

# Revision of the subfamily Bransatoglinirinae (Gliridae, Rodentia, Mammalia)

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Key words – Gliridae, Bransatoglinirinae, classification, new species.

Daams & de Bruijn created the subfamily Bransatoglinirinae for the genus *Bransatoglis* Huguency, and considered *Paraglis* Baudelot and *Oligodyromys* Bahlo to be synonyms of *Bransatoglis*. Twenty two valid species have been classified as *Bransatoglis* or one of its supposed synonyms, ranging in age from Late Eocene (MP17) to Middle Miocene (MN6) and varying in size from very small to very large. Apparently, *Bransatoglis* has become a ‘wastebasket’ and it is impossible to formulate a diagnosis that covers all these species. In this paper the genera *Paraglis* and *Oligodyromys* are restored, new diagnoses are given and the genus *Microdyromys* is transferred from the Dryomyiinae to the Bransatoglinirinae. A new species of *Oligodyromys*, *O. libanicus*, is described from the Lower Oligocene of Montalbán 8 (Teruel, Spain).

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## Introduction

Huguency (1967) published the genus name *Bransatoglis*, based on the name of the village Branssat. When she published her 1969 paper the name of the village had been officially changed into Bransat and Huguency adapted the genus name (*Bransatoglis*). Mrs Huguency drew our attention to the fact that this contravenes Article 33.2.3 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1999), which would consider it an unjustified emendation. However, Article 33.2.3.1 states that “... when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation.” The prevailing usage (see below) makes *Bransatoglis* a justified emendation under this article.

In their classification of the Gliridae, Daams & de Bruijn (1995) created the monogeneric subfamily Bransatoglinirinae for the genus *Bransatoglis* Huguency, 1967, and considered *Paraglis* Baudelot, 1970, and *Oligodyromys* Bahlo, 1975, to be synonyms of

*Bransatoglis*. The diagnosis of the new subfamily was the same as the diagnosis of the type genus, given by Bosma & de Bruijn (1982).

In the concept of Daams & de Bruijn, the genus contained 14 species and since then new species have been described, so that by now 22 valid species names have been classified as *Bransatoglis* or one of its supposed synonyms. These species cover a very wide stratigraphic range, from Late Eocene (MP17) to Middle Miocene (MN6), and their size varies from very small to very large. In such conditions it is impossible to formulate a useful diagnosis that distinguishes it from other taxa. In this paper, the genera *Paraglis* and *Oligodyromys* are restored, new diagnoses are given, and the genus *Microdyromys* is transferred from the Dryomyinae to the Bransatoglininae. A new species of *Oligodyromys*, *O. libanicus*, is described from the Lower Oligocene of Montalbán 8 (Teruel, Spain).

### Methods

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

Measurements are given in 0.1 mm units. The nomenclature of parts of the cheek teeth is as defined by Freudenthal & Martín-Suárez (2006). *V*' is the variability coefficient as defined by Freudenthal & Cuenca Bescós (1984).

*Abbreviations* – IRSNB, Institut Royal des Sciences Naturelles de Belgique; RGM, geological collections of the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

#### Locality codes -

AGT2D	Aguatón 2D	HH7	Headon Hill 7
ANW	Anwil	HRM1	Harami 1
BELCHA	Belchatów A	ITA	Itardies
BELCHC	Belchatów C	KOC	Kocayarma
BEZ	Bézian	LFQ	Lacey's Farm Quarry
BIR	Birosse	LR	La Romieu
BU	Buñol	MIR4B	Mirambueno 4B
CHR6C	Chorrillo 6C	MLB1D	Montalbán 1D
COD	Coderet	MLB3X	Montalbán 3X
EG-ERD	Eggingen-Erdbeerhecke	MLB3Y	Montalbán 3Y
EG-MI1	Eggingen-Mittelhart 1	MLB8	Montalbán 8
EG-MI2	Eggingen-Mittelhart 2	OLA4A	Olalla 4A
EST	Estrepouy	PAG1	Paguera 1
FF3B	Fuenferrada 3B	PHC	Paulhiac
FONS4	Fons 4	SCHW	Schönweg
FORST	Forsthart	SIN	Sineu
GRB3	Gröben 3	SRD	Serido
HB	Hoogbutsel	SS	Sansan
HEIM	Heimersheim	ULMW	Ulm Westtangente
HH3	Headon Hill 3	UMB1B	Fuente Umbría 1B
HH5	Headon Hill 5	WW	Wintershof-West
HH6	Headon Hill 6		

## Systematic palaeontology

### *Oligodyromys libanicus* sp. nov.

Pl. 1.

*Type locality* – Montalbán 8.

*Derivatio nominis* – Montalbán is said to have been founded around 200 B.C. by settlers who called the place Libana.

*Holotype* – MLB8 1183, m1 sin., to be stored in the collections of the ‘Departamento de las Ciencias de la Tierra,’ University of Zaragoza.

*Objective synonymy* – *Bransatoglis* sp. nov. larger than *B. parvus* from MLB8 in Freudenthal (1997a).

*Other localities* – Montalbán 3X, Montalbán 3Y.

*Diagnosis* – Anterotropid only well-developed in m1, poorly developed or absent in the other elements of the lower dentition. Centrolophid and posterotropid generally long. In m3 the posterotropid is frequently connected to the lingual part of the posterolophid. The mesolophid is generally connected to the entoconid. In M1,2 an anterotrope is present in somewhat less than half the specimens, in M3 it is more frequent. The posterotrope is absent in M1, rare in M2 and frequent in M3. In M1,2 there is never a complete endoloph.

The occlusal surface of the lower molars is flat, with an uplifted metaconid and a less pronounced entoconid. The occlusal surface of the upper molars is moderately concave.

*Differential diagnosis* – Largest *Oligodyromys* known; only *O. sjeni* (Ünay-Bayraktar, 1989) is of the same size.

#### Difference with

<i>O. sjeni</i>	much more simple dental pattern.
<i>O. attenuatus</i> (Peláez-Campomanes, 2000)	less-developed anterotropid, prototrope, metatrope and posterotrope.
<i>O. parvus</i> (Freudenthal, 1996)	less-developed anterotropid in m2; more frequently interconnected centrolophs; less-developed endoloph and more complex pattern of M3.
<i>O. bahloi</i> (Bosma & de Bruijn, 1982)	frequent presence of an anterotrope.
<i>O. moyai</i> (Hugueney & Adrover, 1990)	incomplete endoloph and smaller number of crests in m2.
<i>O. planus</i> Bahlo, 1975	slightly larger; endoloph less complete and anterotropid less developed.
<i>Paraglis</i>	same size as various <i>Paraglis</i> species, but never a complete endoloph.
<i>Bransatoglis</i>	much smaller size.

*Material* – MLB8 910 - 913, 1024, 1030, 1042, 1065, 1138 - 1356, 1364, to be stored in the ‘Departamento de Ciencias de la Tierra,’ University of Zaragoza.

*Measurements* – See Table 1, and Figures 1 and 2.

*Description of Oligodyromys libanicus from Montalbán 8 – d4* - The anterolophid is interrupted (3) or continuous (20). The anterotropid is absent (23). The metalophid is free (2), low connected to the metaconid (2) or high connected (17). The centrolophid is absent (6), short (9) or of medium length (5). The centrolophid is not connected to the metaconid (19), low connected (2) or high connected (1). The mesoconid is placed on the labial border (22) or more centrally (2). The mesolophid is of medium length and interrupted (15), of medium length (4), directed towards the metaconid (1) or directed towards the entoconid (3). The posterotropid is absent (1), small (17), of medium length (4) or long (1). In most cases there is no mesolophid properly speaking, but a mesoconid on the labial border, and a longitudinal structure through the centre of the tooth, which frequently reaches the metalophid.

*p4* - The shape is blunt (20) or pointed (2). The anterolophid is interrupted (7) or continuous (12). The anterotropid is absent (16), very small (1), small (3) or of medium length (1). The metalophid is free (1), low connected to the metaconid (6) or high connected (13). The centrolophid is short (1), of medium length (2) or long (19). The centrolophid-metaconid connection is absent (7), low (10), high (3) or the centrolophid is connected to a mesostylid (3). The mesostylid is absent (18), present (1) or it forms a crest (3). The mesoconid is placed on the labial border. The mesolophid is short (1), directed towards the entoconid (6), connected to the entoconid (15) or it reaches the

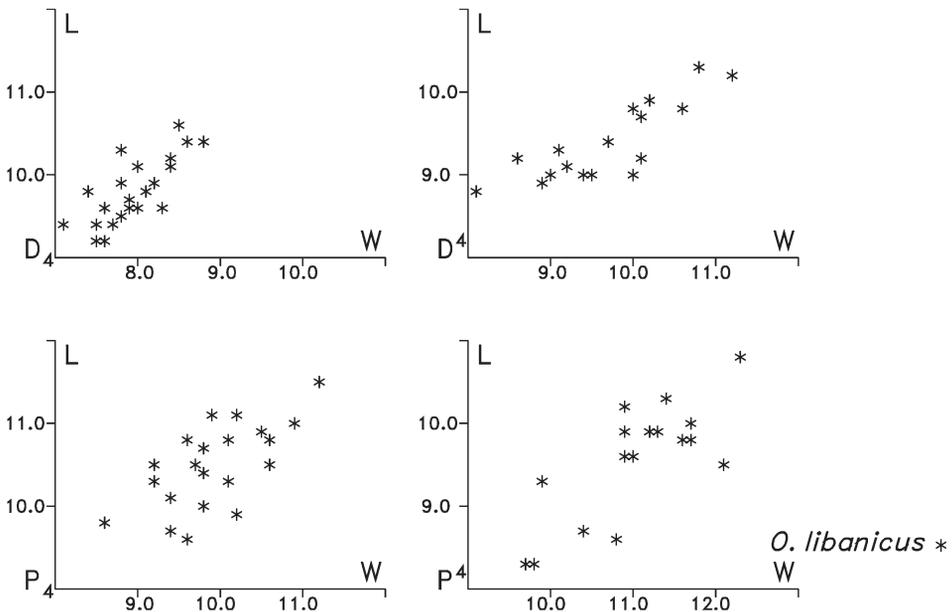


Fig. 1. Length/width diagrams of d4, D4 and p4, P4 of *O. libanicus* from MLB8.

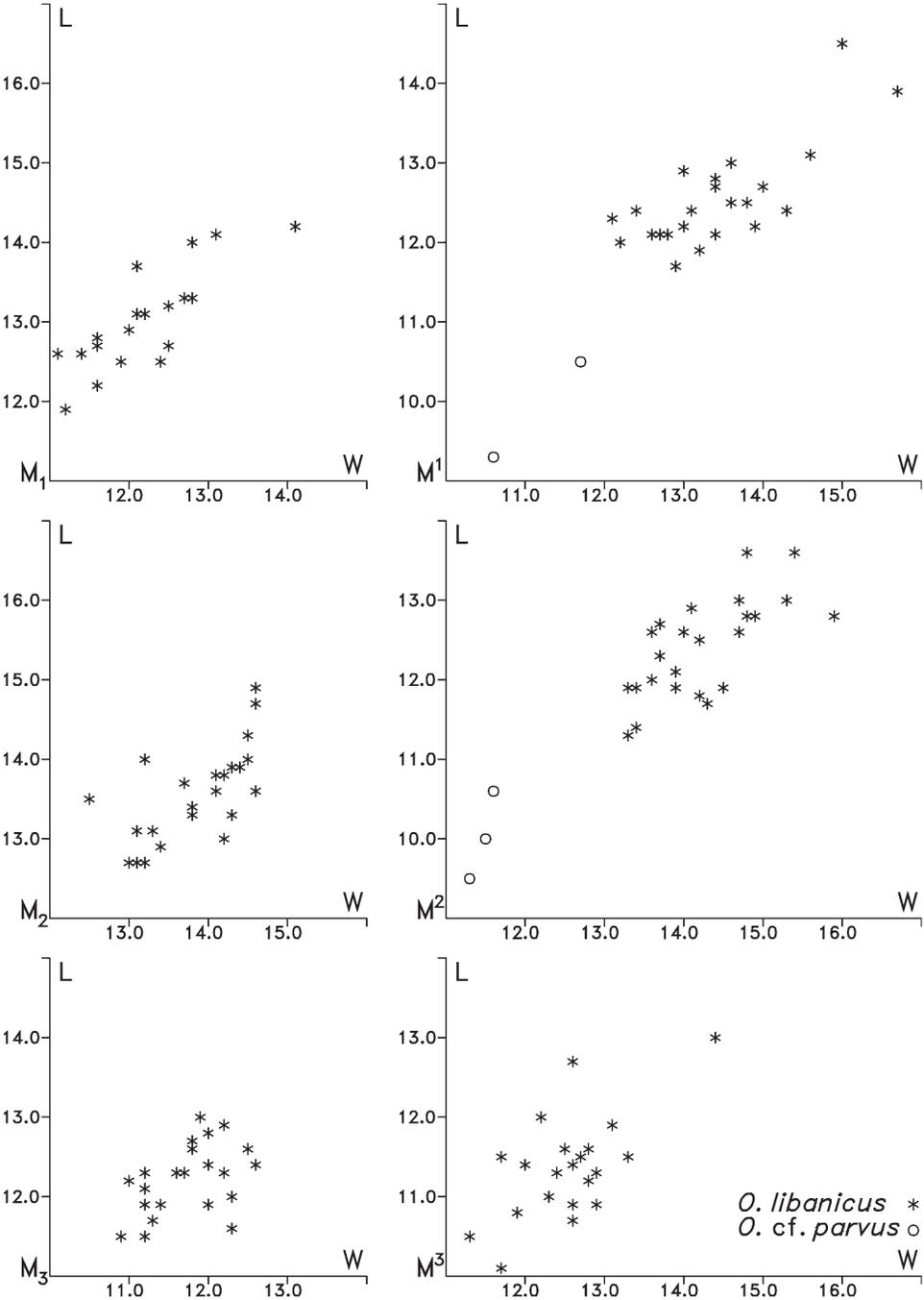


Fig. 2. Length/width diagrams of m1, m2, m3, M1, M2 and M3 of *O. libanicus* and *O. cf. parvus* from MLB8.

Table 1. Measurements of *Oligodyromys libanicus*.

d4	Length					Width						
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
MLB8	22	9.2	9.80	10.6	14.1	0.40	23	7.1	7.95	8.8	21.4	0.42
MLB3Y	1		9.70				1		7.20			
MLB3X	4	9.4	10.30	11.2	17.5	0.98	4	8.0	8.33	9.0	11.8	0.47
p4												
MLB8	22	9.6	10.45	11.5	18.0	0.53	21	8.6	9.92	11.2	26.3	0.62
MLB3Y	8	10.3	10.65	11.4	10.1	0.42	9	8.8	9.77	10.2	14.7	0.44
MLB3X	14	9.9	10.59	11.1	11.4	0.34	13	9.5	10.03	11.2	16.4	0.52
m1												
MLB8	19	11.9	13.02	14.2	17.6	0.64	20	11.1	12.21	14.1	23.8	0.72
MLB3Y	10	12.1	12.96	13.6	11.7	0.50	11	10.8	12.14	13.0	18.5	0.66
MLB3X	10	12.4	13.35	14.0	12.1	0.57	10	11.6	12.85	13.7	16.6	0.64
m2												
MLB8	23	12.7	13.56	14.9	15.9	0.60	23	12.5	13.85	14.6	15.5	0.62
MLB3Y	8	12.3	13.44	14.6	17.1	0.77	8	12.5	13.36	14.7	16.2	0.76
MLB3X	9	12.9	13.52	14.6	12.4	0.54	9	13.5	14.04	14.9	9.9	0.52
m3												
MLB8	23	11.5	12.22	13.0	12.2	0.43	23	10.9	11.73	12.6	14.5	0.49
MLB3Y	8	11.0	12.48	13.6	21.1	0.88	8	11.0	11.96	13.6	21.1	0.88
MLB3X	11	10.9	12.04	13.2	19.1	0.74	12	11.2	12.03	12.9	14.1	0.59
D4												
MLB8	18	8.8	9.38	10.3	15.7	0.46	17	8.1	9.67	11.2	32.1	0.82
MLB3X	9	8.4	9.32	10.3	20.3	0.65	9	9.2	9.90	10.9	16.9	0.52
P4												
MLB8	17	8.3	9.56	10.8	26.2	0.71	17	9.7	11.03	12.3	23.6	0.77
MLB3Y	7	8.5	9.50	10.3	19.1	0.56	7	10.1	10.84	11.5	13.0	0.51
MLB3X	18	9.2	9.76	10.3	11.3	0.36	17	10.2	11.41	12.1	17.0	0.57
M1												
MLB8	23	11.7	12.54	14.5	21.4	0.64	23	12.1	13.43	15.7	25.9	0.88
MLB3Y	7	11.2	12.84	14.8	27.7	1.11	6	12.2	13.57	15.3	22.5	1.05
MLB3X	20	11.5	12.51	13.4	15.3	0.51	18	12.6	13.57	14.8	16.1	0.64
M2												
MLB8	24	11.3	12.40	13.6	18.5	0.62	24	13.3	14.23	15.9	17.8	0.71
MLB3Y	3	12.4	12.53	12.7	2.4		5	13.4	14.02	14.8	9.9	0.53
MLB3X	15	11.9	12.53	13.6	13.3	0.43	15	13.5	14.37	15.3	12.5	0.51
M3												
MLB8	22	10.1	11.37	13.0	25.1	0.66	21	11.3	12.54	14.4	24.1	0.66
MLB3Y	6	10.1	11.08	12.3	19.6	0.82	5	12.2	12.44	13.0	6.3	0.32
MLB3X	4	10.9	11.68	12.4	12.9	0.61	4	12.5	13.03	13.6	8.4	0.46

lingual border (1). The posterotropid is absent (14), very small (1), small (2), of medium length (4) or long (1). Like in d4, though less common, there may be a longitudinal structure between metalophid and mesolophid or centrolophid.

*m1* - The anterolophid is labially free (18) or labially connected (3). The anterotropid is absent (4), very small (3), small (5), of medium length (6) or long (4). The metalophid is low connected to the metaconid (3) or high connected (19). The centrolophid is long. The centrolophid-metaconid connection is absent (2), low (3) or high (17). The meso-

stylid is absent (21) or present (1). The mesoconid is placed on the labial border. The mesolophid is connected to the metaconid (3), directed towards the entoconid (1), connected to the entoconid (17) or it reaches the lingual border (1). The posterotropid is small (1) or long (21).

In a number of cases the aspect of the occlusal pattern is irregular, due to the existence of some longitudinal connection or to the interruption of mesolophid or centrolophid.

*m2* - The anterolophid is labially free. The anterotropid is absent (17), very small (3), small (1), of medium length (2) or long (2). The metalophid is free (1), low connected to the metaconid (17) or high connected (6). The centrolophid is of medium length (1) or long (25). The centrolophid-metaconid connection is absent (2), low (3) or high (18). The mesostylid is absent (23) or there is a small crest (2). The mesoconid is placed on the labial border (26). The mesolophid is directed towards the entoconid (1) or connected to it (25). The posterotropid is long.

Irregularities like those observed in *m1* and may be present in *m2*, too, but they are significantly less common.

*m3* - The anterolophid is labially free (6) or labially connected (18). The anterotropid is absent (18), very small (4) or of medium length (1). The metalophid is free (1), low connected to the metaconid (9) or high connected (11). The centrolophid is of medium length (3) or long (21). The centrolophid-metaconid connection is low (3) or high (18). The mesostylid is absent (13), present (1) or it forms a crest (8). The mesoconid is placed on the labial border. The mesolophid is connected to the metaconid (2), directed towards the entoconid (3) or connected to it (18). The posterotropid is of medium length (2) or long (22). In many specimens the posterotropid is lingually connected to the posterolophid.

*D4* - The anteroloph is of medium length (16) or long (1). The anterotrope is absent (17) or short (1). The precentroloph is long. The postcentroloph is absent (6), short (3) or of medium length (9). The centrolophs are not connected (10) or connected (9). Prototrope, metatrope and posterotrope are absent. The precentroloph may be connected to the middle of the metaloph.

*P4* - The anteroloph is short (1), of medium length (6) or long (10). The anterotrope is absent. The precentroloph is long. The postcentroloph is absent (4), short (5), of medium length (6) or long (2); in six specimens it is not connected to the metacone. The prototrope is absent (13), short (3) or of medium length (1). The metatrope is absent. The centrolophs are not connected (15) or connected (2). The posterotrope is absent. The endoloph is formed by the protocone alone (10), anteriorly interrupted (1) or posteriorly interrupted (2). The lingual border is smooth.

In one case the precentroloph is connected to the middle of the metaloph. In several cases the postcentroloph is not connected to the metacone.

*M1* - The anteroloph is lingually free. The anterotrope is absent (14), short (7) or of medium length (5). The precentroloph is of medium length (4) or long (22). The pre-

centroloph is connected to the paracone (24), free from the paracone (1) or connected to a mesostyl (1). The postcentroloph is of medium length (3) or long (22); it is connected to the metacone (17), free from the metacone (8) or placed centrally (1). The prototrope is absent (14), short (2), of medium length (5) or long (5). The metatrope is absent (22), short (1), of medium length (2) or long (1). The centrolophs are not connected (5), connected lingually (10) or there are two connections (11). The posterotrope is absent. The endoloph is formed by the protocone alone (16) or anteriorly interrupted (1). The lingual border is smooth.

M2 - The anteroloph is lingually free (18) or lingually low connected (2). The anterotrope is absent (13), short (4), of medium length (5) or long (1). The precentroloph is of medium length (3) or long (21). The precentroloph is connected to the paracone (11), free from the paracone (3) or connected to a mesostyl (10). The postcentroloph is of medium length (1) or long (23); it is connected to the metacone (10) or free from the metacone (14); in three specimens it is connected to the middle of the metaloph. The prototrope is absent (3), short (1), of medium length (7) or long (13). The metatrope is absent (14), short (2), of medium length (7) or long (1). The centrolophs are not connected (4), connected lingually (12) or there are two connections (7). The posterotrope is absent (19), short (4) or of medium length (1). The endoloph is formed by the protocone alone. The lingual border is smooth.

M3 - The anteroloph is lingually free (5), lingually low connected (3) or lingually high connected (11). The anterotrope is absent (10), short (3), of medium length (4) or long (5). Inside the trigone are three (10), four (10) or five crests (2). The mesostyl is absent (13) or present (8). The posterotrope is absent (8), short (4), of medium length (5) or long (4). The endoloph is formed by the protocone alone (1), anteriorly interrupted (6), posteriorly interrupted (1) or complete (12). The lingual border is smooth.

In several specimens the pattern is fairly simple, but, in the majority, longitudinal connections between crests are developed that give the tooth a very complicated aspect.

*Oligodyromys libanicus* from Montalbán 3X and 3Y - The populations from MLB3X and 3Y show some minor differences with the type-population. For example, in MLB3X the anterolophid of m1 is more frequently interrupted or constricted midway; the centrolophid-metaconid connection is on average lower; the postcentroloph of D4 and P4 is less developed; the centrolophs are less frequently interconnected and the number of crests inside the trigone is smaller in MLB8.

In the P4 from MLB3X, some specimens have an anteroloph that lies in front of the protocone and not of the paracone, so that the greatest length of the tooth is lingual and not labial. Yet, the width is not much greater than the length and the specimens clearly not belong to a *Gliravus*.

***Oligodyromys* aff. *attenuatus* (Peláez-Campomanes, 2000)**

*Locality* – Barranco del Chorrillo 6C (Sierra Palomera, Teruel, Spain, code CHR6C).

Table 2. Measurements of *Oligodyromys* aff. *attenuatus* from Chorrillo 6C.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
d4							1	7.30				
p4	21	9.1	9.73	10.5	14.3	0.41	21	7.7	8.67	10.0	26.0	0.53
m1	11	10.2	11.15	12.0	16.2	0.64	11	10.3	10.91	11.6	11.9	0.45
m2	13	11.3	11.68	12.2	7.7	0.29	12	11.1	12.00	12.6	12.7	0.45
m3	11	10.5	11.04	12.2	15.0	0.56	10	10.3	11.10	12.6	20.1	0.72
P4	15	7.6	8.43	9.4	21.2	0.57	13	9.6	10.57	11.2	15.4	0.51
M1	13	10.1	11.01	11.9	16.4	0.53	13	11.5	12.19	13.0	12.2	0.48
M2	9	9.9	10.77	11.4	14.1	0.53	10	12.0	12.81	13.6	12.5	0.58
M3	9	8.6	9.36	9.9	14.1	0.55	8	10.0	11.14	12.0	18.2	0.60

*Material* – RGM 418 668-418 673, 418 717-418 738, 418 769; CHR6C 47-100, CHR6C 269-295. CHR6C numbers will be deposited in the 'Departamento de Ciencias de la Tierra', University of Zaragoza, Spain.

*Measurements* – See Table 2.

*Remarks* – There are only minor morphological differences with the type population of *O. attenuatus*. All dental elements are on average larger than in the type population and it may well represent a different species, which may be derived from *O. attenuatus*.

The Paleogene sedimentation in the Sierra Palomera consists of two units; an older one of Eocene-Early Oligocene age and a younger one of Late Oligocene age, separated by an important hiatus (see Freudenthal, 2004). Chorrillo 6C lies only a few metres below this hiatus and is one of the youngest localities in the older unit. It may be classified as MP20. In the Sierra Palomera the only record of younger *Oligodyromys* is from Fuente Umbria (UMB1B, MP20), but that material is too poor to permit an evaluation.

### *Oligodyromys parvus* (Freudenthal, 1996)

*Redefinition* – Freudenthal (1996) described *Bransatoglis parvus* and *Gliravus itardiensis* Vianey-Liaud, 1989, from OLA4A. *Gliravus itardiensis* is now incorporated in the genus *Butseloglis*. By now, a considerably larger collection is available of both species and it has become clear that they were not separated correctly. Distinction is quite difficult, because there is no size difference (see Tables 3, 4), and morphological separation depends on the criteria chosen, which in the end is an arbitrary choice. This situation is remarkably similar to the one in Hoogbutsel, where *B. micio* and *O. planus* are also difficult to separate.

*p4* - Specimens with continuous anterolophid are now considered as *O. parvus* and not *B. itardiensis*. The crests in these specimens are more regular than in *B. itardiensis*, but tropids may be absent. Especially, the mesolophid is longer and generally reaches the entoconid.

*m1,2,3* - All specimens with an anterotropid are assigned to *Oligodyromys*. Freudenthal (1996) mentioned one specimen of *m1* (OLA 920), one *m2* (OLA 951), and two *m3* (OLA 984, 993) of *B. itardiensis* with an anterotropid. These specimens are now determined as *O. parvus*.

The posterotropid is clearly better developed in *O. parvus* than in *B. itardiensis*. In the former it is never absent or small; in the latter this happens in about 33 % of the *m1*, 15 % of the *m2* and 33 % of the *m3*. However, it may be long in *B. itardiensis* as well. So, the presence of a long posterotropid is no argument to attribute the specimen to one species or the other; the absence or very small size of a posterotropid, however, means that the specimen belongs to *B. itardiensis*.

*m1* - The centrolophid in *O. parvus* is on average longer and its connection with the metaconid is usually higher than in *B. itardiensis*. The mesolophid of *m1* is much better developed in *O. parvus* than in *B. itardiensis*. It is longer, frequently connected to the entoconid, and the mesolophid, entoconid and posterolophid may form a continuous garland. In *B. itardiensis* the mesolophid is on average shorter, hardly ever connected to the entoconid and frequently pointing forward, directed more towards the metaconid than towards the entoconid; the posterolophid may reach the entoconid, but generally it does not. Also, in *O. parvus* the mesoconid may be almost as high as the hypoconid, whereas in *B. itardiensis* it is always lower.

Table 3. Measurements of *Oligodyromys parvus* from Olalla 4A.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
d4	8	7.8	8.20	8.8	12.0	0.31	8	6.4	6.68	7.1	10.4	0.27
p4	11	8.1	8.67	9.6	16.9	0.45	10	7.4	8.11	9.1	20.6	0.49
m1	18	9.8	10.82	12.0	20.2	0.51	18	10.0	10.69	12.0	18.2	0.53
m2	14	10.1	11.15	11.7	14.7	0.52	15	10.7	11.53	12.6	16.3	0.51
m3	20	9.5	10.66	12.2	24.9	0.68	18	9.7	10.43	12.1	22.0	0.64
D4	6	8.0	8.47	8.8	9.5	0.37	6	8.5	8.98	9.3	9.0	0.36
P4	9	7.2	8.07	9.1	23.3	0.52	8	9.0	9.97	10.8	18.2	0.66
M1	16	9.5	10.41	11.2	16.4	0.51	15	10.6	11.83	12.5	16.5	0.54
M2	13	9.6	10.39	11.3	16.3	0.42	13	11.3	12.25	13.6	18.5	0.63
M3	17	8.9	9.39	10.2	13.6	0.36	15	10.5	11.27	12.1	14.2	0.57

Table 4. Measurements of *Butseloglis itardiensis* from Olalla 4A.

	Length						Width					
	N	Min.	Mean	Max.	V'	$\sigma$	N	Min.	Mean	Max.	V'	$\sigma$
d4	27	7.5	8.29	9.7	25.6	0.48	24	6.3	7.08	8.4	28.6	0.54
p4	72	8.0	9.13	10.1	23.2	0.47	71	7.6	8.36	9.4	21.2	0.42
m1	59	10.1	10.98	12.2	18.8	0.48	57	9.7	11.07	12.2	22.8	0.52
m2	81	10.1	11.18	12.0	17.2	0.41	77	10.4	11.81	13.1	23.0	0.61
m3	87	8.8	10.39	11.5	26.6	0.56	87	8.0	10.11	11.6	36.7	0.65
D4	13	7.1	7.98	8.6	19.1	0.39	14	7.7	8.51	9.2	17.8	0.44
P4	54	6.7	7.84	8.7	26.0	0.45	55	8.9	10.07	11.4	24.6	0.56
M1	77	8.6	10.45	11.7	30.5	0.50	76	10.0	11.75	13.0	26.1	0.54
M2	68	9.3	10.42	11.3	19.4	0.42	68	11.1	12.35	13.5	19.5	0.50
M3	59	7.8	8.93	10.0	24.7	0.48	57	9.7	11.00	12.2	22.8	0.50

*m2* - The same differences as observed for *m1* occur also in *m2*. Also, in both species the crests of *m2* are better developed than those of *m1*.

*m3* - Centrolophid and posterotropid are much better developed in *O. parvus* than in *B. itardiensis*. The mesolophid of *B. itardiensis* is much better developed than in *m1,2* and has the same degree of development as in *O. parvus*.

*D4* - In *O. parvus* there are generally two centrolophs, but in *B. itardiensis* this is rare.

*P4* - The rounded shape of *P4* distinguishes *O. parvus* from *B. itardiensis*.

*M1,2* - The anterotrope is absent in *B. itardiensis* and common (50 %) in *O. parvus*. The centrolophs in *B. itardiensis* are lower and shorter and the main crests (proto-loph, metaloph) are higher. In *O. parvus* the difference in height is less.

*M3* - The anterotrope is like in *M1,2*. The separation between the two species may be incorrect.

*Remark* – Some *m2* of *B. itardiensis* have a split anterior root; in *m3* this is frequently, maybe always occurring. In *m1* the anterior root is simple, though it may bear a furrow. In the material of *O. parvus*, the roots are not preserved.

### ***Oligodyromys planus* Bahlo, 1975, and *Butseloglis micio* (Misonne, 1957)**

*Remarks* – *Butseloglis micio* from Hoogbutsel (MP21 like OLA4A) is based on the lectotype IRSNB M 1683, designated by Vianey-Liaud (1994). This specimen is an *m2* dext. and its correct catalogue number is M 1143 (M 1683 should not be used; it is a superfluous new number for a specimen that was numbered already). Its anterolophid is widely separated from the protoconid; there is no trace of an anterotropid; the metalophid reaches the base of the steeply rising metaconid and the centrolophid is of medium length, low and weak, especially in its lingual half. The mesolophid is long, ending free, with a tendency to bend forward towards the metaconid; there is a weakly developed posterotropid of medium length. The four main crests (anterolophid, metalophid, mesolophid and posterolophid) are equally high and the centrolophid and the posterotropid are much lower, and weakly developed.

The three specimens present under number M 1142 are *P4*, *M1* and *M2* sin. (not dext., as stated by Vianey-Liaud, 1994). These specimens may well belong to a single individual, because of the degree of wear and the perfect conservation of the roots that may mean that they were conserved in the jaw; however, this is not certain. None of these specimens has even a trace of an extra crest, neither inside nor outside the trigone. They are very concave, with the axis of the concavity through the centre of the molar.

The *P4* has a long, low anteroloph, two long and low centrolophs that are connected to paracone and metacone, respectively, and lingually connected to each other; the post-centroloph is interrupted midway. The posteroloph is low connected to the hypocone. The shape of the specimen is an asymmetrical trapezoid.

The M1 has an anteroloph that is separated from both the protocone and the paracone, two long and very low centrolophs that are lingually connected. The precentroloph is high connected to the paracone, the postcentroloph is low connected to the base of the metacone. The posteroloph is connected to the metaloph and the lingual connection to the hypocone is high.

In M2 the anteroloph is connected to both protocone and paracone. The centrolophs are like in M1, though even lower; the posteroloph is similar to M1.

*Oligodyromys planus* was recognized in Hoogbutsel by Vianey-Liaud (1994). In the lower dentition the premolars have a tiny anterotripid and in the molars this crest is moderately to well developed. Specimens without anterotripid (like M 1733, Vianey-Liaud, 1994, fig. 18h; the anterotripid drawn by Vianey-Liaud is not present) in our opinion belong to *B. micio*.

On the other hand, some specimens attributed to *B. micio* should be transferred to *O. planus*. For example, the m2 sin. M 1686 (Vianey-Liaud, 1994, fig. 14n), with a distinct anterotripid and a mesolophid that is well connected to the entoconid does not fit in *B. micio*. Other specimens of *B. micio*, drawn with a very small anterotripid, do not have that crest. Stains and shines on the specimens are easily misinterpreted in the Hoogbutsel material.

However, tiny anterotripids do occur in some specimens of *B. micio*. This feature, which serves to separate the two species in OLA4A is not 100 % decisive in HB; the anterotripid is constantly present in *O. planus*, but not constantly absent in *B. micio*. The other features used to distinguish *O. parvus* and *B. itardiensis* are valid in the HB populations as well. The measurements of *O. planus* from Heimersheim seem to be consistently smaller than those for Hoogbutsel and it is quite possible that the population from Hoogbutsel does not represent *O. planus*.

*The relative stratigraphic position of Hoogbutsel (HB) and Olalla 4A (OLA4A)* – In the first edition of the MP scheme (Schmidt-Kittler, 1987), Olalla 4A was incorrectly placed in MP22, whereas Hoogbutsel was MP21. In the new edition of this scheme (Biochrom'97, 1997) this was corrected and both were placed in MP21. The present study reveals a remarkable similarity between the glirids of these two localities.

*Glamys* aff. *olallensis* from Hoogbutsel is larger than *G. olallensis*, but morphologically similar.

*Glamys devoogdi* is present in Hoogbutsel and a similar species, *G. umbriae*, has been reported from several Spanish localities that are older than OLA4A (Freudenthal, 2004). In central Spain this group disappears earlier (it is absent in OLA4A), though in northern Spain it exists in Calaf (Anadón *et al.*, 1987), a locality of about the same age as Hoogbutsel and Olalla 4A.

*Butseloglis itardiensis* is present in OLA4A and *B. micio* in HB, and the two populations are highly similar both in size and in morphology. The measurement data given by Vianey-Liaud seem to indicate larger values for Hoogbutsel, but (some of) the larger specimens probably belong to *O. planus*.

*Oligodyromys parvus* from OLA4A is of the same size as *B. itardiensis* from the same locality and *O. planus* from Hoogbutsel overlaps the size distribution of *B. micio* in that locality. In both cases it is difficult to separate the *Butseloglis* and the *Bransatoglis* material reliably.

*Microdyromys misonnei* is not present in Olalla 4A; *Microdyromys* appears somewhat later, in the locality of Montalbán 3X.

HB and OLA4A are probably very close in age. The data do not permit a decision about which of the two localities is older. The absence of *Microdyromys* in OLA4A may mean it is the older one, but that absence may also be caused by geographic and/or climatic differences. Both localities contain several species of *Atavocricetodon*, which show similar degrees of development and do not help to solve the question.

## Classification of Bransatoglirinae

### Subfamily Bransatoglirinae Daams & de Bruijn, 1995

*Original diagnosis* (Daams & de Bruijn, 1995, p. 24-25) – “The diagnosis of the subfamily is the same as the emended diagnosis (Bosma & de Bruijn, 1982) of the type genus: The characteristic features of the dentition of *Bransatoglirinae* are:

- 1) the relatively large, rounded premolars
- 2) the strongly concave occlusal surfaces
- 3) the first and second molars, which are long relative to the width
- 4) the presence of long extra ridges outside the trigone in the M1-2, and the tendency to form a continuous endoloph in these teeth
- 5) the rounded shape of the M3, and the short, curving metaloph of that tooth.

Although none of the above dental features occurs exclusively in the *Bransatoglirinae*, their combination is characteristic.”

*Remarks* – Among these five features, number 1 (the rounded premolars) is identical in *Microdyromys* and *Bransatoglis*, and this feature distinguishes these two genera from many other Gliridae. It appears to be a good argument to classify these two genera in the same subfamily.

The relative size of the premolars for the six subfamilies of Gliridae (*sensu* Daams & de Bruijn, 1995) is compared in Table 5. The total number of populations is about 250, based partly on published data and partly on unpublished material in the collections we have under study. The number of populations (n) per subfamily varies between 25 and 53, sufficiently large to be representative. In each population mean length, mean width and mean surface (approximated as length x width) of P4 and of M1+M2 have been calculated to obtain the relationship P4/M1,2. The same calculations were carried out eliminating populations with only a few specimens, without a noticeable change of the results. It is clear that the Bransatoglirinae do not have relatively large premolars. The relatively largest premolars are found in *Glamys*, and the smallest in the Myomiminae, but the differences are too small to be of any diagnostic importance. Though the diagnosis almost certainly refers to the upper premolars, the same calculations were made for the lower ones, with similar results.

Feature number 2, the concavity of the occlusal surface, is not evident. Most of the species attributed to *Bransatoglis* have a moderately concave occlusal surface. In the type species, *B. concavidens*, only M2 is strongly concave. The P4 is moderately concave and M3 is flat, with an uplifted labial border. m1 is only slightly concave, m2 is flat, with an uplifted metaconid and entoconid, and m3 is flat with an uplifted metaconid.

Table 5. Size relation of P4/M1,2 and p4/m1,2, calculated for the length, the width and the surface, in the six subfamilies of Gliridae according to the interpretation by Daams & de Bruijn (*Microdyromys* placed in the Dryomyinae).

P4/M1,2 subfamily	length			width			surface					
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.
Gliravinae	49	0.66	0.80	0.93	47	0.77	0.86	0.94	48	0.54	0.69	0.85
Bransatoglririnae	40	0.71	0.78	0.90	39	0.69	0.84	0.95	39	0.52	0.66	0.85
Dryomyinae	53	0.65	0.73	0.88	53	0.70	0.79	0.92	53	0.46	0.58	0.78
Glamys	31	0.79	0.87	0.97	31	0.76	0.88	0.95	31	0.63	0.77	0.91
Myomiminae	53	0.50	0.71	0.89	53	0.53	0.75	0.88	53	0.27	0.54	0.71
Glirinae	25	0.65	0.74	0.98	25	0.67	0.78	0.98	25	0.45	0.58	0.96
p4/m1,2												
Gliravinae	48	0.69	0.84	0.93	48	0.61	0.73	0.89	48	0.47	0.61	0.80
Bransatoglririnae	39	0.75	0.84	0.92	39	0.66	0.75	0.87	39	0.52	0.63	0.80
Dryomyinae	58	0.61	0.75	0.85	58	0.61	0.72	0.84	58	0.38	0.55	0.67
Glamys	31	0.82	0.88	1.01	32	0.69	0.78	0.87	31	0.59	0.68	0.81
Myomiminae	44	0.49	0.70	0.85	44	0.52	0.69	0.79	44	0.25	0.49	0.64
Glirinae	24	0.65	0.71	0.79	24	0.63	0.73	0.87	24	0.41	0.52	0.65

Comparing the holotype of *B. concavidens* with the profiles of M1,2 of *Oligodyromys planus* published by Bahlo (1975), one comes to the conclusion that their degree of concavity is not much different and the majority of the species are slightly to moderately concave, not strongly. Freudenthal & Martín-Suárez (2007a) chose the radius of the circle that best fits the occlusal profile (see Fig. 3) as measure of concavity. For further details the reader is referred to that paper.

Feature number 3 is not evident. Since it is not clear whether this feature refers to the upper or lower molars, length/width ratios have been calculated per population for the mean length and width of the four elements in question, separated into the same groups as in Table 5. Table 6 shows that the L/W ratio of m1 and m2 of Bransatoglririnae is not fundamentally different from that of other glirids. In the upper molars the highest values are those of Bransatoglririnae, but the differences are so small that the L/W ratio cannot be considered to be of diagnostic value.

As far as feature number 4 is concerned, a continuous endoloph is indeed common in Bransatoglririnae; it is even more frequent in the species attributed to *Microdyromys* and present in several other glirid genera. Extra ridges outside the trigone are rare, though not absent,

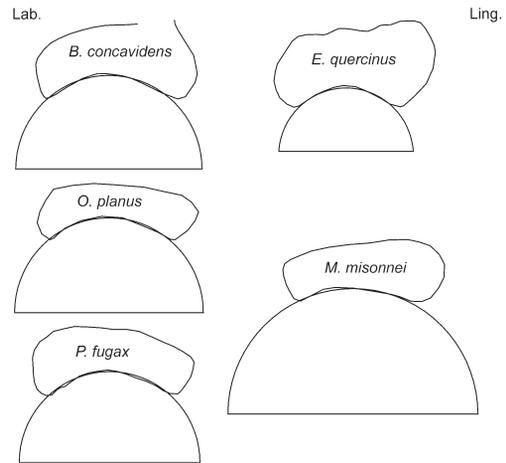


Fig. 3. Anterior profiles of M2 of several species of Bransatoglririnae, compared with *Eliomys quercinus*. All figures are drawn at the same size, ignoring scale. The profiles are drawn over protocone, protoloph and paracone. The radius of the best-fitting circle appears to be a good measure of concavity.

Table 6. Minimum, mean and maximum values of the ratio mean length/mean width of upper and lower M1 and M2 in the six subfamilies of Gliridae according to the interpretation by Daams & de Bruijn (*Microdyromys* placed in the Dryomyinae).

group	L/W M1				L/W M2			
	n	min.	mean	max.	n	min.	mean	max.
Gliravinae	37	0.77	0.87	1.02	36	0.78	0.83	0.92
Bransatoglirinae	39	0.80	0.95	1.08	48	0.79	0.90	1.08
Dryomyinae	37	0.78	0.89	0.98	38	0.79	0.85	0.95
Glamys	31	0.69	0.84	0.94	27	0.74	0.82	0.87
Myomiminae	22	0.78	0.91	1.03	26	0.69	0.87	0.96
Glirinae	24	0.79	0.90	1.03	25	0.79	0.85	0.91
group	L/W m1				L/W m2			
	n	min.	mean	max.	n	min.	mean	max.
Gliravinae	45	0.95	0.99	1.12	47	0.88	0.93	1.02
Bransatoglirinae	48	0.95	1.04	1.16	49	0.89	0.98	1.11
Dryomyinae	62	1.00	1.06	1.19	62	0.93	1.01	1.13
Glamys	34	0.83	1.00	1.04	37	0.91	0.95	1.02
Myomiminae	54	0.93	1.06	1.15	57	0.89	1.01	1.13
Glirinae	27	0.99	1.06	1.15	26	0.90	1.02	1.09

in *Microdyromys*, and common in *Glirudinus*, *Myoglis* and many other genera, and they are far from frequent in many Bransatoglirinae.

Feature number 5, the short, curving metaloph of M3, may be present in *Microdyromys*, too, though it may be less frequent and many M3 of *Bransatoglis* do not present it. On the other hand, it is often difficult to interpret the pattern of M3 and often one cannot be sure which one of the posterior crests is the metaloph, especially when they are discontinuous.

*Microdyromys* shares the feature of the rounded premolars with *Bransatoglis*. Especially in the case of the small Early Oligocene species like *B. misonnei*, it is not evident to which genus they belong. The crenulation of the lingual wall of the upper molars, common in *Microdyromys*, is less frequent and above all less developed in *Bransatoglis*. However, there are no fundamental morphological differences and these two genera should be classified in one and the same subfamily, the Bransatoglirinae.

We propose the following diagnosis, based on the one by Daams & de Bruijn (1995): Very small to very large Gliridae with rounded upper premolars and trapezium-shaped lower premolars. Weakly to strongly concave molars. Seven to twelve crests in the lower molars, six to eleven in the upper molars. Tendency to form a continuous endoloph in the upper molars. Rounded or triangular M3, often with a backwards-curving metaloph.

### Genus *Bransatoglis* Huguene, 1967

*Type species* – *Bransatoglis concavidens* Huguene, 1967, from Coderet, Allier, France, Upper Oligocene, MP30.

*Original diagnosis* (translated from Huguene, 1967, p. 92) – Large Gliridae, with concave occlusal surface, due to the uplifting of the internal and external border; the blunt and thick crests are separated by narrow and shallow grooves; the trigonodont design is clearly visible.

*Emended diagnosis* (translated from Vianey-Liaud, 1994, p. 138) – Glirid with the anterior branch of the zygomatic arch hardly tilted up, and masseter insertion on its inner side; foramen infraorbitale protrogomorphous; apophysis coronoideus of the mandible long; P3 present; P4/p4 relatively large; occlusal surface weakly to strongly concave; tendency to the development of centrolophs and extra crests outside the trigone in the upper molars; base of the trigone widened (U-shape); tendency to form a continuous endoloph; M1 slightly asymmetrical; in the lower molars tendency to form extra crests besides the four main ones.

*Diagnosis by Daams & de Bruijn* (1995) – See the diagnosis of the subfamily (above).

*Remarks* – Apart from the taxa described as *Bransatoglis*, *Paraglis* or *Oligodyromys*, several species that were originally classified as *Peridyromys* Stehlin & Schaub, 1951, *Gliravus* Stehlin & Schaub, 1951, or *Vasseuromys* Baudelot & de Bonis, 1966, have at some time been attributed to *Bransatoglis*. All potential *Bransatoglis* have been listed in Table 7 in stratigraphic order, a total of 23 species, ranging in age from Late Eocene (MP17) to Middle Miocene (MN6). These include two names, *B. parvus* Peláez-Campomanes, 1993, and *B. rimosus* Peláez-Campomanes, 1993, which are *nomina nuda*, because they were never published. Furthermore, Engesser (1972) described a Gliride X in open nomenclature from Anwil, which most authors consider to be *B. astaracensis*.

Apparently, *Bransatoglis* has become a wastebasket. The genera *Glis* and *Muscardinus* are the next richest, and have each about ten species. It is clear that it will be very difficult, if not impossible, to formulate a diagnosis that covers both the oldest and the youngest, the smallest and the largest, of these 21 species. In the following, a short characterization of each attributed species is given.

*Gliravus meridionalis* from Fons 4 (MP17). This species was classified by Vianey-Liaud (1994) as a *Bransatoglis*, without giving any argument for that decision, except for a possible ancestor-descendent relationship with *B. bahloi*, which is far from proven. *Gliravus meridionalis* does not share a single morphological character with any of the species that might belong to *Bransatoglis*. Freudenthal (2004) placed it tentatively in *Glamys*.

*Bransatoglis bahloi* from HH3 (Isle of Wight, MP18 and MP19). Characterized by six or seven crests in the lower molars or, in other words, by the constant presence of a centrolophid and a posterotropid, and the occasional presence of an anterotropid. The mesolophid is often, but not always, connected to the entoconid. In M1,2 there are always two centrolophs, which are frequently connected; the trigone is U- or V-shaped, the protocone and hypocone are separated or low connected, the anteroloph is separated from the protocone and there is no anterotrope, except for one case (HH3 1097), nor a posterotrope. The shape of P4 is oval.

Bosma & de Bruijn (1982) incorporated this species in *Bransatoglis*, because “it shows at least incipiently a number of *Bransatoglis* characteristics.” They extrapolated the features of the oldest known species at that time (*Oligodyromys planus*) back in time and came to the conclusion that *B. bahloi* fulfills the requirements of an ancestor of *Bransatoglis*.

However, we now know *B. attenuatus* from Aguatón 2D, which is partly contemporaneous with the time range of *B. bahloi* and has typical features of *Bransatoglis* perfectly

Table 7. Species that have been classified as *Bransatoglis*, with the number of crests and the mean length of m1.

	Type locality	Species	crests		length
			m1,2	M1,2	m1
MN6	SS	<i>Paraglis astaracensis</i> Baudelot, 1970	7	8	16.8
MN5	SCHW	<i>Bransatoglis mayri</i> Rabeder, 1984	7	9	21.6
MN4A	BEZ	<i>Bransatoglis cadeoti</i> Bulot, 1978	7-8	9-10	21.9
MN3	EST	<i>Paraglis infralactorensis</i> Baudelot & Collier, 1982	7	8	12.9
MN3	WW	<i>Glis? spectabilis</i> Dehm, 1950	7	9-10	18.2
MN2	HRM1	<i>Bransatoglis complicatus</i> Ünay, 1994	8-11	8-10	13.2
MP30	ULMW	<i>Paraglis ingens</i> Werner, 1994	7	7-8	12.9
MP30	COD	<i>Pseudodyromys fugax</i> Hugueney, 1967	7	8-9	12.4
MP30	COD	<i>Bransatoglis concavidens</i> Hugueney, 1967	7	9	18.2
MP25	SIN	<i>Vasseuromys moyai</i> Hugueney & Adrover, 1990	10-12	11	12.8
MP24	GRB3	<i>Bransatoglis heissigi</i> Uhlig, 2001	7	6-8	7.9
MP24	HEIM	<i>Oligodyromys planus</i> Bahlo, 1975	7	7-8	11.3
MP24?	KOC	<i>Bransatoglis sjeni</i> Ünay, 1989	7	7-10	13.3
MP23/24	PAG1	<i>Bransatoglis adroveri</i> Hugueney, 1997	7-9	10-11	16.7
MP23	ITA	<i>Gliravus itardiensis</i> Vianey-Liaud, 1989	6	6	11.6
MP22	MLB8	<i>Bransatoglis libanicus</i> sp. nov.	6-7	6-9	13.0
MP21	OLA4A	<i>Bransatoglis parvus</i> Freudenthal, 1996	7	6-8	10.8
MP21	OLA4A	<i>B. parvus</i> Peláez-Campomanes, 1993			
MP21	OLA4A	<i>B. rimosus</i> Peláez-Campomanes, 1993			
MP21	HB	<i>Peridyromys micio</i> Misonne, 1957	4-6	4-6	11.4
MP21	HB	<i>Bransatoglis misonnei</i> Vianey-Liaud, 1994	7	6-8	9.0
MP19	AGT2D	<i>Bransatoglis attenuatus</i> Peláez-Campomanes, 2000	7	6-8	10.3
MP18	HH3	<i>Bransatoglis bahloi</i> Bosma & de Bruijn, 1982	6-7	6	9.9
MP17	FONS4	<i>Gliravus meridionalis</i> Hartenberger, 1971	5	5	10.1

developed (see below). That makes it necessary to reconsider whether *B. bahloi* really is a *Bransatoglis*, because the typical *Bransatoglis* pattern is developed much earlier than Bosma & de Bruijn assumed.

The same authors mentioned the presence of *B. bahloi* in the higher level of Whitecliff Bay 2A (MP19), and of a second species, *B. aff. bahloi*, in HH5, HH6, and HH7 (MP19). The latter material is restricted to some m3 and M3 that are larger than *B. bahloi*.

*Bransatoglis attenuatus* from Aguatón 2D (MP19; Peláez-Campomanes mistakenly places AGT2D in MP21). There are always seven crests in the lower molars; their general aspect is very regular, and parallel; the anterotropid is constantly present, of medium length or long, and centrolophid and posterotropid are nearly always long and the mesolophid is connected to the entoconid in the vast majority of the cases. In the upper molars there are two long centrolophs, connected to each other in about half the cases; there may be an anterotrope (40 %), rarely there is a posterotrope and the prototrope is generally present. The protocone is connected to the hypocone in half the specimens; the anteroloph generally remains separated and only in a few cases there is a complete endoloph. The shape of P4 is oval. The metaloph of M3 reaches far backwards in half the specimens. The precentroloph is long, but not in contact with the endoloph.

*Peridymomys micio* from Hoogbutsel (MP21). In both lower and upper molars the number of crests varies between four and six. Centrolophid and posterotropid, where present, are much lower than the other crests. The mesolophid is generally of medium length, it rarely reaches the entoconid and it is frequently directed, or even connected, to the posterior part of the metaconid instead of to the entoconid. The main crests are low and, in comparison with them, the metaconid is extremely high; the labial wall of the metaconid is very steep; in relation with this the upper molars are very much concave. The P4 is triangular or trapezoid, not oval. In the upper molars the centrolophs are poorly developed, occasionally absent. There are no extra crests, neither inside nor outside the trigone. Vianey-Liaud (1994) classified *P. micio* as a *Bransatoglis*, probably because she incorporated some specimens that should be attributed to *O. planus* from the same locality. The size ranges of these two species are identical and distinction is difficult. The bulk of the material, however, shows no features that justify its characterization as a *Bransatoglis* and, consequently, Vianey-Liaud (2004) removed it and chose it as the type species of her new genus *Butseloglis*. Freudenthal (2004) incorporated *P. micio* in his new genus *Schizoglivavus*, which is a junior synonym of *Butseloglis*, because Freudenthal's publication appeared several months later.

*Gliravus itardiensis* from Itardies (MP23) was put into synonymy with *B. micio* by Vianey-Liaud (1994). It may well coincide with the material from Hoogbutsel; there is no anterotropid, nor an anterotrope. According to Vianey-Liaud (1989), there are six crests in both the upper and lower molars, though some of the figures give the impression that a very weak seventh crest may be present in the upper molars. The P4 is triangular, not rounded. It is a *Butseloglis* and might be synonymous with *B. micio*, although the time difference with Hoogbutsel makes that improbable.

*Bransatoglis misonnei* from Hoogbutsel (MP21) is characterized by lower molars with seven crests, the four main ones, a long centrolophid and posterotropid, and an anterotropid of variable length. The P4 is oval, with one or two centrolophs, the precentroloph being dominant. There are six to eight crests in the upper molars, the four main ones, two centrolophs, a prototrope and/or, rarely, a small cusp-like anterotrope. In size it agrees with the species attributed to *Microdymomys*. In the lower molars mesolophid, entoconid and posterolophid frequently form a continuous garland. In the upper molars the centrolophs are interconnected in less than 20 % of the cases. In M3 the metaloph is oblique towards the labial border or backwards towards the posterior border in equal proportions. On the basis of size, and the not connected centrolophs, this species is best placed in *Microdymomys*.

*Bransatoglis parvus* from Olalla 4A (MP21). The tropids and tropes are less developed than in AGT2D, with the exception of the anterotrope, which is more frequent and longer. The general aspect of the teeth presents the same degree of complexity as in AGT2D. The centrolophs are interconnected in about 60 % of the specimens. The P4 is oval. In the majority of the M3 the metaloph reaches far backwards. Just like in Hoogbutsel, the *Butseloglis* and *Bransatoglis* from OLA4A are not easily separated, and a number of specimens with poorly developed tropids, previously assigned to *Butseloglis itardiensis*, has to be transferred to *B. parvus*. This changes the characterization of both

species, as shown before. *Bransatoglis parvus* is roughly the same size as *O. planus* from Heimersheim. In Heimersheim, the anterotrope seems to be better developed.

*Bransatoglis parvus* Peláez-Campomanes, 1993, and *B. rimosus* Peláez-Campomanes, 1993, were listed by Daams & de Bruijn (1995), but are *nomina nuda*, because they were never published. Daams & de Bruijn (1995) mention OLA4A as their type locality. Freudenthal (1996) discussed the possibility of two species being present in that locality, so we may assume the valid name of both *nomina nuda* is *B. parvus*.

*Bransatoglis libanicus* sp. nov. from Montalbán 8 (MP22; not MP21 as indicated in table 3 in Biochrom '97, 1997) has lower molars with the four main crests, a long centrolophid and a well-developed posterotropid; in m1 the anterotropid is generally present and fairly well developed, in m2 that crest is practically absent. In the upper molars, apart from the main crests, there are always two long centrolophs, interconnected in more than 80 % of the cases; anterotrope, prototrope and metatrope may be present in varying combinations; when present, these crests are poorly developed. The P4 is oval. In the majority of the M3 the metaloph reaches far backwards.

*Bransatoglis adroveri* from Paguera (MP23-24) is among the biggest *Bransatoglis* known and has a very complex dental pattern; it has seven to nine crests in the lower molars and ten to eleven in the upper ones. The P4 is more or less oval. The centrolophs are interconnected, not connected to the endoloph, and form an irregular pattern together with prototrope and metatrope. The metaloph in M3 is obliquely directed towards the posterolabial corner of the tooth in the figured specimen. The endoloph is incomplete, the protocone is isolated from both anteroloph and posteroloph. This species is exceptionally large in view of its stratigraphic position. Huguenev (1997) suggested there may be a certain degree of (island) isolation that might explain this.

*Bransatoglis sjeni* from Kocayarma (MP24?) has lower molars with seven well-developed crests. The entoconid/mesolophid connection is always realized, though weak in quite a number of cases. There is an oval or subtriangular P4 with nearly always two centrolophs. In the upper molars there are from seven to ten ridges: in the latter case these are the four main crests, two centrolophs, anterotrope, prototrope, metatrope and posterotrope. The centrolophs are interconnected or parallel and not connected. The precentroloph is long, but not connected to the endoloph. The endoloph is interrupted. In M3 the metaloph reaches far backwards.

*Oligodyromys planus* from Heimersheim (MP24) has seven ridges in the lower molars; anterotropid, centrolophid and posterotropid are low, but quite long. The mesolophid is connected to the entoconid. The P4 is oval and has a precentroloph. The upper molars have seven or eight ridges, the anterotrope is quite well developed. The centrolophs are interconnected, not connected to the endoloph. The endoloph is complete or anteriorly interrupted. The metaloph of M3 reaches the posterior border of the tooth.

Vianey-Liaud (1994) recognized *Bransatoglis planus* in Hoogbutsel. Though the material from Heimersheim is quite poor, the dimensions of M1,2 appear to be smaller

than those of the population from Hoogbutsel; the latter probably represents a different species. In the m1,2 from Hoogbutsel, the mesolophid/entoconid connection may be absent.

*Bransatoglis heissigi* from Gröben 3 (MP24). The lower molars have seven ridges, the upper ones six to eight. It is of very small size. Anterotrope and posterotrope may be present, though poorly developed; the precentroloph is long, the postcentroloph shorter and may be absent; the centrolophs are parallel, rarely interconnected; the endoloph is anteriorly interrupted in M1, complete in M2. The metaloph of M3 reaches the labial border.

*Vasseuromys moyai* from Sineu (MP25). The lower molars have ten to twelve crests, due to the presence of two anterotropids, a crest between metalophid and centrolophid, a second centrolophid behind the main one and one to three posterotropids. The P4 is oval and has seven ridges. Upper molars with 11 crests: the four main ones, two centrolophs, anterotrope, prototrope, midcentroloph, metatrope and posterotrope. All extra crests are quite long and have a somewhat irregular aspect. The centrolophs do not reach the endoloph. The endoloph is complete.

*Bransatoglis concavidens* from Coderet (MP30). The lower molars have nine ridges, due to the presence of additional crests in front of the centrolophid, and behind it; except for these two crests, all other crests have more or less the same height. The upper molars also have nine ridges (up to eleven in the populations from Eggingen-Mittelhart). The endoloph is incomplete, being connected to the posteroloph only. The centrolophs are not interconnected and not in contact with the endoloph.

P4 and M3 are not known in Coderet. In the figured specimens from Eggingen-Mittelhart (Werner, 1994) the P4 is rounded, and the metaloph of M3 reaches far backward.

*Pseudodryomys fugax* from Coderet (MP30). 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 ingens* from Ulm-Westtangente (MP30). Lower molars with seven, upper molars with seven to eight crests. The P4 is rounded. The centrolophs are basically parallel and may show some longitudinal connection. The precentroloph is not connected to the endoloph. The endoloph is (almost) complete. The metaloph of the figured M3 from the type locality is directed obliquely towards the labial border; in the figured specimen from Jungingen it is more backwards.

*Bransatoglis complicatus* from Harami 1 (MN2) has eight to eleven ridges in the lower molars and eight to ten in the upper ones. The P4 has a rounded outline. The

centrolophs are not interconnected. The precentroloph reaches the endoloph. The endoloph in M1,2 is complete. The metaloph of M3 is directed to the labial border, not to the posterior border.

*Glis? spectabilis* from Wintershof West (MN3) has seven ridges in the lower molars and nine to ten in the upper ones, including two centrolophs, an anterotrope, prototrope and a posterotrope. The crests are regular and parallel. The endoloph is complete or anteriorly interrupted. The precentroloph reaches the endoloph in the holotype; in other specimens it is slightly shorter.

*Paraglis infralactorensis* from Estrepouy (MN3) has lower molars with seven well-developed crests, including a long anterotropid and posterotropid, and a medium-sized to long centrolophid. In the upper molars there are eight crests, with a well-developed anterotrope, a long precentroloph and a shorter postcentroloph and a prototrope. The endoloph is almost complete in M1 and complete in M2. According to Baudelot & Collier (1982), the anterotrope is absent in a specimen from Petit Camon. The isolated position of the centroloph, which forms a mesostyl, is remarkably similar to the situation in *P. astaracensis*. The precentroloph does not reach the endoloph.

*Bransatoglis cadeoti* from Bézian (MN4) has seven crests in the lower molars and nine or ten in the upper ones, presenting both anterotrope and posterotrope. The P4 is rounded. The endoloph is complete. The metaloph of M3 is directed to the labial wall of the tooth. The centrolophs are detached from paracone and metacone, and the precentroloph forms a mesostyl. The crests within the trigone are interconnected. The precentroloph is not connected to the endoloph.

*Bransatoglis mayri* from Schönweg (MN5) has seven crests in the lower molars and nine in the upper ones; the anterotrope is present. The endoloph is continuous. In M3 the metaloph reaches backwards. The precentroloph does not reach the endoloph.

*Paraglis astaracensis* from Sansan (MN6) has seven crests in the lower molars, and eight in the upper ones. According to Baudelot (1970), this species is characterized by a small number of extra crests. In her figure 1b one can observe seven crests, less than in *B. concauidens*, but the normal number in other species. The precentroloph is connected to the endoloph. The interpretation of the homologies of the crests is not easy, but we think Rabeder (1984) did it correctly, calling the central labial cusp mesostyl. That means that there probably are two centrolophs, both connected to the mesostyl, and a metatrope, connected to the posteroloph, and no crests outside the trigone. The endoloph is complete. Absence of anterotrope and posterotrope is part of the diagnosis of the genus *Paraglis*, but Mayr (1979) reported the occasional presence of these crests in the Sansan material.

*Proposed classification* – Several of the above mentioned species do simply not belong to *Bransatoglis*, not even to the Bransatoglirinae; *G. itardiensis* and *P. micio* belong to *Butseloglis* (Gliravinae). *Gliravus meridionalis* may be a *Glamys* (Gliravinae). They are not further considered here.

Among the remaining ones four groups may be distinguished on the basis of size as may be seen in Figures 4 and 5:

1. A group of large species (mean length m1 between 16.8 and 21.8), per definition *Bransatoglis*, because it contains the type species *B. concavidens*.
2. A group of medium-sized species (mean length m1 between 12.4 and 16.8), around *Paraglis astaracensis*.
3. A group of small to medium-sized species (mean length m1 between 9.9 and 13.0), which contains *Oligodyromys planus*.
4. A group of small-sized species (mean length m1 between 8.6 and 9.2), which includes *B. misonnei* (not in Figures 4, 5).

Whether these groups are different genera is a matter of subjective interpretation. De Bruijn *et al.* (2004, p. 61) gave as their opinion that 'size difference is considered not to be characteristic at the genus level', but in the same paper the diagnoses of two of the three new genera begin with a reference to size, so apparently they did consider size to be an important factor at genus level. Daams & de Bruijn (1995) assembled the diagnoses of all glirid genera and that listing makes it easy to verify that size forms part of the diagnosis of the majority of them. In fact, size is as good a criterion as any other one and should be used whenever it serves a good purpose, as is common practice, not only in palaeontology, but also in zoology, where a much wider choice of criteria is available.

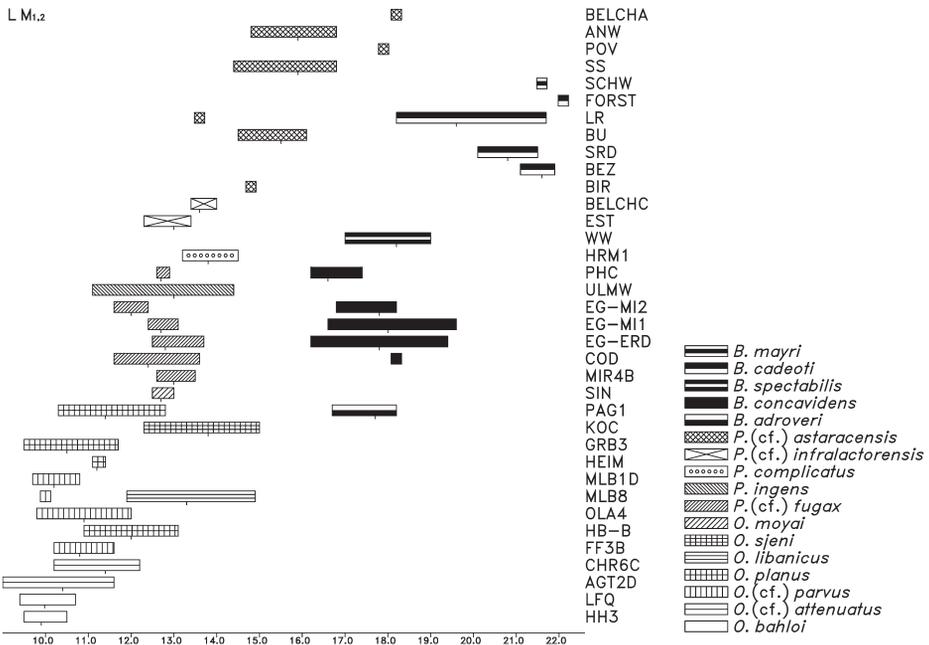


Fig. 4. Length of m1,2 of various Bransatoglririnae populations; data for POV and FORST have been estimated from M1,2.

A genus like *Bransatoglis* in its present concept, with 21 species ranging from very small to very large, and from Late Eocene to Middle Miocene, is a taxon that is no longer useful. When a logical subdivision is possible on whatever criterion, one should do it. And when such a subdivision leads to groups that show a higher degree of relationship within groups than among groups, they certainly deserve to be distinguished as genera. This leads to the following classification of the Bransatoglririnae.

**Genus *Bransatoglis* Huguency, 1967**

*Type species* – *Bransatoglis concavidens* Huguency, 1967.

*Diagnosis* – Large Bransatoglririnae. Lower molars with seven to nine ridges, the four main ridges plus an anterotripid, centrolophid and posterotripid, all well-developed, regular, quite long, straight and parallel. In the upper molars there are nine or ten crests; anterotrope and/or posterotrope usually present. The centrolophs are generally not interconnected. The endoloph is usually complete. The precentroloph is long and rarely reaches the endoloph; it may be detached from the paracone. The metaloph of M3 is frequently directed towards the posterior border of the molar.

*Species included* - *Glis spectabilis* Dehm, 1950; *Bransatoglis cadeoti* Bulot, 1978; *Bransatoglis mayri* Rabeder, 1984; *Bransatoglis adroveri* Huguency, 1997.

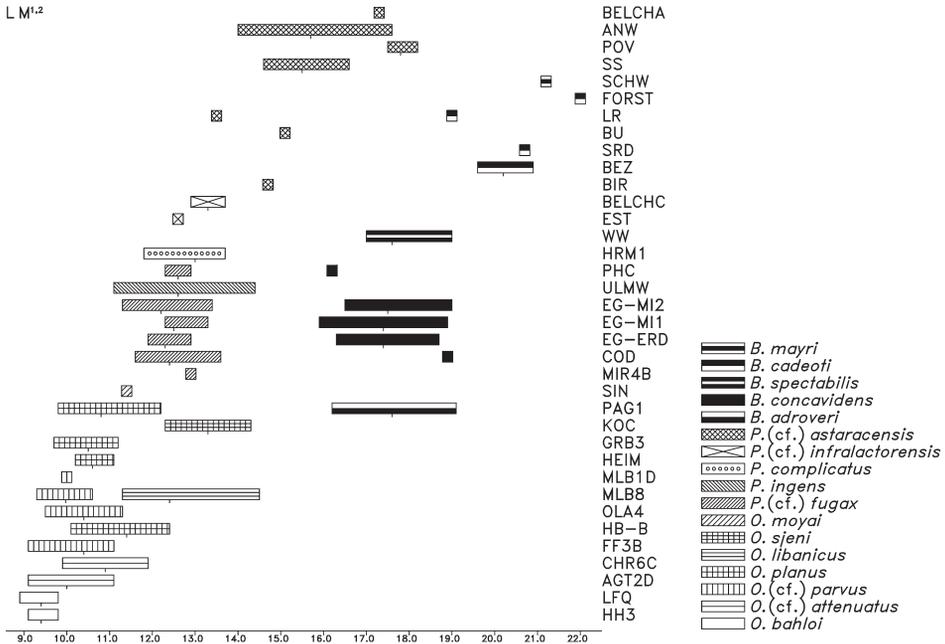


Fig. 5. Length of M1,2 of various Bransatoglririnae populations; data for SRD, BIR, MIR4B, and LFQ have been estimated from m1,2.

*Remarks* – *Bransatoglis adroveri* is placed in *Bransatoglis* on the basis of size. Its morphology is certainly not typical of *Bransatoglis*. The protocone in M1,2 is isolated from anteroloph and posteroloph, and the centrolophs are irregular and interconnected. One might consider it to occupy an intermediate position between *Oligodyromys* and *Bransatoglis*.

### Genus *Paraglis* Baudelot, 1970

*Type species* – *Paraglis astaracensis* Baudelot, 1970.

*Diagnosis* – Medium-sized Bransatoglininae. 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.

*Species included* – *Pseudodryomys fugax* Hugueney, 1967; *Paraglis infralactorensis* Baudelot & Collier, 1982; *Paraglis ingens* Werner, 1994; *Bransatoglis complicatus* Ünay, 1994.

*Remarks* – *Paraglis astaracensis* has been cited from Belchatów A and Povia de Santarem; in both cases it is larger than the type material and should be placed in the group of large-sized species. A revision of this material seems to be necessary. In the case of Belchatów, the larger size may be related to the fact that that locality is much younger (MN9) than the type locality.

Povia de Santarem (MN6) is of about the same age as Sansan. One of the two specimens is much more complicated than the type of the species.

The material from Anwil (Gliride X in Engesser, 1972) has a high metric variability due to the presence of one very large specimen and one very small specimen. The other specimens are within the variability of the Sansan population. This material needs revision, too.

Most of the published populations contain not more than a few specimens. Only two populations are quite numerous, Anwil and La Grive. The description of the Anwil material by Engesser (1972) is not exhaustive, because he intended to publish it elsewhere; the La Grive material is unpublished. Knowledge of these populations is essential to get a better idea of *P. astaracensis* and the genus *Paraglis*.

*Bransatoglis complicatus* falls in this size group, but its dental pattern is much more complicated than in the other species. Its complete endoloph in M1,2 shows resemblance with *Paraglis*. However, anterotrope and posterotrope are well developed in *B. complicatus*, and absent or poorly developed in *Paraglis*. It is classified as *Paraglis*, though that is far from satisfactory. The geographic factor may explain the differences.

The distinction between *Paraglis* and *Bransatoglis* is far from clear. The type species are clearly different, but the other species show overlapping morphologies. Size is a good criterion, but other morphological features are less decisive. Part of the problem may be caused by the fact that nearly all populations are very poor in specimens and

intra-population variability is practically unknown. It is not impossible that this lack of material has led to some misidentifications. Only when larger populations are known will it be possible to give a good definition of these two genera.

### Genus *Oligodyromys* Bahlo, 1975

*Type species* – *Oligodyromys planus* Bahlo, 1975.

*Diagnosis* – Small to medium-sized Bransatoglininae. There are six or seven crests in the lower molars and six to nine in the upper ones. The crests are frequently irregular, and the centrolophs are often interconnected. The endoloph is usually incomplete. The position of the metaloph in M3 is variable.

*Species included* – *Bransatoglis bahloi* Bosma & de Bruijn, 1982; *Bransatoglis sjeni* Ünay-Bayraktar, 1989; *Bransatoglis parvus* Freudenthal, 1996; *Vasseuromys moyai* Hugueney & Adrover, 1990; *Bransatoglis attenuatus* Peláez-Campomanes, 2000; *Oligodyromys libanicus* sp. nov.

*Remarks* – *Oligodyromys bahloi* is reported from MP18 and MP19, and there is a larger species, *B. aff. bahloi* from HH5, 6 and 7 (MP19). In AGT2D (MP19), *Oligodyromys* coexists with a smaller species that is considered to be a *Microdyromys*. One cannot rule out that in the Isle of Wight a similar situation occurs; *O. bahloi* might be a *Microdyromys* and the larger *O. aff. bahloi* a true *Oligodyromys*. This would be in agreement with the absence of ridges outside the trigone in *O. bahloi*.

*Vasseuromys moyai* from Sineu (MP25) has a large number of crests (10-12), but it is small (length m2 12.5-13.0). Since Sineu is situated on an island (Majorca), one might consider the surplus of crests being a result of insularity. However, none of the other components of the fauna shows adaptations that can be related to island isolation, so, insularity is not a good argument to explain its morphology. Hugueney & Adrover (1990, p. 160) said that “*Oligodyromys planus* d’Heimersheim (MP24) est la forme qui, d’allure générale, semble la plus proche” and that *V. moyai* might be derived from a form close to *O. planus*. Supposing its descendance from a form close to *O. planus* it is placed in *Oligodyromys*, in spite of the large number of crests.

By its size, *B. sjeni* belongs to *Oligodyromys* or *Paraglis*. Ünay-Bayraktar (1989) found it to be more similar to *O. planus* than to any other *Bransatoglis* species known at the time, but one M1 and one M2 have ten crests, more complicated than in other *Oligodyromys*, which sheds doubt on its classification. Furthermore, the upper premolars do not always show the rounded shape thought to be typical for this group. *Bransatoglis sjeni*, according to Ünay-Bayraktar (1989), has two centrolophs in the P4 and double centrolophs in P4 are quite common in *Oligodyromys*, but they occur in *Paraglis*, too. The endoloph is like in *Oligodyromys* and the centrolophs of M1,2 may be interconnected. It seems to belong to *Oligodyromys* and the large number of crests may be explained by the fact that it is probably the youngest representative of the genus. However, its relative complexity, considered to be an advanced feature, may also be related to its presence in a very different geographic area.

### Genus *Microdyromys* de Bruijn, 1966

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

*Diagnosis* – 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. Extra crests outside the trigone rare.

*Species included* – *Dryomys praemurinus* Freudenberg, 1941; *Microdyromys complicatus* de Bruijn, 1966; *Microdyromys monspeliensis* Aguilar, 1977; *Microdyromys legidensis* Daams, 1981; *Microdyromys orientalis* Wu, 1986; *Microdyromys sinuosus* Alvarez Sierra, 1986; *Bransatoglis misonnei* Vianey-Liaud, 1989; *Bransatoglis heissigi* Uhlig, 2001; *Microdyromys puntarronensis* Freudenthal & Martín-Suárez, 2007b; *Microdyromys* sp. from AGT2D.

*Remarks* – *Bransatoglis misonnei* and *B. heissigi* are smaller than all species of *Oligodyromys*, and of the same size as several species of *Microdyromys*. Interconnection of centrolophs is rare (like in *Microdyromys*), the endoloph of M1,2 is incomplete and the metaloph of M3 is frequently directed towards the labial border of the molar. They are considered to be *Microdyromys*, and *B. misonnei* may well be the link between that genus and *Oligodyromys*. Daams & de Bruijn (1995) supposed *Microdyromys* to be derived from the Gliravinae. Uhlig (2002, fig. 6) was the first to relate *Microdyromys* with the Bransatoglininae. She supposed a lineage *B. misonnei* - *M. praemurinus* and saw *Microdyromys* as a ramification of a lineage that starts with *B. bahloi*. Basically that may be right, though the situation could be more complicated, because that doesn't account for the record of *Microdyromys* in AGT2D (MP19, see Freudenthal, 1997a; Freudenthal & Martín-Suárez, 2007b). As said before, one might consider whether *O. bahloi* is a *Microdyromys*.

### Biostratigraphy and phylogeny

In Figure 6, the distribution of Paleogene and Neogene Bransatoglininae, except *Microdyromys*, is given. The oldest Bransatoglininae known is *Oligodyromys bahloi* (MP18) from the Upper Eocene of the Isle of Wight; it shows the lowest degree of development of Bransatoglininae features.

The next record is *Oligodyromys attenuatus* from Aguatón 2D (MP19), which shows a well advanced development of Bransatoglininae features. It appears in Spain in the Sierra Palomera in a large number of localities that are classified as MP19 and MP20. The youngest of these localities is Chorrillo 6C where all dental elements are on average larger than in the type population of *B. attenuatus*; it is classified as *O. aff. attenuatus*.

A few specimens from AGT2D are assigned to *Microdyromys* sp. That material is very poor and this very old record of the genus must be considered with some doubt, but it seems to prove a very early origin of *Microdyromys*.

*Oligodyromys parvus* appears in Fuenferrada 2B and 3B (MP20) (Freudenthal, 1997b), and its type locality is Olalla 4A (MP21). Between Fuenferrada 3B and Olalla 4A, the faunal change of the 'Grande Coupure' implies the disappearance of most of the Euro-

		<i>M. misomnei</i>	<i>M. praemurinus</i>	<i>O. bahloi</i>	<i>O. aff. bahloi</i>	<i>O. attenuatus</i>	<i>O. planus</i>	<i>O. parvus</i>	<i>O. libanicus</i>	<i>O. sjeni</i>	<i>O. moyai</i>	<i>P. fugax</i>	<i>P. ingens</i>	<i>P. complicatus</i>	<i>P. infralactorensis</i>	<i>P. astaracensis</i>	<i>B. adroveri</i>	<i>B. concavidentis</i>	<i>B. spectabilis</i>	<i>B. cadeoti</i>	<i>B. mayri</i>	
MIOCENE		MN9														+						
		MN7														+						
		MN6														X						+
		MN5														+					cf.	X
		MN4	?									+				cf.	+			aff.	X	
		MN3													X						X	
		MN2										cf.		X								?
		MN1										+										+
OLIGOCENE	Late	MP30		+								X	X								X	
		MP29		+									+									
		MP28		X			?						aff.									
		MP27		+									aff.									
		MP26		+			?						?									
	MP25		+								X	aff.										
	MP24	cf.				X			X												X	
	Early	MP23	cf.				?			+												
		MP22	cf.				?	X														
		MP21	X				+	X														
	MP20					?		+														
EOCENE	MP19	sp.	+	X	X																	
	MP18		X																			

Fig. 6. Distribution of Bransatoglririnae, except for Miocene *Microdyromys*. X = type level; + = other occurrences; cf. and aff. as mentioned in the original publication; ? = doubtful occurrences.

pean mammal taxa. It is surprising that *Oligodyromys* survives this event. In this respect it is important to note that *O. attenuatus* from AGT2D has a more developed ‘*Bransatoglrilis* pattern’ than the species from OLA4A, HB and MLB. If they form a phylogenetic lineage, its tendency would be characterized by reduction of accessory crests; maybe the Oligocene *Oligodyromys* are immigrants, not directly related with *O. attenuatus*.

Hoogbutsel and Olalla 4A are of about the same age (both placed in MP21), and show a remarkable similarity in composition of the fauna, though the species are not the same. Hoogbutsel has yielded the first doubtless record of *Microdyromys*, which arrived in Spain somewhat later. *Microdyromys* may be derived from *Oligodyromys* or it may be a component of the migration wave of the ‘Grande Coupure’ and be derived from an unknown Eastern stock.

The *Oligodyromys* from Hoogbutsel has been classified as *O. planus*, a species originally described from Heimersheim (MP24); this long existence is not certain, because the species from Hoogbutsel is possibly misidentified. Its Spanish counterpart is *O. parvus*.

In Montalbán 8 (MP22), *O. libanicus* appears, which is clearly larger than the previous species, accompanied by the first certain appearance of *Microdyromys* in Spain. Furthermore, MLB8 contains a second, poorly documented, species of *Oligodyromys* of smaller size that may well be *O. parvus*.

In MP18 to MP22, *Oligodyromys* is a common element of the faunas, but in Montalbán 1D (MP23) it becomes rare, being represented only by a few specimens of *O. cf. parvus*. This precedes the extinction of the genus at the Early/Late Oligocene transition. *Microdyromys*, on the other hand, is quite common in this level.

Hugueneý (1997) suggested a late Early Oligocene age (MP23-24) for the locality Paguera, because of similarities with Montalbán 1D and Heimersheim. The faunal list of Paguera 1 given in Hugueneý & Adrover (1982) strongly suggests an Early Oligocene age, except for *Eucricetodon aff. dubius*, which is not known before MP26. However, this citation of *E. dubius* appears to be incorrect and the material in question shows more affinities with *Atavocricetodon* (Hugueneý, pers. comm.). There is no certainty about the age of Paguera; it might be latest Early Oligocene (later than Heimersheim), but certainly not younger.

Hugueneý & Adrover (1990) concluded an early Late Oligocene age (MP25) for Sineu. In the area of Montalbán this age is represented by MIR4B, a locality that has yielded a few specimens of *Paraglis fugax*; *Oligodyromys* has disappeared.

In the Montalbán area there is no fossil record of the Lower/Upper Oligocene boundary. There is an important hiatus in the register, because the sedimentation is formed by a thick conglomerate body that is not liable to yield any fossils. The fossiliferous beds below and above this level have yielded faunas that are completely different. They have not a single species in common, and there are at least eight newcomers at genus level; *Protechimys*, *Issiodoromys*, *Allocricetodon*, *Eucricetodon*, *Heterocricetodon*, *Melissiodon*, *Paraglis*, *Gliravus* and slightly later *Plesiosminthus*. Apparently, this interval is characterized by an important migration wave and an almost complete renewal of the fauna, in which typical Early Oligocene genera like *Blainvillymys*, *Sciurumys*, *Elfomys*, *Atavocricetodon*, *Butseloglis*, *Glamys* and *Oligodyromys* disappear. Some of these changes may be due to a change of genus name within an evolutionary lineage, but most of the newcomers have no direct relationship with any Early Oligocene taxon and must be considered immigrants.

Because this interval is not fossiliferous we cannot know whether all these immigrants arrived exactly at the same time or whether it is a step-wise renewal of the fauna. A remarkable fact is that several typical Early Oligocene genera like *Glamys* and *Oligodyromys*, instead of disappearing suddenly, gradually lose importance during the later part of the Early Oligocene and are reduced to very low percentages at the level of Montalbán 1D before their final disappearance. In the oldest Late Oligocene locality, Mirambueno 4B (MP25), all the new elements are present, but their arrival is not necessarily synchronous.

In the two Majorca localities, Paguera and Sineu, one gets the impression that some relicts of Early Oligocene taxa co-exist with some of the immigrants. In Paguera, *Oligodyromys planus* coexists with the supposed immigrant *B. adroveri*. The rest of the fauna has affinities with Early Oligocene forms and not with the Late Oligocene.

*Oligodyromys moyai*, a possible end-of-lineage form of *Oligodyromys*, coexists in Sineu with *Eomys molassicus* and *Allocricetodon*, which are present in MIR4B, and with *Pseudocricetodon thaleri*, which appears in continental European localities much later (MP27). *Paracricetodon*, also present in Sineu, is not known in the Montalbán area.

These considerations lead to one of two hypotheses:

1. Paguera and the somewhat younger locality Sineu correspond to the period of time at the Early/Late Oligocene transition that is not documented in the Montalbán area.
2. These two localities are of latest Early Oligocene age and the early Late Oligocene migration wave reaches Majorca somewhat earlier than the Iberian Peninsula.

One of the elements of this migration wave is *Paraglis fugax*, present in Mirambueno 4B (MP25), and constantly present in our record until Vivel del Río (MP28), the youngest locality in the Montalbán area. Such a long-lasting record is not usual and maybe more than one species is involved; however, the material is very poor and does not permit differentiation. None of the later *Paraglis* populations in France is rich, either; the only rich population is that of *P. ingens* from Ulm-Westtangente (Germany). The poor record does not even permit an attempt to discover ancestor-descendant relationships between *P. fugax*, *P. infralactorensis* and *P. astaracensis*.

In MIR4B, *Microdyromys* is represented by *M. praemurinus* or a predecessor of it, and from that moment onwards *Microdyromys* is a constant element of the Spanish faunas until the Late Miocene (MN10). True *Bransatoglis* is not recorded in Spain, except for *B. adroveri*, which might be a predecessor of *B. concavidens*. All Late Oligocene and Miocene occurrences in Spain are referred to *Paraglis*. The total record of *Bransatoglis* from France and Germany is very scarce, and the populations are generally comprised of few specimens, except for those described by Werner (1994) from the area around Ulm (Germany). The centre of distribution of this genus seems to be Central and maybe Eastern Europe. That pleads against the oldest record (*B. adroveri* from Majorca) being a *Bransatoglis*, unless Majorca had a direct relationship with Central Europe.

This leaves us with the two citations of Bransatoglirinae from Turkey, *O. sjeni* and *P. complicatus*. The age of *O. sjeni* is uncertain, but is supposed to be late Early Oligocene. Morphologically and in size it is quite similar to other *Oligodyromys* species like *O. planus* and *O. libanicus* that are of about the same age.

The age of *P. complicatus* is supposed to be Early Miocene (MN2), one of the oldest Miocene records of Bransatoglirinae. Ünay (1994) said that morphologically it is quite similar to *O. moyai* from Majorca. It certainly is much more complicated than the other *Paraglis* species. We arrange it in *Paraglis*, though it may be a representative of another branch of Bransatoglirinae that is unknown in Europe.

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### Plate 1

*Oligodyromys libanicus* sp. nov. from Montalbán 8.

- Fig. 1. d4 sin., MLB8 913  
Fig. 2. d4 dext., MLB8 1154  
Fig. 3. p4 sin., MLB8 1169  
Fig. 4. p4 dext., MLB8 1175  
Fig. 5. m1 sin., MLB8 1183 holotype  
Fig. 6. m1 dext., MLB8 1200  
Fig. 7. m2 sin., MLB8 1210  
Fig. 8. m2 dext., MLB8 1218  
Fig. 9. m3 sin., MLB8 1231  
Fig. 10. m3 dext., MLB8 1249
- Fig. 11. D4 sin., MLB8 1252  
Fig. 11. D4 dext., MLB8 1264  
Fig. 13. P4 sin., MLB8 1271  
Fig. 14. P4 dext., MLB8 1280  
Fig. 15. M1 sin., MLB8 1287  
Fig. 16. M1 dext., MLB8 1303  
Fig. 17. M2 sin., MLB8 1315  
Fig. 18. M2 dext., MLB8 1331  
Fig. 19. M3 sin., MLB8 1336  
Fig. 20. M3 dext., MLB8 1346

Scale bar represents 1 mm.

