SPANISH JOURNAL OF PALAEONTOLOGY

New ideas on the systematics of Gliridae (Rodentia, Mammalia)

Matthijs FREUDENTHAL[1] & Elvira MARTÍN-SUÁREZ[2]*

[1] Departamento de Estratigrafía y Paleontología, Campus Fuentenueva, Universidad de Granada, 18071 Granada, Spain, and Netherlands Centre for Biodiversity, Naturalis, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands; mfreuden@ugr.es
[2] Departamento de Estratigrafía y Paleontología, Campus Fuentenueva, Universidad de Granada, 18071 Granada, Spain; elvirams@ugr.es

* Corresponding author

Freudenthal, M. & Martín-Suárez, E. 2013. New ideas on the systematics of Gliridae (Rodentia, Mammalia). [Nuevas ideas sobre la sistemática de Gliridae (Rodentia, Mammalia)]. *Spanish Journal of Palaeontology*, 28 (2), 239-252.

Manuscript received 04 March 2013
Manuscript accepted 07 June 2013

ABSTRACT

Extant members of the family Gliridae lack a caecum and are not capable of digesting hard (cellulose) plant material. We assume that they did have a caecum at some time in the past and consequently may have had a different diet. We think that during the period of their maximum diversity in the Early Miocene, about 16 My ago, they still possessed the caecum, which allowed for a much greater variety in diet, as may be reflected by the existence of hypsodont taxons, and that they lost it afterwards. It is, however, unlikely that the three recent subfamilies that existed in the Miocene, Glirinae, Myomiminae and Dryomyinae, lost the caecum independently; the alternative is that all modern glirids are derived from one single Middle Miocene species. If that is true the few occurrences of the recent genera in MN4 or older, should be transferred to other, eventually new, genera. This is consistent with the fact that the distributions of the extant genera before MN9 are discontinuous and that, except for *Muscardinus*, they are absent in MN6-MN8 (14-11 My ago).

Keywords: Gliridae, Rodentia, systematics.

RESUMEN

Los glíridos actuales (lirones) no son capaces de digerir la celulosa porque carecen de ciego intestinal. Entre los glíridos fósiles hay mayores diferencias en los patrones dentarios, existen incluso taxones con los dientes de corona alta (hipsodontos). Por ello suponemos que tenían dietas más variadas y también que tenían ciego durante el período de su máxima diversidad en el Mioceno temprano, hace aproximadamente 16 millones de años. Posteriormente lo perdieron. Pero es poco probable que las tres subfamilias actuales que existían en el Mioceno, Glirinae, Myomiminae y Dryomyinae, perdieran el ciego independientemente. La alternativa es que todos los lirones actuales provienen de una sola especie del Mioceno Medio. Si es así, las pocas especies de los géneros actuales conocidas de MN4 y anterior deben ser transferidas a otros géneros, en su caso nuevos. Esto es consistente con el hecho de que las distribuciones de los géneros actuales son discontinuas y no están representados (excepto *Muscardinus*) entre 14 y 11 millones de años.

Palabras clave: Gliridae, Rodentia, sistemática.

https://doi.org/10.7203/sjp.28.2.17857

1. INTRODUCTION

Gliridae Muirhead, 1819 is a rodent family with a mainly European distribution and a limited number of extant species. Throughout the Oligocene glirids are constantly present and quite diverse in European faunas. With the extinction of Theridomorpha and Oligocene Cricetidae (Eucricetodontinae and Pseudocricetodontinae) at the Oligocene/Miocene transition they reach their maximum species diversity in the Early Miocene, and at that time they often are the dominant family, with up to 90 % of the rodent specimens. From MN5 onwards the new Cricetidae become the dominant group and the number of glirid species and their specimen frequency decrease (see Daams & de Bruijn, 1995, figs 2, 9 and 10).

Tullberg (1899) was the first to recognize that extant Gliridae lack a caecum and this was confirmed by later workers, e.g., Storch (1995). The caecum is a blind sac, placed at the transition from the small intestine to the large intestine, containing bacteria that are capable of fermenting hard plant material (cellulose) through the enzyme cellulase. This hindgut fermentation is typical of Perissodactyla and Rodentia, among others. The size of the caecum is directly related with the percentage of cellulose in the food; it is large in herbivores and small in carnivores. Laboratory experiments have shown that the size of the caecum in rodents increases with the amount of cellulose in the food (Dominguez-Bello & Robinson, 1991).

The lack of the caecum means that extant Gliridae are not capable of digesting hard (cellulose) plant material; they feed on soft plant tissue, nuts and seeds, young birds, eggs and invertebrates. It is hard to give preferences because the diet is determined by the seasonal availability of food sources.

The only available fact about the diet of fossil glirids is the paper by Storch & Seiffert (2007), who concluded that the Eocene *Eogliravus wildi* Hartenberger, 1971, had a similar diet as extant Gliridae, but that does not mean that all fossil glirids had that same diet. It seems reasonable to suppose that they did have a caecum at some time in the past and consequently may have had a different diet.

Contrary to Gliridae, all other extant rodents for which data are available do have a caecum. During the period of their maximum diversity, around MN4/5, about 16 to 15 My ago, Gliridae may represent up to 90 % of the rodent fauna and almost certainly occupied all niches and used all available food sources. Consequently, at that time they must have had the caecum, which allowed for a much greater variety in diet, as may be reflected by the existence of hypsodont taxons, like *Armantomys* de Bruijn, 1966a. Hypsodonty is strongly correlated with the digestion of hard plant material (Daams & van der Meulen, 1984; Kaiser *et al*., 2011). The latter authors said about *Armantomys*: "The dental morphology and the food-abraded enamel in the valleys and dentine exposed in the ridges indicate adaptation to very tough plant material".

According to the current classification (Daams & de Bruijn, 1995) the three subfamilies Glirinae, Myomiminae and Dryomyinae are already present in the Early Miocene. In our opinion it is unconceivable that their Miocene members, when evolving towards their extant relatives, would have lost the caecum independently.

The alternative is a completely new concept of glirid evolution, in which the modern species are derived from one single Middle Miocene genus, e.g., a *Microdyromys* de Bruijn, 1966a. The few occurrences of the recent genera (see Fig. 1) in MN4 or older should be transferred to other, eventually new, genera. Table 1 gives the FAD and LAD (first and last appearance dates) of a selection of genera; discontinuous distributions are represented on separate lines. Bibliographic references for these data are given in Table 2.

2. MATERIAL AND METHODS

The current classification (Daams & de Bruijn, 1995, emended by Freudenthal & Martín-Suárez, 2007b) recognizes seven subfamilies: Glirinae, Dryomyinae, Myomiminae, Graphiurinae, and the extinct Gliravinae, Glamyinae and Bransatoglirinae. We use that classification as the basis of our work.

Several authors have described cranial characters of fossil glirids, e.g., Vianey-Liaud (1989), but systematics of fossil glirids is mainly based on the morphology of the dental pattern: number and position of ridges, connections between ridges, and concavity, e.g., Daams & de Bruijn (1995) explicitly state: "The criterion used for subdividing the Gliridae is the morphology of the cheek teeth because this is the only character known for all taxa".

Classification of recent glirids is based on a wide variety of characters, like cranial morphology, dental pattern, incisor enamel, and soft tissue like mastication muscles, genital morphology, and auditory region (Wahlert *et al*., 1993; Storch, 1995). A recent development is molecular distance (Montgelard *et al*., 2003).

In this paper we focus on the absence of the caecum, which seems to be the only character shared by all extant Gliridae. Through the analysis of the fossil record (time range, discontinuous distribution, number of species, relative frequency and hypsodonty) we try to estimate the moment they lost the caecum.

Montgelard *et al*. (2003) gave ages for the origin of the modern genera on the basis of molecular distance. Her calculations are based on a supposed base age of 50 My (Eocene MP10, the age of the oldest known glirid, *Eogliravus wildi*). We recalculated their results, multiplying them by 0.33, for a base age of 16 My, which we postulate as the age at which glirids still had the caecum.

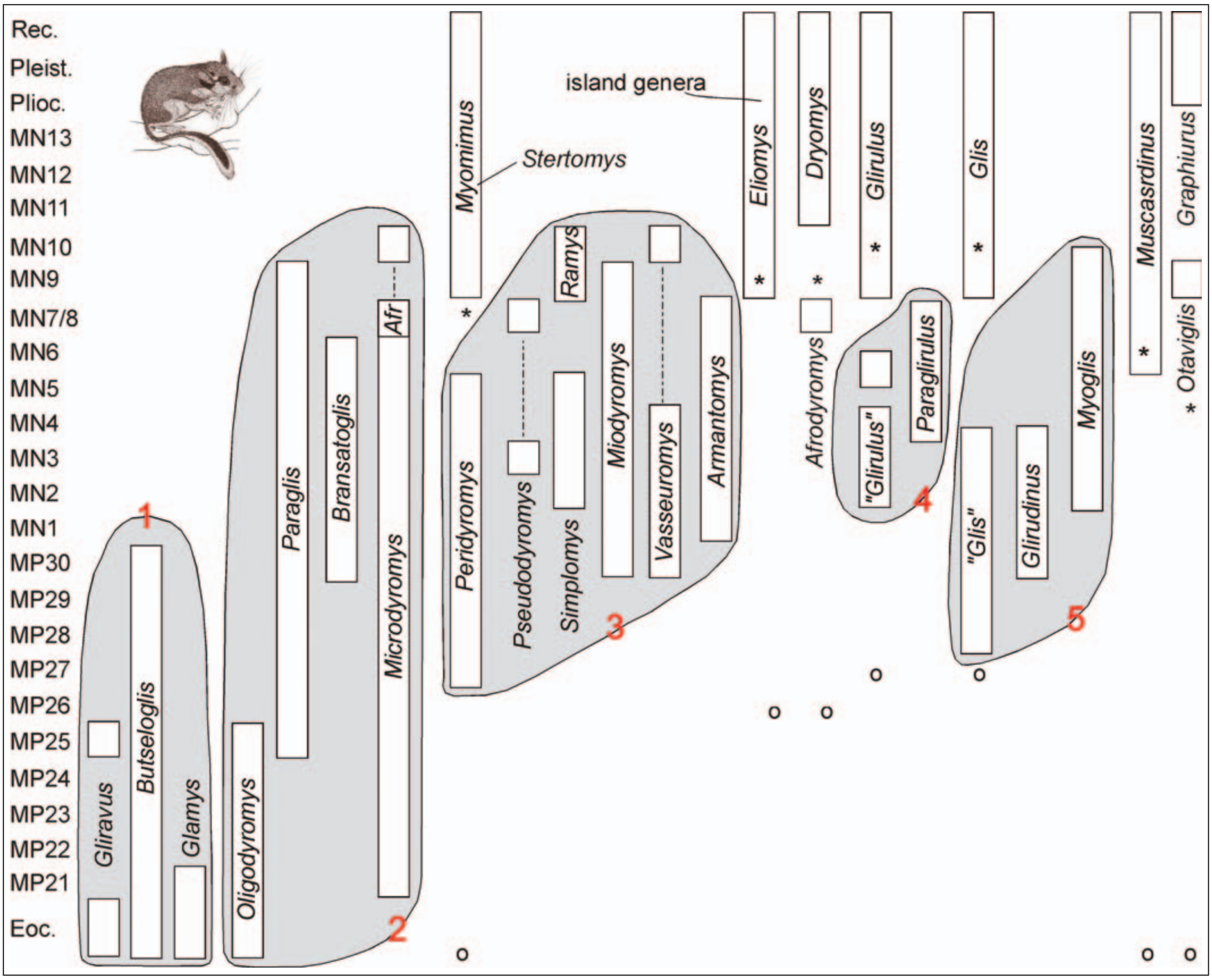

Figure 1. Distribution of glirid genera. The time of appearance of the extant genera based on the molecular clock is indicated by asterisks (base age 16 My) and circles (base age 50 My). Grey fields represent subfamilies. 1: Gliravinae and Glamyinae; 2: Bransatoglirinae; 3: Peridyromyinae; 4 and 5: unnamed subfamilies.

For relative ages we use MP units (Biochrom'97, 1997) and MN units (de Bruijn *et al*., 1992). Absolute ages are based on ATNTS (Lourens *et al*., 2004).

3. SYSTEMATIC PALAEONTOLOGY

In the following we will analyze the stratigraphic record and the contents of the extant genera, and of *Microdyromys*, which we consider to be the ancestor of recent Gliridae. Records of *Glis*, *Glirulus* and *Myomimus* from MN4 and older are transferred to other genera.

Subfamily **Bransatoglirinae** Daams & de Bruijn, 1995

Genus *Microdyromys* de Bruijn, 1966a

Microdyromys appears in MP21, possibly derived from an Eocene *Gliravus* Stehlin & Schaub, 1951 or *Glamys* Vianey-Liaud, 1989, and is continuously present from MP21 through MN6. If *Afrodyromys ambiguus* is a *Microdyromys* (see Jaeger, 1977a) its distribution is extended to MN7/8. The genus reappears in MN10 with *Microdyromys sinuosus* (Alvarez-Sierra, 1986) and possibly ?*Afrodyromys chaabi* Jaeger, 1977b, though we can't be sure that these MN10 occurrences really belong to this genus.

In MP27 it gives rise to *Peridyromys* Stehlin & Schaub, 1951, which is the origin of the other genera that were previously placed in Myomiminae and which we group in the new subfamily Peridyromyinae. Another possibility is that *Peridyromys* is derived from *Butseloglis* Vianey-Liaud, 2004 (Fig. 2).

Table 1. FAD's and LAD's (first and last appearance date) of selected genera of Gliridae.

GENUS	FAD		LAD		FAD	LAD
	SPECIES	LOCALITY	SPECIES	LOCALITY		
Graphiurus	sp.	Langebaanweg	spp.	Recent	Plioc.	Recent
Otaviglis	*daamsi*	Harasib			MN9	
Dryomys	sp.	Dorn-Dürkheim	*nitedula*	Recent	MN11	Recent
Eliomys	*assimilis*	Hammerschmiede	*quercinus*	Recent	MN9	Recent
Muscardinus	*thaleri*	Manchones	*avellanarius*	Recent	MN6	Recent
Eomuscardinus	*sansaniensis*	Sansan	cf. *vallesiensis*	Castell de Barbera	MN6	MN7/8
Eomuscardinus	*vallesiensis*	Can Llobateres	*helleri*	Gundersheim 4	MN9	MN15
Glirulus	*conjunctus*	Marktl	*japonicus*	Recent	MN9	Recent
Glirulus	*daamsi*	Çandir			MN5/6	
Glirulus	aff. *ekremi*	Harami 1	*minor*	Petersbuch 2	MN2	MN4A
Paraglirulus	*agelakisi*	Aliveri	*werenfelsi*	Anwil	MN4A	MN7/8
Glis	*vallesiensis*	Ballestar	*glis*	Recent	MN9	Recent
Glis	*guerbuezi*	Kocayarma	*galitopouli*	Aliveri	MP28	MN4A
Glirudinus	*glirulus*	Gunzenheim	*undosus*	Erkertshofen	MP30	MN4A
Myoglis	sp.	Lespignan	*meini*	Soblay	MN2B	MN10
Miodyromys	*hugueneyae*	Fraga 11	*hamadryas*	Can Ponsich	MP30	MN9
Myomimus	*dehmi*	Pedregueras 2C	*personatus*	Recent	MN9	Recent
Myomimus	sp.	Keseköy	sp.	Çandir	MN3	MN5/6
Peridyromys	*murinus*	Mirambueno 1	*sondaari*	Vargas 2B	MP27	MN5
Ramys	*perezi*	Ampudia 9	*multicrestatus*	Torremormojón 1	MN9	MN10
Simplomys	*aljaphi*	Montaigu-le-Blin	*simplicidens*	Las Umbrías 17	MN2A	MN5
Vasseuromys	*bergasensis*	Bergasa	*cristinae*	Pico del Fraile 2	MP30	MN4/5
Vasseuromys	*pannonicus*	Széchenyi Hill			MN10	MN10
Armantomys	*bijmai*	Santa Cilia	*tricristatus*	Escobosa	MN1	MN7/8
Pseudodryomys	*rex*	Torremormojón 6B			MN7/8	
Pseudodryomys	*ibericus*	Ateca 1			MN3	
Oligodyromys	*bahloi*	Headon Hill 3	*moyai*	Sineu	MP17	MP25
Paraglis	*fugax*	Mirambueno 4B	*astaracensis*	Belchatów A	MP25	MN9
Bransatoglis	*concavidens*	Coderet	*mayri*	Sandelzhausen	MP30	MN6
Microdyromys	*misonnei*	Hoogbutsel	*complicatus*	Sansan	MP21	MN6
Microdyromys	*sinuosus*	Ampudia 3			MN10	MN10
Afrodyromys	*ambiguus*	Beni Mellal	*chaabi*	Oued Zra	MN7/8	MN10
Gliravus	*pyrenaicus*	Sossis 1			MP17	MP17
Gliravus	*caracensis*	Pareja			MP25	MP25
Glamys	*robiacensis*	Robiac Sud	*olallensis*	Olalla 4A	MP16	MP21
Butseloglis	*daamsi*	Headon Hill 2	*bruijni*	Coderet	MP17	MP30

Subfamily **Glirinae** Muirhead, 1819

Genus *Glis* Brisson, 1762

Glis is recorded from MP28 to Recent, with an important gap in MN5-MN8. The oldest record after the gap is *G. vallesiensis* Agustí, 1981 from Ballestar (MN9), which may be considered a true *Glis*, but the older records from MP28 to MN4 in our opinion represent a different genus. One of these, *Glis truyolsi* Daams, 1976 from Cetina de Aragón (MN2) was placed in *Myoglis* Baudelot, 1965 by Werner (1994) and that may be a good solution for the other *Glis* species from MN4 and older: *G. apertus* Mayr, 1979; *G. galitopouli* van der Meulen & de Bruijn, 1982; *G. guerbuezi* Ünay-Bayraktar, 1989; *G. major* de Bruijn & Rümke, 1974 and *G. transversus* Ünay, 1994. *Myoglis*, *Glirudinus* de Bruijn, 1966a and *Heteromyoxus* Dehm, 1938 form a subfamily of their own, different from Glirinae.

This hypothesis is supported by Daams & de Bruijn (1995), who stated: "We can now trace *Glis* to the Oligocene, and dispute about generic allocation is whether or not to include *Glis guerbuezi* Ünay- Bayraktar, 1989 from the Middle Oligocene of Turkey into *Glis.* For a rodent genus a stratigraphic range of more than thirty million years seems very long and is probably not biologically correct, but the effect of our parsimonious knowledge of fossil species."

Genus *Muscardinus* Kaup, 1829

Aguilar & Lazzari (2006) described *Muscardinus sansaniensis* (Lartet, 1851) from MN4/5 of Blanquatère 1.

Table 2. Bibliographic references for the data in Table 1.

SPECIES	LOCALITY	REFERENCE
Afrodyromys ambiguus	Beni Mellal	Lavocat, 1961
Afrodyromys chaabi	Oued Zra	Jaeger, 1977b
Armantomys bijmai	Santa Cilia	Lacomba & Martínez-Salanova, 1988
Armantomys tricristatus	Escobosa	Daams, 1990
Bransatoglis concavidens	Coderet	Hugueney, 1967
Bransatoglis mayri	Sandelzhausen	Rabeder, 1984
Butseloglis bruijni	Coderet	Hugueney, 1967
Butseloglis daamsi	Headon Hill 2	Bosma & de Bruijn, 1982
Dryomys sp.	Dorn-Dürkheim	Franzen & Storch, 1975
Eliomys assimilis	Hammerschmiede	Mayr, 1979
Eomuscardinus helleri	Gundersheim 4	García-Alix et al., 2008a
Eomuscardinus sansaniensis	Sansan	Daams, 1985
Eomuscardinus vallesiensis	Can Llobateres	García-Alix et al., 2008a
Glamys olallensis	Olalla 4A	Freudenthal, 1996
Glamys robiacensis	Robiac Sud	Vianey-Liaud, 1994
Gliravus caracensis	Pareja	Daams et al., 1989
Gliravus pyrenaicus	Sossis 1	Agustí & Arcas, 1997
Glirudinus glirulus	Gunzenheim	Dehm, 1935
Glirudinus undosus	Erkertshofen	Mayr, 1979
Glirulus aff. *ekremi*	Harami 1	Ünay, 1994
Glirulus conjunctus	Marktl	Mayr, 1979
Glirulus daamsi	Çandir	de Bruijn et al., 2003
Glirulus minor	Petersbuch 2	Wu, 1993
Glis galitopouli	Aliveri	van der Meulen & de Bruijn, 1982
Glis guerbuezi	Kocayarma	Ünay-Bayraktar, 1989
Glis vallesiensis	Ballestar	Agustí, 1981
Graphiurus sp.	Langebaanweg	Pocock, 1976
Microdyromys complicatus	Sansan	Daams & de Bruijn, 1995
Microdyromys misonnei	Hoogbutsel	Freudenthal & Martín-Suárez, 2007a
Microdyromys sinuosus	Ampudia 3	Alvarez Sierra, 1986
Miodyromys hamadryas	Can Ponsich	Daams & de Bruijn, 1995
Miodyromys hugueneyae	Fraga 11	Agustí & Arbiol, 1989
Muscardinus thaleri	Manchones	de Bruijn, 1966a
Myoglis meini	Soblay	Nemetschek & Mörs, 2003
Myoglis sp.	Lespignan	Aguilar, 1974
Myomimus dehmi	Pedregueras 2C	de Bruijn, 1966b
Myomimus sp.	Çandir	de Bruijn et al., 2003
Myomimus sp.	Keseköy	Ünay, 1994
Oligodyromys bahloi	Headon Hill 3	Hugueney & Adrover, 1990
Oligodyromys moyai	Sineu	Hugueney & Adrover, 1990
Otaviglis daamsi	Harasib	Mein et al., 2000
Paraglirulus agelakisi	Aliveri	van der Meulen & de Bruijn, 1982
Paraglirulus werenfelsi	Anwil	Engesser, 1972
Paraglis astaracensis	Belchatów A	Freudenthal & Martín-Suárez, 2007b
Paraglis fugax	Mirambueno 4B	Freudenthal & Martín-Suárez, 2007b
Peridyromys murinus	Mirambueno 1	Freudenthal, 1997
Peridyromys sondaari	Vargas 2B	Daams, 1999
Pseudodryomys ibericus	Ateca 1	de Bruijn, 1966a
Pseudodryomys rex	Torremormojón 6B	García Moreno, 1986
Ramys multicrestatus	Torremormojón 1	García Moreno & López Martínez, 1986
Ramys perezi	Ampudia 9	Alvarez Sierra, 1986
Simplomys aljaphi	Montaigu-le-Blin	García-Paredes et al., 2009
Simplomys simplicidens	Las Umbrías 17	García-Paredes et al., 2009
Vasseuromys bergasensis	Bergasa	Ruiz Sánchez et al. (in prep.)
Vasseuromys cristinae	Pico del Fraile 2	Ruiz-Sánchez et al., 2012
Vasseuromys pannonicus	Széchenyi Hill	Kretzoi, 1980

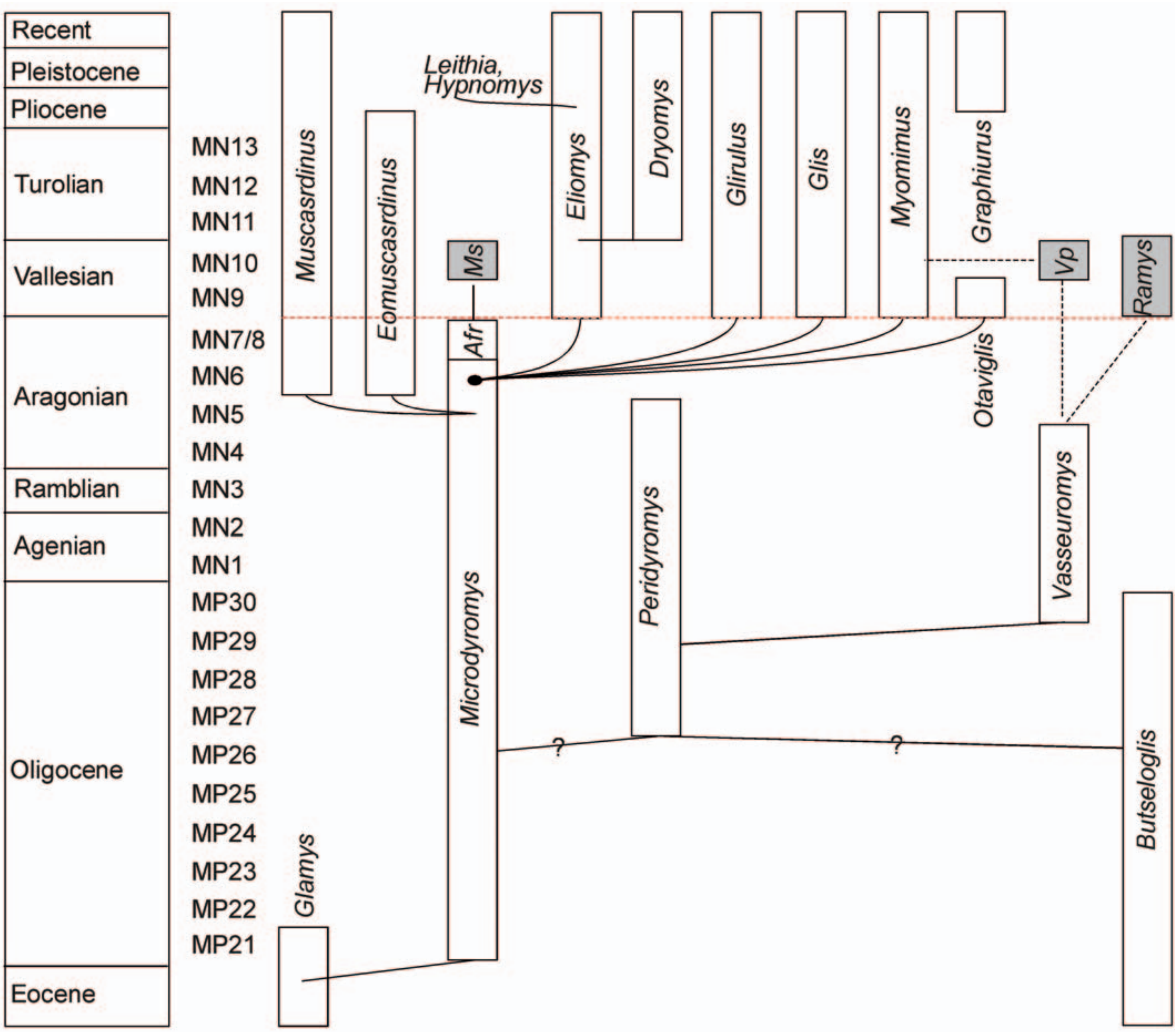

Figure 2. Proposed phylogeny of extant Gliridae. Grey fields are records for which the phylogeny is uncertain.

We think, however, that that fauna is a mixture of various ages and that the genus does not appear before MN6 (see Fig. 2).

García-Alix *et al*. (2008a) distinguished two lineages within *Muscardinus*:

M. thaleri (MN6)-*hispanicus-pliocaenicus-avellanarius* (Recent) and *M. sansaniensis* (MN6)-*vallesiensis-vireti-meridionalis-helleri* (MN15). The first lineage contains the oldest record of modern glirids, but we are not sure that it is derived from *M. sansaniensis.* The second one may be a lineage of "old" glirids (with caecum) and in that case the genus name *Eomuscardinus* Hartenberger, 1967 is available. Whether or not *Eomuscardinus* is considered a separate genus is not decided here. It depends on the question whether it had a caecum or not, and that cannot be resolved. The coexistence of two species in Can Llobateres may be an indication in favour of separating them.

Subfamily **Dryomyinae** de Bruijn, 1967
Genus *Dryomys* Thomas, 1906

According to Daams & de Bruijn (1995) the oldest occurrence in Europe of *Dryomys* may be that of *Dryomys* sp. from the Late Miocene (MN11) of Dorn-Dürkheim (Franzen & Storch, 1975), but it is essentially restricted to the Pleistocene and Holocene. *Dryomys ambiguus* from MN7/8 of Beni Mellall was placed in *Dryomys* by Lavocat (1961). Jaeger (1977a) placed it in *Microdyromys* and Jaeger (1977b) created the new genus *Afrodyromys* for it. *Afrodyromys* was considered a synonym of *Dryomys* by

Daams (1981). Whether or not *Afrodyromys* deserves to be considered a separate genus is not clear, but its taxonomic history may well be an indication of the ancestral position of *Microdyromys* with respect to *Dryomys*.

Genus *Eliomys* Wagner, 1840

The oldest records of *Eliomys* are *E. assimilis* and *E. reductus* from the Late Miocene of Hammerschmiede (MN9, Germany). *S*everal species, e.g., *E. truci* Mein & Michaux, 1970 are recorded from the Late Miocene-Pliocene (MN12-16, García-Alix *et al*., 2008b) of France and Spain. It is not clear why they are attributed to *Eliomys*, and not to *Dryomys*, and one of these species might be the ancestor of *Dryomys apulus* Freudenthal & Martín Suárez, 2006. *Eliomys* is considered to be the origin of *Dryomys* and of a number of Plio-Pleistocene genera from Mediterranean islands, like *Hypnomys* Bate, 1918, *Leithia* Lydekker, 1896, etc. *Hypnomys* was placed in synonymy with *Eliomys* by Bover & Alcover (2008).

Genus Glirulus Thomas, 1906

Glirulus conjunctus (Mayr, 1979) from Marktl (MN9) was originally described as *Paraglirulus* Engesser, 1972. Daams & de Bruijn (1995) placed it in *Glirulus*. If that is correct it is the oldest record of *Glirulus* after the gap between MN4 and MN9.

Older records of *Glirulus* range between *G.* aff. *ekremi* from Harami 1 (MN2; Ünay, 1994) and *G. daamsi* from Çandir (MN5/6?; de Bruijn *et al*., 2003).

According to Daams & de Bruijn (1995) *Paraglirulus* contains two species: the type species *P. werenfelsi* Engesser, 1972 from Anwil (MN7/8) and *P. agelakisi* van der Meulen & de Bruijn, 1982 from Aliveri (MN4A). For the moment the *Glirulus* records from MN2 to MN5/6 may be placed in *Paraglirulus*: *P. diremptus* Mayr, 1979; *G. daamsi* de Bruijn *et al*., 2003; *G. ekremi* Ünay, 1994 and *G. minor* Wu, 1993. In Figure 1 they form the unnamed subfamily 4.

Subfamily **Myomyinae** Daams, 1981
Genus *Myomimus* Ognev, 1924

The oldest record of *Myomimus* is *Myomimus* sp. from Keseköy (MN3, Ünay, 1994). De Bruijn *et al*. (2003) postulated the synonymy of *Myomimus* and *Peridyromys*, as already suggested by de Bruijn *et al*. (1970). The oldest record of *Peridyromys* is *P. murinus* Pomel, 1853 from Mirambueno 1 (MP27, Freudenthal, 1997); the youngest record is *P. sondaari* from Vargas 2A (MN5, Daams, 1999). Neither *Myomimus* nor *Peridyromys* are recorded in MN6 through MN8 (the dating of Çandir as MN6 is questionable; see de Bruijn *et al*., 2003), and true *Myomimus* appears in MN9: *Myomimus dehmi* (de Bruijn, 1966b). In the concept proposed here the records from MN5 and older should be placed in *Peridyromys,* and those from MN9 and younger in *Myomimus.*

If one wishes to maintain the subfamily Myomiminae it should be restricted to *Myomimus*, and the other genera previously placed in Myomiminae form a new subfamily, Peridyromyinae (Number 3 in Fig. 1):

Subfamily **Peridyromyinae** subfamilia nov.

Type-genus. *Peridyromys* Stehlin & Schaub, 1951

Diagnosis. Daams (1981) gave the following diagnosis for the Myomiminae: “Concave occlusal surface, main cusps fairly well developed, extra ridges narrower than main ridges, relatively high-crowned molars in some genera, generally no endoloph in the M1,2 and a simple dental pattern.”

This is in fact the diagnosis of Peridyromyinae, and if one wishes to maintain the subfamily Myomiminae a much more restricted diagnosis can be made.

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

Of these *Vasseuromys* and *Ramys* do not fit the diagnosis, especially with respect to the simple dental pattern. Their inclusion in Peridyromyinae is provisional and based on the supposed origin in *Peridyromys*.

Daams & de Bruijn (1995) thought *Peridyromys* to be derived from *Gliravus* s.l.; since then the genus *Gliravus* has been split in *Gliravus*, *Glamys* and *Butseloglis* (=*Schizogliravus* Freudenthal, 2004). The type-species of *Gliravus* and two closely related species are restricted to MP24; five other species are attributed to *Gliravus*, simply because no action was taken when *Glamys* and *Butseloglis* were split off. They all are from the Eocene (MP17) and this discontinuous distribution may mean that *Gliravus* in its present concept is heterogeneous. Some of these five species may be placed in *Glamys* (*G. robiacensis* Hartenberger, 1971), but others not (*G. meridionalis* from Sossís 1, figured by Agustí & Arcas, 1997) (see Freudenthal, 2004).

This makes *Butseloglis* a possible ancestor of *Peridyromys* in view of its stratigraphic distribution (and in agreement with Daams & de Bruijn (1995), since *Butseloglis* is part of their *Gliravus* s.l.). However, *Microdyromys* cannot be ruled out as a possible ancestor (see Fig. 2).

Subfamily **Graphiurinae** Vianey-Liaud & Jaeger, 1996

Genus *Graphiurus* Smuts, 1832

Vianey-Liaud & Jaeger (1996) created the family Graphiuridae for the extant African genus *Graphiurus* on the basis of its hystricomorphous skull. The oldest record of *Graphiurus* is *Graphiurus* sp. from the Pliocene of Langebaanweg (Pocock, 1976). According to Mein *et al.* (2000) *Graphiurus* may be a descendent of *Otaviglis* Mein *et al.*, 2000 from MN9 of Harasib, and these authors think that *Otaviglis* may be a descendent of *Microdyromys*. We think that the oval shape of the upper premolar, typical for Bransatoglirinae, and the broad lower molars, strengthen this point.

4. MOLECULAR SYSTEMATICS

Montgelard *et al.* (2003) gave ages for the origin of the modern genera on the basis of molecular distance and observed that the calculated origins are much older than the appearance in the fossil record. Similar results were obtained by Nunome *et al.* (2007). Their calculations are based on a supposed base age of 50 My (Eocene MP10, the age of the oldest known glirid, *Eogliravus wildi*). We recalculated their results, multiplying them by 0.33, for a base age of 16 My, which we postulate as the age at which glirids still had the caecum (see Table 3). In Figure 1, the ages by Montgelard *et al.* (2003) are indicated by circles and our recalculated ages by asterisks. The FAD's of the extant genera, except *Graphiurus*, give a remarkably good fit with the latter calculations. The first occurrence of *Graphiurus* is *Graphiurus* sp. from the Pliocene of Langebaanweg (Pocock, 1976), dated at 5 My ago, which is 11 My younger than the recalculated age (see Fig. 2). *Otaviglis* Mein, Pickford & Senut, 2000, the ancestor of *Graphiurus*, is reported to have an age of 10-11 My, which is still 5 My younger (see Montgelard *et al.*, 2003).

Table 3. Divergence times of recent Gliridae from Montgelard et al. (2003) and recalculated ages for a base age of 16 My, compared with the oldest known records.

	My	MN	My	MN	FAD
base age	50 My		16 My		
Glirulus	27.7	MP27	9.2	MN10	MN9
Glis	27.7	MP27	9.2	MN10	MN9
Dryomys	28.5	MP26	9.5	MN9/10	MN11
Eliomys	28.5	MP26	9.5	MN9/10	MN9
Myomimus	38.1	MP16	12.7	MN7	MN9
Muscardinus	40.8	MP15	13.6	MN6	MN6
Graphiurus	50.0	MP10	16.0	MN4	Pliocene
Otaviglis					MN9

5. DISCUSSION

Wahlert *et al.* (1993) grouped living glirids, on the basis of cranial, mandibular, and dental morphology, in two subfamilies: their Leithiinae (=Dryomyinae) and Myoxinae (=Glirinae). Leithiinae consists of two tribes, the Leithiini (*Eliomys* and *Dryomys)* and the Myomimini (*Myomimus* and *Selevinia).* Myoxinae includes *Myoxus* (=*Glis*), *Glirulus* and *Muscardinus.*

Storch (1995) placed *Myomimus* in Seleviniinae (=Myomiminae), *Eliomys* and *Dryomys* in Dryomiinae and *Myoxus* (=*Glis*), *Glirulus and Muscardinus* in Glirinae. Characters used are the dental occlusal pattern, skull, enamel ultrastructure of the lower incisors, muscles of mastication, external male genital morphology, and auditory region.

Among living glirids Daams & de Bruijn (1995) recognized the subfamilies Glirinae, Myomiminae and Dryomyinae and they included several extinct subfamilies. At present this classification, based exclusively on dental morphology is widely accepted. Basically these three classifications are the same, though the actual names and the taxonomic level may be different. The similarities in the dental pattern led Daams & de Bruijn to classify a number of fossil species in recent genera.

We consider these similarities to be convergencies. The almost complete absence of the modern genera in MN6-8, the simultaneous (re)appearance of the modern genera and the absence of the caecum are arguments for a fundamentally different concept of the systematics of Gliridae.

Gliridae reached their maximum species diversity in the Early Miocene, and at that time they often were the dominant family, with up to 90 % of the rodent specimens. This diversity and the presence of hypsodont forms make us suppose that until MN5 they still had a caecum. It is highly unlikely that the loss of the caecum happened independently in all lineages of extant glirids, so we hypothesize that they are derived from one single taxon without caecum, not older than MN5 (around 15/16 My ago). Diversification starts in MN6 with the appearance of *Muscardinus*, whereas the other modern genera appear in MN9 (between 11 and 10 My ago). That makes the usefulness of the subfamily names Myomiminae and Dryomyinae questionable; one subfamily, Glirinae, is sufficient to house the extant genera and several genera from Mediterranean Late Miocene to Pleistocene island faunas, like *Stertomys* Daams & Freudenthal, 1985 and *Leithia*. There is, however, no argument against maintaining them as separate subfamilies, or reducing them to tribe rank. In any case, in this concept, they no longer include the records from the Middle Miocene and older that were previously classified in Glirinae (*Glis*, *Heteromyoxus*, *Glirudinus* and *Myoglis*) or in Dryomyinae (*Glirulus* and *Paraglirulus*), and Myomiminae is reduced to the type-genus only. The hystricomorph condition is an argument to maintain the subfamily Graphiurinae.

Among the fossil glirids the subfamilies Bransatoglirinae (*Bransatoglis* Hugueney, 1967, *Oligodyromys* Bahlo, 1975, *Paraglis* Werner, 1994 and *Microdyromys*), Gliravinae (*Gliravus*, *Eogliravus* Hartenberger, 1971 and *Butseloglis*) and Glamyinae (*Glamys*) remain unchanged.

The subfamily Myomiminae is restricted to *Myomimus*, and a new subfamily, Peridyromyinae, type-genus *Peridyromys*, is created to house the genera from MN5 or older that were previously assigned to Myomiminae.

Ramys (MN9-10) may be a Peridyromyinae, related to *Vasseuromys* (Agustí *et al*., 2011), but it may also be related to the modern *Myomimus* lineage that starts in MN9. Neither can we be sure about *Microdyromys sinuosus*, a reappearance of the genus in MN10 after its extinction in MN6, and a similar case is *Vasseuromys pannonicus* Kretzoi, 1980 from MN10. These doubtful cases are indicated as shaded fields in Fig. 2.

One of the most remarkable facts is the moment of first appearance of the modern Gliridae. *Muscardinus* appears in MN6 and is regarded to be the first of the modern glirids. Its derived dental pattern, however, excludes it as a possible ancestor of the other genera.

The first occurrence of *Graphiurus* is *Graphiurus* sp. from the Pliocene of Langebaanweg (Pocock, 1976), dated at 5 My ago and *Dryomys* appears in MN11, probably as an off-shoot from *Eliomys*. The other extant Gliridae appear simultaneously in the Early Vallesian, MN9, including *Otaviglis*, which is the ancestor of *Graphiurus*. The time gap between *Otaviglis* and *Graphiurus* is probably due to lack of data.

We think the origin of all extant glirids is a *Microdyromys* from MN5/6, which had lost the caecum. Other possibilities cannot be excluded, but *Microdyromys* has the least derived dental pattern. The radiation of *Eliomys*, *Glirulus*, *Glis*, *Myomimus* and *Graphiurus* took place shortly before the beginning of the Vallesian (see Fig. 2).

The loss of the caecum appears to be a negative factor because it puts limits to the ecological possibilities of the glirids and for that reason alone it is unlikely that it would have happened several times in different lineages. In fact it is an exceptional phenomenon that offers no evident advantages; otherwise it certainly would have occurred in some of the other 2,250 rodent species, and that has not been observed. An unresolved question is, why the “better equipped” ancient glirids became extinct around MN9, at the same time that the modern glirids, with an apparent disadvantage, began to flourish.

We are well aware that our new concept is quite unorthodox, and impossible to prove with hard paleontological material, but we did not find any other plausible explanation. In fact, the question is whether the loss of the caecum is the result of the glirid diet or the cause of it. We think the latter is the most probable because it requires only one event. Its logical consequence is the taxonomy presented here.

6. CONCLUSIONS

The current classification implies that the loss of the caecum would have taken place independently in a number of already separated subfamilies. We find that improbable and propose a monophyletic phylogeny, starting about 15/16 million years ago. This hypothesis means that:

All extant Gliridae are derived from one single Middle Miocene species, probably a *Microdyromys*.

The occurrences of *Glis* and *Glirulus* from MN5 and older belong to other genera. *Peridyromys* is a separate genus and not a synonym of *Myomimus*.

Muscardinus is the only modern glirid in the Middle Miocene; the other genera appear simultaneously in the Early Vallesian.

The divergence data based on molecular systematics and a base age of 50 My, calculated by Montgelard *et al*. (2003) show strong discrepancies with the fossil record. Recalculation for a base age of 16 My gives a remarkable good fit with the FAD of the recent taxons.

The loss of the caecum is an exceptional phenomenon that offers no evident advantages, and did not occur in any other rodent group. We have no explanation for the fact that the ancient Gliridae became extinct simultaneously with the radiation of the modern genera.

ACKNOWLEDGEMENTS

Thanks are due to Drs H. de Bruijn, P. Mein and F.J. Ruiz-Sánchez for critically reading the manuscript. Two anonymous referees and the editor of Paleontologia Electronica helped to improve the text. This study was carried out in the framework of the program “Huellas isotópicas en micromamíferos fósiles como indicadores del cambio climático (RNM 8011)” of the “Junta de Andalucía”.

REFERENCES

Aguilar, J.P. 1974. Les Rongeurs du Miocène inférieur en Bas-Languedoc et les corrélations entre échelles stratigraphiques marine et continentale. *Géobios*, 7, 4, 345-398.

Aguilar, J.P. & Lazzari, V. 2006. Nouvelles espèces de gliridés du gisement karstique de Blanquatère 1 (Miocène moyen, sud de la France). *Geodiversitas*, 28, 277-295.

Agustí, J. 1981. *Glis vallesiensis* n. sp. Nouveau Gliride (Rodentia, Mammalia) du Néogène de Seu d'Urgell (Catalogne, Espagne). *Géobios*, 14, 4, 543-547.

Agustí, J. & Arbiol, S. 1989. Nouvelles espèces de rongeurs (Mammalia) dans l'Oligocène supérieur du Bassin de l'Ebre (N.E. de l'Espagne). *Géobios*, 22, 3, 265-275.

Agustí, J. & Arcas, A. 1997. Gliridae (Mammalia, Rodentia) from the Late Eocene of Sossis. *Münchner Geowissenschaftliche Abhandlungen, A, Geologie Paleontologie*, 34, 23-32.

Agustí, J., Pérez-Rivarés, F.J., Cabrera, L., Garcés, M., Pardo, G. & Arenas, C. 2011. The Ramblian-Aragonian boundary and its significance for the European Neogene continental chronology. Contributions from the Ebro Basin record (NE Spain). *Géobios*, 44, 121-134.

Alvarez Sierra, M.A. 1986. In: Alvarez Sierra, M.A. & E. García Moreno, 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. *Stvdia Geologica Salmanticensia*, 22, 145-189.

Bahlo, E. 1975. Die Nagetierfauna von Heimersheim bei Alzey (Rheinhessen, Westdeutschland) aus dem Grenzbereich Mittel/Oberoligozän und ihre stratigrafische Stellung. *Abhandlungen Hessisches Landesamt für Bodenforschung*, 71, 1-182.

Bate, D.M.A. 1918. On a new genus of extinct Muscardine Rodent from the Balearic Islands. *Proceedings Zoological Society London*, 209-222.

Baudelot, S. 1965. Complément à l'étude de la faune des rongeurs de Sansan: les Gliridés. *Bulletin Société Géologique France*, 7, 8, 758-764.

Baudelot, S. & de Bonis, L. 1966. Nouveaux Gliridés (Rodentia) de l'Aquitanien du Bassin d'Aquitainie. *Comptes Rendus sommaires Société Géologique de France*, 1966, 9, 341-342.

Biochrom'97 1997. Syntheses and correlation tables. In: Actes du Congrès BiochroM'97 (eds. Aguilar, J.P., Legendre, S. & Michaux, J.), *Mémoires Travaux E.P.H.E., Institut Montpellier*, 21, 337-352.

Bosma, A. & de Bruijn, H. 1982. Eocene and Oligocene Gliridae (Rodentia, Mammalia) from the Isle of Wight, England. Part II. *Gliravus minor* n.sp., *Gliravus daamsi* n.sp., *Bransatoglis bahloi* n.sp. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 85, 4, 365-380.

Bover, P. & Alcover, J.A. 2008. Extinction of the autochthonous small mammals of Mallorca (Gymnesic Islands, Western Mediterranean) and its ecological consequences. *Journal of Biogeography*, 35, 1112-1122.

Brisson, A.D. 1762. Regnum Animale in Classes IX. Distributum, sive Synopsis Methodica. *T. Haak, Leiden*, 1-296.

Bruijn, H. de 1966a. Some new Miocene Gliridae (Rodentia, Mammalia) from the Calatayud Area (prov. Zaragoza, Spain). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 69, 1, 1-21.

Bruijn, H. de 1966b. On the Mammalian fauna of the Hipparion-Beds in the Calatayud-Teruel Basin (prov. Zaragoza, Spain). Part II. The Gliridae (Rodentia). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 69, 58-78.

Bruijn, H. de 1967. Gliridae, Sciuridae y Eomyidae (Rodentia, Mammalia) miocenos de Calatayud (provincia de Zaragoza, España) y su relación con la bioestratigrafía del área. *Boletín Instituto Geológico Minero España*, 78, 187-373.

Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy*, 26, 2-3, 65-118.

Bruijn, H. de, Dawson, M.R. & Mein, P. 1970. Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 73, 5, 535-584.

Bruijn, H. de, van den Hoek Ostende, L., Kristkoiz-Boon, E., Rummel, M., Theocharopoulos, C. & Ünay, E. 2003. Rodents, lagomorphs and insectivores from the middle Miocene hominoid locality of Çandir (Turkey). *Courier Forschungs-Institut Senckenberg*, 240, 51-87.

Bruijn, H. de & Rümke, C. 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 77, 1, 45-79.

Daams, R. 1976. Miocene Rodents (Mammalia) from Cetina de Aragón (Prov. Zaragoza) and Buñol (Prov. Valencia), Spain. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 79, 3, 152-182.

Daams, R. 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins, Special Publication*, 3, 1-115.

Daams, R. 1985. Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain). *Scripta Geologica*, 77, 1-20.

Daams, R. 1990. Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and the Oligocene-Miocene boundary interval of Spain. *Scripta Geologica*, 95, 1-63.

Daams, R. 1999. *Peridyromys darocensis* and *Peridyromys sondaari*, two new species of Gliridae (Rodentia, Mammalia) from the Lower Miocene (MN3-5) of the Calatayud-Daroca Basin, Zaragoza, Spain. *Deinsea*, 7, 83-90.

Daams, R. & de Bruijn, H. 1995. A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix*, 6, 1-2, 3-50.

Daams, R. & M. Freudenthal, 1985. *Stertomys laticrestatus*, a new glirid (dormice, Rodentia) from the insular fauna of Gargano (Prov. of Foggia, Italy). *Scripta Geologica*, 77, 21-27.

Daams, R., Freudenthal, M., Lacomba, J.I. & Alvarez, M.A. 1989. Upper Oligocene micromammals from Pareja, Loranca Basin, prov. of Guadalajara, Spain. *Scripta Geologica*, 89, 27-56.

Daams, R. & van der Meulen, A.J. 1984. Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of north central Spain. *Paléobiologie Continentale*, 14, 2, 241-257.

Dehm, R. 1935. Über tertiäre Spaltenfüllungen im Fränkischen und Schwäbischen Jura. *Abhandlungen Bayerische Akademie Wissenschaften, math. nat. Abt.*, 29, 1-86.

Dehm, R. 1938. *Heteromyoxus* n.g. und *Dryomys* Thomas, zwei Schlafmäuse im Untermiocän (Aquitanium) von Ulm. *Zentralblatt Mineralogie, B*, 9, 2, 337-343.

Díaz Molina, M. & López Martínez, N. 1979. El Terciario continental de la Depresión Intermedia (Cuenca). Bioestratigrafía y Paleogeografía. *Estudios Geológicos*, 35, 149-167.

Dominguez-Bello, M.G. & Robinson, M.D. 1991. A comparison of digestive adaptation in two neotropical cricetid rodents (*Holochilus venezuelae* and *Zygodontomys microtinus). Physiological Zoology*, 64, 1542-1551.

Engesser, B. 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). *Tätigkeitsberichte Naturforschenden Gesellschaft Baselland*, 28, 35-363.

Franzen, J. L. & Storch, G. 1975. Die unterpliozäne (turolische) Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 1. Entdeckung, Geologie, Mammalia: Carnivora, Proboscidea, Rodentia. *Senckenbergiana Lethaea*, 56, 4-5, 233-303.

Freudenthal, M. 1996. The Early Oligocene rodent fauna of Olalla 4A (Teruel, Spain). *Scripta Geologica*, 112, 1-67.

Freudenthal, M. 1997. Paleogene rodent faunas from the province of Teruel (Spain). In: Actes du Congrès BiochroM'97 (eds. Aguilar, J.P., Legendre, S. & Michaux, J.), *Mémoires Travaux E.P.H.E., Institut Montpellier*, 21, 397-415.

Freudenthal, M. 2004. Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). *Treballs del Museu de Geologia de Barcelona*, 12, 97-173.

Freudenthal, M. & Martín-Suárez, E. 2006. Gliridae (Rodentia, Mammalia) from the late Miocene fissure filling Biancone 1 (Gargano, province of Foggia, Italy). *Palaeontologia Electronica*, 9, 2, 1-23.

Freudenthal, M. & Martín-Suárez, E. 2007a. *Microdyromys* (Gliridae, Rodentia, Mammalia) from the Early Oligocene of Montalbán (Prov. Teruel, Spain). *Scripta Geologica*, 135, 179-211.

Freudenthal, M. & Martín-Suárez, E. 2007b. Revision of the subfamily Bransatoglirinae (Gliridae, Rodentia, Mammalia). *Scripta Geologica*, 135, 241-273.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E. & Freudenthal, M. 2008a. *Muscardinus meridionalis* sp. nov., a new species of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of *Muscardinus*. *Journal of Vertebrate Paleontology*, 28, 2, 568-573.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E. & Freudenthal, M. 2008b. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica*, 136, 1-37.

García Moreno, E. 1986. El género *Megacricetodon* (Cricetidae, Rodentia) en el Aragoniense y Vallesiense de la Cuenca del Duero. Relaciones filogenéticas. *COL-PA*, 41, 51-106.

García Moreno, E. & López Martínez, N. 1986. *Ramys*, a new genus of Gliridae (Rodentia) from the Lower Vallesian of Spain. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 89, 4, 337-355.

García-Paredes, I., Peláez-Campomanes, P. & Alvarez Sierra, M.A. 2009. Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene. *Zoological Journal of the Linnean Society*, 157, 622-652.

Hartenberger, J.L. 1967. Les rongeurs du Vallésien (Miocène supérieur) de Can Llobateres (Sabadell, Espagne): Gliridae et Eomyidae. *Bulletin de la Société Géologique de France*, 7, 8, 596-604.

Hartenberger, J.L. 1971. Contribution à l'étude des genres *Gliravus* et *Microparamys* (Rodentia) de l'Eocène d'Europe. *Palaeovertebrata*, 4, 97-135.

Hugueney, M.1967. Les Gliridés (Mammalia, Rodentia) de l'Oligocène supérieur de Coderet-Branssat (Allier). *Comptes Rendus sommaires Société Géologique de France*, 1967, 3, 91-92.

Hugueney, M. & Adrover, R. 1990. Rongeurs (Rodentia, Mammalia) de l'Oligocène de Sineu (Baleares, Espagne). *Paleontologia i Evolució*, 23, 157-169.

Jaeger, J.J. 1977a. Rongeurs (Mammalia, Rodentia) du Miocène de Beni Mellal. *Palaeovertebrata*, 7, 4, 91-125.

Jaeger, J.J. 1977b. Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata*, 8, 1, 1-166.

Kaiser, T.M., Müller, D.W.H., Fortelius, M., Schulz, E., Codron, D. & Clauss, M. 2011. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Review*. doi: 10.1111/j.1365-2907.2011.00203.x.

Kaup, J. 1829. Skizzierte Entwicklungs-Geschichte und Natürliches System der Europäischen Thierwelt. *C.W. Leske, Darmstadt/Leipzig*, 1, 1-203.

Kretzoi M. 1943. Ein neuer Muscardinide aus dem Ungarischen Miozän. *KüIönlenyomat a Földtani Közlöny,* 73, 1-3, 271- 273.

Kretzoi, M. 1980. Wichtigere Streufunde in der wirbeltierpaläontologischen Sammlung der Ungarischen Geologischen Anstalt.1. Wirbeltierfauna des pliozänen Süßwasserkalkes am Széchenyi-Berg in den Budaer Bergen. *Magyar Allami Földtami Intézet Évi Jelentése*, 1978, 347-358.

Lacomba, J.I. & Martínez-Salanova, J. 1988. *Quercomys bijmai* gen. nov. sp. nov. (Gliridae, Rodentia, Mammalia) del tránsito Oligoceno-Mioceno Español. *Estudios Geológicos*, 44, 107-118.

Lartet, E., 1851 Notice sur la colline de Sansan. *Portes, Auch*, 1-47

Lavocat, R. 1961. Le gisement de vertébrés miocènes de Beni Mellal (Maroc). Etude systématique de la faune de mammifères et conclusions générales. *Notes Mémoires Service Géologique Maroc*, 155, 1-145.

Lourens, L.J., Hilgen, F.J., Shackleton, N.J., Laskar, J. & Wilson, D.S. 2004. The Neogene period. In: *A Geologic Time Scale 2004* (eds. Gradstein F.N., Ogg, J.G. & Smith, A.G.). *Cambridge University Press*, 409-440.

Lydekker, R. 1896. On the Affinities of the so-called Extinct Giant Dormouse of Malta. *Proceedings Zoological Society London*, 1895, 860-863.

Mayr, H. 1979. *Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands*. PhD Thesis, University Munich.

Mein, P. & Michaux, J.J. 1970. Un nouveau stade dans l'évolution des rongeurs pliocènes de l'Europe sud-occidentale. *Comptes rendus Académie des Sciences Paris, D*, 270, 2780-2783.

Mein, P., Pickford, M. & Senut, B. 2000. Late Miocene micromammals from the Harasib karst deposits, Namibia. Part 1. Large muroids and non-muroid rodents. *Communications of the Geological Survey of Namibia*, 12, 375-390.

Meulen, A.J. van der & de Bruijn, H. 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2: The Gliridae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 85, 4, 485-524.

Montgelard, C., Matthee, C.A. & Robinson, T.J. 2003. Molecular systematics of dormice (Rodentia: Gliridae) and the radiation of Graphiurus in Africa. *Proceedings Royal Society London, B*, 270, 1947-1955.

Muirhead, L. 1819. *Mazology. In: The Edinburgh Encyclopedia* (ed. Brewster, D.). W. Blackwood, Edinburgh, 13, 393-486.

Nemetschek, A. & Mörs, T. 2003. *Myoglis meini* (de Bruijn, 1965 [1966]) (Mammalia: Gliridae) aus dem Miozän von Hambach 6C (NW-Deutschland). *Paläontologische Zeitschrift*, 77, 401-416.

Nunome, M., Yasuda, S.P., Sato, J.J., Vogel, P. & Suzuki, H. 2007. Phylogenetic relationships and divergence times among dormice (Rodentia, Gliridae) based on three nuclear genes. *Zoologica Scripta*, 36, 6, 537-546.

Ognev S.I. 1924. Nature and sport in Ukraine. *Kharkov*, 1 p.

Pocock, T.N. 1976. Pliocene mammalian microfauna from Langebaanweg: a new fossil genus linking the Otomyinae with the Murinae. *South African Journal of Science*, 72, 58-60.

Pomel, A. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire et surtout dans la vallée de son affluent principal, l'Allier. *J.B. Baillière, Paris*, 1-193.

Rabeder, G. 1984. *Bransatoglis* (Gliridae, Rodentia, Mammalia) aus dem Mittelmiozän von Schönweg bei St. Andrä im Lavanttal (Kärnten) *Beiträge Paläontologie Österreich*, 11, 511-519.

Ruiz-Sánchez, F.J., Murelaga, X., Freudenthal, M., Larrasoaña, J.C. & Garcés, M. 2012. A new species of glirid rodent *Vasseuromys* from the Aragonian (Miocene) of the Ebro Basin (north–eastern Spain). *Acta Palaeontologica Polonica*, 57, 2, 225-239.

Ruiz-Sánchez, F.J., Lacomba-Andueza, J.I, Freudenthal, M. & Álvarez-Sierra, M.Á. (in prep). A new species of *Vasseuromys* (Gliridae, Mammalia) from the Upper Oligocene of the Ebro Basin (Spain). *Paläontologische Zeitschrift*.

Smuts, J. 1832. Enumerationem mammalium Capensium. *J.C. Cyfveer, Leiden*, 1-105.

Stehlin, H.G. & Schaub, S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweizerische Paläontologische Abhandlungen*, 67, 1-385.

Storch, G. 1995. Affinities among living dormouse genera. *Hystrix (n.s.)*, 6, 1-2, 51-62.

Storch, G. & Seiffert, C. 2007. Extraordinarily preserved specimen of the oldest known glirid from the middle Eocene of Messel (Rodentia). *Journal of Vertebrate Paleontology*, 27, 1, 189-194.

Thomas O. 1906. The Duke of Bedford's zoological exploration in eastern Asia. l. List of mammals obtained by Mr. M.P. Anderson in Japan. *Proceedings Zoological Society London*, 1905, 2, 331-363.

Tullberg, T. 1899. Ueber das System der Nagethiere. Eine phylogenetische Studie. *Nova Acta Regalis Societatis Scienciarum Upsaliensis*, 3, 1-514.

Ünay-Bayraktar, E. 1989. Rodents from the middle Oligocene of Turkish Thrace. *Utrecht Micropaleontological Bulletins*, 5, 1-119.

Ünay, E. 1994. Early Miocene rodent faunas from the eastern Mediterranean area. Part IV. The Gliridae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, 97, 4, 445-490.

Vianey-Liaud, M. 1989. Parallelism among Gliridae (Rodentia): the genus *Gliravus* Stehlin & Schaub. *Historical Biology*, 2, 213-226.

Vianey-Liaud, M. 1994. La radiation des Gliridae (Rodentia) à l'Eocène supérieur en Europe Occidentale et sa descendance Oligocène. *Münchner Geowissenschaftliche Abhandlungen, A*, 26, 117-160.

Vianey-Liaud, M. 2004. Gliridae (Mammalia, Rodentia) de l'Oligocène européen origine de trois genres miocènes. *Coloquios de Paleontología, Volumen Extraordinario*, 1, 669-698.

Vianey-Liaud, M. & Jaeger, J.J. 1996. A new hypothesis for the origin of African Anomaluridae and Graphiuridae (Rodentia). *Palaeovertebrata*, 25, 349-358.

Wagner, J.A. 1840. Beschreibung einiger neuer Nager. *Abhandlungen mathematisch-physische Classe, Koenigliche Bayerische Akademie Wissenschaften München*, 3, 173-218.

Wahlert, J.H., Sawitzke, S.L. & Holden, M.E. 1993. Cranial Anatomy and Relationships of Dormice (Rodentia, Myoxidae). *American Museum Novitates*, 3061, 1-32.

Weerd, A. van de 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins, spec. publ.*, 2, 1-217.

Werner, J. 1994. Beiträge zur Biostratigraphie der Untern Süsswasser-Molasse Süddeutschlands - Rodentia und Lagomorpha (Mammalia) aus den Fundstellen der Ulmer Gegend. *Stuttgarter Beiträge Naturkunde, B*, 200, 1-263.

Wu, W. 1993. Neue Gliridae (Rodentia, Mammalia) aus untermiozänen (orleanischen) Spaltenfüllungen Süddeutschlands. *Documenta Naturae*, 81, 1-149.