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## New data on early Oligocene dormice (Rodentia, Gliridae) from southern Europe: phylogeny and diversification of the family

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Rodents of the extant family Gliridae, commonly called dormice, are common in European faunas since the early Eocene. Here we study for the first time specimens from St-Martin-de-Castillon C (France, early Oligocene) previously reported as *Gliravus* aff. *majori* and *Pseudodryomys* aff. *fugax*. We now refer them to *Butseloglis tenuis* and *Microdryomys misonnei*. Besides the French material, new specimens from Montalbán 1D (Spain, early Oligocene) are studied. They include: *Butseloglis montisalbani* and *M. misonnei* already known in the locality, but also *Oligodyromys libanicus* and *Glirudinus* aff. *glirulus* reported here for the first time. Previous phylogenies of the family only focused on extant taxa. Here we propose the first phylogenetic analysis of Gliridae including both extant and fossil taxa. The relationships between the taxa show several paraphylies at the generic level and suggest that the classification of the family needs a revision. Two main clades are revealed in our analysis, including most extant taxa, both of them being closely related to the Oligocene genus *Microdryomys*. By comparing the phylogeny to the evolution of species-richness through time, we show that glirids underwent three major diversification phases. The first diversification event involves several clades of late Eocene and early Oligocene glirids. The second diversification event involves the two main clades still represented today. They both started diversifying in the late Oligocene and led the species richness of the family to reach a peak at the end of the early Miocene. Finally, the third diversification starts in the middle Pliocene and involves mostly extant genera. These diversification phases might have been triggered by successive glaciation events that occurred in the Oligocene, Miocene and Pliocene. A potential evolutionary advantage of this family successfully facing cold climatic events could be the ability to hibernate, acquired as early as the early Oligocene.

**Keywords:** Gliridae; phylogeny; subfamily; diversity

## Introduction

Gliridae Thomas, 1897 is a monophyletic group of rodents, widely spread in the Old World today. The first occurrence in the fossil record can be traced back to *Eogliravus* Hartenberger, 1971 from the early Eocene of France (Thaler 1966). Additionally, most fossils and the oldest taxa have been recorded from Europe, thus strongly supporting a European origin of the family. Glirids, relatively poorly diversified in the Eocene, started diversifying in the Oligocene and underwent their biggest diversification during the Miocene with both generic and species richness much higher than today (nine genera and 28 species today [Wilson & Reeder 2005] vs. 18 genera and 36 species for the late early Miocene of Europe only [Daams 1999]). Some extant glirid genera originated from this Miocene diversification, as the oldest fossil records of *Eliomys* Wagner, 1840, *Dryomys* Pallas, 1778, *Muscardinus* Kaup, 1829 and *Myomimus* Ognev, 1924 date back to

the Miocene. Outside Europe, the oldest Asian glirid, *Miodryomys asiamediae* Maridet, Wu, Ye, Ni & Meng, 2011, is known in the early Miocene of China, but occurrences of this taxon remain rare. The only genus known from Africa is *Graphiurus* Smuts, 1832. Its oldest record dates back to the Pliocene of South Africa (Daams & de Bruijn 1995). In comparison with other extant genera, *Graphiurus* is the most species-rich genus today (14 species, Wilson & Reeder 2005), representing half of the whole family richness. This observation suggests that other significant diversification events occurred in the evolutionary history of the family. However, the lack of phylogenetic hypotheses including both fossil and extant taxa prevents a better understanding of its evolutionary history.

As far as extant taxa are concerned, two phylogenetic hypotheses have been proposed by Montgelard *et al.* (2003) and Nunome *et al.* (2007) based on nuclear genes, and one by Wahlert *et al.* (1993) based on cranial and tooth morphology. The different zygomasseteric

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**Figure 1.** Map of the localities studied in this work.

structures of the skulls are indeed important for the classification of extant glirids. However, few fossil skulls are well preserved enough to use cranial anatomy for phylogenetic analysis including fossil taxa. The typical lophodont morphology of the teeth turns out to be the main basis for the identification and classification of fossil taxa. The only phylogenetic analysis of fossil glirids so far focused on the paraphyletic genus *Vasseuromys* Baudelot & de Bonis, 1966 (Sinitis & Nesin 2018). As a result, several palaeontologists proposed hand-drawn phylogenetic hypotheses (Daams & de Brujin 1995; Berger 2008; Freudenthal & Martín-Suárez 2007a, 2013), despite sometimes noticeable discrepancies with the phylogenetic relationships of extant taxa and the neontological classification. Here, we propose the first phylogenetic analysis of the whole family, extant and fossil taxa together, using molecular data as a backbone.

In this paper, we also describe new specimens from early Oligocene localities: St-Martin-de-Castillon C (France) and Montalbán 1D (Teruel, Spain; collected during Franco-Spanish scientific exchanges; Fig. 1). These two rich localities share a similar age (Aguilar *et al.* 1997; Escarguel & Aguilar 1997). In previous studies, two fossil glirids have been identified from the French locality (*Gliaravus* aff. *majori* and *Pseudodryomys* aff. *fugax*) but never studied in detail

(Hugueneuy *et al.* 1971). By contrast, the early Oligocene fauna of Montalbán has been well studied before. *Butseloglis itardiensis* Vianey-Liaud, 1989, *Butseloglis montisalbani* Freudenthal, 2004, *Microdryomys misonnei* Vianey-Liaud, 1994, *Glamys olallensis* Freudenthal, 1996 and some *affinis* species have already been described from different layers by Vianey-Liaud (2003), Freudenthal (2004), Freudenthal & Martín-Suárez (2007a, b) and García-Paredes *et al.* (2010). These new data increase the diversity of early Oligocene glirids and constitute the basis of our phylogenetic analysis, allowing us to address the question of the different phases of diversification of the family, and in turn to better understand its evolution from the early Eocene to the present.

## Material and methods

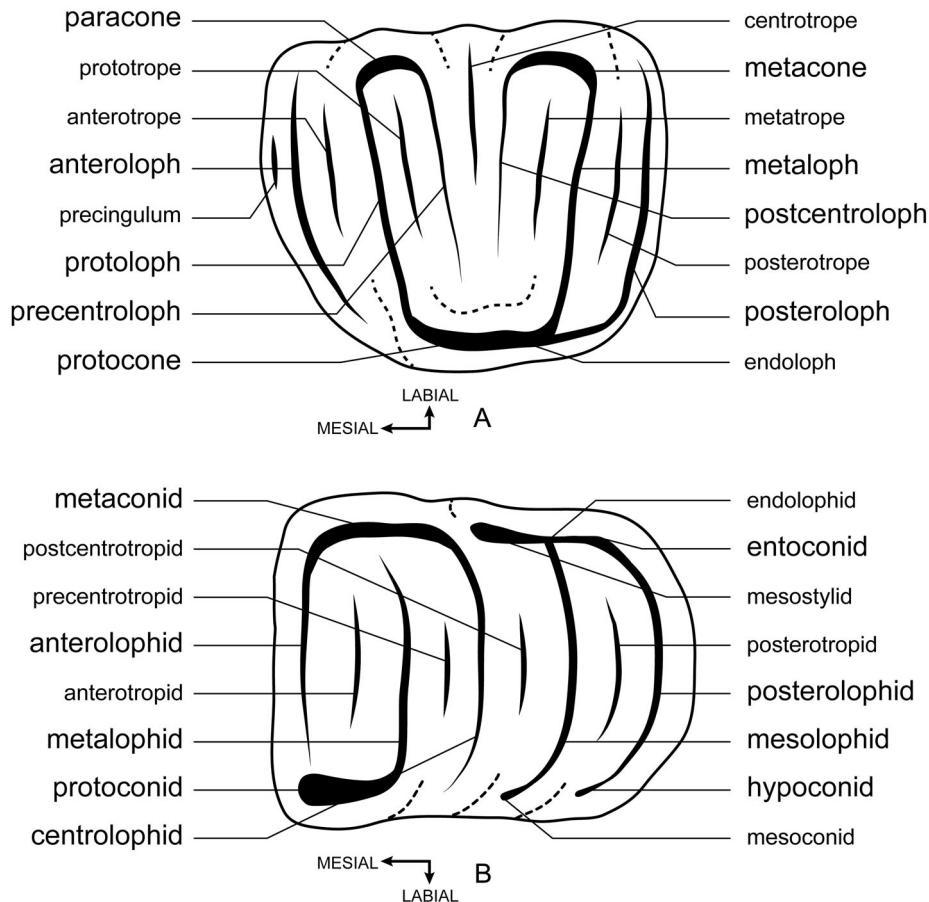
### Abbreviations

**dp/DP**, lower/upper deciduous premolar; **HLMD**, Hessisches Landesmuseum Darmstadt, Darmstadt, Germany; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussel, Belgium; **m/M**, lower/upper molar; **MLB1D**, Montalbán 1D; **MLB8**, Montalbán 8; **p/P**, lower/upper premolar; **Slg. München**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **SMC**, St-Martin-de-Castillon C; **UCBL-FSL**, Faculté des Sciences de Lyon, University Claude Bernard Lyon 1, Lyon, France.

### Material

The specimens of glirid included here were collected from the early Oligocene localities of St-Martin-de-Castillon C (France) and Montalbán 1D (Spain). All the described specimens are deposited in the collections of the Faculté des Sciences de Lyon, University Claude Bernard Lyon 1 (UCBL-FSL), and are catalogued under the numbers UCBL-FSL\_218048 to 218067, 218070, 218073 and 218074 for Saint-Martin-de-Castillon (France), and UCBL-FSL\_218025 to 218047, 218068, 218069, 218071 and 218072 for Montalbán 1D.

The specimen images were produced using the Bruker Skyscan 2211 CT scanner at the CT Imaging Laboratory of the University of Fribourg, Switzerland. The specimens were CT-scanned with beam energy of 180 kV and a flux of 90 µA at a detector resolution of 2.2 µm per pixel using a 360° rotation with a step size of 0.2° and an aluminium filter. Three-dimensional reconstructions were produced in Amira 6.0.



**Figure 2.** Dental terminology used for the descriptions of glirid teeth. **A**, upper left molar; **B**, lower left molar.

### Species richness

We collected occurrence data for the whole family, from the oldest record of *Eoglravus wildi* Hartenberger, 1971 (Mas de Gimel, France, MP10) to the extant ones. *Affinis* species were not taken into account. The dataset includes 222 species from 190 localities. In order to minimize potential sample biases, the data have been corrected by range-through completion of the fossil record (assuming a continuous occurrence of a taxon through time between its first and its last observed occurrences; Barry *et al.* 2002).

### Cladistic analysis

A new matrix was established with 124 characters (see **Supplemental material, Appendix 1 – Character states**) for 52 taxa. Of these, 44 characters based on cranial morphology were selected from the matrix of extant species by Wahlgren *et al.* (1993). However, the preservation of skull elements is rare in the fossil record, so

80 additional dental characters have been defined for this study. The scoring of taxa is based on the observations of actual specimens or casts; only *Chaetocauda sichuanensis* Wang, 1985 has been scored on the basis of published figures.

### Specimens and terminology

The material described here is solely composed of isolated teeth. The terminology used to describe teeth in this study (Fig. 2) is modified after Freudenthal (2004). All extra crests have their own name. In lower molars, each lophid, cuspid and their connections are usually easy to observe; however, upper molars generally show more variation than lower molars, making the identification of morphological features more difficult. Here we consider that the centrolophs, the precentroloph and the postcentroloph (whether they are well developed or not) are main lophs, as are the protoloph and the metaloph. The extra crests located between these main lophs are called tropes. Depending on the morphological variation,

tropes can sometimes be as developed as lophs, making their differentiation difficult, but we identify them considering that the precentroloph and postcentroloph always are the lophs connecting to the paracone and metacone, respectively. However, in some species like *Glis minor* Kowalski, 1956 and *Glis glis* Linnaeus, 1766, the precentroloph and postcentroloph are free labially. In this case the assumption is made that tropes cannot exist if the main centrolophs (precentroloph and postcentroloph) are not present. Isolated central crests are consequently first identified as lophs (not tropes). Among all tropes, the centrotrope between the precentroloph and postcentroloph is rare and only exists in some rare species characterized by numerous crests like *Myomimus dehmi* de Bruijn, 1966a (centrotrope weak) and *Vasseuromys rugosus* Baudelot & de Bonis, 1966 (centrotrope developed). We consider the term ‘endoloph’ as the whole lingual wall in upper molars. For the condition in which the crest-like protocone connects to the anteroloph and posteroloph, like *Glirulus* de Bruijn, 1966a, the protocone is located on the ‘endoloph’. A clear distinction between the first and second molars was not always possible; both teeth are consequently not separated and described as M1/2 and m1/2. Measurements consist of maximal length (L) and width (W) of teeth, in millimetres. They follow the method presented by Prieto *et al.* (2016, fig. 3). In addition, the third molars have been measured following Freudenthal (2004): length perpendicular to the anterior border and width parallel to the anterior border. For MLB1D, the given measurements provided only take into account the specimens studied here (see Supplemental material, Appendix 2 – Detailed measurements).

### Biochronological framework

The biochronological framework is based on the European Land Mammal Ages (ELMA: Lindsay 1997; Vandenberge *et al.* 2012) which are subdivided into a succession of European mammal reference levels for the Palaeogene (MP; Schmidt-Kittler 1987), each of them being correlated with the Palaeogene geological time scale (Luterbacher *et al.* 2004; Vandenberge *et al.* 2012). For the age of the localities Montalbán 1D (MP23) and St-Martin-de-Castillon C (MP23/24, Hugueney & Mödden 1996), we follow the biochronological ages provided by Freudenthal & Martín-Suárez (2007a) and Maridet *et al.* (2011), respectively.

### Systematic palaeontology

Order **Rodentia** Bowdich, 1821  
Family **Gliridae** Thomas, 1897

#### Genus *Butseloglis* Vianey-Liaud, 2003

**Type species.** *Butseloglis micio* (Misonne, 1957)

*Butseloglis tenuis* (Bahlo, 1975)

(Fig. 3A–H)

1971 *Gliravus* aff. *majori*; Hugueney *et al.*: 2432.

**Type locality.** Heimersheim, Germany, MP24.

**Holotype.** HLMD/Hhm 409, right M2.

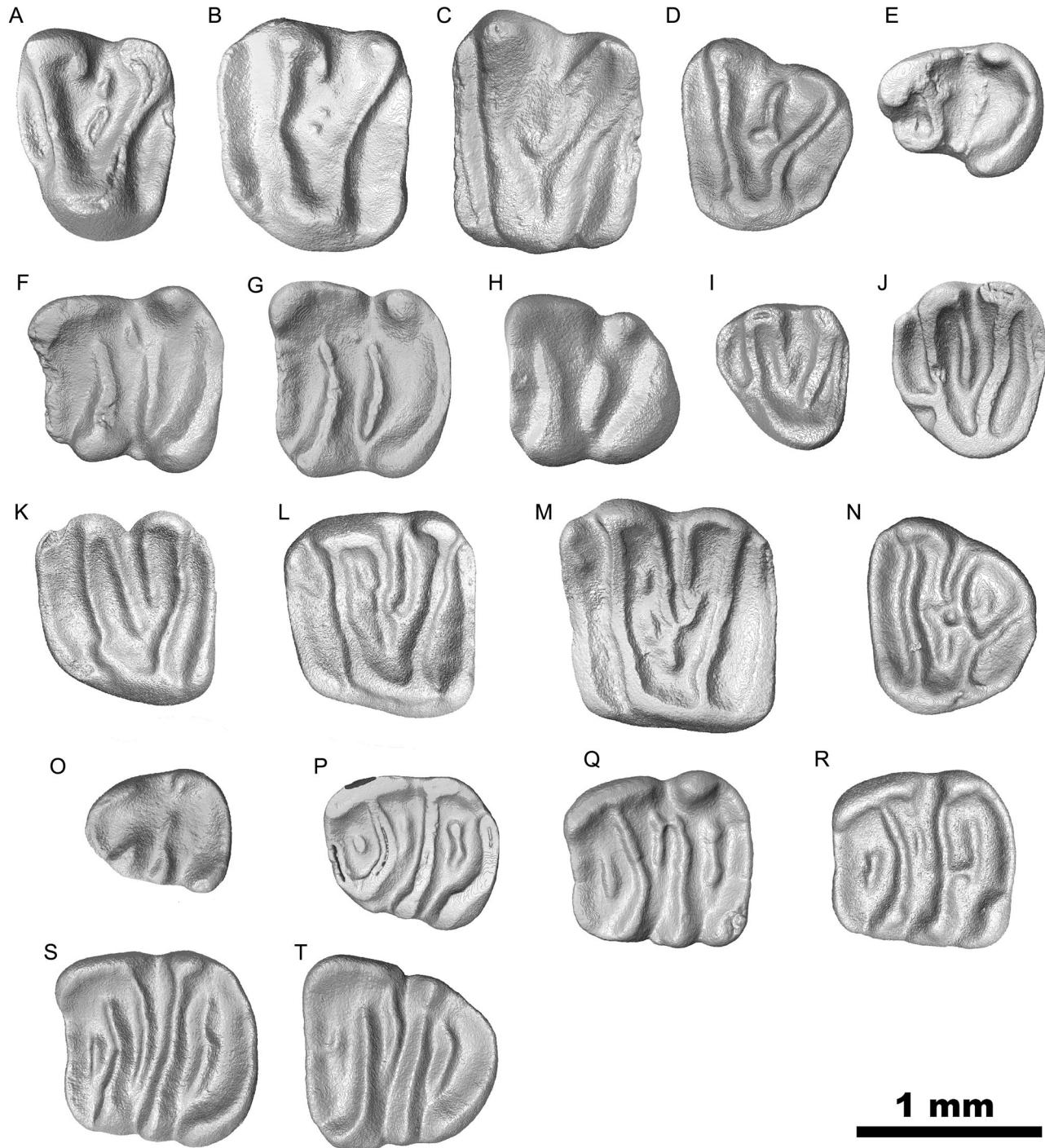
**Specimens and measurements from St-Martin-de-Castillon C.** UCBL-FSL\_218048 to 218055 and 218070, for measurements see Table 1 and Supplemental material, Appendix 2 (Fig. 3A–H).

**Description of the specimens from St-Martin-de-Castillon C.** The occlusal surface of P4 is strongly concave and cusps are well developed. The paracone is slightly higher than the protocone. The anteroloph and posteroloph are weak and shorter than other lophs. The protoloph is straight and as developed as the metaloph. A weak precentroloph is the only centroloph in the ‘V’-shaped trigone; it is interrupted and connects to the paracone. All tropes are absent.

**M1/M2.** The pattern is as simple as P4 but with a trapezoid shape. The occlusal surface of M1 is usually more concave than M2. The cusps are strong. The anteroloph is longer than the posteroloph in M2, and both of them are straight and as high and developed as the other lophs in upper molars. The protoloph and metaloph are slightly bent anteriorly in their middle. A weak unique centroloph is present; it either connects usually to the paracone (precentroloph) or more rarely to the metacone (postcentroloph).

**M3.** Only one M3 has been found; it is smaller than M1 and M2 and about the size of P4. The shape is more triangular than other teeth but the pattern is otherwise similar to M1 and M2. Although the anteroloph and protoloph are transverse, the metaloph extends substantially posterolabially with a bend which results in the metacone being located more lingually than the paracone. The precentroloph is free labially. The posteroloph is oblique (instead of transverse in M1 and M2) due to the reduction of the posterolingual side of the tooth.

**p4.** The tooth is strongly concave on the lingual side. The metaconid is the highest cuspid. The entoconid and hypoconid are distinct and connected to each other by a well-developed and rounded posterolophid. Comparatively other lophids are weak. The anterolophid and the mesolophid are very weakly developed. The metalophid connects to both the metaconid and



**Figure 3.** Upper and lower teeth of glirids from St-Martin-de-Castillon. *C. Butseloglis tenuis*: **A**, right P4, UCBL-FSL\_218048 (reversed); **B**, right M1, UCBL-FSL\_218049 (reversed); **C**, right M2, UCBL-FSL\_218050 (reversed); **D**, right M3, UCBL-FSL\_218051 (reversed); **E**, left p4, UCBL-FSL\_218052; **F**, left m1, UCBL-FSL\_218053; **G**, right m2, UCBL-FSL\_218054 (reversed); **H**, left m3, UCBL-FSL\_218055; *Microdyromys misonnei*: **I**, left DP4, UCBL-FSL\_218056; **J**, left P4, UCBL-FSL\_218057; **K**, right M1, UCBL-FSL\_218058 (reversed); **L**, left M1, UCBL-FSL\_218059; **M**, left M2, UCBL-FSL\_218060; **N**, right M3, UCBL-FSL\_218061 (reversed); **O**, right dp4, UCBL-FSL\_218062 (reversed); **P**, right p4, UCBL-FSL\_218063 (reversed); **Q**, left m1, UCBL-FSL\_218064; **R**, left m1, UCBL-FSL\_218065; **S**, right m2, UCBL-FSL\_218066 (reversed); **T**, right m3, UCBL-FSL\_218067 (reversed). Scale bar = 1 mm.

protoconid. There is no connection between the mesolophid and the entoconid. No tropid is observed between the main lophids.

**m1/m2.** They are trapezoidal in shape but m2 is slightly wider in the anterior part. All main cusps are distinct and lophids are transverse and parallel. The posterior arm of the metaconid and the mesolophid do not join. The anterolophid is very weak and disconnected from the protoconid. The metalophid extends from the protoconid but does not connect to the metaconid. In the unique m1, the short and weak centrolophid is located anterolingually to the mesolophid and is free. However, in m2s, the centrolophid and all tropids are absent. The posterolophid only connects to the base of the entoconid.

**m3.** The unique m3 is smaller than m2, with a rounded posterior border. Its pattern is the same as other lower molars; however, the lophids seem more robust. The centrolophid is difficult to observe (either weakly developed or poorly preserved), but it seems to connect to the posterior arm of the metaconid. There is a deep groove between the posterolophid and the entoconid.

**Remarks.** *Butseloglis tenuis* was initially described under the genus *Gliravus* Stehlin & Schaub, 1951, then referred to genus *Schizoglravus* Freudenthal, 2004, which is now a junior synonym of genus *Butseloglis* (Vianey-Liaud 2003). The material of *Gliravus tenuis* in Vianey-Liaud (1994) from Montalbán S was later referred to *B. montisalbani* (Freudenthal 2004). Likewise, *B. montisalbani* is also present in MLB1D but not *B. tenuis* (Freudenthal & Martín-Suárez 2007a). The size of *B. tenuis* is indeed similar to that of *B. montisalbani* but its dental pattern is simpler than both *B. montisalbani* and *Butseloglis hispanicus* van Dam, 1998: the posterotropid is absent, and only one centroloph is present in upper molars. Here we report for the first time the occurrence of this species in SMC (MP24).

#### *Butseloglis montisalbani* Freudenthal, 2004 (Fig. 4A–I)

**Type locality.** Montalbán 1D (MP23).

**Holotype.** Departamento de las Ciencias de la Tierra, University of Zaragoza, MLB1D 1050, left M1.

**Specimens and measurements from Montalbán 1D.** UCBL-FSL\_218025 to 218033 and 218071, for measurements see Table 1 and Supplemental material, Appendix 2 (Fig. 4A–I).

**Description of the new specimens from Montalbán 1D.** In upper molars, the anteroloph and posteroloph are free lingually and labially. The anterotrope and posterothrope are absent. The protocone is anterior to the metacone. DP4s are triangular. Only the weak centroloph is

visible in DP4. P4s display an oval shape with a well-developed precentroloph. Both M1s and M2s are rectangular. The anteroloph of M1 is shorter than that of M2. The precentroloph and postcentroloph are present in M1 and M2. The precentroloph is always developed, but the postcentroloph is sometimes weak. There is a strong reduction in M3 posteriorly. The state of the centrolophs is the same as M1/M2. The metaloph bends posterolabially but the posteroloph remains free.

In lower molars, the anterotropid is absent. The anterolophid becomes longer through m1 to m3. The metalophid is free lingually and labially, curved posteriorly only in m1. The centrolophid is long and free, without the precentrotropid and postcentrotropid nearby. A very weak posterotropid is only present in a few m2s.

**Remarks.** *Butseloglis montisalbani* was originally described as the type species of *Schizoglravus*, itself a junior synonym of *Butseloglis*. This species was not found in St-Martin-de-Castillon C. The type materials from Montalbán 1D have been fully described by Freudenthal (2004). The new specimens from Montalbán 1D are characterized by two equally important centrolophs which are always present in the upper molars; the centrolophid is frequently present, but not well developed; the mesolophid is well developed together with a weakly developed posterotropid. Our specimens consequently show no significant difference with the population described by Freudenthal (2004).

#### Genus *Microdyromys* de Bruijn, 1966b

**Type species.** *Microdyromys koenigswaldi* de Bruijn, 66b.

#### *Microdyromys misonnei* (Vianey-Liaud, 1994) (Fig. 3I–T)

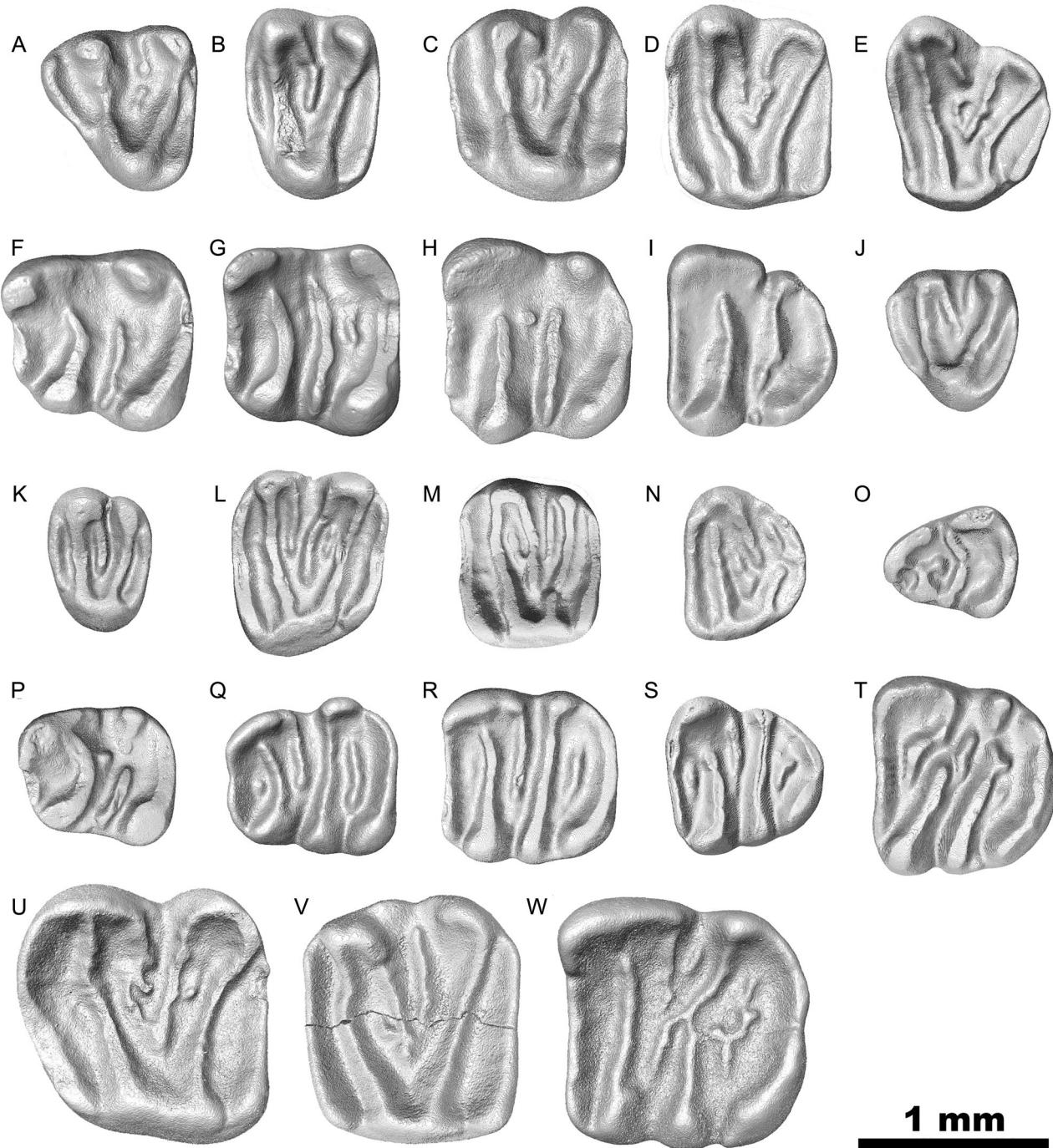
1971 *Pseudodryomys* aff. *fugax* Hugueney *et al.*: 2432.  
1994 *Branssatoglis misonnei* Vianey-Liaud: 147–149.

**Type locality.** Hoogbutsel (MP21).

**Holotype.** IRSNB M1786, right M2.

**Specimens and measurements.** UCBL-FSL\_218056 to 218067 and 218073 to 218074 for St-Martin-de-Castillon C; UCBL-FSL\_218034 to 218043 and 218072 for Montalbán 1D; for measurements see Table 1 and Supplemental material, Appendix 2 (Figs 3I–T, 4j–s).

**Description of the specimens from St-Martin-de-Castillon C.** DP4s are more-or-less triangular. The occlusal surface is moderately concave. The protocone is the highest cusp. The paracone and metacone are about the same height but lower than the protocone. The



**Figure 4.** Upper and lower teeth of glirids from MLB1D. *Butseloglis montisalbani*: **A**, right DP4, UCBL-FSL\_218025 (reversed); **B**, left P4, UCBL-FSL\_218026; **C**, right M1, UCBL-FSL\_218027 (reversed); **D**, left M2, UCBL-FSL\_218028; **E**, left M3, UCBL-FSL\_218029; **F**, right m1, UCBL-FSL\_218030 (reversed); **G**, left m1, UCBL-FSL\_218031; **H**, right m2, UCBL-FSL\_218032 (reversed); **I**, left m3, UCBL-FSL\_218033; *Microdyromys misonnei*; **J**, right DP4, UCBL-FSL\_218034 (reversed); **K**, left P4, UCBL-FSL\_218035; **L**, left M1, UCBL-FSL\_218036; **M**, left M2, UCBL-FSL\_218037; **N**, left M3, UCBL-FSL\_218038; **O**, left dp4, UCBL-FSL\_218039; **P**, right p4, UCBL-FSL\_218040 (reversed); **Q**, left m1, UCBL-FSL\_218041; **R**, right m2, UCBL-FSL\_218042 (reversed); **S**, left m3, UCBL-FSL\_218043; *Glirudinus aff. glirulus*; **T**, right m2, UCBL-FSL\_218044 (reversed). *Oligodyromys libanicus*: **U**, left M1, UCBL-FSL\_218045; **V**, right M2, UCBL-FSL\_218046 (reversed); **W**, left m2, UCBL-FSL\_218047. Scale bar = 1 mm.

anteroloph is relatively long and lower than other transverse crests, about half of the width of the tooth. It is curved and free, following the anterior side of the tooth. In the central valley, the precentroloph is well developed and connects to the paracone, whereas the postcentroloph is absent. The posteroloph also connects to the protocone but remains free labially.

**P4.** All teeth display an oval shape. The occlusal surface is strongly concave, with the protocone, paracone and metacone all the same height. The main pattern of the tooth is similar to that of DP4. The anteroloph is still curved and connects to the protocone and metacone, but longer and higher than in DP4; in some specimens, it is as high as other crests. The precentroloph is more developed than in DP4 and the postcentroloph is absent as in DP4. The posteroloph can be either free or connected to metacone on the labial side.

**M1/M2.** Teeth display a sub-rectangular shape. The anterior part of M2 is generally wider than M1 but the rest of the morphology is similar. The occlusal surface is concave at all wear stages. The protocone is included in the endoloph and forms a short lingual wall connecting to the posteroloph. The anteroloph is free on both sides, occasionally connecting with the protocone on some M2; it is curved posteriorly on its lingual side. The protoloph is straight and transverse, but the metaloph bends anteriorly near the protocone. The anterotrope and posterotrope are both absent. The precentroloph is well developed, almost reaching the protocone. The postcentroloph is less developed than the precentroloph, about half the length of the central valley, and it connects lingually to the precentroloph in some specimens. A very weak prototrope can be observed in most of the teeth whereas the metatrophe is absent. The posteroloph is free labially.

**M3.** All teeth display a sub-triangular shape, strongly reduced posteriorly. The occlusal surface is slightly concave and the pattern is more complicated than on other teeth due to a stronger morphological variation. The anteroloph is straight and connects with the protocone. There is either the prototrope or the metatrophe in the central valley, never both together. The precentroloph and the postcentroloph can be weak or well developed and in some specimens they are discontinuous. The posteroloph extends posterolabially and connects with protocone and metacone.

**dp4.** It is slightly narrower than p4. The metaconid is strong and elongated posteriorly, but disconnected from the entoconid. The anterotropid and centrolophid are absent. The metalophid is robust and connects to the metaconid and protoconid. The anterolophid is very weak. The mesolophid is free and also weak. The

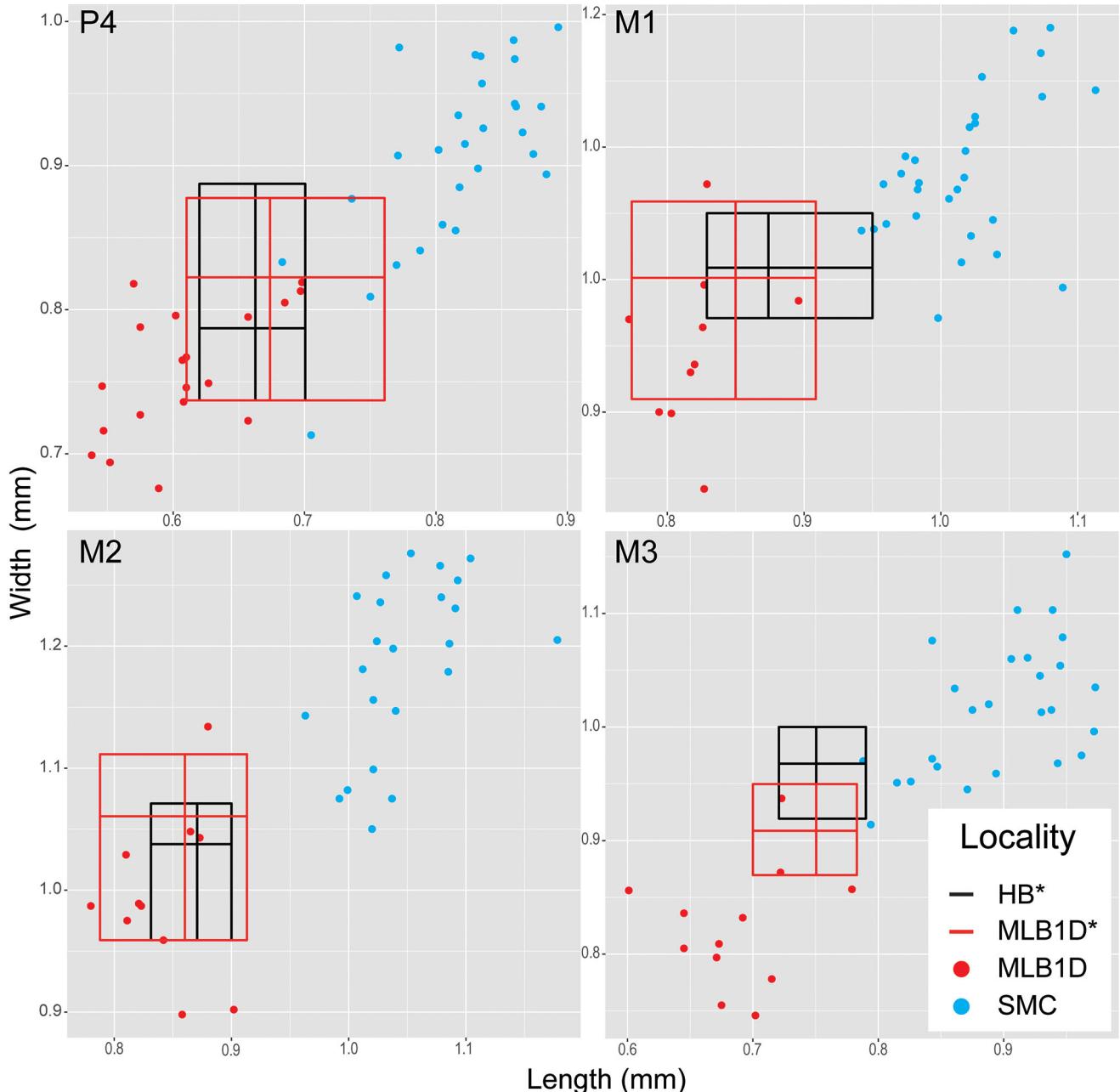
posterotropid is absent. The posterolophid is more robust than the metalophid and forms a rounded wall on the posterior border of the tooth.

**p4.** The morphology is similar to that of dp4. However, the anterolophid is present and also a short anterotropid; it is oblique, weak and short, shorter than in m1. The metalophid is curved posteriorly near the labial side. The centrolophid is present but very low and difficult to observe. The posterolophid is transverse in the middle.

**m1/m2.** All teeth are rectangular and strongly concave. m1 differs from m2 in having the posterior part slightly wider than the anterior part. The main cuspids are distinct from the crests. The metaconid is elongated and forms a robust lingual crest. The entoconid is strong and connects to the posterolophid in a low level. In most specimens, the entoconid connects with the mesolophid; in some rare cases this connection is absent. All transverse crests are about the same height. The anterolophid disconnects from the protoconid labially. There is only one weak anterotropid. The metalophid bends backward but does not reach the metaconid lingually. Both the precentrotropid and postcentrotropid are absent. The centrolophid can be weak or developed, even lingually free in some cases. The mesolophid is straight and connects with the mesoconid. The posterotropid is well developed.

**m3.** It displays a triangular shape, reduced posteriorly. The main pattern of the teeth is similar to that of m1 and m2, but the cuspids are weaker except the metaconid. The anterotropid is weak and the metalophid is completely straight. The centrolophid is well developed in all specimens. Because of the reduction of the posterior part of teeth, the posterotropid and posterolophid are strongly curved backward.

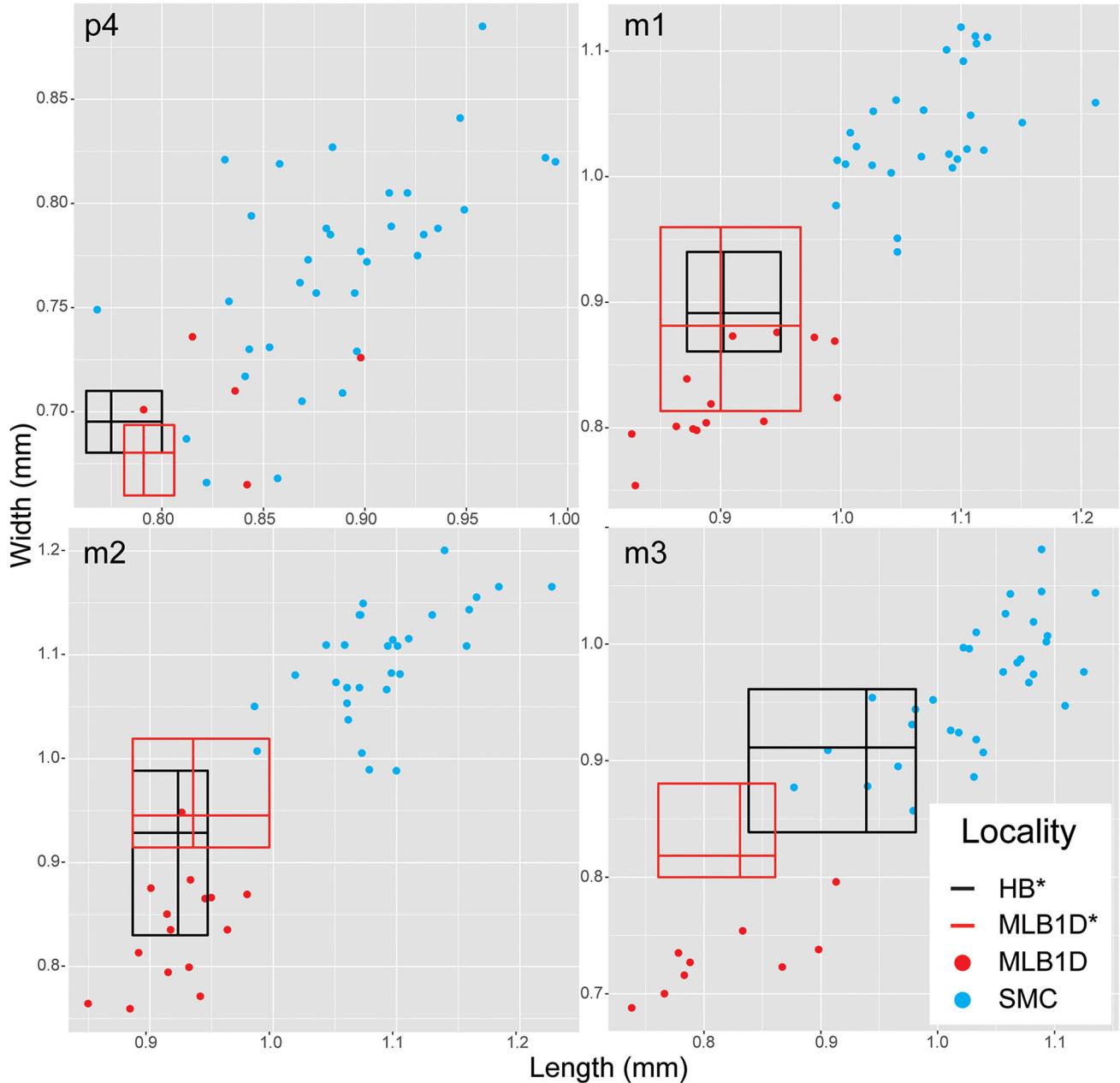
**Remarks.** *Microdyromys misonnei* was initially described as *Branssatoglis misonnei*. It was transferred to the genus *Microdyromys* by Freudenthal & Martín-Suárez (2007a). Most of the new specimens from Montalbán 1D (MP23) are referred to this species. Freudenthal & Martín-Suárez (2007a) made a complete description of the population from Montalbán. Our specimens from Montalbán 1D are characterized as upper molars, by the prototrope which can be either absent, short or long; the anterotropid in lower molars always present but weak; and a well-developed posterotropid in m1 and m2. These characteristics fit the description and variability described by Freudenthal & Martín-Suárez (2007a). Apart from the material from Montalbán 1D, some specimens from St-Martin-de-Castillon C (MP24) are also referred to the same species (see Description, above). The new specimens from



**Figure 5.** Size for the upper cheek teeth of *Microdyromys misonnei* from different localities. Boxes show the maximum, minimum and mean of the measurements. Abbreviations: **HB**, Hoogbutsel; **MLB1D**, Montalbán 1D; **SMC**, St-Martin-de-Castillon C; \*, measurements from Freudenthal & Martín-Suárez (2007a).

Montalbán 1D seem smaller than the former collection for P4 and M3 (Figs 5, 6). In lower cheek teeth, the length of teeth is similar, but they are noticeably narrower than in the old collection. Such differences for the same locality are difficult to explain as the method used to measure the teeth is the same as the one used by Freudenthal & Martín-Suárez (2007a). Discrepancies between the two studies in identifying premolars and third molars at specific level could explain such

differences. Additionally, for m3 only, the material from Hoogbutsel is slightly larger than that from Montalbán 1D. These differences do not seem to be the result of an evolution of a lineage with time but might partly be due to a previously underestimated size variability of the species. However, our new specimens from St-Martin-de-Castillon C are much larger than in the two other localities. Vianey-Liaud (1994) noticed a noticeable size evolution for the genera *Glamys*, *Gliravus* and



**Figure 6.** Size for the lower cheek teeth of *Microdyromys misonnei* from different localities. Boxes show the maximum, minimum and mean of the measurements. Abbreviations: HB, Hoogbutsel; MLB1D, Montalbán 1D; SMC, St-Martin-de-Castillon C; \*, measurements from Freudenthal & Martín-Suárez (2007a).

*Branssatoglis* along the course of the Palaeogene. She hypothesized that geographic isolation of taxa might lead to significant size differentiations whereas morphological changes often remain weak. Likewise, we hypothesize here that the different sizes might also be due to a biogeographic factor considering the distance between the different localities. Waiting for further data or additional comparisons with other localities, we tentatively refer the specimens of St-Martin-de-Castillon C to *M. misonnei* due to the morphological similarities and

despite the size differences with Hoogbutsel and Montalbán 1D.

Genus *Glirudinus* de Bruijn, 1966b

Type species. *Glirudinus gracilis* (Dehm, 1950).

*Glirudinus* aff. *glirulus* (Dehm, 1935)  
(Fig. 4T)

**Type locality.** Gunzenheim, Germany (MP30).

**Holotype.** Slg. München 1934 V21, fragment of the left lower jaw with incisor and m1.

**Specimens and measurements.** UCBL-FSL\_218044, right m2, L = 0.97 W = 0.93 (Fig. 4T); UCBL-FSL\_218069, right m3, L = 1.10 W = 1.14.

**Description of the specimens from Montalbán 1D.**

**m2.** Only one tooth was found in Montalbán 1D. The occlusal surface is slightly concave. The anterotropid connects to the metalophid on its lingual side. The metaloiphid extends from the posterior arm of the metaconid to the protoconid with a gap near the lingual side. The centrolophid is weak and free. The entoconid is also free. The posterotropid is very weak, almost absent. All tropids and lophids are straight and form an angle of approximately 45° to the longitudinal axis of the tooth, except the anterolophid and posterolophid.

**m3.** The pattern of m3 is similar to m2 and slightly concave. The talonid is noticeably narrower than the trigonid. The anterotropid is absent. The centrolophid is not connected to the metaconid. It is interrupted and more developed than in m2. The entoconid weakly connects with the mesolophid and the posterolophid at a low level. The posterotropid is well developed.

**Remarks.** The pattern is composed of an association of straight lophids with an oblique centrolophid, all forming a right triangle shape of the trigonid which is a typical character of the genera *Glirudinus* and *Glirulus*. In addition, *Glirulus* is only known in the Miocene and has more crests than *Glirudinus*, especially the existence of precentrotropid and postcentrotropid in lower molars, while *Glirudinus* traces back to the early Oligocene of Itardies (MP23) with fewer and more robust crests (Vianey-Liaud 2003). Consequently, despite some variation of the anterotropid and metalophid observed in our specimens, we refer them to *Glirudinus* because of the lower number of crests and of their robustness. *Glirudinus antiquus* Vianey-Liaud, 2003 from Itardies is the only species known so far in the early Oligocene. The size of our m2 fits within the size range of the type population from Itardies (m2: mean length = 1.02; mean width = 0.98; Vianey-Liaud 2003); however, the m3s are much larger (m3: mean length = 0.89; mean width = 0.85; Vianey-Liaud 2003). Additionally, the metalophid is transverse and the trigonid is not triangular as in the type population. The interrupted centrolophid in m3 also occasionally appears in *G. antiquus*. Thus, considering both morphology and size, our specimen is more similar to the late Oligocene species *Glirudinus glirulus* (Gunzenheim, Dehm 1950; Pech Desse and Pech du Fraysse, Vianey-Liaud 2003). Even if the identification at

specific level is uncertain and needs more specimens for a confirmation, the new specimens can without doubt be referred to the genus *Glirudinus*, which has never been identified in Montalbán 1D before.

Genus *Oligodyromys* Bahlo, 1975

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

***Oligodyromys libanicus*** Freudenthal & Martín-Suárez, 2007b  
(Fig. 4U–W)

1971 *Pseudodryomys* aff. *fugax* Hugueney et al.: 2432.

**Type locality.** Montalbán 8 (MP22).

**Holotype.** Departamento de las Ciencias de la Tierra, University of Zaragoza, MLB8 1183, left m1.

**Specimens and measurements.** UCBL-FSL\_218045, left M1, L = 1.38 W = 1.31 (Fig. 4U); UCBL-FSL\_218068.001, left M1, L = 1.15 W = 1.33; UCBL-FSL\_218046, right M2, L = 1.09 W = 1.32 (Fig. 4V); UCBL-FSL\_218068.002, right M2, L = 1.25 W = 1.52; UCBL-FSL\_218068.003, broken right M2, L = 1.25 W = 1.44; UCBL-FSL\_218047, left m2, L = 1.34 W = 1.44 (Fig. 4W).

**Description of the specimens from Montalbán 1D.**  
**M1/M2.** The occlusal surfaces of M1 and M2 are strongly concave. Both M1 and M2 display a rectangular shape, but M1 is slightly longer labially. All cusps are well developed. The anteroloph connects with paracone labially in M1, but remains free in M2. Both anterotrope and posterotrope are absent. The central valley is ‘V’-shaped; on its lingual side the endoloph of M1 is more developed and longer than in M2, which results in the metaloph being slightly bent posteriorly. In contrast it is always straight in M2. Both the precentroloph and the postcentroloph are well developed, with no tropes in the central valley. Sometimes there are some bulges in between the centrolophs and main lophs. Because they are not crest-like, we consider them as the variation of the centrolophs. The posteroloph is free in all specimens.

**m2.** The only m2 shows irregular tropids. All cusps are well developed and the metaconid is much higher than other cusps. Six crests are present in our specimen. The anterotropid is absent. The metalophid is parallel to the anterolophid, it connects with the protoconid and reaches the base of the rising metaconid. The centrolophid is well developed and originates from the posterior arm of the metaconid. It is interrupted in the middle of the tooth, and the labial part extends posteriorly to connect with mesolophid. The mesoconid connects with the

entoconid through the mesolophid. The posterotropid is well developed and twisted. There is a weak crest in the valley between the centrolophid and the mesolophid, but this crest is as high as the centrolophid. We consider it as a variation of the centrolophid.

**Remarks.** *Oligodyromys* was referred to Glirinae Thomas, 1897 by Bahlo (1975) and was later transferred to the Myomiminae Daams, 1981 because of the concave occlusal surface. Bosma & de Bruijn (1982) synonymized *Oligodyromys* with *Branssatoglis* Hugueney, 1967. However, Freudenthal & Martín-Suárez (2007b) restored the genus because too many species are classified inside the genus *Branssatoglis*. As a result, *Branssatoglis* has been used as a wastebasket taxon; however, the different species of *Oligodyromys* and the type species of *Branssatoglis* (*Branssatoglis concavidens* Hugueney, 1967), being distant in our phylogeny, indicate that both genera are clearly differentiated and that *Oligodyromys* is valid. *O. libanicus* is described from the early Oligocene of Montalbán 8 as the largest known *Oligodyromys*; only *Oligodyromys sjeni* Ünay, 1989 from Kocayarma (Turkey) is of similar size (Freudenthal & Martín-Suárez 2007b). The anterotropid of *O. libanicus* is only well developed on m1. Unfortunately, we do not have any large-sized m1. The anterotrope in M1/2 is infrequently present in the type locality and also absent in all our specimens. Six crests exist on both upper and lower molars. The patterns are also similar to *Butseloglis micio* and *B. itardiensis*, the latter species possibly being synonymous with *B. micio* (Vianey-Liaud, 1994). Freudenthal & Martín-Suárez (2007b) considered that the larger specimens of *B. itardiensis* from Hoogbutsel probably belongs to *O. planus*; our specimens differ from it by lacking the anterotropid and having fewer crests in upper molars. Considering that on the one hand our specimens are larger than *B. micio* and *B. itardiensis*, and that the patterns are simpler than *O. planus* and *O. sjeni*, and on the other hand the size is close to that of *O. libanicus* from Montalbán 8 (M1: mean length = 1.25, mean width = 1.34; M2: mean length = 1.24, mean width = 1.42; m2: mean length = 1.36, mean width = 1.38; Freudenthal & Martín-Suárez 2007b), we tentatively refer our specimens to *O. libanicus*. *Oligodyromys* is common from MP18 to MP22, but remains rare in Montalbán 1D (MP23), only represented by a few specimens of *O. cf. parvus* (Freudenthal & Martín-Suárez 2007b). This is the first occurrence of *O. libanicus* or such a large species in this locality.

## Phylogenetic analysis

We followed the strategy of Wahlert *et al.*'s (1993) phylogeny by selecting *Paramys* as an outgroup taxon

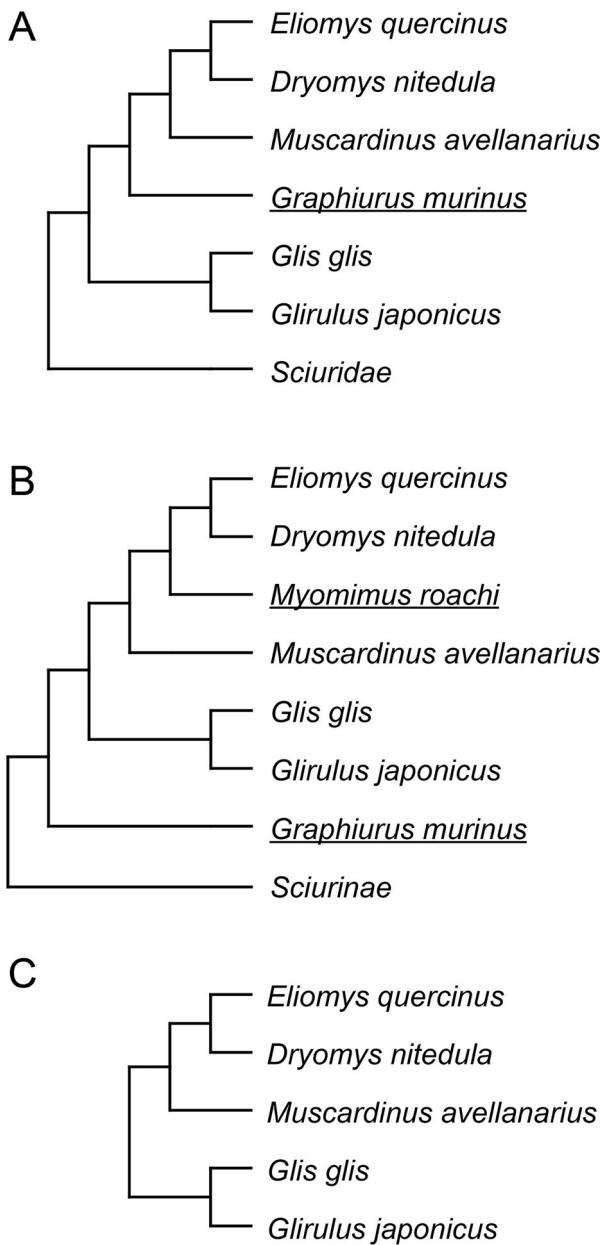
(here *Paramys copei* Loomis, 1907), and added *Paleosciurus goti* Vianey-Liaud, 1974 as a second outgroup, as sciurids are often considered to be closely related to glirids based on both morphological and genetic evidence (e.g. Vianey-Liaud & Jaeger 1996; Bentz & Montgelard 1999; Montgelard *et al.* 2003). For the analysis we used the semi-ordered character configuration. The data matrix was edited in Mesquite v. 3.6 software and saved in NEXUS format (see *Supplemental material*, Appendix 3 – Phylogenetic matrix). A parsimony analysis was performed using PAUP v. 4.0a (tree analysis using heuristic search). Optimal scores were searched with 10,000 replications. Considering the variety of glirids, all characters were unordered and set with equal weight (e.g. Wahlert *et al.* 1993). A backbone constraint has been established after the phylogenetic result of the nuclear gene analysis inferred from the maximum-likelihood analyses of Montgelard *et al.* (2003) and Nunome *et al.* (2007). The main differences between these studies are the position of *Graphiurus* and the absence of *Myomimus* in Nunome *et al.* (2007). We created the constrained tree by selecting the common part of their results (Fig. 7). Phylogenetic analyses were performed both with the backbone method for the extant species, and without. The results with and without backbone are identical, implying that our phylogenetic result including fossil taxa is compatible with the phylogenetic relationship known for extant taxa. The best trees and the strict consensus trees were obtained using PAUP.

The phylogenetic analysis resulted in 27 most parsimonious trees with tree lengths of 533 steps, a consistency index (CI) of 0.415 and a retention index (RI) of 0.667. In our strict consensus tree (Fig. 8), the most basal clade of the family is a monophyletic group composed of *Chaetocauda* and *Graphiurops* Bachmayer & Wilson, 1980. In the Palaeogene, most basal genera like *Glamys* Vianey-Liaud, 1989, *Butseloglis*, *Oligodyromys* and *Microdyromys* are paraphyletic. By the middle Oligocene, two main clades split including most extant genera: the first clade mainly contains the extant genera *Glirudinus*, *Glis* Brisson, 1762 and *Glirulus*, and the second one includes *Graphiurus*, *Dryomys*, *Eliomys*, *Myomimus* and *Muscardinus*. However, several genera also appear paraphyletic when taxa from the fossil record are included, such as *Prodryomys* Mayr, 1979, *Myomimus*, *Glis*, *Glirudinus* and *Eliomys*.

## Discussion

### Phylogenetic results

For extant genera, *Glis* forms a monophyletic group, except '*Glis*' *guerbuezi* Ünay, 1989 from the middle

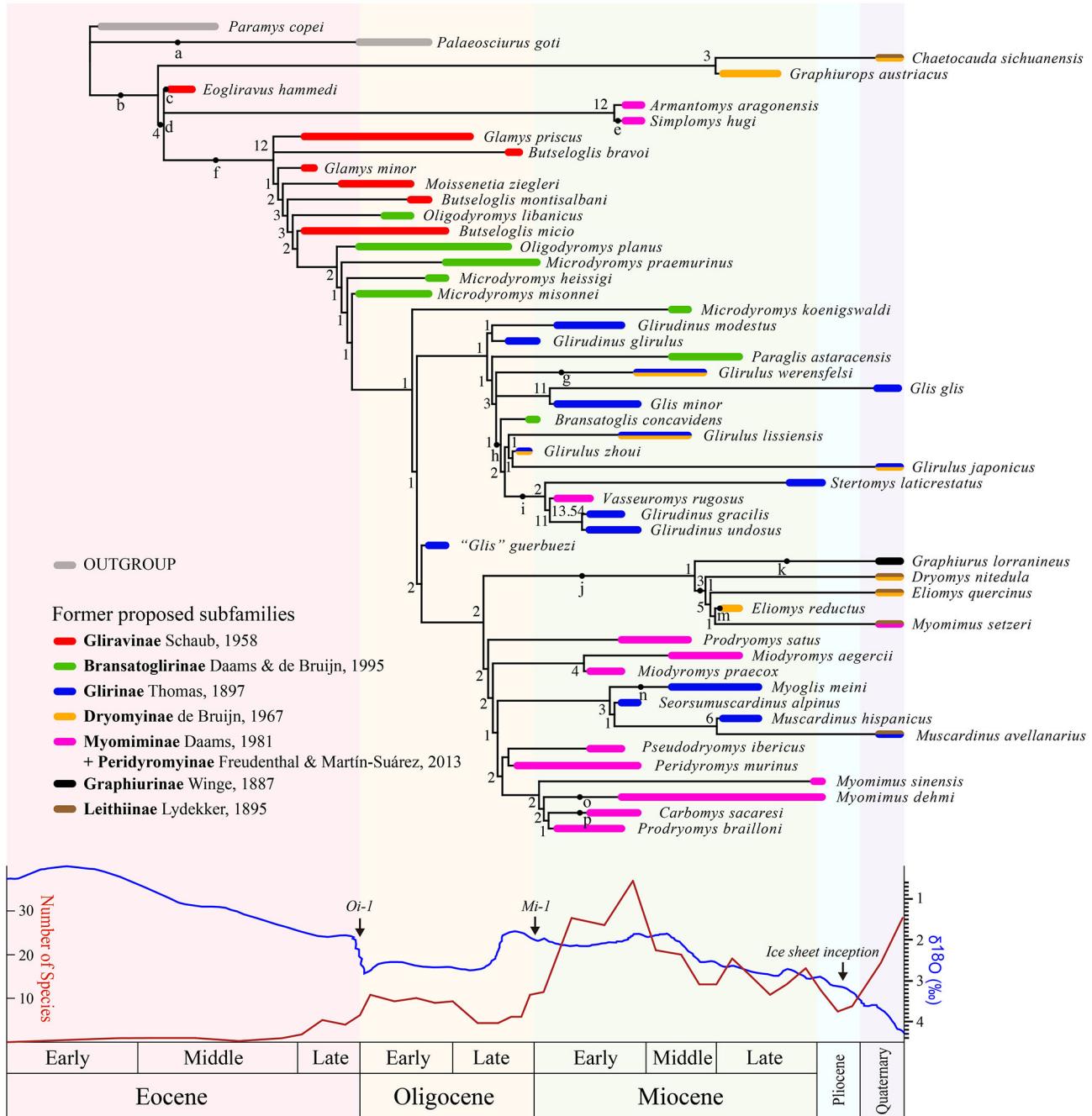


**Figure 7.** The tree used for back-bone analysis. **A**, simplified phylogenetic tree inferred from maximum-likelihood analyses of Nunome *et al.* (2007) concatenated sequences (six-gene analysis; APOB + IRBP + RAG1+ SPTBN + TH + LCAT; 5084 bp dataset); **B**, simplified phylogenetic tree using the concatenation of Montgelard *et al.* (2003) (SPTBN, TH, LCAT and 12S rRNA); **C**, consensus tree used for back-bone analysis excluding the underlined species whose position differs between Nunome *et al.* (2007) and Montgelard *et al.* (2003).

Oligocene of Turkey for which the generic attribution seems doubtful (Ünay 1989). It is common in *Glis* that the protoloph and metaloph are separated lingually, which is not the case for ‘*Glis*’ *guerbuezi*. In our result,

‘*Glis*’ *guerbuezi* is recovered in a basal position within the other big clade, suggesting a closer relationship to the genus *Microdyromys*. The genus *Myomimus* also shows noticeable differences between the extant and fossil species. The extant species *Myomimus setzeri* Rossolimo, 1976 has a simple dental pattern with a well-developed precentroloph, but lacking the postcentroloph in upper molars, whereas the fossil species *M. sinensis* and *M. dehmi* differ in having longer P4 with a precentroloph and a free anteroloph, in having a postcentroloph in M1/2 and M3 and a metatrophe in M3, and in having a posterotropid in m1/2. As a result, the extant species has a close relationship with the extant genus *Eliomys*, whereas the fossil species are closer to *Carbomys* Mein & Adrover, 1982 and *Prodryomys* and form a monophyletic clade with them.

The Asian extant genus *Chaetocauda* has a close relationship with the Austrian Miocene genus *Graphiurops* which has been described from Kohfidisch (MN10; Bachmayer & Wilson 1980). They form a monophyletic clade with the simplest dental pattern, and are recovered in the basal-most position of Gliridae. All cheek teeth are without any tropes and tropids, hence resemble the primitive glirids of the genus *Eoglravus*. Most main lophs and lophids as precentroloph, postcentroloph, centrolophid and mesolophid are also absent. In contrast, the cusp(id)s of *Eoglravus* are more developed with a generally bunolophodont morphology, similar to the outgroups. In *Chaetocauda* and *Graphiurops* the more lophodont morphology with the endoloph forming a lingual wall and the lack of mesolophid precludes closer relationships to outgroups. Based on recent genetic analyses, the position of *Graphiurus* remains uncertain (Fig. 7). It could be either a basal clade (Montgelard *et al.* 2003), or a sister group to Leithiinae (*Dryomys*, *Eliomys*, *Muscardinus*) and form a monophyletic clade together with them (Nunome *et al.* 2007). According to the presence of a small zygomatic plate, Hautier *et al.* (2008) hypothesize that the initial state of graphiurines could be morphologically close to *Branssatoglis*. Our results do not support any close phylogenetic relationship between *Graphiurus* and *Branssatoglis* but rather support *Graphiurus* as a sister group to extant Leithiinae as proposed by Nunome *et al.* (2007). Bachmayer & Wilson (1980) and Montgelard *et al.* (2003) suggested that *Graphiurops* bears a close relationship with the extant African dormice *Graphiurus*. They used *Graphiurops* to discuss the evolution of Graphiurinae Winge, 1887, and proposed the possibility that the group originated in Europe before migrating to Africa, or that a primitive clade of African Graphiurinae migrated into Europe during the Miocene. In contrast, in our study, *Graphiurops* is closely related to the extant Asian



**Figure 8.** Phylogeny of glirids. Strict consensus tree is from 27 most parsimonious trees. Numbers for each node are Bremer support values. Blue line, oxygen isotopic curve from Zachos *et al.* (2001); Red line, species richness curve; Unambiguous morphological synapomorphies: **a**, 126 (0→1); **b**, 121 (0→1); **c**, 109 (1→2); **d**, 109 (0→1); **e**, 64 (0→1); **f**, 69 (0→2); **g**, 50 (0→1); **h**, 104 (0→1), 113 (0→1); **i**, 72 (0→1); **j**, 23 (0→2), 41 (0→1); **k**, 8 (1→2); **l**, 36 (0→1), 40 (0→1); **m**, 32 (1→2); **n**, 85 (0→1), 113 (0→2); **o**, 72 (0→1); **p**, 69 (2→1); arrows indicate the glaciation events from Zachos *et al.* (2001). Abbreviations: **Mi-1**, early Miocene Glaciation; **Oi-1**, early Oligocene Glaciation; **pIS**, permanent ice-sheets on both hemispheres.

dormouse *Chaetocauda*, both forming a monophyletic basal clade. The upper teeth patterns of *Graphiurus* are indeed more complicated than both *Graphiurus* and *Chaetocauda* with a lot of spurs developed from the centrolophs in the central valley. As a result, *Graphiurus*

appears to be a genus strictly endemic to Africa of which an origin in Eurasia remains so far unknown.

Daams & de Bruijn (1995) created the monogeneric subfamily *Bransatogliniae* Daams & de Bruijn, 1995 for the genus *Bransatoglis*. Freudenthal & Martín-Suárez

(2007b) discussed the relationships within the clade Bransatoglirinae extensively. The genera *Paraglis* Baudelot, 1970 and *Oligodyromys* used to be in synonymy with *Bransatoglis* (Daams 1976; Bosma & de Bruijn 1982), and were then restored by Freudenthal & Martín-Suárez (2007b). Additionally, the genus *Microdyromys* was transferred to Bransatoglirinae from Dryomyinae de Bruijn, 1967 by Freudenthal & Martín-Suárez (2007b). In our result, Bransatoglirinae becomes a paraphyletic group. *Oligodyromys* is the most basal genus of this subfamily as suggested by Freudenthal & Martín-Suárez (2007b).

Freudenthal & Martín-Suárez (2013) also created a new subfamily Peridyromyinae Freudenthal & Martín-Suárez, 2013 based on the diagnosis of the genus *Peridyromys* Stehlin & Schaub, 1951, which was previously referred to Myomiminae (Daams 1981; Daams & de Bruijn 1995). In addition to *Peridyromys*, they also include the genera *Altomiramys* Díaz-Molina & López-Martínez, 1979, *Armantomys* de Bruijn, 1966b, *Miodyromys* Kretzoi, 1943, *Praearmantomys* de Bruijn, 1966b, *Pseudodryomys* de Bruijn, 1966a, *Simplomys* García-Paredes et al., 2009, *Tempestia* van de Weerd, 1976, *Ramys* García-Moreno & Lopez-Martínez, 1986 and *Vasseuromys* in this new subfamily. However, the morphology of both *Vasseuromys* and *Ramys* differ from the ‘simplified pattern’ considered as diagnostic for this subfamily. Sinitza & Nesin (2018) made a full systematic analysis for *Vasseuromys*, also including *Ramys*, and considered it as paraphyletic, rather used as a waste-basket glirid taxon. Many species were placed inside this genus. Our analysis does not include *Ramys* and the number of species of *Vasseuromys* is insufficient to support the conclusions of Sinitza & Nesin (2018), but its phylogenetic position is far from the other genera included in the subfamily Peridyromyinae. Likewise, in our result, *Armantomys* and *Simplomys* form a monophyletic clade also far from other species considered to belong to Peridyromyinae. This clade is characterized by the simple pattern and the elongated protocone. The subfamily Peridyromyinae appears here as polyphyletic, thus questioning its validity.

The main differences between the traditional palaeontological classification and the biological classification are the definition of the subfamilies. All palaeontological classifications are based on studies by Daams (1981) and Daams & de Bruijn (1995). They suggested six subfamilies: Glirinae, Dryomyinae, Myomiminae, Graphiurinae, Bransatoglirinae and Gliravinae Schaub, 1958. In a later study, more subfamilies were created focusing on the basal taxa described from the Palaeogene of Europe (Glamyninae Vianey-Liaud, 1994, a synonym of Gliravinae according to Freudenthal 2004, and Peridyromyinae). By contrast, the

classification used by biologists remains unchanged since Lydekker (1895). Only three subfamilies exist: Graphiurinae is a monogenic subfamily including only species within the genus *Graphiurus*; Glirinae includes two genera, *Glis* and *Glirulus*. The subfamily Leithiinae Lydekker, 1895 is not included in any palaeontological classification. The type genus of Leithiinae is *Leithia* Lydekker, 1895, a large fossil insular taxon with specialized sciromorph characters. Hennekam et al. (2020) studied the type species, *L. melitensis* Adams, 1863, and considered that this kind of endemic species tends to display a composite morphology strongly constrained by its insular environment. We tried to add it to our phylogeny in order to address the question of the subfamily Leithiinae. However, the position of *L. melitensis* is unstable among the numerous most parsimonious trees (the consensus tree with 50% majority rule of 702 most parsimonious trees is provided in Supplemental material, Appendix 4 – Phylogenetic result). Apart from *Leithia*, Leithiinae also includes *Dryomys*, *Eliomys*, *Myomimus* and *Muscardinus*. Molecular-based hypotheses indicate that these four extant genera form a monophyletic group (Montgelard et al. 2003; Nunome et al. 2007). The only noticeable result drawn from our majority rule tree is that *L. melitensis* does not seem to be closely related to these taxa, thus suggesting that a revision of this subfamily is needed, or that insular taxa are too derived to help decipher fine scale phylogenetic affinities.

The peculiar morphology of *L. melitensis* due to its insular condition and the difficulty to obtain a reliable phylogeny including this species justifies, *a posteriori*, its exclusion from our main phylogenetic analysis (Fig. 8) in order to correctly decipher the phylogenetic relationships between non-insular glirid taxa.

In contrast, in the traditional palaeontological classification, *Dryomys* and *Eliomys* are referred to Dryomyinae, the species of *Myomimus* form the subfamily Myomiminae, whereas *Muscardinus* belongs to Glirinae. Our result contradicts both classifications by grouping *Dryomys*, *Eliomys* and *Myomimus* in a clade together with *Graphiurus*, but *Muscardinus* in a different clade. It is also noteworthy that the fossil species of *Myomimus* are not grouped with the extant species, thus indicating that they should be referred to a different genus, the type species of *Myomimus* being the extant *M. personatus* Ognev, 1924. All subfamilies turn out to be paraphyletic or polyphyletic in our study.

### Implications for the classification of Gliridae

Although the proposal of formally naming clades is beyond the scope of the present study, a few remarks can be made, potentially serving as guidelines for further work on the topic. Our phylogenetic hypothesis

supports the existence of two well-supported and diversified clades, including all extant genera with the exception of *Chaetocauda*. The first clade includes the genera *Glirudinus*, *Glis*, *Glirulus*, *Paraglis*, *Stertomys* Daams & Freudenthal, 1985, *Vasseuromys* and *Branssatoglis*. Inside this group, we agree with the extant classification that *Glirulus* is closely related with *Glis* and *Glirudinus*, and should be part of Glirinae, not Dryomyinae. Our result includes *Vasseuromys* in this clade: however, it has to be considered with caution because of the paraphyly within the genus (Sinitza & Nesin 2018). Likewise, *Branssatoglis* has been used as a wastebasket and several species previously referred to this genus are now distributed to other basal genera like *Butseloglis*, *Oligodyromys*, *Microdyromys* and *Paraglis* (Freudenthal & Martín-Suárez 2007b). So far, beside the type species, other species previously referred to *Branssatoglis* cannot always be referred with certainty. The whole clade is mostly composed of taxa previously considered as Glirinae (with the exception of *Myoglis*, *Seormuscardinus* and *Muscardinus*); additionally, the subfamily name Glirinae would have the priority, and potential further monophyletic subdivisions could then be regarded as tribes.

The other main monophyletic clade splits into two monophyletic groups. One well-supported group includes the extant genera *Graphiurus*, *Dryomys*, *Eliomys* and *Myomimus*. However, morphologically, *Graphiurus* noticeably differs from these three other genera by its unique pattern of prominent peripheral crests on upper molars (Wahlert *et al.* 1993). In addition, the posterior edge of the anterior root of the zygoma is anterior to the first cheek tooth. As a result, the skull presents a hystricomorphous condition (Hautier *et al.* 2008) which does not fit with any other known pseudo-myomorphic type of skull proposed by Vianey-Liaud (1985) for Eurasian glirids. However, despite those morphological differences, *Graphiurus* groups with *Dryomys*, *Eliomys* and *Myomimus*, forming a potential subfamily for which the name Graphiurinae would have the priority. Within this clade, *Myomimus* turns out to be polyphyletic. As a result, the fossil forms of *Myomimus* should probably be referred to a different genus (or genera) and a systematic revision will be needed for these taxa in the future.

The other monophyletic group includes the genera *Prodryomys*, *Midyromys*, *Myoglis*, *Seormuscardinus* de Bruijn 1998, *Muscardinus*, *Peridyromys*, *Myomimus* and *Carbomys*. *Muscardinus*, previously regarded as falling within Glirinae in the molecular analysis of Bentz & Montgelard (1999), was later suggested to be included in Leithiinae (Montgelard *et al.* 2003), which fits better with our results where it is grouped with most

of the extant species referred to Leithiinae (with the exception of *Chaetocauda*). Additionally, our phylogeny also supports a close relationship with the genera *Muscardinus*, *Seormuscardinus* and *Myoglis* McKenna & Bell, 1997 outside of Glirinae due to a typical flat surface and narrow crests pattern. This group includes most of the species referred to the subfamily Peridyromyinae (*sensu* Freudenthal & Martín-Suárez 2013) and could potentially be named Peridyromyinae.

In addition, two other smaller monophyletic clades are revealed by our analysis. *Armantomys* and *Simplomys* form a monophyletic clade due to their simple tooth pattern. Most of the species having a simplified pattern were included in *Armantomys*, *Praearmantomys* and *Pseudodryomys* before García-Paredes *et al.* (2009) erected the genus *Simplomys*. Four of the six species in *Simplomys*, including the type species *Simplomys simplicidens* de Bruijn, 1966a, were defined previously under the genus *Pseudodryomys* (de Bruijn 1966a; García-Paredes *et al.* 2009; Prieto *et al.* 2019). Although Kälin & Kempf (2009) still consider *Simplomys* to be a junior synonym of *Pseudodryomys*, in our study *Pseudodryomys* is closer to *Peridyromys* as they both form a monophyletic clade. The patterns of *Armantomys* and *Simplomys* are indeed simpler than *Pseudodryomys ibericus* de Bruijn, 1966a, the type species of *Pseudodryomys*. It fits with the assumption of the close relationships between *Armantomys* and *Simplomys* of García-Paredes *et al.* (2009), due to a presumably same origin on the Iberian Peninsula. But the morphological similarities could also be the result of convergent evolution under similar environments (García-Paredes *et al.* 2009) which would not be detected by the analysis.

Another monophyletic group, potentially the most basal among dormice, is composed by the extant genus *Chaetocauda* and the fossil genus *Graphiurops*. Our study is the very first to suggest a close relationship between these two genera, whereas *Graphiurops* is usually compared with *Graphiurus* (Bachmayer & Wilson 1978, 1980). Vianey-Liaud & Jaeger (1996) considered *Graphiurops* to be very close to the small European late Eocene glirid *Tenuiglis*. We do not know a lot about the rare genus *Tenuiglis*, which is incidentally not included in our analysis but our result shows that *Graphiurops* is closer to *Chaetocauda* rather than any other fossil taxon (see discussion, above).

However, these two small clades include only two taxa each so far and further analyses are necessary to confirm these monophyletic relationships before considering possible implications in terms of classification.

**Table 1.** Measurements for new specimens of St-Martin-de-Castillon C (**SMC**) and Montalbán 1D (**MLB1D**), in mm.

Species	Locality	Position	N.	Length			Width		
				Min.	Mean	Max.	Min.	Mean	Max.
<i>Butseloglis tenuis</i>	SMC	P4	2	0.745	0.802	0.859	1.019	1.045	1.071
		M1	2	0.914	0.986	1.057	1.093	1.185	1.276
		M2	4	0.914	0.962	1.034	1.117	1.207	1.301
		M3	1	—	0.913	—	—	1.012	—
		p4	1	—	0.898	—	—	0.742	—
		m1	3	0.957	1.026	1.063	1.023	1.093	1.209
		m2	4	0.986	0.993	0.998	0.993	1.084	1.171
		m3	1	—	0.957	—	—	0.946	—
		DP4	7	0.744	0.794	0.922	0.719	0.813	0.864
		P4	23	0.585	0.688	0.772	0.812	0.921	1.014
<i>Butseloglis montisalbani</i>	MLB1D	M1	33	0.886	0.975	1.086	0.916	1.029	1.200
		M2	20	0.881	0.961	1.026	1.018	1.094	1.175
		M3	7	0.796	0.830	0.874	0.863	0.941	1.041
		m1	22	0.852	0.979	1.089	0.838	0.955	1.110
		m2	30	0.948	1.024	1.137	0.942	1.037	1.155
		m3	14	0.817	0.966	1.121	0.803	0.929	1.029
		DP4	18	0.687	0.725	0.769	0.673	0.720	0.794
		P4	28	0.683	0.816	0.893	0.713	0.907	0.996
		M1	29	0.942	1.015	1.113	0.971	1.081	1.190
		M2	23	0.963	1.047	1.178	1.050	1.186	1.276
<i>Microdyromys misonnei</i>	SMC	M3	26	0.788	0.897	0.973	0.914	1.017	1.152
		dp4	12	0.749	0.774	0.810	0.580	0.640	0.684
		p4	34	0.768	0.887	0.994	0.666	0.770	0.885
		m1	27	0.996	1.074	1.212	0.940	1.038	1.119
		m2	30	0.988	1.093	1.229	0.988	1.094	1.200
		m3	32	0.877	1.034	1.135	0.857	0.964	1.081
		DP4	7	0.565	0.663	0.720	0.688	0.763	0.806
		P4	19	0.538	0.608	0.698	0.676	0.757	0.819
		M1	10	0.772	0.821	0.896	0.842	0.949	1.072
		M2	11	0.780	0.842	0.902	0.898	0.996	1.134
<i>Microdyromys misonnei</i>	MLB1D	M3	12	0.601	0.687	0.779	0.746	0.823	0.937
		dp4	22	0.620	0.745	0.909	0.490	0.616	0.807
		p4	5	0.791	0.836	0.898	0.665	0.708	0.736
		m1	14	0.826	0.906	0.997	0.754	0.823	0.876
		m2	15	0.853	0.926	0.982	0.759	0.835	0.948
		m3	9	0.738	0.818	0.913	0.688	0.731	0.796

## Diversification of Gliridae

We measured species-richness for the whole family through time (see [Supplemental material, Appendix 5](#) – Diversity raw data) and compared our phylogenetic result with the global climatic curve of Zachos *et al.* (2001). The species-richness curve shows that glirids diversified at least three times along the course of their evolution. The first event occurred in the late Eocene and early Oligocene. This diversification involves numerous clades including the genera *Glamys*, *Butseloglis*, *Moissenetia* Hugueney & Adrover, 1995, *Oligodyromys* and *Microdyromys*. The diversification could be linked to the glaciation event that occurred at the end of the Eocene inducing a drastic temperature drop at the beginning of the Oligocene (O1-1 Glaciation; Zachos *et al.* 2001). It triggered a large faunal turnover in the European faunas known as the ‘Grande Coupure’ (Stehlin 1909). At the Oligocene–Miocene boundary,

the second diversification event, arguably the most important one, involves the two main clades discussed above, noticeably with the appearance of the genera *Glirudinus*, *Branssatoglis*, *Vasseuromys*, *Glis* and *Glirulus* in one clade, and *Peridyromys*, *Prodryomys*, *Carbomys*, *Seorsumuscardinus* and *Midyromys* in the other. It is noteworthy that among the late Eocene and early Oligocene taxa involved in the first diversification phase, *Microdyromys* (although paraphyletic) is the genus most closely related to these clades, supporting the hypothesis proposed by Freudenthal & Martin-Suárez (2013) that most modern glirids (*Chaetocauda* excluded) derive from this genus. As for the previous diversification event, this diversification phase seems to be coeval with another glaciation event (Mi-1 Glaciation; Zachos *et al.* 2001). However, unlike the previous climatic event, this glaciation event is short and the diversification reaches its optimum at the late

early Miocene climatic optimum (Zachos *et al.* 2001; Böhme 2003). From this point onward, the species richness continuously reduces until the Pliocene. The third diversification event is the recent one starting from the middle Pliocene when the onset of the northern hemisphere ice sheet expansion started (e.g. Hill *et al.* 2007; Gradstein *et al.* 2012; Contoux *et al.* 2015). It reached its peak through the Quaternary until today. However, it is worth noting that the recent species richness of the family is mostly related to the diversification of the African *Graphiurus*, and consequently of one single African clade, whereas the species from Eurasia remain relatively poorly diversified following the decreasing trend initiated in the mid-Miocene.

These different observations suggest that glaciation events may have been responsible for triggering the three main diversification phases of the family. One peculiarity of extant dormice is the ability of species living in temperate zones to hibernate during the cold season (Nowak & Walker 1999). This strategy enables them to cope with difficulties of maintaining body temperature during the season when less food is available (Vaughan *et al.* 2011). Although the origin of hibernation in mammals, and more specifically for dormice, remains uncertain, one hypothesis suggests that it occurs in the phylogenetically old groups and that this ability could derive from an ancestral characteristic lost in most modern groups of larger mammals (Geiser 1998), rather than a late adaptation during Quaternary glaciations (Goodwin *et al.* 2005). Our observations linking the main diversification phases of dormice to cold climatic events as soon as the early Oligocene suggest that dormice possessed an adaptive advantage at the time, triggering their successful diversifications. Such an observation lends support to the hypothesis of an ancestral origin of this ability, although definite proofs of hibernation remain to be found in the fossil record prior to the Quaternary (Selkova 2003; Goodwin *et al.* 2005; Klevezal & Potapova 2010).

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## Supplemental material

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