	0.98	10.8	0.044
m1,2												
VIV	46	0.84	0.924	1.01	18.4	0.040	45	0.82	0.911	1.00	19.8	0.043
MIR2A	13	0.86	0.933	1.00	15.1	0.040	11	0.80	0.912	1.01	23.2	0.052
MIR1	29	0.82	0.942	1.01	20.8	0.042	27	0.81	0.937	1.03	23.9	0.046
MIR4D	1		0.890				1		0.870			
MIR4C	11	0.80	0.894	0.96	18.2	0.045	10	0.79	0.885	0.96	19.4	0.052
MIR4B	8	0.88	0.909	0.95	7.7	0.024	8	0.86	0.906	0.98	13.0	0.047
m3												
VIV	17	0.75	0.807	0.87	14.8	0.037	16	0.68	0.779	0.86	23.4	0.049
MIR2A	2	0.80	0.825	0.85	6.1		2	0.73	0.770	0.81	10.4	
MIR1	12	0.74	0.818	0.90	19.5	0.044	12	0.74	0.803	0.85	13.8	0.036
MIR4C	1		0.890				1		0.800			
MIR4B	2	0.85	0.865	0.88	3.5		2	0.84	0.850	0.86	2.4	
D4												
VIV	3	0.61	0.643	0.71	15.2		3	0.72	0.723	0.73	1.4	
MIR4C	1		0.920				1		0.970			
P4												
VIV	14	0.59	0.630	0.68	14.2	0.024	13	0.71	0.758	0.80	11.9	0.037
MIR2A	1		0.650				1		0.780			
MIR1	13	0.58	0.632	0.68	15.9	0.033	13	0.73	0.790	0.84	14.0	0.035
MIR4D	1		0.650				1		0.760			
MIR4C	3	0.61	0.620	0.63	3.2		3	0.71	0.740	0.76	6.8	
M1												
VIV	31	0.79	0.877	0.95	18.4	0.040	28	0.90	0.974	1.05	15.4	0.037
MIR2A	8	0.84	0.889	0.96	13.3	0.042	8	0.95	0.986	1.03	8.1	0.030
MIR1	7	0.86	0.910	0.97	12.0	0.045	6	0.96	1.023	1.08	11.8	0.042
MIR4C	6	0.80	0.880	0.93	15.0	0.045	6	0.87	0.975	1.04	17.8	0.061
MIR4B	5	0.81	0.846	0.89	9.4	0.036	5	0.93	0.964	0.99	6.2	0.026
M2												
VIV	35	0.79	0.882	0.97	20.5	0.040	35	0.98	1.038	1.12	13.3	0.038
MIR2A	7	0.85	0.900	0.95	11.1	0.036	6	1.00	1.047	1.08	7.7	0.029
MIR1	15	0.80	0.885	0.98	20.2	0.048	14	0.94	1.059	1.12	17.5	0.055
MIR4C	2	0.85	0.880	0.91	6.8		2	1.03	1.055	1.08	4.7	
MIR4B	1		0.830				1		1.010			
M1,2												
VIV	66	0.79	0.880	0.97	20.5	0.040	63	0.90	1.010	1.12	21.8	0.049
MIR2A	15	0.84	0.894	0.96	13.3	0.038	14	0.95	1.012	1.08	12.8	0.042
MIR1	22	0.80	0.893	0.98	20.2	0.048	20	0.94	1.048	1.12	17.5	0.053
MIR4C	8	0.80	0.880	0.93	15.0	0.041	8	0.87	0.995	1.08	21.5	0.065
MIR4B	6	0.81	0.843	0.89	9.4	0.033	6	0.93	0.972	1.01	8.2	0.030
M3												
VIV	24	0.63	0.703	0.83	27.4	0.046	23	0.79	0.866	0.96	19.4	0.051
MIR2A	5	0.70	0.734	0.79	12.1	0.034	5	0.89	0.912	0.94	5.5	0.026

interrupted (3), or complete (2). Lingual border smooth (3) or crenulated (3).

M2. Anteroloph lingually free. Anterotrope absent (1) or short (1). Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph long. Postcentroloph placed centrally. Prototrope long. Metatrope absent. centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted . Lingual border crenulated.

Description of *Microdyromys* cf. *legidensis* from Mirambueno 1. (Fig. 12, Table 10).

d4. Anterolophid interrupted (1) or continuous (3). Anterotropid absent (2) or very small (2). Metalophid free (3) or high connected to the metaconid (1). Centrolophid absent (2), of medium length (1), or long (1). Centrolophid-metaconid connection absent (2), low (1), or high (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid of medium length (1), directed towards the entoconid (1), or connected to the entoconid (2). Posterotropid absent (1), very small (1), of medium length (1), or long (1).

p4. Shape blunt. Anterolophid interrupted. Anterotropid absent (1) or very small (1). Metalophid free (1), low connected to the metaconid (1), or high connected to the metaconid (1). Centrolophid long. Centrolophid-metaconid connection absent (2) or low (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (1) or connected to the entoconid (2). Posterotropid long.

m1. Anterolophid labially connected. Anterotropid absent (4), very small (3), of medium length (2), or long (3). Metalophid free (4), low connected to the metaconid (4), or high connected to the metaconid (5). Centrolophid long. Centrolophid-metaconid connection absent (3), low (2), or high (8). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the metaconid (1), connected to the metaconid (1), directed towards the entoconid (1), connected to the entoconid (9), or long and straight (1). Posterotropid long.

m2. Anterolophid labially connected. Anterotropid absent (4), very small (2), small (1), of medium length (9), or long (1). Metalophid free (9), low connected to the metaconid (5), or high connected to the metaconid (3). Centrolophid long. Centrolophid-metaconid connection absent (1), low (2), or high (14). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid of medium length (4) or long (13).

m3. Anterolophid labially free (3) or labially connected (7). Anterotropid absent (10) or small (2). Metalophid free (4), low connected to the metaconid (6), or high connected to the metaconid (1). Centrolophid of medium length (7) or long (5). Centrolophid-metaconid connection absent (2), low (1), or high (9). Mesostylid absent (11) or crest (1). Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (1) or connected to the entoconid (11). Posterotropid absent (2), very small (3), small (3), of medium length (2), or long (2).

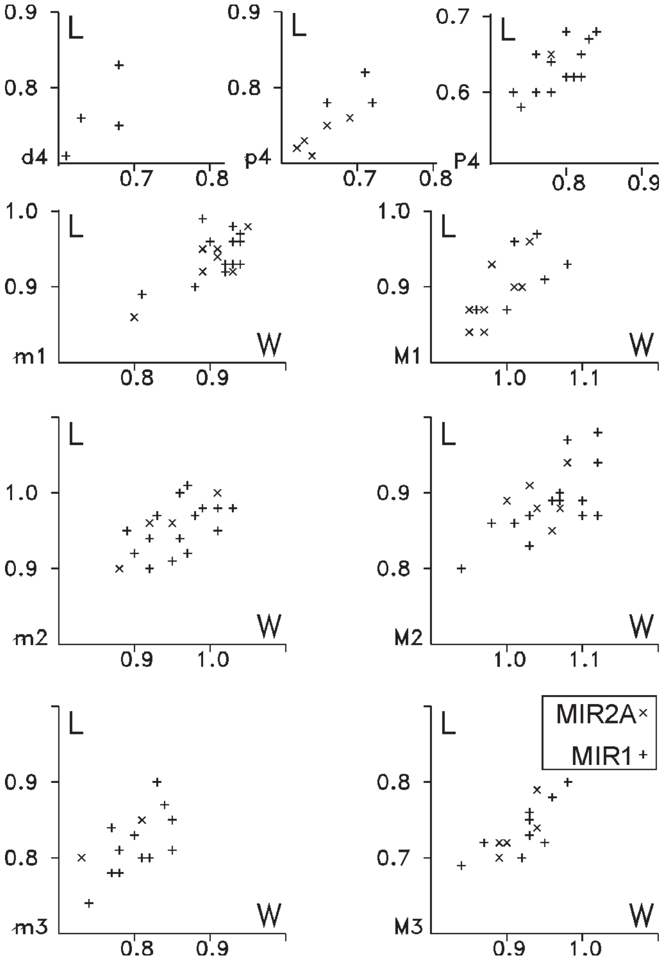

Figure 12. Length/width diagrams of *Microdyromys* cf. *legidensis* from Mirambueno 1 and 2.

P4. Anteroloph short (1), of medium length (8), or long (4). Anterotrope absent. Precentroloph absent (3) or long (10). Midcentroloph absent. Postcentroloph absent (6), short (4), or long (3). Prototrope absent. Metatrope absent (12) or short (1). Centrolophs not connected (12) or connected (1). Posterotrope absent. Endoloph formed by the protocone alone (2), anteriorly interrupted (1), posteriorly interrupted (3), or complete (7). Lingual border smooth.

M1. Anteroloph lingually free (2), lingually low connected (2), or lingually high connected (3). Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph long. Postcentroloph connected to the metacone (6) or placed centrally (1). Prototrope absent (1), of medium length (2), or long (4). Metatrope absent. Centrolophs not connected (4) or connected lingually (3). Posterotrope absent.

Endoloph formed by the protocone alone (1) or complete (6). Lingual border smooth (1) or crenulated (6).

M2. Anteroloph lingually low connected (2) or lingually high connected (11). Anterotrope absent (11) or short (3). Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph short (1) or long (14). Postcentroloph connected to the metacone (7), free from the metacone (3), or placed centrally (4). Prototrope absent (1), of medium length (5), or long (8). Metatrope absent (13) or long (1). Centrolophs not connected (13), connected lingually (1), or connected midway (1). Posterotrope absent. Endoloph anteriorly interrupted (2) or complete (10). Lingual border smooth (1) or crenulated (10).

M3. Anteroloph lingually high connected . Anterotrope absent (9) or long (1). Precentroloph long. Postcentroloph long. Prototrope absent. Metatrope short. Centrolophs not connected (8) or connected (3). Crests inside the trigone: three crests. Mesostyl absent (8) or present (3). Posterotrope absent. Endoloph complete. Lingual border smooth (3) or crenulated (6).

Description of *Microdyromys* cf. *legidensis* from Mirambueno 2A. (Fig. 12, Table 10).

p4. Shape blunt. Anterolophid interrupted (1) or continuous (3). Anterotropid absent. Metalophid low connected to the metaconid (1) or high connected to the metaconid (3). Centrolophid absent (2), short (1), of medium length (1), or long (1). Centrolophid-metaconid connection high. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid absent (2), very small (2), or long (1).

m1. Anterolophid labially connected. Anterotropid very small (1), small (1), of medium length (4), or long (1). Metalophid free (1), low connected to the metaconid (1), or high connected to the metaconid (5). Centrolophid long. Centrolophid-metaconid connection absent (1), low (1), or high (5). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

m2. Anterolophid labially free (2) or labially connected (5). Anterotropid absent (2), small (3), or of medium length (2). Metalophid free (1), low connected to the metaconid (2), or high connected to the metaconid (4). Centrolophid long. Centrolophid-metaconid connection absent (1), low (4), or high (2). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the metaconid (1) or connected to the entoconid (6). Posterotropid long.

m3. Anterolophid labially connected. Anterotropid absent (1) or small (1). Metalophid free (1) or high connected to the metaconid (1). Centrolophid of medium length (1) or long (1). Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

P4. Anteroloph long. Anterotrope absent. Precentroloph long. Midcentroloph absent. Postcentroloph long. Prototrope absent. Metatrope absent. Centrolophs connected. Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

M1. Anteroloph lingually free (5), lingually low connected (2), or lingually high connected (1). Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph long. Postcentroloph connected to the metacone (4) or free from the metacone (4). Prototrope of medium length (6) or long (2). Metatrope absent. centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted (5) or complete (3). Lingual border smooth (4) or crenulated (4).

M2. Anteroloph lingually free (3), lingually low connected (1), or lingually high connected (3). Anterotrope absent. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph of medium length (1) or long (6). Postcentroloph connected to the metacone (5) or free from the metacone (2). Prototrope short (2), of medium length (1), or long (4). Metatrope absent (6) or short (1). Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted (3) or complete (4). Lingual border smooth (4) or crenulated (3).

M3. Anteroloph lingually high connected . Anterotrope absent. Precentroloph long. Postcentroloph absent (1), short (2), or of medium length (1). Prototrope absent (1), short (1), or long (2). Metatrope absent. Centrolophs not connected. Crests inside the trigone: two crests (2) or three crests (3). Mesostyl absent (2) or present (3). Posterotrope absent. Endoloph complete. Lingual border smooth (3) or crenulated (2).

Description of *Microdyromys* cf. *legidensis* from Vivel del Río. (Figs. 4.17-4.20, Fig. 13, Table 10).

d4. Anterolophid interrupted (1) or continuous (6). Anterotropid absent. Metalophid lingually free (6) or high connected to the metaconid (1). Metalophid labially free (4) Centrolophid absent (6) or short (1). Centrolophid-metaconid connection absent (6) or high (1). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid of medium length and interrupted (1) or connected to the entoconid (6). Posterotropid absent (1), very small (1), small (1), of medium length (1), or long (3).

p4. Shape blunt. Anterolophid interrupted (3) or continuous (11). Anterotropid absent (9), very small (5), or small (1). Metalophid free (1), low connected to the metaconid (1), or high connected to the metaconid (13). Centrolophid absent (1), short (2), of medium length (3), or long (9). Centrolophid-metaconid connection absent (2), low (7), or high (5). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (2) or connected to the entoconid (12). Posterotropid absent (2), small (1), of medium length (4), or long (8).

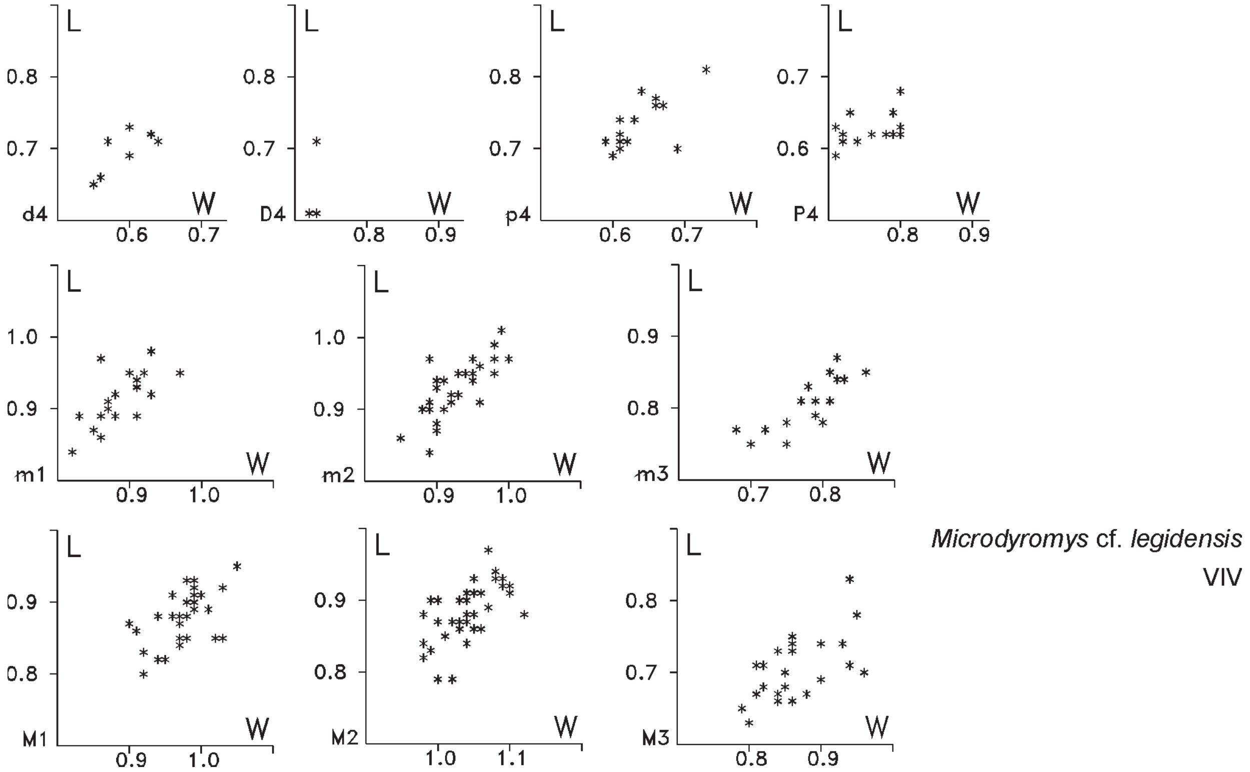

Figure 13. Length/width diagrams of *Microdyromys* cf. *legidensis* from Vivel del Río.

m1. Anterolophid labially connected. Anterotropid absent (2), very small (2), small (2), of medium length (6), or long (6). Metalophid free (6), low connected to the metaconid (1), or high connected to the metaconid (11). Centrolophid long. Centrolophid-metaconid connection absent (3) or high (15). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (1) or connected to the entoconid (17). Posterotropid of medium length (2) or long (16).

m2. Anterolophid labially connected. Anterotropid absent (4), very small (4), small (5), of medium length (10), or long (7). Metalophid free (18), low connected to the metaconid (7), or high connected to the metaconid (5). Centrolophid of medium length (2) or long (30). Centrolophid-metaconid connection absent (4), low (2), or high (25). Mesostylid absent (28) or crest (3). Mesoconid placed on the labial border. Mesolophid directed towards the entoconid (1) or connected to the entoconid (30). Posterotropid of medium length (4) or long (28), double in one case.

m3. Anterolophid labially free (10) or labially connected (6). Anterotropid absent (9), very small (4), small (3), or of medium length (1). Metalophid free (14), low connected to the metaconid (1), or high connected to the metaconid (2). Centrolophid of medium length (2) or long (15). Centrolophid-metaconid connection absent (3), low (1), or high (11). Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid of medium length (3) or long (13).

D4. Anteroloph short. Anterotrope absent. Precentroloph long. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted (2) or complete (1). Lingual border smooth.

P4. Anteroloph short (1), of medium length (7), or long (6). Anterotrope absent. Precentroloph long. Midcentroloph absent. Postcentroloph absent (8), short (4), of medium length (1), or long (1). Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph formed by the protocone alone (1), anteriorly interrupted (10), or complete (2). Lingual border smooth (9) or crenulated (4).

M1. Anteroloph lingually free (16), lingually low connected (7), or lingually high connected (9). Anterotrope absent (30), short (5), or of medium length (1). Precentroloph of medium length (1) or long (35). Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph of medium length (3) or long (33) nearly always shorter than precentroloph. Postcentroloph connected to the metacone (22), free from the metacone (8), or placed centrally (3). Prototrope short (4), of medium length (17), or long (15). Metatrope absent. Centrolophs not connected (33), connected lingually (2), or connected midway (1). Posterotrope absent (33), short (2), or of medium length (1). Endoloph anteriorly interrupted (16), posteriorly interrupted (1), or complete (16). Lingual border smooth (3) or crenulated (32).

M2. Anteroloph lingually free (4), lingually low connected (2), or lingually high connected (32). Anterotrope absent (28), short (8), of medium length (2), or long (1). Precentroloph long, generally longer than postcentroloph. Precentroloph connected to the paracone (38) or free from the paracone (1). Midcentroloph absent. Postcentroloph of medium length (1) or long (38). Postcentroloph connected to the metacone (17), free from the metacone (12), or placed centrally (8). Prototrope absent (3), short (2), of medium length (14), or long (20). Metatrope absent (31), of medium length (2), or long (5). centrolophs not connected (32), connected lingually (1), or connected midway (6). Posterotrope absent. Endoloph anteriorly interrupted (3) or complete (35). Lingual border smooth (4) or crenulated (30).

M3. Anteroloph lingually free (1), lingually low connected (2), or lingually high connected (20). Anterotrope absent (18), short (5), or of medium length (1). Postcentroloph short (3), of medium length (3), or long (17). Centrolophs not connected (16) or connected (5). Crests inside the trigone: two crests (1), three crests (17), or four crests (2). Mesostyl absent (14) or present (3). Posterotrope absent (21), short (1), or of medium length (1). Endoloph posteriorly interrupted (3) or complete (21). Lingual border smooth (8) or crenulated (13).

Discussion. The *Microdyromys* from Vivel was described as *M. praemurinus* by Hugueney *et al*. (1987), but that species is clearly smaller (Figs 9-10). Daams (1981) said that *M. praemurinus* differs from *M. legidensis* by the not-ornamented lingual wall of M1,2, and by the centrolophid which is not connected to the metaconid in 10 out of 14 specimens. Here we will discuss the features used by Daams (op. cit.):

1) Prototrope M1,2. In *M. legidensis* from its type-locality VL2A 3 out of 21 specimens (16%) lack a prototrope. In Vivel and Mirambueno this is the case in only 6 out of 124 specimens (5%). In this respect (morphotype H) our material resembles *M. legidensis* fairly well.

2) Ornamentation. The lingual wall of M1,2 of *M. legidensis* is "generally ornamented" (Daams, 1981). In our material, 21 out of 115 (18%) specimens have a smooth lingual wall. Also in this feature our material resembles *M. legidensis* (Table 11).

According to Daams (1981) such ornamentation is absent in the M1,2 of *M. praemurinus* from Gaimersheim; Kristkoiz (1992) mentions this feature, but apparently referred to something different from other authors, and furthermore said it to be subjective.

Table 11. Ornamentation of the lingual border of M1,2 in *Microdyromys*.

Ornamentation M1,2	locality	n	state	source
M. heissigi	GRB3	20	few small holes 4/20	Uhlig (2001)
M. monspeliensis	NFM	12	absent	Aguilar (1977)
M. monspeliensis sensu Daams	Spain		generally present	Daams (1981)
M. praemurinus	GAIM	11	absent	Daams (1981)
M. praemurinus	GAIM	20	12/20 present ?	Kristkoiz (1992)
M. hildebrandti	ULMW	189	strong	Werner (1994)
M. cf. legidensis	VIV	69	absent 7/69	this paper
M. cf. legidensis	MIR	46	absent 14/46	this paper
M. legidensis	VL2A		generally present	Daams (1981)

3) Metaconid-centrolophid connection. Daams reported a metaconid-centrolophid connection constantly present in VL2A and absent in 10 out of 14 m1,2 from Gaimersheim. In our material from Vivel and Mirambueno, the connection is established in 66 out of 80 specimens (over 80%), quite compatible with *M. legidensis*, and not with *M. praemurinus* (Table 12).

Table 12. Metaconid-centrolophid connection in m1,2 of *Microdyromys* cf. *legidensis*.

		n	absent %	present %	source
M. praemurinus	GAIM	14	71%	29%	Daams (1981)
M. praemurinus	GAIM	34	44%	56%	Kristkoiz (1992)
M. cf. *legidensis*	VIV	49	14%	86%	ths work
M. cf. *legidensis*	MIR	62	15%	85%	ths work
M. legidensis	VL2A	?	0%	100%	Daams (1981)

4) Other features. In the other features used by Daams *Microdyromys* and *Peridyromys* are treated together, and we don't know the character distribution of *M. legidensis* from VL2A. That means we cannot decide whether our material really belongs to *M. legidensis* and therefore we call it *M.* cf. *legidensis.*

According to Daams (1981) in the M1,2 of *M. legidensis* from VL2A the postcentroloph is not connected to the metacone in 73% (n=15); in our material of *M.* cf. *legidensis* the postcentroloph is predominantly connected (Table 13).

In view of the data from Daams (1981), *M. legidensis* from VL2A seems to have less-developed tropids than our material. However, the data from VL2A include *Peridyromys murinus* (Table 14).

Phylogeny of *Microdyromys*. The phylogeny of *Microdyromys* was discussed by Freudenthal & Martín-Suárez (2007a). Here we present a revised version of their figure 5 (Fig. 14).

Table 13. Connection of the postcentroloph in M1,2 of *Microdyromys*. cf. *legidensis*.

M1	MIR4B	MIR4C	MIR1	MIR2A	VIV
	%	%	%	%	%
postcentroloph	N=5	N=6	N=7	N=8	N=33
to metacone	80.0	33.3	85.7	50.0	66.7
free	20.0	16.7	0.0	50.0	24.2
central	0.0	50.0	14.3	0.0	9.1
M2					
postcentroloph	N=0	N=2	N=14	N=7	N=37
to metacone	0.0	0.0	50.0	71.4	45.9
free	0.0	0.0	21.4	28.6	32.4
central	0.0	100.0	28.6	0.0	21.6

Table 14. Absence/presence of tropids in m1,2 of *M.* cf. *legidensis*; * includes *Peridyromys*.

	MIR4B	MIR4C	MIR1	MIR2A	VIV	VL2A*
m1	%	%	%	%	%	%
anterotropid	N=2	N=4	N=12	N=7	N=18	N=35
absent	0.0	50.0	33.3	0.0	11.1	71.4
present	100.0	50.0	66.7	100.0	88.9	28.6
posterotropid	N=2	N=4	N=13	N=7	N=18	N=35
absent	0.0	0.0	0.0	0.0	0.0	65.7
present	100.0	100.0	100.0	100.0	100.0	34.3
m2						
anterotropid	N=6	N=7	N=17	N=7	N=30	N=30
absent	83.3	57.1	23.5	28.6	13.3	76.6
present	16.7	42.9	76.5	71.4	86.7	23.3
posterotropid	N=6	N=7	N=17	N=7	N=32	N=30
absent	16.7	0.0	0.0	0.0	0.0	76.6
present	83.3	100.0	100.0	100.0	100.0	23.3

Freudenthal & Martín-Suárez (2007a) mentioned *Microdyromys* sp. from the Eocene of Aguatón, but the oldest formally described species is *M. misonnei* (Vianey-Liaud, 1994) from the lower Oligocene (MP21) of Hoogbutsel, which is thought to be the ancestor of *M. heissigi* (Uhlig, 2001) from GRB3 (MP25). In *M. misonnei*, the anterotropid is absent in a few m1,2 and the postcentroloph is always present. In *M. heissigi*, a species of smaller size, the anterotropid is absent in some m2, the postcentroloph is absent in two out of 19 M1,2 and anterotropes are relatively frequent.

Microdyromys monspeliensis Aguilar, 1977 from NFM (lower Miocene, MN2) is one of the smallest *Microdyromys* known; it is characterized by a very simple dental pattern. In the m1,2, the anterotropid is absent and there is a well-developed posterotropid. In M1, the postcentroloph is absent (morphotype F as defined by Daams, 1981), in M2 it is absent or incipient in four out of six specimens (morphotype F or G).

Among the stratigraphically older species, in the M1 of *M. hildebrandti* Werner, 1994 from Ulm-Westtangente (lower Miocene, MN2) the postcentroloph may be absent and in these specimens a posterotrope is present. Werner (1994) interprets this posterotrope as the labial part of the original metaloph and the present metaloph as a postcentroloph connected to the lingual part of the original metaloph. The curved shape of the metaloph makes this quite plausible, the more so since posterotropes are practically absent in all other species of Oligocene and lower Miocene *Microdyromys*: among a total of 225 M1 and 216 M2 from 12 populations examined by us, only 3 M1 and 3 M2 have a posterotrope. This crest becomes more frequent in younger populations, from Armantes 7 (MN8) onwards. If Werner's interpretation is correct *M. monspeliensis* and *M. hildebrandti*, both from MN2, cannot be directly related.

On the other hand *M. monspeliensis* may be a descendant of *M. heissigi*, characterized by a simplification of the dental pattern. *M. monspeliensis* may well be the ancestor of *M. monspeliensis* sensu Daams, 1981 from various Spanish localities, which is also characterized by the absence of anterotropids and postcentrolophs, but which is larger than *M. monspeliensis* Aguilar, 1977.

The other small *Microdyromys* species are *M. praemurinus* (Freudenberg, 1941) from Gaimersheim (MP28), and *M. hildebrandti* Werner, 1994 (MN2). These may form a phylogenetic lineage derived from *M. heissigi*, and characterized by an increasing complication of the dental pattern; however *M. praemurinus* is larger than *M. heissigi* and *M. hildebrandti*.

Uhlig (2002) described *M. praemurinus* from Bumbach 1(MP25), but these specimens are larger than *M. praemurinus* and the lingual wall of M1 is crenulated. We attribute this population to *M.* cf. *legidensis*.

All other *Microdyromys* species are larger. Two species from the lower Oligocene are considered here: *M. misonnei* and *M. puntarronensis* Freudenthal & Martín-Suárez, 2007 from several MP22 localities in the Montalbán area (Teruel, Spain). *M. puntarronensis* is thought to be derived from *M. misonnei*. This lineage is characterized by the better-developed anterotropid, anterolophid-protoconid connection, and centrolophid-metaconid connection, the better developed prototrope, and the frequently detached postcentroloph. All these are considered to be advanced characters.

In the MP23 localities from the same area a species that cannot be distinguished from *M. misonnei* replaces *M. puntarronensis*. In these populations the anterotropid and prototrope are less developed, and the postcentroloph is less frequently detached than in the MP22 samples. Both species are equal in size and distinguished only on the basis of percentages of character states. If the two co-occur in a locality they are impossible to separate.

In the upper Oligocene localities, *M.* cf. *legidensis* Daams, 1981 appears. MIR4B (MP25) and MIR4C (MP26) are too poor to make reliable comparisons, but fairly good samples are available from MIR1 (MP27), MIR2A

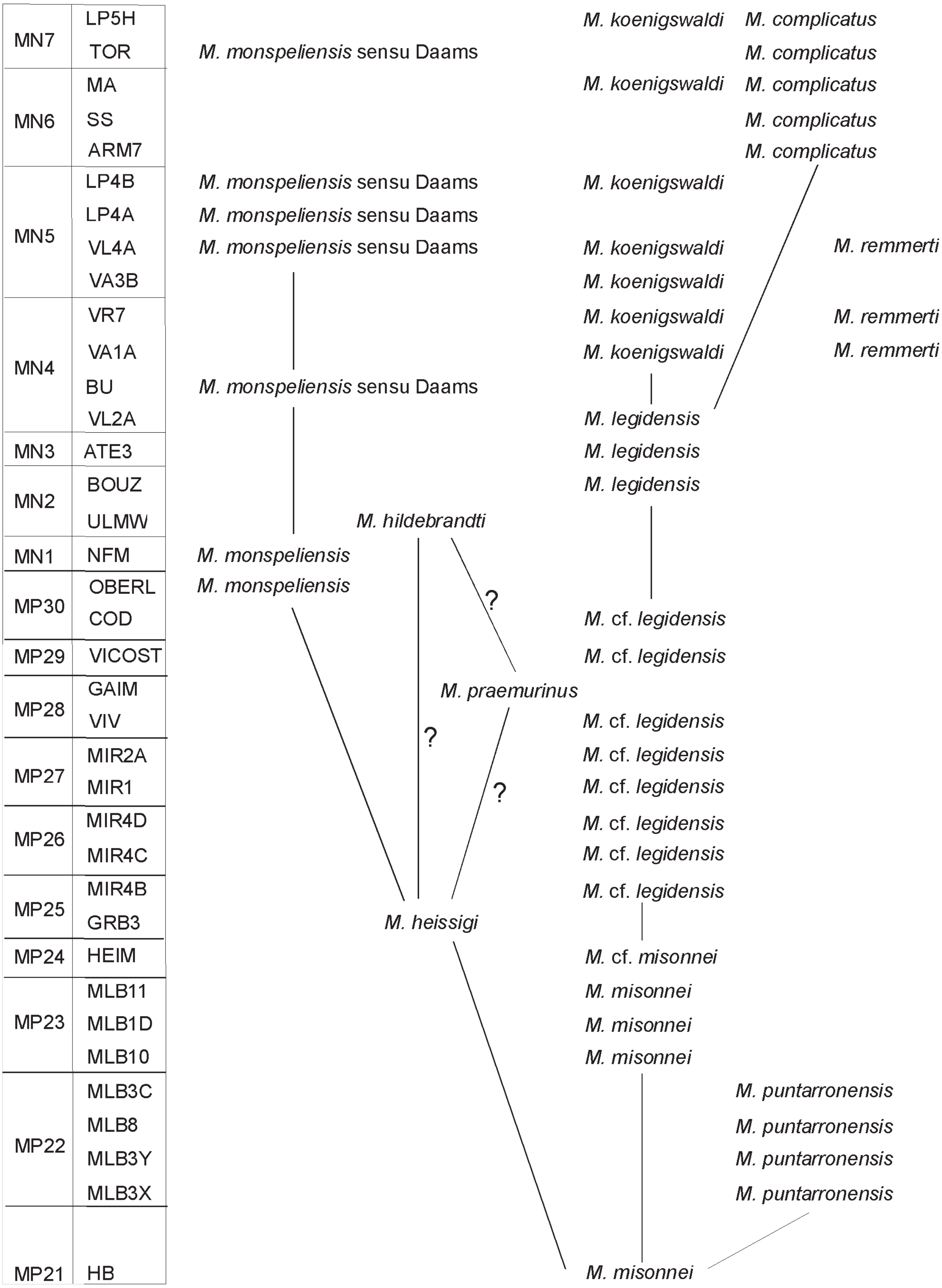

Figure 14. Phylogeny of *Microdyromys*.

(MP27) and VIV (MP28). These are morphologically advanced in comparison with their ancestor *M. misonnei* (Vianey-Liaud, 1994). In the first and second molars, the anterolophid is always connected to protoconid, the centrolophid-metaconid connection is better developed, the anteroloph more frequently connected, the prototrope on average longer, the endoloph more complete, and -except for MIR2A- the lingual border of M1,2 is nearly always crenulated. *M. puntarronensis* cannot be excluded as the ancestor, but in that species the anterotropid is already more developed. It might be true *M. legidensis*, but the description of the lower molars of that species by Daams (1981) includes *Peridyromys murinus*, which makes comparison impossible. However, the oldest population, MIR4B, is from MP25, the type-locality of *M. legidensis* is VL2A (MN2) and it is reported from MN4, implying a time range of 13 Ma, which seems to be little probable. We therefore call it *M.* cf. *legidensis*.

The other Miocene species, *M. koenigswaldi* de Bruijn, 1966 and *M. complicatus* de Bruijn, 1966, are derived from *M. legidensis*. For *M. remmerti* García-Paredes *et al*., 2010, we are not sure.

Extra crests outside the trigone are frequent in *M. complicatus*, rare in *M. remmerti*, present in *M. sinuosus* (Alvarez Sierra & García Moreno, 1986). According to Freudenthal & Martín-Suárez (2013), *M. sinuosus* from the late Miocene of Ampudia 3 (MN10) belongs to the modern Gliridae that diversified in the Vallesian; consequently it is not a *Microdyromys*.

Genus *Paraglis* Baudelot, 1970

Type species *Paraglis astaracensis* Baudelot, 1970.

Diagnosis. (From Freudenthal & Martín-Suárez, 2007b). “Medium-sized Bransatoglirinae. Number of crests in the lower molars like in *Bransatoglis*; upper molars with seven or eight crests, rarely more. In the lower molars the crests are often irregular and interrupted, in contrast with the parallel, well-developed, straight crests of *Bransatoglis* and *Oligodyromys*. The anterotrope may be absent and the posterotrope is usually absent or poorly developed; the extra crests are found inside the trigone. The precentroloph tends to get detached from the paracone and form a mesostyl, and it is often connected to the endoloph. The endoloph is complete, except for the oldest species”.

Paraglis fugax (Hugueney, 1967)

Holotype. M2 sin., no 96223, Lyon

Type locality. Coderet, France (MP30).

Paraglis fugax was described as *Pseudodryomys* and Baudelot (1972) transferred it to the genus *Paraglis*. De Bonis (1973) synonymized *Paraglis* with *Bransatoglis*, an opinion shared by many later authors. Freudenthal & Martín-Suárez (2007b) returned to the use of *Paraglis*.

Werner (1994) described *P.* aff. *fugax* from several MP30 localities in Germany, and stated that this material shows more accessory structures (tropids and tropes) that are subordinate or absent in the type material from Coderet.

Freudenthal & Martín-Suárez (2007b) characterized *Paraglis fugax* as follow: the lower molars have seven ridges, the upper molars eight or nine. In the lower molars, the crests are quite discontinuous. Anterotrope and posterotrope are poorly developed. The endoloph is anteriorly interrupted. The centrolophs are not interconnected. The precentroloph almost reaches the endoloph. The metaloph of M3 is directed towards the labial border of the tooth. P4 is not known from the type locality, but a specimen from Paulhiac (de Bonis, 1973, fig. 7) shows a rounded shape and in this material the centrolophs may be interconnected.

Paraglis cf. *fugax* (Hugueney, 1967)

Our material is very scarce; one specimen from MIR1, three from MIR4B, and a small collection from MIR2A. For material and measurements see Table 15.

Description of *Paraglis* cf. *fugax* from Mirambueno 4B. (Figs. 4.21-4.22).

p4. Shape blunt. Anterolophid continuous. Anterotropid long. Metalophid high connected to the metaconid. Centrolophid long. Centrolophid-metaconid connection low. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

m1. Worn specimen. Centrolophid long. Centrolophid-metaconid connection low. There is a second centrolophid, formed by a small cusp. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

m2. Anterolophid labially free. Anterotropid long. Metalophid low connected to the metaconid. Centrolophid long. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

Description of *Paraglis* cf. *fugax* from Mirambueno 1.

P4. Anteroloph long. Anterotrope absent. Precentroloph long. Midcentroloph absent. Postcentroloph short. Prototrope very thin and low. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted. Lingual border smooth.

Description of *Paraglis* cf. *fugax* from Mirambueno 2A.

d4. Anterolophid continuous. Anterotropid of medium length. Metalophid high connected to the metaconid. Centrolophid of medium length. Centrolophid-metaconid

Table 15. Measurements of *Paraglis* cf. *fugax*.

	Length						Width					
d4	N	Min.	Mean	Max.	V'	σ	N	Min.	Mean	Max.	V'	σ
MIR2A	1		0.980				1		0.780			
p4												
COD	3	0.98	1.02	1.09	10.6		3	0.81	0.88	1.01	22.0	
MIR2A	2	1.05	1.140	1.23	15.8		2	0.94	0.990	1.04	10.1	
MIR4B	1		1.090				1		1.000			
m1												
MIR2A	5	1.26	1.356	1.49	16.7	0.106	5	1.14	1.290	1.37	18.3	0.092
MIR4B	1		1.260				1		1.240			
m2												
MIR2A	1		1.350				1		1.360			
MIR4B	1		1.350				1		1.470			
m1,2												
COD	9	1.16	1.24	1.36	15.9		9	1.26	1.33	1.44	13.3	
MIR2A	6	1.26	1.355	1.49	16.7	0.095	6	1.14	1.302	1.37	18.3	0.087
MIR4B	2	1.26	1.305	1.35	6.9		2	1.24	1.355	1.47	17.0	
m3												
COD	2	1.16	1.21	1.26	8.3		2	1.16	1.20	1.25	7.5	
D4												
COD	1		1.10				1		1.04			
P4												
COD	1		0.99				1		1.10			
MIR1	1		0.980				1		1.150			
MIR2A	2	0.87	0.910	0.95	8.8		3	1.01	1.110	1.17	14.7	
M2												
MIR2A	2	1.27	1.280	1.29	1.6		2	1.47	1.515	1.56	5.9	
M1,2												
COD	6	1.16	1.24	1.36	15.9		5	1.26	1.33	1.44	13.3	
MIR2A	2	1.27	1.280	1.29	1.6		2	1.47	1.515	1.56	5.9	
M3												
COD	2	1.04	1.06	1.09	4.7		1		1.34			
MIR2A	3	0.88	1.000	1.07	19.5		3	1.22	1.253	1.30	6.3	

connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid directed towards the entoconid. Posterotropid long.

p4. Shape blunt. Anterolophid continuous. Anterotropid very small. Metalophid high connected to the metaconid. Centrolophid long. Centrolophid-metaconid connection low. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

m1. Anterolophid labially free (4) or labially connected (1). Anterotropid of medium length (2) or long (3). Metalophid low connected to the metaconid (4) or high connected to the metaconid (1). Centrolophid of medium length (1) or long (4). Centrolophid-metaconid connection low. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the metaconid through the centrolophid (1) or connected to the entoconid (4). Posterotropid long.

There may be a small second centrolophid. The posterotropid may be double or ramified.

m2. Anterolophid labially free. Anterotropid long. Metalophid low connected to the metaconid. Centrolophid long. Centrolophid-metaconid connection absent. Mesostylid absent. Mesoconid placed on the labial border. Mesolophid connected to the entoconid. Posterotropid long.

P4. Anteroloph of medium length (1) or long (2). Anterotrope absent. Precentroloph long. Midcentroloph absent. Postcentroloph absent. Prototrope absent. Metatrope absent. Centrolophs not connected. Posterotrope absent. Endoloph anteriorly interrupted (1) or complete (2). Lingual border smooth.

M2. Anteroloph lingually high connected . Anterotrope long. Precentroloph long. Precentroloph connected to the paracone. Midcentroloph absent. Postcentroloph long. Postcentroloph connected to the metacone. Prototrope absent. Metatrope long. Centrolophs not connected (1) or connected lingually (1). Posterotrope absent (1) or short (1). Endoloph complete. Lingual border smooth.

M3. Anteroloph lingually high connected . Anterotrope absent. Precentroloph of medium length. Postcentroloph long. Prototrope absent. Metatrope of medium length. Centrolophs not connected. Crests inside the trigone: 1 crest (1) or three crests (2). Mesostyl absent. Posterotrope absent. Endoloph complete. Lingual border smooth.

4. RESULTS AND CONCLUSIONS

Several fossil mammal localities in the upper Oligocene of the Montalbán depression contain rich populations of Gliridae. The first one of these is Vivel del Río, discovered by E. Moissenet in 1978 and first published by Hugueney *et al*. (1985). The other localities are Mirambueno 1, 2A, 4B, 4C and 4D, discovered and exploited by our team in the years 1986-1991.

The study of the Gliridae has permitted us to identify six species pertaining to five genera as one may see in Table 16, which gives the faunal lists for the taxonomic groups studied so far.

In our concept (see Freudenthal & Martín-Suárez, 2013), the genus *Gliravus* is restricted to three upper Oligocene species (MP25-26): *G. majori* Stehlin & Schaub, 1951, *G. alvarezae* Lacomba & Morales, 1987, and *G. caracensis* Daams, Freudenthal, Lacomba & Alvarez, 1989. *Gliravus majori*, the single species found in our area, was described by Stehlin and Schaub on the basis of a single skull fragment from the Quercy; its variability and exact age are unknown. In our material, *Gliravus majori* is typically restricted to MP26. We call it *Gliravus majori* because it differs from the other two known species of *Gliravus*. Whether it really belongs to the same species as the holotype is impossible to know.

The genus *Butseloglis* is represented by two species: *Butseloglis bruijni* is present in the oldest localities (MP26-27). From MIR4 to MIR1 the dental pattern becomes more simple: tropes are lost, centroloph(id)s are lost. The mesoconid leaves the lingual border and may connect to the hypoconid. The metalophid-metaconid connection becomes more frequent. In the youngest locality *B. bruijni* has been replaced by *Butseloglis bravoi,* known only from its type locality Vivel; it may be derived from *B. bruijni*.

Peridyromys murinus appears for the first time in MP27 and its origin is not clear. Freudenthal & Martín-Suárez (2013) suggested that it may be derived either

Table 16. Faunal distribution.

	MP26			MP27		MP28
	MIR4B	MIR4C	MIR4D	MIR1	MIR2A	VIV
Gliravus majori	X	X	X			
Butseloglis bruijni		X	X	X	X	
Butseloglis bravoi						X
Peridyromys murinus				X	X	X
Microdyromys cf. *legidensis*	X	X	X	X	X	X
Paraglis fugax	X			X	X	
Eucricetodon aff. *dubius*		X		X	X	X
Eucricetodon martinensis		X	X			
Pseudocricetodon aff. *simplex*	X	X	X			
Pseudocricetodon philippi		X				
Pseudocricetodon adroveri					X	X
Pseudocricetodon sp.				X		
Allocricetodon incertus	X	X	X			X
Allocricetodon landroveri		X	X			X
Allocricetodon cornelii				X	X	X
Heterocricetodon hausi	X					
Heterocricetodon cf. *stehlini*		X	X	X		
Plesiosminthus cf. *margaritae*				X		X
Plesiosminthus aff. *conjunctus*					X	
Plesiosminthus sp.					X	

from *Microdyromys* or from *Butseloglis*, but it cannot be discarded that it is an immigant with unknown roots. *P. murinus* seems to have a very long stratigraphical range.

Microdyromys is present in all our samples; in fact it has a very long distribution range from early Oligocene through middle Miocene. Our populations (MP26-27-28) are morphologically advanced in comparison with their ancestor *M. misonnei* (Vianey-Liaud, 1994).

Our material of *Paraglis* is so poor, that it permits no conclusions.

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