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

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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 gliridos actuales (lirones) no son capaces de digerir la celulosa porque carecen de ciego intestinal. Entre los gliridos 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 periodo 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.
1. INTRODUCTION

Gliroid Muirhead, 1819 is a rodent family with a mainly European distribution and a limited number of extant species. Throughout the Oligocene gliroids 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 gliroid 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 Gliroid 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 Gliroidae 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 gliroids is the paper by Storch & Seiffert (2007), who concluded that the Eocene Eogliravus wildi Hartenberger, 1971, had a similar diet as extant Gliroidae, but that does not mean that all fossil gliroids 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 Gliroidae, 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, Gliroidae 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 & de Bruijn, 1995). Hypsodonty is strongly correlated with the existence of hypsodont taxons, like Armantomys de Bruijn, 1966a. Hypsodonty is strongly correlated with the digestion of hard plant material (Daams & 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: Gliroidae, Dryomyinae, Myomiminae, Graphiurinae, and the extinct Gliroidinae, Glamyninae and Bransatogliroidinae. We use that classification as the basis of our work.

Several authors have described cranial characters of fossil gliroids, e.g., Vianey-Liaud (1989), but systematics of fossil gliroids 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 Gliroidae is the morphology of the cheek teeth because this is the only character known for all taxa”.

Classification of recent gliroids 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 Gliroidae. 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 fossil 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 gliroid, 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 gliroids still had the caecum.

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 Gliroidinae, 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 gliroid 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.
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).
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 concavidentes     | Codet        | Hugueneey, 1967                |
| Bransatoglis mayri             | Sandelhausen | Rabeder, 1984                  |
| Buteeloglis bruijni            | Codet        | Hugueneey, 1967                |
| Buteeloglis daamsi             | Headon Hill 2| Bosma & de Bruijn, 1982        |
| Dryomys sp.                    | Dorn-Dürkheim| Franzen & Storch, 1975         |
| Eliomys assimilis              | Hammerschmied| Mayr, 1979                     |
| Eomuscardinus kellneri         | 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             | Robiá Sud    | Vianey-Liaud, 1994             |
| Glivus caracensis              | Paipa        | Daams et al., 1989             |
| Glivus pyrenaicus              | Sossis 1     | Agüst & Arcas, 1997            |
| Glirodinus glirulus            | Gunzenheim   | Dehm, 1935                     |
| Glirodinus undosus             | Erkertshofen | Mayr, 1979                     |
| Glirolus aff. ekremi           | Haram 1      | Ünay, 1994                     |
| Glirolus conjunctus            | Markt        | Mayr, 1979                     |
| Glirolus daamsi                | Çandin       | de Bruijn et al., 2003         |
| Glirolus minor                 | Petersbuch 2 | Wu, 1993                       |
| Glis gallipouli                | Aliveri      | van der Meulen & de Bruijn, 1982 |
| Glis guerbeucle                | Kocayarma    | Ünay-Bayraktar, 1989           |
| Glis vallesiensis              | Ballestar    | Agüst, 1981                    |
| Graphium sp.                   | Langebaanweg | Pocock, 1976                   |
| Microdyromys complicatus       | Sansan       | Daams & de Bruijn, 1995        |
| Microdyromys misonei           | Hoogbutsel   | Freudenthal & Martín-Suárez, 2007a |
| Microdyromys sinuosus          | Ampudia 3    | Alvarez Sierra, 1986           |
| Miodyromys hamadryas           | Can Ponsich  | Daams & de Bruijn, 1995        |
| Miodyromys hugueneveae         | Fraga 11     | Agüst & Arbiol, 1989           |
| Muscardinus thaleri            | Manchoines   | de Bruijn, 1966a               |
| Myoglis meini                  | Soblay       | Nemetschek & Mörs, 2003        |
| Myoglis sp.                    | Lespignan    | Aguilar, 1974                  |
| Myomimus dehmi                 | Pedregueras 2C| de Bruijn, 1966b               |
| Myomimus sp.                   | Çandin       | de Bruijn et al., 2003         |
| Myomimus sp.                   | Keseköy      | Ünay, 1994                     |
| Oligodryomys bahloai           | Headon Hill 3| Hugueneey & Adrover, 1990      |
| Oligodryomys moyai             | Sineu        | Hugueneey & Adrover, 1990      |
| Otavilis daamsi                | Harasib      | Mein et al., 2000              |
| Paraglirulus agelakisi         | Aliveri      | van der Meulen & de Bruijn, 1982 |
| Paraglirulus werafelsi         | Anwil        | Engesser, 1972                 |
| Paraglis asteracensis           | Belchatów A  | Freudenthal & Martín-Suárez, 2007b |
| Paraglis fugax                  | Mirambueno 4B| Freudenthal & Martín-Suárez, 2007b |
| Peridyromys marinus            | Mirambueno 1 | Freudenthal, 1997              |
| Peridyromys sondaari           | Vargas 2B    | Daams, 1999                    |
| Pseudodryomys ibericus         | Ateca 1      | de Bruijn, 1966a               |
| Pseudodryomys rex              | Torremorromojón 6B| García Moreno, 1986          |
| Ramys multirecastatus          | Torremorromojón 1| García Moreno & López Martínez, 1986 |
| Ramys perezi                   | Ampudia 9    | Alvarez Sierra, 1986           |
| Simplomys aljaphi              | Montagu-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                  |
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

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**Figure 2.** Proposed phylogeny of extant Gliridae. Grey fields are records for which the phylogeny is uncertain.
Engesser, 1972. 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). Several 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 & Martin 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 Myomynae 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 Myomyninae it should be restricted to Myomimus, and the other genera previously placed in Myomyninae form a new subfamily, Peridyromyninae (Number 3 in Fig. 1):

Subfamily Peridyromyninae subfamilia nov.

Type-genus. Peridyromys Stehlin & Schaub, 1951

Diagnosis. Daams (1981) gave the following diagnosis for the Myomyninae: “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 Peridyromyninae, and if one wishes to maintain the subfamily Myomyninae a much more restricted diagnosis can be made.

Genera included. Peridyromys; Altomiramys Díaz-Molina & López-Martínez, 1979; Armanomys; Miodyromys Kretzoi, 1943; Praearmantomys de Bruijn, 1966a; Pseudodyromys de Bruijn, 1966a; Simplomys García-Paredes et al., 2009; Tempesta 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 Peridyromyninae is provisional and based on the supposed origin in Peridyromyninae.

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 Agusti & 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).

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 Leithini (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 Dryomyinae 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

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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.

| Subfamily            | Genus          | My | MN  | My | MN  | FAD  |
|----------------------|----------------|----|-----|----|-----|------|
| base age             | 50 My          | 16 My |
| Glirurus             | 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  |
include the records from the Middle Miocene and older that were previously classified in Glirinae (Glis, Heteromomyxus, 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), Glirininae (Gliravus, Eogliravus Hartenberger, 1971 and Butseloglis) and Glamyninae (Glamyis) 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.

Ramous (MN9-10) may be a Peridyromyinae, related to Vasseuromys (Agusti 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 taxa.

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.

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NEW IDEAS ON THE SYSTEMATICS OF GLIRIDAE (RODENTIA, MAMMALIA)
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