

## A CLASSIFICATION OF THE GLIRIDAE (RODENTIA) ON THE BASIS OF DENTAL MORPHOLOGY

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**ABSTRACT** – The supra-familiar relationships of the Gliridae are discussed. The criterion used for subdividing the Gliridae is the morphology of the cheek teeth because this is the only character known for all taxa. This limitation leads to the undesirable "synonymy" of *Glamys* and *Gliravus*, two genera whose type species have a very different skull morphology, and to the incorporation into the Dryomyinae of *Graphiurus* and *Leithiu*, despite the fact that *Dryomys* has a myomorph, *Graphiurus* a hystricomorph and *Leithiu* a sciurormorph skull. The hundred and seventy-seven species and thirty eight genera of dormice are grouped into five subfamilies. One of these, the Bransatoglirinae, is new. The subfamily Graphiurinae is suppressed and *Graphiurus* is assigned to the Dryomyinae. The genera of the Gliridae and the species allocated to them are listed in the appendix in alphabetical order. The original diagnoses of the genera are given in English and the type locality, type level and synonymy of each species is given.

**Key words:** Gliridae, Systematics, Taxonomy, Dental morphology, Palaeontology.

**RIASSUNTO** – *Una classificazione di Gliridae (Rodentiu) sulla base della morfologia dentale* – Vengono discusse le relazioni soprafamiliari dei Gliridi. Il criterio utilizzato per la suddivisione dei Gliridi è la morfologia dei denti molari poiché è l'unico carattere noto per tutti i taxa. Questa limitazione porta alla "sinonimia" non voluta di *Glamys* e *Gliravus*, due generi le cui specie tipiche presentano una struttura del cranio molto diversa, ed alla incorporazione di *Graphiurus* e *Leithiu* nei Dryomyinae, sebbene *Dryomys* abbia un cranio miomorfo, *Graphiurus* un cranio isticomorfo e *Leithiu* un cranio sciurormorfo. Le centosettantasette specie ed i trentotto generi di Gliridi sono raggruppati in cinque sottofamiglie. Una di queste, Bransatoglirinae, è nuova. La sottofamiglia Graphiurinae viene soppressa e *Graphiurus* è incluso nei Dryomyinae. I generi dei Gliridi e le specie in essi incluse sono elencati in appendice in ordine alfabetico. Le diagnosi originali dei generi sono date in inglese e vengono date località tipica, livello stratigrafico tipico e sinonimie di ogni specie.

**Parole chiavi:** Gliridae, Sistematica, Tassonomia, Morfologia dentale, Paleontologia.

### PREAMBLE

The Rodentia are by far the most diverse order of mammals. In spite of this diversity similar structures have developed repeatedly in different groups. The occurrence of parallel and convergent evolutionary trends seems to be the rule rather than the exception. So it seems that genetic limitations inherent to the order allow a restricted number of efficient morpho-functional adaptations. Reconstructing phylogeny requires the recognition of primitive and derived character states. However, the oldest known representatives, *Paramys* in N. America and *Cocomys* in Asia, are already very specialised and very different.

Consequently, the evolutionary relationships among major groups of rodents have not been resolved conclusively in spite of the extensive biological and palaeontological analyses carried out during the last forty years.

The working hypothesis of Hartenberger (1980) who, on fossil evidence, postulated a dichotomy of the unknown Asiatic ancestor of the Rodentia into ischyromyoid and ctenodactyloid groups, is supported by biological data sets (George, 1985) and therefore appealing.

The ischyromyoid branch, characterized by molariform premolars, a small infraorbital foramen and molars that do not increase in size from M1 through M3, reached N. America and Europe during the Early Eocene, but seems to have persisted in S. Asia (de Bruijn et al., 1982). In North America, the Ischyromyoidea seem to be the ancestors of Sciuravidae who in turn seem to be at the base of the Geomyoidea. The Muroidea (= Muridae, Cricetidae, Tachyoryctidae, Spalacidae, Rhizomyidae, Gerbilidae and Platacanthomyidae as well as a number of "families" known as fossils only) and the Dipodoidea, who arrived as immigrants in Europe and N. America during the Early Oligocene, cluster in many biological aspects with the Geomyoidea. They are therefore considered to have descended from the Ischyromyoidea in Asia. On the basis of tooth morphology and their arrival as immigrants in Europe and N. America, a similar source is suggested for the Sciuroidea and possibly the Aplodontoidea and Castoroidea. In Europe the Ischyromyoidea seem to have radiated, shortly after the opening of the North Atlantic, into the Gliroidea (Hartenberger, 1971; Vianey-Liaud, 1985) and the Theridomyoidea. We think that the separate position of the Gliroidea and their descent from protrogomorphous ancestors has been demonstrated beyond reasonable doubt (Vianey-Liaud, 1985). Since the myomorph skull morphology has apparently evolved independantly in the Gliridae in Europe and the Muroidea and Dipodoidea in Asia (Vianey-Liaud, 1985) we disagree with Wahlert et al. (1993) who state: "The Myoxidae (= Gliridae) is the sister taxon to the combined Muroidea plus Dipodoidea; these three superfamilies constitute the rodent suborder Myomorpha".

The ctenodactyloid branch of the rodents, originally characterized by a relatively large infraorbital foramen, non-molariform premolars and cheek teeth that increase in size from M1 through M3 etc., shows rapid diversification in Asia during the Eocene. This group seems to be the stock from which not only the Hystricognaths from the Old as well as the New World may be derived, but also the Phiomyoidea. The fossil record suggests that these two entities along with the Anomaluridae may have originated in Africa, while the Ctenodactylidae, Chapattimyidae, Yuomyidae and Pedetidae, who share the same ancestral stock (the Cocomyidae ?), originated in Asia. The genus *Diatomys* that seems to be the only chapattamyid of the Indian subcontinent to have survived the Early Miocene immigration of rodents from Central Asia, seems to be a good candidate for the ancestry of the Pedetidae. The ctenodactyloids never seem to have reached N. America and the European mainland unless the specimens described as Chapattitnyidae indet. (Pelaez-Campomanes et al., 1989) from the Middle Eocene of Spain are what they seem to be.

This discussion on possible evolutionary relationships among rodents as seen

by a paleontologist has taken us far away from the goal of our paper: the presentation of a revised classification of the Gliridae. However, we consider it necessary to explain why we see the Gliroidea as a separate superfamily that is not part of the Myomorpha, although most of the genera and species included seem to have a myomorphous skull morphology and all have uniserial incisor enamel.

## INTRODUCTION

The Gliridae (dormice) are a monophyletic family that is represented by only eight genera and some thirteen or fourteen species in the extant fauna. The geographical range of the family (fossil and extant) is limited to Europe, Asia and Africa. The oldest record is from Europe (*Eogliravus wildi*, Mas de Gimel, France; MP10, Early Eocene) if the genus *Eogliravus*, with its dental pattern that is intermediate between the ischyromyoid *Microparamys* (*Sparnacomys*) and the true glirid *Gliravus*, is allocated to the Gliridae.

The fossil record of the dormice suggests that they are of European origin and that they have developed from the ischyromyoid branch of the Rodentia during a radiation that followed the opening of the North Atlantic during the Early Eocene. The only other rodent family of European origin - the Theridomyidae - represents another branch of the same radiation.

The diversification of the Gliridae that began in the Early Eocene continued during the Oligocene and culminated in the Late Early Miocene (MN3-4A) of Europe, where they seem to have occupied many ecological niches that remained filled with "cricetids" in the Muroid-dominated assemblages of Asia. The decline of the Gliridae in terms of diversity as well as of relative abundance in assemblages of fossil rodents becomes apparent during the Late Middle Miocene (MN7/8) (Figs. 9 and 10), that is, before the arrival of the first Muridae in Europe. From the Late Miocene onwards (MN11) the Gliridae are represented in Europe, Asia and Africa by a few genera only, excluding the insular forms, a situation that has essentially continued until the present.

Our classification of the Gliridae based on the morphology of the cheek teeth recognizes five subfamilies, thirty eight genera and one hundred and seventy-seven species. The number of species will certainly grow rapidly when new information from Western Asia becomes available, but the general picture is expected to remain essentially unchanged. This study is intended to show the rise and decline of the family during its geological history and to facilitate access to the, often specialized, literature. The Seleviniidae, which belong to the Superfamily Gliroidea together with the Gliridae, and consisting of the extant *Selevinia* and the Pliocene *Plioselvinia* are not considered in this paper, as we were not able to study the scarce material. Moreover, hitherto nothing is known about their dental patterns.

## PREVIOUS CLASSIFICATIONS

Opinions on the contents of the family Gliridae have not diverged much during the last hundred and fifty years. Some have included the Platanthomyidae while others assigned that family to the Muroidea. In contrast to this conformity, the

dormice have appeared under four different names: Gliridae Muirhead, 1819 (or Thomas, 1897), Myoxidae Zimmermann, 1780 (or Waterhouse, 1839), Leithiidae Lydekker, 1895 and Muscardinidae Palmer, 1899. The latter two names are obviously junior synonyms, but the semantics about the correct name for the family may well continue into the next century. Much depends on whether or not *Glis* Brisson, 1762 is considered to be a valid genus name and on the interpretation of the Code of Zoological Nomenclature.

Holden (1993) and Wahlert et al. (1993) use the name Myoxidae because they argue that the name *Glis* does not fulfill the requirements of the Code. We continue to use the name Gliridae because the stability of Zoological Nomenclature is not enhanced by resurrecting a name that has become obsolete since Ellerman's (1940) and Simpson's (1945) classification of the rodents. Pending the opinion of the International Commission of Zoological Nomenclature on the request to preserve Brisson's generic names *Philander*, *Pteropus*, *Glis*, *Cuniculus*, *Hydrochoerus*, *Meles*, *Tragul* and *Giraffa* (Gentry, 1994) we also consider it premature to replace the name Gliridae by Myoxidae now.

Reuvens (1890) summarizes the literature and gives diagnoses for five subgenera of the genus *Myoxus* to which all the extant forms are assigned.

Kretzoi (1943) divides the Leithiidae (=Gliridae) into three subfamilies: Graphiurinae, Leithiinae and Glirinae on the basis of their dental pattern, assigning the extinct as well as the extant genera to these subfamilies. Unfortunately the logic behind his allocations and his usage of the Leithiidae (while considering *Glis* a valid name) is not understood.

The classification of Simpson (1945) summarizes the literature on fossil and extant dormice and is not based on first hand knowledge. His grouping of the three families Gliridae, Platacanthomyidae and Seleviniidae in the superfamily Gliroidea is not followed. The Platacanthomyidae are allocated to the Muroidea (Qiu Zhuding, 1989) and the Seleviniidae seem to be a synonym of Gliridae (von Koenigswald, 1993). This leaves us with two subfamilies: the Graphiurinae for the African dormice South of the Sahara and the Glirinae for all the other members of the family.

The classification of de Bruijn (1967) based on dental morphology is an attempt to organize the, then rapidly growing, number of fossil genera and species that are defined by their dental pattern only. Although it was meant to be purely typological, the influence of phylogenetic thinking was unfortunately not rigorously avoided. Hence *Peridyromys* and *Pseudodryomys* with a style of dental pattern as in *Myomimus* were grouped with *Glirulus* (instead of with *Myomimus*), because I (H.d.B) considered *Peridyromys* the ancestor of *Glirulus* at the time. Another source of misjudgment is that I was never aware of the great antiquity of some of the dental patterns that characterize extant genera. In other words: the perspective has changed since 1967. A good example of this phenomenon is provided by *Glis* (= *Myoxus*). In 1967 this genus was known from the Pleistocene to the Recent only. However, I postulated a much longer stratigraphical range on the basis of its unique dental pattern (de Bruijn, 1967). We can now trace *Glis* to the Oligocene, and dispute about generic allocation is whether or not to include *Glis guerbuezi* Unay, 1989 from the Middle Oligocene of Turkey into *Glis*. For a

rodent genus a stratigraphic range for more than thirty million years seems very long and is probably not biologically correct, but the effect of our parsimonious knowledge of fossil species.

The classification proposed by Daams (1981) is also exclusively based on the dental morphology of the cheek teeth and as such an improved version of the arrangement of genera suggested by de Bruijn (1967). Daams' classification maintains a subdivision of the family into five subfamilies. Four of these (the Gliravinae, Glirinae, Dryomyinae and Graphiurinae) are the same as in de Bruijn (1967) although the content of the Dryomyinae is essentially different. Inclusion of *Glirulus* into the Dryomyinae made Glirulinae de Bruijn a synonym of Dryomyinae. A new subfamily Myomiminae was therefore proposed to house a large number of fossil genera with a style of dental pattern similar to extant *Myomimus*. Many of these were included in the Dryomyinae by de Bruijn. The island forms *Leithia*, *Hypnomys* and *Tyrrhenoglis* were classified as Gliridae incertae sedis.

Von Koenigswald (1993) divided the Gliridae into three groups on the basis of differences in the microstructure of the enamel of the lower incisors and suggested that the observed character differences could well be of great systematic importance and define major groups. The reason for von Koenigswald not formally defining subfamilies is that too few fossil glirid enamels could be analysed. The introduction of this new set of characters for subdividing the Gliridae is interesting and it is to be hoped that this line of research will be pursued. However, the poor correlation between the type of enamel, the characteristics of the cheek teeth and the cranial anatomy (Wahlert et al., 1993) suggests that the microstructure of the enamel of the lower incisor is yet another morpho-functional character and therefore no more suitable for taxonomy than any of the other data sets. What we need at this stage is information on the evolution of the enamel structure within one lineage.

The most recent classification of the extant Gliridae is by Wahlert et al. (1993). This study provides very complete information on the cranial morphology and dentition of the majority of the extant genera. Unfortunately *Selevinia* and *Chaetocauda* were not available to these authors and they did not consider the few skulls of fossil species preserved. This procedure results in a, basically classic classification in which the Gliridae are seen as the sister group of the combined Muroidea and Dipodoidea (for comments, see above). By applying the rule of priority rigorously in combination with refraining from studying the type genera of some of the higher categories used, considerable nomenclatural instability is introduced. The revival of the subfamily Leithiinae Lydekker, 1896 with the tribes Leithiini Lydekker, 1896 and Seleviniini Bashanov and Belosludov, 1939 to replace Dryomyinae de Bruijn, 1967 and Myomiminae Daams, 1981 respectively does not seem a good idea because:

1. The genus *Leithia* presumably has a sciuriform skull (Lydekker, 1895) and an angular process of the lower jaw that is not perforated (de Bruijn, 1966 c). These characters do not match the requirements for Leithiinae (sensu Wahlert et al., 1993).
2. The genus *Selevinia* is said to have two upper molars or premolars and no

lower d4 or p4 when very young. Although we are inclined to think that this very peculiar dental formula may have been inferred on incorrect observations, this "genus" which has type 3 enamel in the lower incisor but is otherwise virtually unknown, can hardly serve as the type genus of the tribe Seleviini. We therefore maintain Dryomyinae and Myomiminae until it can be shown that these concepts cover the same set of characters as Leithiini and Seleviini.

3. Character polarities of cranial data were assessed using *Paramys copei* Loomis, 1907 from the Lower Eocene of North America as the standard for primitive states. This does not seem a good choice, as this species is already very specialised and as it lacks any relation with the Gliridae, whose origin is situated in Western Europe.

One last remark concerns *Graphiurus* which has a hystricomorphous skull (Wahlert et al., 1993), type 3 enamel in the lower incisors (von Koenigswald, 1993) and a derived dental pattern that is reminiscent of *Eliomys*. Wahlert et al. interpret the skull characters of *Graphiurus* as primitive among living dormice and consequently suggest that it is an old branch of the family. However, fossil evidence shows that the primitive state of the skull of dormice is protrogomorphous. Since the genus is not known from deposits older than the Late Pliocene, and since its dental pattern resembles that of *Eliomys*, we think that *Graphiurus* is a descendant of *Eliomys*.

## CLASSIFICATION

### Subfamily **GLIRAVINAE** Schaub, 1958

Genus *Eoglravus* Hartenberger, 1971

Type species: *E. hammeli* (Thaler, 1966)

Other species: *E. moltzeri* Pelaez-Campomanes, 1995

*E. wildi* Hartenberger, 1971

Genus *Gliravus* Stehlin & Schaub, 1951 (= *Glamys* Vianey-Liaud, 1989)

Type species: *G. majori* Stehlin & Schaub, 1951

Other species: *G. alvarezae* Lacombe & Morales, 1987

*G. bravoii* Hugueney, Adrover & Moissenet, 1985

*G. bruijini* Ilugueney, 1967

*G. caracensis* Daams, Frcudenthal, Lacombe & Alvarez, 1989

*G. daamsi* Bosma & de Bruijn, 1982

*G. devoogdi* Bosma & de Bruijn, 1979

*G. fordii* Bosma & de Bruijn, 1979

*G. itardiensis* Vianey-Liaud, 1989

*G. meridionalis* Hartenberger, 1971

*G. micio* (Misonne, 1957)

*G. minor* Bosma & de Bruijn, 1982

*G. priscus* Stehlin & Schaub, 1951

*G. robiacensis* Hartenberger, 1965

*G. tenuis* Bahlo, 1975

### Subfamily **GLIRINAE** Thomas, 1897 (Fig. 2)

Genus *Glis* Brisson, 1762

Type species: *Glis glis* (Linnaeus, 1766)

Other species: *G. apertus* Mayr, 1979

*G. galitopouli* Van der Meulen & de Bruijn, 1982

*G. guerbuezi* Unay, 1990

*G. major* de Bruijn & Riimkc, 1974

*G. minor* Kowalski, 1956

*G. sackdillingensis* (Heller, 1930)

*G. sussenbornensis* Soergel, 1919

*G. transversus* Unay, 1994

*G. truyolsi* Daams, 1976

*G. vallesiensis* Agusti, 1981 a

Genus *Muscardinus* Kaup, 1829 (= *Eomuscardinus* Hartenberger, 1966; = *Pentaglis* Krcetoi, 1943)

Type species: *M. avellanarius* (Linnaeus, 1758)

Other species: *M. cyclopeus* Agusti, Moya-Sola & Pons Moya, 1982

*M. dacicus* Kormos, 1930

*M. davidi* Hugueney & Mein, 1965

*M. heintzi* Aguilar, 1981

*M. helleri* Fejfar & Storch, 1990

*M. hispanicus* de Bruijn, 1966b (= *Muscardinus crusafonti* Hartenberger, 1966)

*M. pliocaenicus* Kowalski, 1963

*M. sansaniensis* (Lartet, 1851)

*M. thaleri* de Bruijn, 1966a

*M. vallesiensis* Hartenberger, 1966

*M. vireti* Hugueney & Mein, 1965

Genus *Heteromyoxus* Dehm, 1938

Type species: *H. wetzleri* (Schlosser, 1884)

Other species: *H. schlosseri* Dehm, 1950

Genus *Myoglis* Baudelot, 1965

Type species: *M. meini* (de Bruijn, 1966a) (= *Myoglis larteti* Baudelot, 1965)

Other species: *Myoglis antecessens* Mayr, 1979

Genus *Glirudinus* de Bruijn, 1966a (= *Muscardinulus* Thaler, 1966)

Type species: *G. gracilis* (Dehm, 1950)

Other species: *G. engesseri* Unay, 1994.

*G. euryodon* Van der Meulen & de Bruijn, 1982

*G. glirulus* (Dehm, 1935)

*G. haramiensis* Unay, 1994.

*G. minutus* Wu, 1993

*G. modestus* (Dehm, 1950) (= *G. bouziguensis* (Thaler, 1966))

*G. undosus* Mayr, 1979

Genus *Stertomyx* Daams & Freudenthal, 1985

Type species: *S. laticrestatus* Daams & Freudenthal, 1985

Subfamily **DRYOMYINAE** de Bruijn, 1967

Genus *Dryomys* Thomas, 1906 (= *Afrodryomys* Jaeger, 1975)

Type species: *D. nitedula* (Pallas, 1778)

Other species: *D. ambiguus* Lavocat, 1961

*U. chaabi* (Jacger, 1977)

*D. laniger* Felten & Storch, 1968

Genus *Elionzys* Wagner, 1840

Type species: *E. quercinus* (Linnaeus, 1766) (= *Elionzys melanurus* Wagner, 1843)

Other species: *E. assimilis* Mayr, 1979

*E. intermedius* Priant, 1953

*E. reductus* Mayr, 1979

*E. truci* Mein & Michaux, 1970

Genus *Leithia* Lydekker, 1895

Type species: *L. melitensis* (Adams, 1863)

Other species: *L. cartei* (Adams, 1863)

Genus *Graphiurus* Smuts, 1832

Type species: *G. ocularis* (Smith, 1829)

Other species: *G. murinus* (Desmarest, 1822)

*G. parvus* (True, 1893)

*G. platyops* Thomas, 1897

Genus *Glirulus* Thonias, 1906

Type species: *G. japonicus* (Schinz, 1845) (= *G. elegans* Temminck, 1845; = *G. lasiotis* Thomas, 1880)

Other species: *G. direptus* (Mayr, 1979)

*G. ekremi* Ünay, 1994

*G. gemmula* Kretzoi, 1962

*G. lissiensis* (Hugueney & Mein, 1965)

*G. minor* Wu, 1993

*G. pusillus* (Heller, 1936)

Genus *Hypnomys* Batc, 1918

Type species: *H. mahonensis* Bate, 1918

Other species: *H. eliomyoides* Agusti, 1980

*H. onicensis* Reunicr. in press

*H. morpheus* Bate, 1918

*H. waldreni* Reumer, 1979

Genus *Microdyromys* de Bruijn, 1966 a

Type species: *M. koenigswaldi* de Bruijn, 1966 a

Other species: *M. complicatus* de Bruijn, 1966 a (= *Glirulus miocaenicus* Baudelot, 1965;

*Paraglrulus scalabicensis* Antunes & Mein, 1977)

*M. legidensis* Daams, 1981

*M. monspeliensis* Aguilar, 1977

*M. orientalis* Wu, 1986

*M. praemurinus* (Freudentberg, 1941)

*M. sinuosus* (Alvarez Sierra, 1986 in: Alvarez Sierra & Garcia Moreno, 1986)

Genus *Graphiurops* Bachmayer & Wilson, 1980

Type species: *G. austriacus* Bachniayer & Wilson, 1980

Genus *Paraglrulus* Engesser, 1972

Type species: *P. werenfelsi* Engesscr, 1972

Other species: *P. agelakisi* Van der Meulen & de Bruijn, 1982

*P. conjunctus* Mayr, 1979

Genus *Tyrrhenoglis* Engesscr, 1976

Type species: *T. majori* Engesser, 1976

Other species: *T. figariensis* Zammit Maempel & de Bruijn, 1982

Genus *Maltamys* Zammit Maempel & de Bruijn, 1982

Type species: *M. gollcheri* (de Bruijn, 1966c)

Other species: *M. wiedincitensis* Zammit Maempel & de Bruijn, 1982

Genus *Anthracoglis* Engesser, 1983

Type species: *A. marinoi* Engesser, 1983

Genus *Eivissia* Alcover & Agusti, 1985

Type species: *E. canarreiensis* Alcover & Agusti, 1985

Genus *Chaetocauda* Wang, 1985

Type species: *C. sichuanensis* Wang, 1985

#### Subfamily MYOMIMINAE Daams, 1981

Genus *Myomimus* Ognev, 1924 (= *Philistomys* Batc, 1937)

Type species: *M. personatus* Ognev, 1924 (= *M. setzeri* Rossolimo, 1976 a; = *M. bulgaricus* Rossolimo, 1976 b)

Other species: *M. compositus* (Bachniayer & Wilson, 1970)

*M. dehmi* (de Bruijn, 1966 b)

*M. maritsensis* de Bruijn, Dawson & Mein, 1970

*M. qafzensis* (Haas, 1973)

*M. roachi* (Bate, 1937) (= *Myomimus judaicus* Tchernov, 1968)

*M. sinensis* Wu, 1985

*M. sumbalenwalicus* Munthc, 1980

Genus *Miodyromys* Kretzoi, 1943



- Type species: *M. hamadryas* (Forsyth Major, 1899)  
 Other species: *M. aegercii* (Baudelot, 1972)  
*M. biradiculus* Mayr, 1979  
*M. hugueneyae* Agusti & Arbiol, 1989  
*M. praecox* Wu, 1993  
*M. prosper* (Thaler, 1966)  
*M. vagus* Mayr, 1979
- Genus *Peridyromys* Stchlin & Schaub, 1951  
 Type species: *P. murinus* (Pomel, 1853) (= *Peridyromys occitanus* Baudelot & De Bonis, 1966)  
 Other species: *P. aquatilis* (de Bruijn & Moltzer, 1974)  
*P. columbarii* Daams, 1989b  
*P. jaegeri* Aguilar, 1974  
*P. ordinasi* Mein & Adrover, 1982  
*P. turbatus* Alvarez et al., 1990
- Genus *Dryomimus* Kretzoi, 1959  
 Type species: *D. eliomyoides* Kretzoi, 1959  
 Genus *Vasseuromys* Baudelot & De Bonis, 1966 (= *Szechenyia* Kretzoi, 1978; = *Ebromys* Cuenca, 1985)  
 Type species: *V. rugosus* Baudelot & De Bonis, 1966  
 Other species: *V. autolensis* (Cuenca, 1985)  
*V. bacchius* (Martinez-Salanova, 1987)  
*V. duplex* Ünay, 1994  
*V. elegans* Wu, 1993  
*V. pannonicus* (Kretzoi, 1978) (= *Vasseuromys thenii* Daxner-Hock & de Bruijn, 1981)  
*V. priscus* De Bonis, 1973
- Genus *Pseudodryomys* de Bruijn, 1966a  
 Type species: *P. ibericus* de Bruijn, 1966a  
 Other species: *P. aljaphi* Huguency et al., 1978  
*P. julii* Daams, 1989a  
*P. granatensis* Agusti 1993 in Martin Suarez et al., 1993  
*P. rex* (Garcia Moreno 1986 in Alvarez Sierra & Garcia Moreno, 1986)  
*P. robustus* de Bruijn, 1967  
*P. simplicidens* de Bruijn, 1966a  
 (= *Psetrodryomys meini* Adrover, 1978)
- Genus *Praearmantomys* de Bruijn, 1966a  
 Type species: *P. crusafonti* de Bruijn, 1966a (= *P. ginsburgi* Antunes & Mein, 1971)
- Genus *Armantomys* de Bruijn, 1966a (= *Quercomys* Lacomba & Martincz-Salanova, 1988)  
 Type species: *A. aragonensis*, de Bruijn, 1966a  
 Other species: *A. bijniai* (Lacomba & Martinez-Salanova, 1988)  
*A. daamsi* (De Visser, 1990 in Alvarez et al., 1990)  
*A. jaspersi* Daams, 1990  
*A. parsani* Daams, 1990  
*A. tricristatus* López, 1977 in Lopez et al., 1977
- Genus *Nievella* Daams, 1976  
 Type species: *N. mayri* Daams, 1976
- Genus *Tempestia* Van de Weerd, 1976  
 Type species: *T. hartenbergeri* (de Bruijn, 1966b)  
 Other species: *T. ovilis* Daams, 1989a
- Genus *Altomiramys* Diaz & Lopez, 1979  
 Type species: *A. daanisi* Diaz & López, 1979
- Genus *Prodryomys* Mayr, 1979  
 Type species: *P. satus* Mayr, 1979  
 Other species: *P. brailloni* (Thaler, 1966) (= *Pseudodryomys aguirrei* Adrover, 1978)  
*P. gregarius* (Dehm, 1950)
- Genus *Carbomys* Mein & Adrover, 1982

Type species: *C. sacaresi* Mein & Adrover, 1982

Genus *Margaritamyx* Mein & Adrover, 1982

Type species: *M. allulli* Mein & Adrover, 1982

Genus *Ramys* Garcia Moreno & Lopez Martinez, 1986

Type species: *R. multicrostatus* (de Bruijn, 1966 b)

Other species: *R. perezi* Alvarez Sierra, 1986 (in Alvarez Sierra & Garcia Moreno, 1986)

Subfamily **BRANSATOGLIRINAE** nov. subfam.

Genus *Bransatoglis* Huguency, 1967 (= *Paraglis* Baudelot, 1970; = *Oligodyromys* Bahlo, 1975)

Type species: *B. concavidens* Huguency, 1967

Other species: *B. astaracensis* (Baudelot, 1970)

*B. attenuatus* Pelacz-Campomanes, 1993

*B. bahloi* Bosma & de Bruijn, 1982

*B. cadeoti* Bulot, 1978

*B. complicatus* Unay, 1994.

*B. fugax* (Huguency, 1967)

*B. infralactorensis* (Baudelot & Collier, 1982)

*B. moyai* (Huguency & Adrover, 1990)

*B. parvus* Pelacz-Campomanes, 1993

*B. planus* (Bahlo, 1975)

*B. rimosus* Peláez-Campomanes, 1993

*B. sjeni* Unay, 1990

*B. spectabilis* (Dehm, 1950)

## STRATIGRAPHIC RANGES AND PHYLOGENETIC CONTEXT

The stratigraphic schemes used are the M.P. zonation for the Paleogene (Schmidt-Kittler, ed., 1987) and the M.N. zonation for the Neogene (de Bruijn et al., 1992). The zones MN2 and MN4 are each divided into a lower part (a) and an upper part (b) because the European fossil record shows major breaks within these units.

The nomenclature of parts of the Gliridae cheek teeth are after de Bruijn (1966), and slightly modified by Daams (1981) (Fig. 1).

Subfamily **GLIRAVINAE** Schaub, 1958

*Range* - Early Eocene (MP10) - Late Oligocene (MP30)

*Characteristic features* - Occlusal surface concave, main cusps well developed, ridges poorly developed, protocone of upper molars situated centrally.

This is considered to be the stemgroup of all Gliridae. *Eoglriravus* with the most primitive dental pattern is known from the Lower and Middle Eocene of France (Thaler, 1966; Hartenberger, 1971) and the Middle Eocene of Spain (Peláez-Campomanes, 1993). Hartenberger (1971) as well as Peláez-Campomanes (1993) reached the conclusion that this genus is probably not the ancestor of *Gliravus*, but we think it is.

The oldest species of *Gliravus* is *G. robiacensis* Hartenberger, 1965 from the Upper Eocene of Robiac, the youngest representative is *G. bruijini* from Coderet. *Gliravus* is well represented in the Upper Eocene and Lower Oligocene of Western Europe. Shevyreva (1992) described *Chaibulakomys angos* from the Upper Eocene of Eastern Kazakhstan and assigned it to the Gliravinae. This taxon, based on one

P<sub>4</sub>, is of uncertain affinity and considered a nomen dubium.

Skulls are known of the Gliravinae "*Glamys*" *priscus* from the Late Eocene and Early Oligocene, *Gliravus itardiensis* from the Early Oligocene, and *Gliravus nzajori* from the Late Oligocene. The first species is inyomorphous and the other two are protrogomorphous (Vianey-Liaud, 1989). We consider the protrogomorphous arrangement as the original character state of the Gliridae.

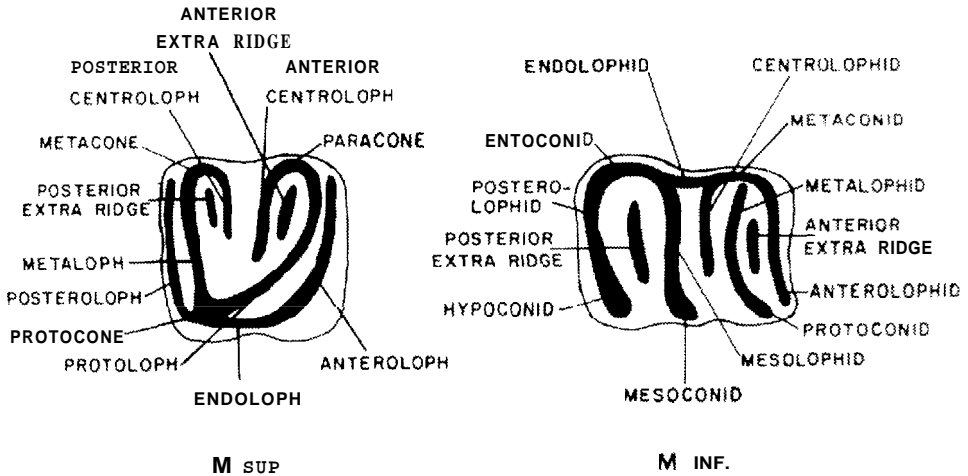


Fig. 1 — Nomenclature of parts of the Gliridae cheek teeth (after Daams, 1981).

Subfamily **GLIRINAE** Thomas, 1897 (Fig. 3)

*Range:* Late Oligocene (MP28) - Recent

*Characteristic features:* Occlusal surface flat or slightly concave, main cusps weak or indistinct, crown and ridges low, extra ridges tend to be situated labially in the upper molars and lingually in the lower ones. Dental pattern usually complex. In several genera the roots are small and occupy a relatively central position. In these enamel continues on the lower side of the crown until it meets the roots.

The first record of this subfamily is *Glirudinus glirulus* from various Late Oligocene (MP28) localities of Western Europe (Gunzenheim, Germany, Dehm, 1935; St. Victor-la-Coste, S France; Huguency, 1968 and Vivel del Rio, Central Spain; Huguency et al., 1987). The dental pattern in this species is relatively simple, and the masticatory stroke in this genus is oblique to the longitudinal axis of the dentition. *G. cf. gracilis* from the Middle Miocene (MN6) of Anwil (Switzerland; Engesser, 1972) and Sansan (France; Engesser, 1972) is the last evidence of this genus in the fossil record. Geologically younger representatives of *Glirudinus*, *G. modestus* (MN2-MN4), *G. undosus* (MN4), and *G. gracilis* (MN3) have complex dental patterns.

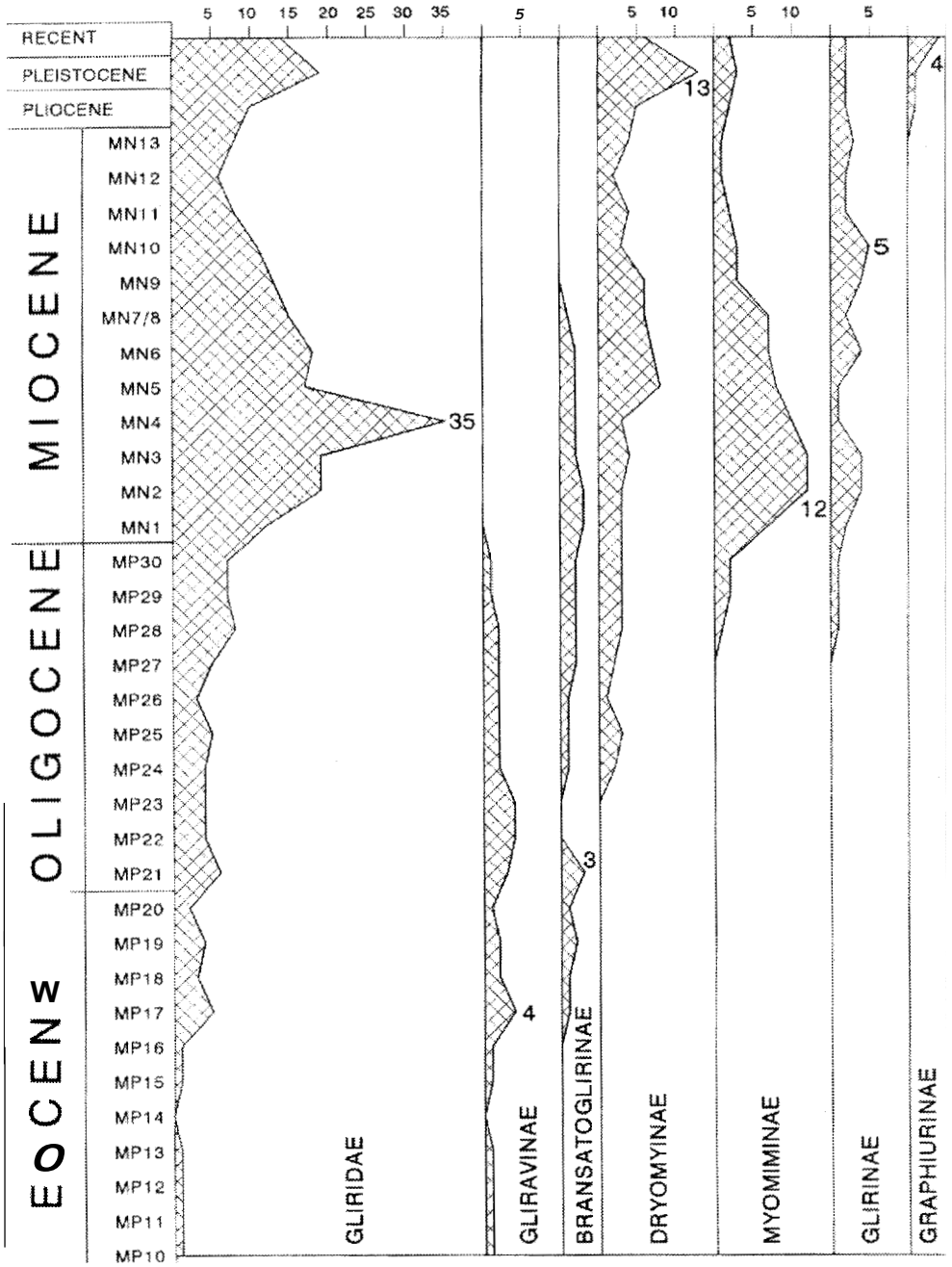


Fig. 2 – Number of Gliridae species from the entire fossil and extant record. The number in each column refers to the maximum number of species per (sub)family and per zone.

The first evidence of *Glis* (*G. guerbuezi*) is from the Middle Oligocene of Kocayarma, Turkey (Unay, 1989). The dental features of this species are a mixture of those of its theoretical ancestor and those of *G. glis*. The dental pattern of *Glis*

*apertus* from the Early Miocene (MN1) of Weissenburg 6, S. Germany, (Mayr, 1979) is basically the same as that of extant *Glis*. In Miocene faunas this genus is rare. *Glis tuyolsi* is known by two teeth from the Lower Miocene (MN2A) of Cetina de Aragon (Spain) and *Glis major* from the Lower Miocene (probably MN2) fauna of Oschiri (Sardinia, Italy) is represented by two teeth only. From the Pliocene onwards, *Glis* is common in central European, but absent or very rare in western European faunas.

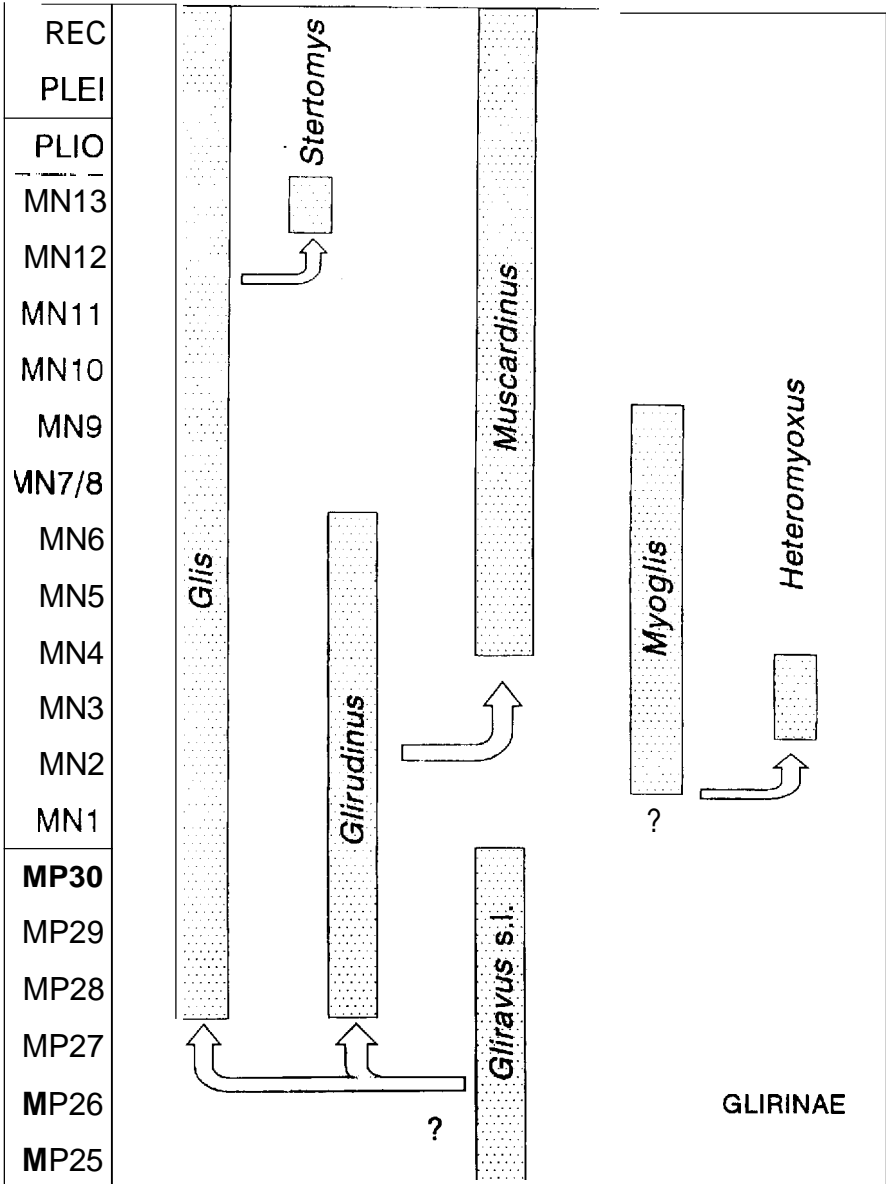


Fig. 3 – Tentative reconstruction of the phylogenetic relationships of the genera of the Glirinae.

The first evidence of *Muscardinus* (*M. thaleri*) is from the Middle Miocene (MN4B) of Spain (Daams, 1985). The very low crowns are completely flat and the masticatory stroke is longitudinal. The dental pattern of *Muscardinus* is easily derivable from *Glirudinus*. During the Middle Miocene the genus is represented by *Muscardinus thaleri* in Spain and by *M. sansaniensis* in France and Central Europe. From the Vallesian onwards, several lineages have been recognized in Europe. The only extant representative is *M. avellanarius*. The *Muscardinus* from MN6 and MN7/8 have a somewhat more complex dental pattern than the extant species.

*Myoglis* sp. from the Lower Miocene (MN2B) of Lespignan (Aguilar, 1974) is the oldest record of this genus. Its ancestor is not known. *Myoglis* sp. has a simpler dental pattern and is somewhat smaller than the Middle Miocene *M. meini* from Manchones, Anwil and Sansan. The last occurrence is *Myoglis* sp. from the Upper Miocene (MN9) of Can Llobateres, Spain (Hartenberger, 1966). The lineage of *Myoglis* sp. - *M. antecedens* - *M. meini* is characterized by a trend towards increased size and towards a somewhat more complex dental pattern.

*Heteromyoxus* has a short stratigraphic range (MN3-MN4A of S. France and S. Germany; Baudelot & Collier, 1982 and Dehm, 1950 respectively) and seems to be a descendant of *Myoglis*. The upper teeth of *Heteromyoxus* and *Myoglis* are very similar, but in the lower cheek teeth of *Heteromyoxus* the transverse ridges are connected by short longitudinal and oblique ridges.

*Stertomyys laticrestatus* from the Upper Miocene (MN13 ?) of Gargano (S. Italy) is an insular giant dormouse which is thought to have descended from *Glis* because in both genera the protoloph and metaloph end separately at the lingual border.

Subfamily **DRYOMYINAE** de Bruijn, 1967 (Figs. 4 and 5)

*Range:* Early Oligocene (MP24) - Recent

*Characteristic features:* Occlusal surface concave, extra ridges generally narrower than the main ridges, upper molars with endoloph. Dental pattern generally relatively complex.

The oldest representative of this subfamily is *Microdyronzys praemurinus* from the Lower Oligocene (MP24) of Heimersheim (Germany). In the assemblage from the Lower Oligocene fauna of Montalbán (MP23, Spain) the endoloph of the upper molars may be complete or incomplete. This assemblage constitutes the transition between the Gliravinae and the Dryomyinae morphotype. Until the end of the Oligocene *M. praemurinus* remains the only species of this subfamily. In the Lower Miocene *Microdyronzys* is represented by *M. monspeliensis* and by *M. legidensis*. The last occurrence of *Microdyromys* is *M. sinuosus* from the Upper Miocene (MN10) of Ampudia 3, Spain (Alvarez Sierra et al., 1987).

The first evidence of *Eliomys* is *E. truci* (Fig. 4) from the Middle Miocene (MN4B) of Spain (Daams & Freudenthal, 1988). The dental pattern of this species is not very different from *Microdyronzys legidensis*. *Eliomys truci* continues to be present until the Ruscian (Van de Weerd, 1976 and Daams et al., 1988). Mayr (1979) described two *Eliomys* species, *E. assimilis* and *E. reductus* from the Upper

Miocene of S. Germany, but it is not known whether or not these have anything to do with the later *E. intermedius*.

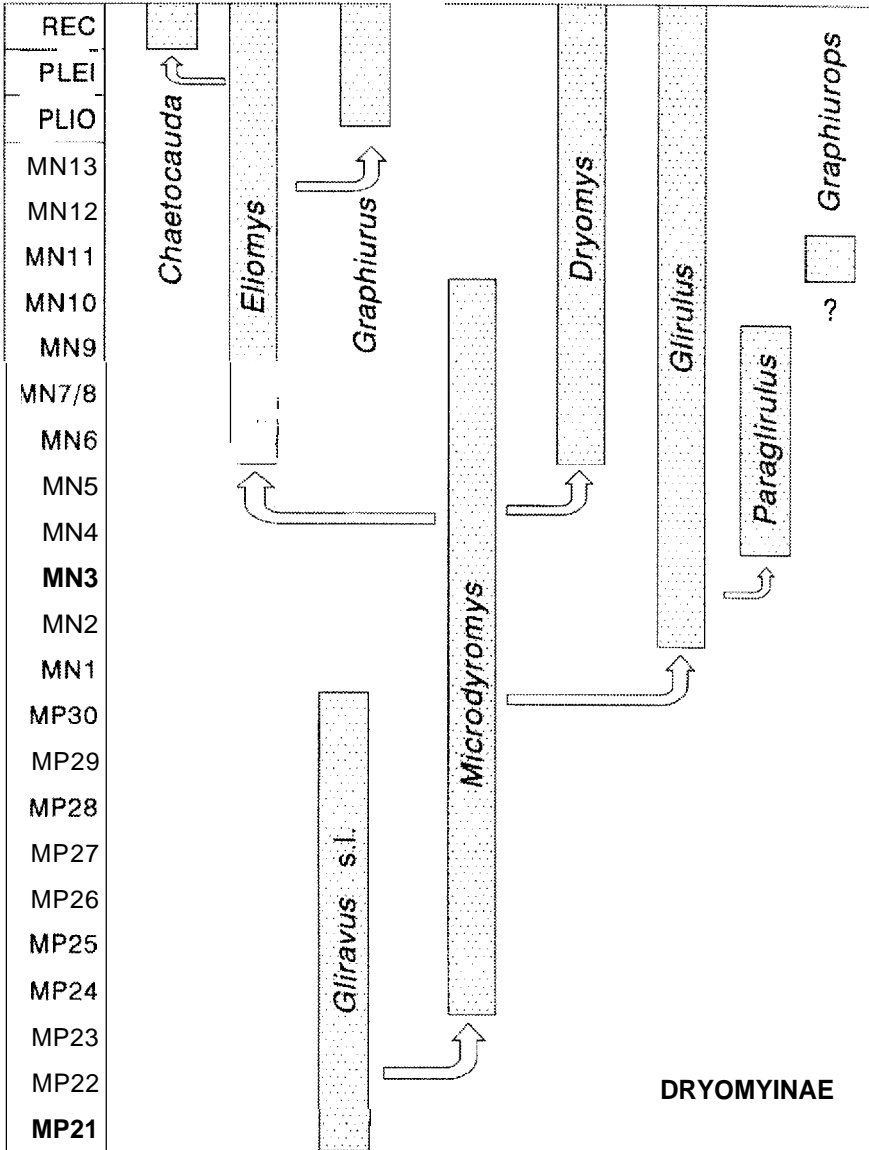


Fig. 4 – Tentative reconstruction of the phylogenetic relationships of the genera of the continental Dryomyinae.

The first evidence of *Dryomys* is from the Middle Miocene (MN6) of North Africa (Lavocat, 1961; Jaeger, 1975). Daams (1981) pointed out that the dental pattern of the two *Dryomys* species from Africa fall morphologically within the range of variation of extant *Dryomys nitedula*. *Dryomys* is thought to have descended from *Microdryomys*. *Dryomys* is extremely rare in the fossil record. The

oldest find in Europe may be that of *Dryomys* sp. from the Late Miocene (MN11) of Dorn-Durkheim (Franzen & Storch, 1975 and Daams, 1981).

The first evidence of *Glirulus* is *G. aff. ekremi* from the Lower Miocene (MN2) of Harami 1, Turkey (Ünay, 1994). The difference between *Glirulus* and *Paraglrulus* is extensively discussed in Van der Meulen & de Bruijn (1982). Mayr (1979) suggests that *Glirulus* is an off-shoot of *Microdyromys*, an opinion we share. Evolutionary trends in the dentition of *Glirulus* have not been observed. Information on the extant *G. japonicus* is given by Kawamura (1989) and Wahlert et al. (1993).

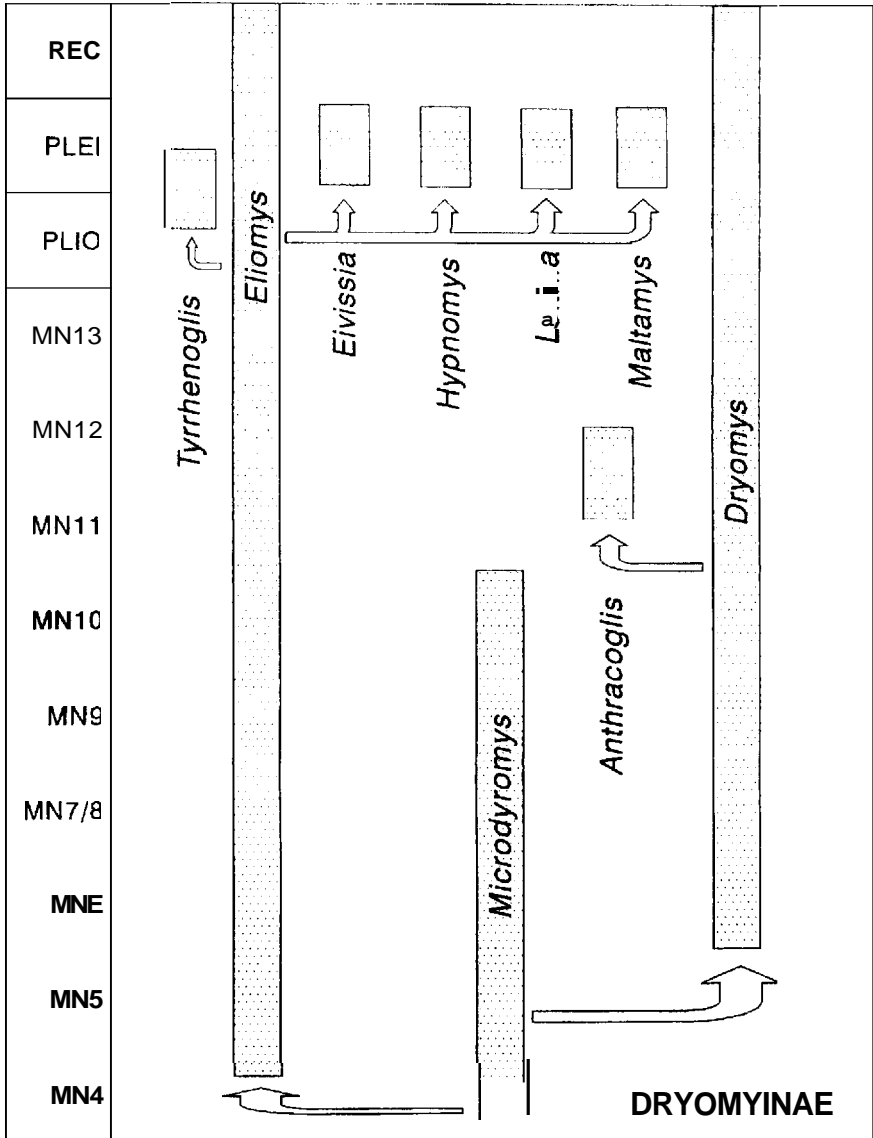


Fig. 5 – Tentative reconstruction of the phylogenetic relationships of the genera of the insular Dryomyinae.



The first record of *Paraglrulus* is *P. agelakisi* from the Lower Miocene (MN4A) of Aliveri, Greece (Van der Meulen & de Bruijn, 1982). The last occurrence is *P. werenfelsi* from the Late Miocene (MN9) of Can Llobateres, Spain (Fig. 4). Van der Meulen & de Bruijn (1982) suggest that *Paraglrulus* may have descended from either *Microdyromys* or *Bransatoglis*. The presence of a long, labially isolated, anterior centroloph in the upper cheek teeth and the symmetrical shape of  $M^2$  are reminiscent of *Bransatoglis*, but the regular shape and arrangement of the ridges, and the size of the teeth are more similar to *Microdyromys*. We therefore think that *Paraglrulus* is closer to *Microdyromys* than to *Bransatoglis*. *Paraglrulus* is more common in central Europe than it is in the Iberian Peninsula.

The insular dormice *Leithia*, *Hypnomys*, *Tyrrhenoglis*, *Maltamys* and *Eivissia* (Fig. 5) are considered to have descended from *Eliomys* (Zammit-Maempel & de Bruijn, 1982; Alcover & Agustí, 1985). The insular *Anthracoglis* from the Upper Miocene of Baccinello (Italy) however, is more similar to *Microdyromys* (Engesser, 1983) and *Dryomys*. Since the last record of *Microdyromys* is from MN10 and thus older than *Anthracoglis* we think that it is most probable that *Anthracoglis* descended from *Dryomys*.

The first remains of *Graphiurus* date from the Plio/Pleistocene of Angola (Pickford et al., 1992) and Botswana (Pickford & Mein, 1988). The four extant species (Webb & Skinner, 1993) are all from Africa south of the Sahara. The Graphiurinae have a hystricomorphous skull (Wahlert et al., 1993) and not a myomorphous skull as most other Gliridae. The dental pattern resembles that of *Eliomys* which makes us postulate a direct relationship between the two genera (Fig. 3). We do not consider the hystricomorphous condition of *Graphiurus* to be the original character state for the Gliridae so there is no reason to suppose that the family reached Africa as early as the Paleocene.

The extant, monospecific genus *Chaetocauda* is only known by a few specimens from China. Wang (1985) assigns *Chaetocauda sichuanensis* to the Myorniminae but the presence of a continuous endoloph in the upper cheek teeth (Wang, 1985, Fig. 1), made us tentatively transfer it to the Dryomyinae. The general appearance of the ridge pattern is reminiscent of a simplified *Eliomys*.

Subfamily **MYOMIMINAE** Daams, 1981 (Figs. 6 and 7)

*Range:* Late Eocene (MP 17) - Recent

*Characteristic features:* Occlusal surface concave, main cusps fairly well developed, extra ridges narrower than main ridges, relatively high-crowned molars in some genera, endoloph generally absent in  $M^{1,2}$ , dental pattern from simple to very complex.

The first record of *Myomimus* is from the Lower Miocene (MN3) of Kilçak, Central Anatolia, Turkey (Unay, 1994), an area where the last representative of the genus, *M. personatus* is still living. *Myomimus dehmi*, a species with a relatively complex dental pattern arrived in central Spain during the Late Aragonian (Daams & Freudenthal, 1988) and is a common constituent of assemblages from the Lower Vallesian (MN9) of Europe. The genus seems to have become extinct in S.W.



one or more extra ridges in both upper and lower molars. The oldest species is *M. hugueneyae* from the Upper Oligocene (MP30) of Northern Spain (Agusti & Arbiol, 1989) and the youngest one is *M. hamadryas* from the Upper Miocene (MN9) of Can Ponsich (Fig. 7). The possible synonymy of *Miodyromys*, *Prodryonzys*, *Pseudodryomys* and *Peridyromys* is not discussed here because these genera are presently under study by the first author.

*Peridyromys* is the oldest genus of the Myomiminae (Figs. 6 and 7). Its teeth are relatively small, and its first representative has a moderately complex dental pattern (*P. murinus* from St. Victor-la-Coste and Coderet, Upper Oligocene (MP30), France; Hugueney, 1968, 1969; *P. columbarii* from the Upper Oligocene (MP30) of Sayatón 6, Spain (Daams, 1989 b). *Peridyromys* is thought to be the ancestor of a number of other genera such as *Armantomys*, *Praearmantomys*, *Pseudodryomys* etc. (see below). The last occurrence of *Peridyromys* (*P. murinus*, is in MN4B of Spain (Daams & Freudenthal, 1988).

*Dryomimus* is hitherto represented by one species; *D. eliomyoides* from the Plio/Pleistocene of Hungary (Kretzoi, 1959) and Greece (de Bruijn & Van der Meulen, 1975). The general features of the simple dental pattern and the three-rooted lower molars suggest that it may have descended from *Myomimus*.

The first evidence of *Vasseuromys* is *V. priscus* in the Lower Miocene (MN1) of France (Baudelot & De Bonis, 1966) and Spain (Fig. 7) and *V. aff. duplex* in MN1 of Turkey (Unay, 1994). According to De Bonis (1973) *V. priscus* from MN1 would be the ancestor of *V. rugosus* from MN2B of France. Alvarez et al. (1990) discuss the characteristic features of *Vasseuromys* and express doubt about the allocation of the species *priscus* to *Vasseuromys*. A number of *Vasseuromys* species (*V. autolensis* from MN1 of Spain, *V. bacchius* from MN2A of Spain, *V. rugosus* from MN1-2B of France and Spain, *V. pannonicus* from MN11 of Central Europe) have a very complex dental pattern. *V. pannonicus* from the Upper Miocene (MN11) of Austria and Hungary is the last representative of the genus.

The first evidence of *Pseudodryomys* is from the Early Miocene (MN1) of central Spain (Daams et al., 1986 and Lacomba, 1988, unpublished thesis, Madrid). Several species of this genus are characterized by their simple dental pattern (*P. simplicidens*, *P. robustus* and *P. julii*), others have a more complex dental pattern (*P. ibericus*, *P. aljaphi* and *P. rex*). Some species, such as *P. simplicidens*, have a long stratigraphic range (MN2A-MN5), but others have a very short one (*P. julii*; MN4A). The genus *Pseudodryomys* is diverse and abundant in S.W. Europe and its last occurrence (*P. simplicidens*) is from the Middle Miocene (MN6) of S. Germany (Mayr, 1979).

*Praearmantomys* has been extensively discussed by Daams (1990). This monospecific genus with its simple dental pattern is exclusively known from the Lower Miocene (MN2B-MN4A) of central Spain and Portugal (Figs. 6). Its slightly hypsodont molars show a modest simplification through time. It is thought to have descended from *Peridyromys murinus*.

*Armantomys* has also been discussed in detail in Daams (1990). It is thought to have descended from *Peridyromys murinus*. The first occurrence of *Armantomys* is *A. cf. bijmai* from the Upper Oligocene (MP29) of the unpublished fauna of Parrales (Loranca Basin, Spain) and its last occurrence is *A. tricristatus* from the

Middle Miocene (MN7/8) fissure filling of Escobosa, Spain. Two lineages are recognized in this genus: the *A. bijmai* - *A. jasperi* lineage, characterized by relatively small teeth and the *A. aragonensis* - *A. tricristatus* lineage characterized by relatively large teeth. *Armantomys* has the most hypsodont cheek teeth of all Gliridae. Both lineages are characterized by a trend towards completion of the posterolophid of  $M_3$ . Descendants are not known.

*Nievella* is represented by a few teeth from the Lower Miocene (MN2A) of Cetina de Aragon, Spain only (Daams, 1976). These teeth are relatively large and the dental pattern is moderately complex. Neither ancestors nor descendants are known (Fig. 6).

*Tempestia* is known by two species that succeed each other in time. *T. ovilis* makes its appearance in central Spain in MN4B and its successor *T. hartenbergeri* appears in MN7/8 of the same area. Hitherto this genus is not known outside the Calatayud-Teruel Basin. Its last occurrence is in the Late Vallesian (MN10) (Fig. 6). Evolutionary trends are towards a slight size increase, the loss of the anterior centroloph of the upper molars and the shortening of the centrolophid in the lower ones.

*Altomiramys* is known by *A. daamsi* from the Lower Miocene (MN2B) of central Spain only (Diaz Molina & Lopez Martinez, 1979 and Daams, 1989 a). Its simple dental pattern and low-crowned molars are reminiscent of *Pseudodryomys*, but it differs in the presence of a relatively long anterior centroloph, the absence of a posterior centroloph, the wide and shallow valleys, and the two-rooted lower molars. Unpublished *Altomiramys* teeth from MN1 and MN2A from central Spain show a close resemblance to *Peridyromys murinus*.

The validity of *Prodryomys* is still under discussion because of similarities with *Miodryomys* and *Pseudodryomys*. The first record of this genus is *Prodryomys brailloni* from MN2B of Bouzigues and the last representative (*P. satus*) is present in MN6 of Sandelzhausen. Mayr (1979) and Wu (1993) suggest that *P. satus* may be a descendant of *Prodryomys brailloni* from MN2B and MN3 of Western Europe. *Prodryomys satus* from MN6 of South Germany is supposed by Mayr (1979) to be the ancestor of *Dryomys*. However, the absence of an endoloph in most of the upper molars of *Prodryomys*, and the presence of *Dryomys* in MN6 in North Africa (Jaeger, 1975) make this improbable. Neither ancestors nor descendants of *Prodryomys* are known (Fig. 7).

*Carbomys* is known from the Middle Miocene of Mallorca, Spain only (Mein & Adrover, 1982) (Fig. 7). Its dental pattern can easily be derived from that of *Pseudodryomys ibericus* from the Spanish mainland. Features such as the posterior centroloph joining the metaloph midway, the relatively high-crowned teeth, the three-rooted second and third lower molars, the accessory ridge in the posterior valley, and the relatively large  $M_3$  are shared by *Carbomys sacaresi* and *P. ibericus*. The differences are in the large size of the cheek teeth and the relatively larger size of the premolars in *Carbomys*.

*Margaritamys* is present in the Middle Miocene of Mallorca only (Mein & Adrover, 1982). This genus may have descended from *Peridyromys murinus* (Fig. 7). Features that these two genera have in common are the simple dental pattern,

relatively high-crowned teeth and two-rooted lower molars. *Margaritamys* is larger and has higher crowned teeth than *P. murinus*

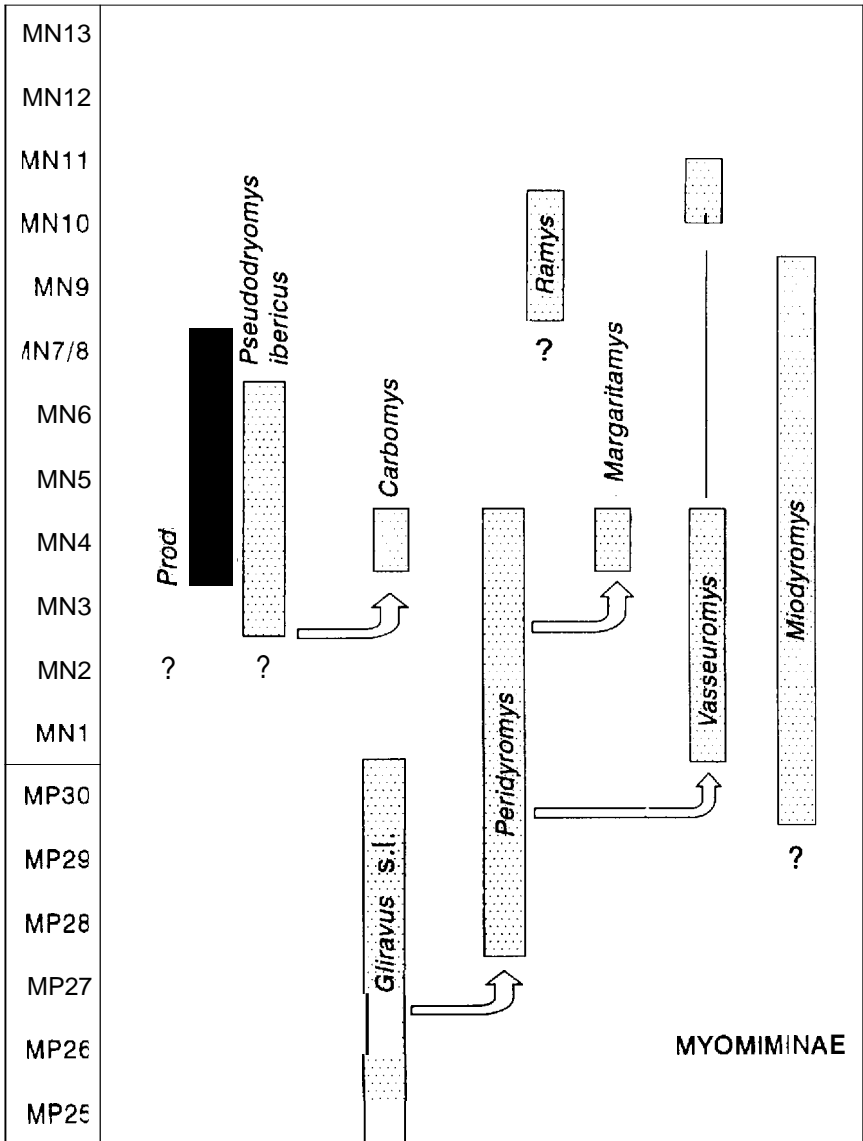


Fig. 7 – Tentative reconstruction of the phylogenetic relationships of the genera of the Myomiminae.

The first record of *Ramys* is *R. perezi* from MN9 of Ampudia 9, Duero Basin, Spain, and its last occurrence (*R. multicrestatus*) is in MN 10 from Torremormojon 1 in the same basin (Fig. 7). This genus is characterized by its medium-sized teeth and its relatively complex dental pattern. The lineage *R. perezi* - *R. multicrestatus*, (Alvarez Sierra and Garcia Moreno, 1986 and Garcia Moreno and López Martínez,

1986), shows tendencies towards a slight size decrease, a more complex dental pattern and the formation of a continuous endoloph in the upper cheek teeth through time.

Subfamily **BRANSATOGLIRINAE** nov. subfam. (Fig. 8)

The diagnosis of the subfamily is the same as the emended diagnosis (Bosma & de Bruijn, 1982) of the type genus: The characteristic features of the dentition of *Bransatoglirinae* are:

- 1) the relatively large, rounded premolars
- 2) the strongly concave occlusal surfaces

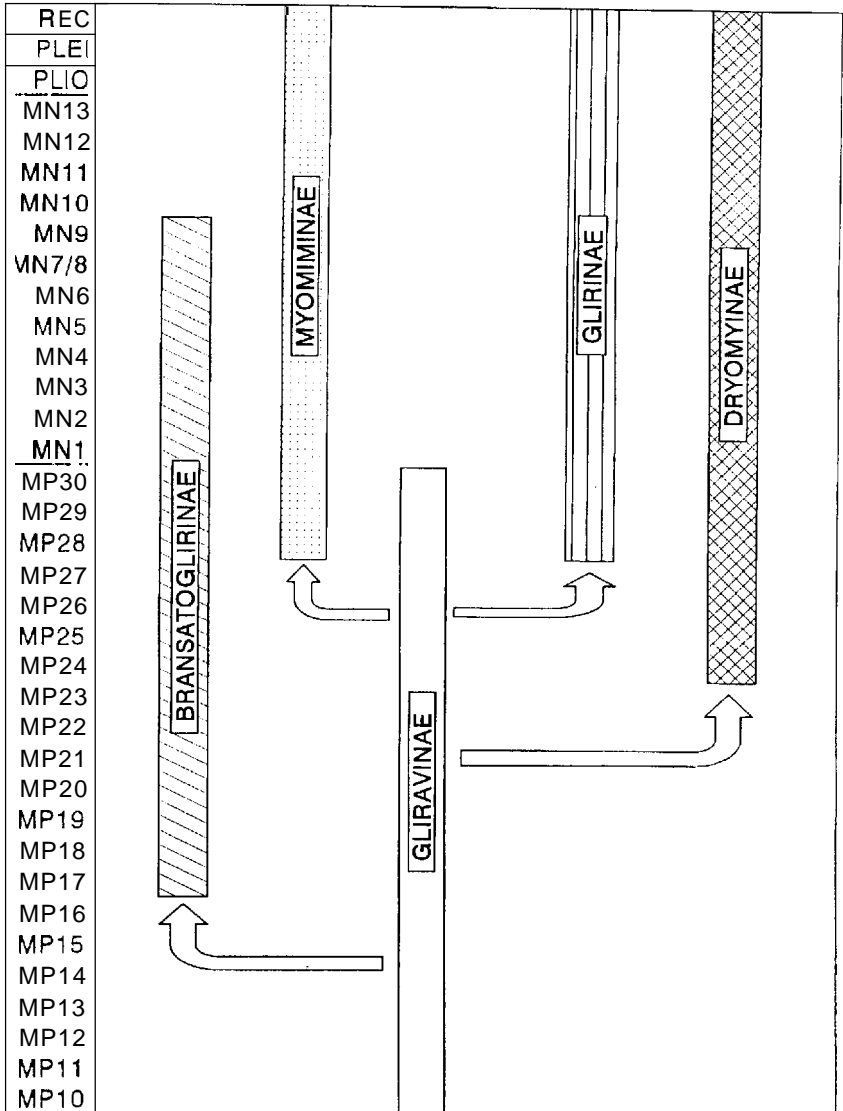


Fig. 8 – Tentative reconstruction of the phylogenetic relationships of the Gliridae subfamilies.

- 3) the first and second molars which are long relative to the width
- 4) the presence of long extra ridges outside the trigone in the  $M^{1-2}$ , and the tendency to form a continuous endoloph in these teeth
- 5) the rounded shape of the  $M^3$ , and the short, curving metaloph of that tooth.

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

Type genus: *Bransatoglis* Huguenev, 1967

Type species of *Bransatoglis*: *B. concavidens* Huguenev, 1967

Range of the subfamily: Late Eocene (MP17) - Late Miocene (MN9)

Daams (1976) synonymized *Paraglis* Baudelot, 1970 with *Bransatoglis* and Bosma & de Bruijn (1982) synonymized *Bransatoglis* with *Oligodyromys* Bahlo, 1975.

The dental pattern of early *Bransatoglis* species is not very different from that of *Gliravus*. Vianey-Liaud (1989) noted a great resemblance between *B. bahloi* from the Upper Eocene of the Isle of Wight and *Gliravus itardiensis* from the Lower Oligocene of the Quercy (S France).

The geologically oldest *Bransatoglis* is *B. bahloi* from the Late Eocene (MP17) of Headon Hill 3 (Island of Wight, England) and the last occurrence is *B. astaracensis* from MN9 in Spain. During the Eocene/Oligocene transitional interval various species of *Bransatoglis* were present in western Europe (Peláez-Campomanes, 1993). Two lineages can be recognized during the Late Oligocene and the Miocene of western and central Europe. *Bransatoglis* has, in our opinion, not given rise to another genus. Daams (1981) assigned *Bransatoglis* to the Dryomyinae, but new information clearly demonstrates its independent evolutionary history. We therefore think that the systematic position of the group within the dormice is best expressed by formally giving it the rank of subfamily.

## CONCLUSIONS

The extant dormice are relics of a once very successful and diverse family. In European Paleogene assemblages they are always present, but almost never dominant. In the Early Miocene a massive adaptive radiation took place in Europe (Fig. 2) and they formed there the major part of many rodent assemblages (Figs. 9 and 10). Up to 8 genera and 11 species may be present in one fauna (Fig. 9). Even in faunas where Gliridae are rare, such as the ones from MN7/8 (Fig. 10), the diversity may be high (Fig. 9). After the Early to Middle Miocene transitional period dormice never regained the same position as they had before.

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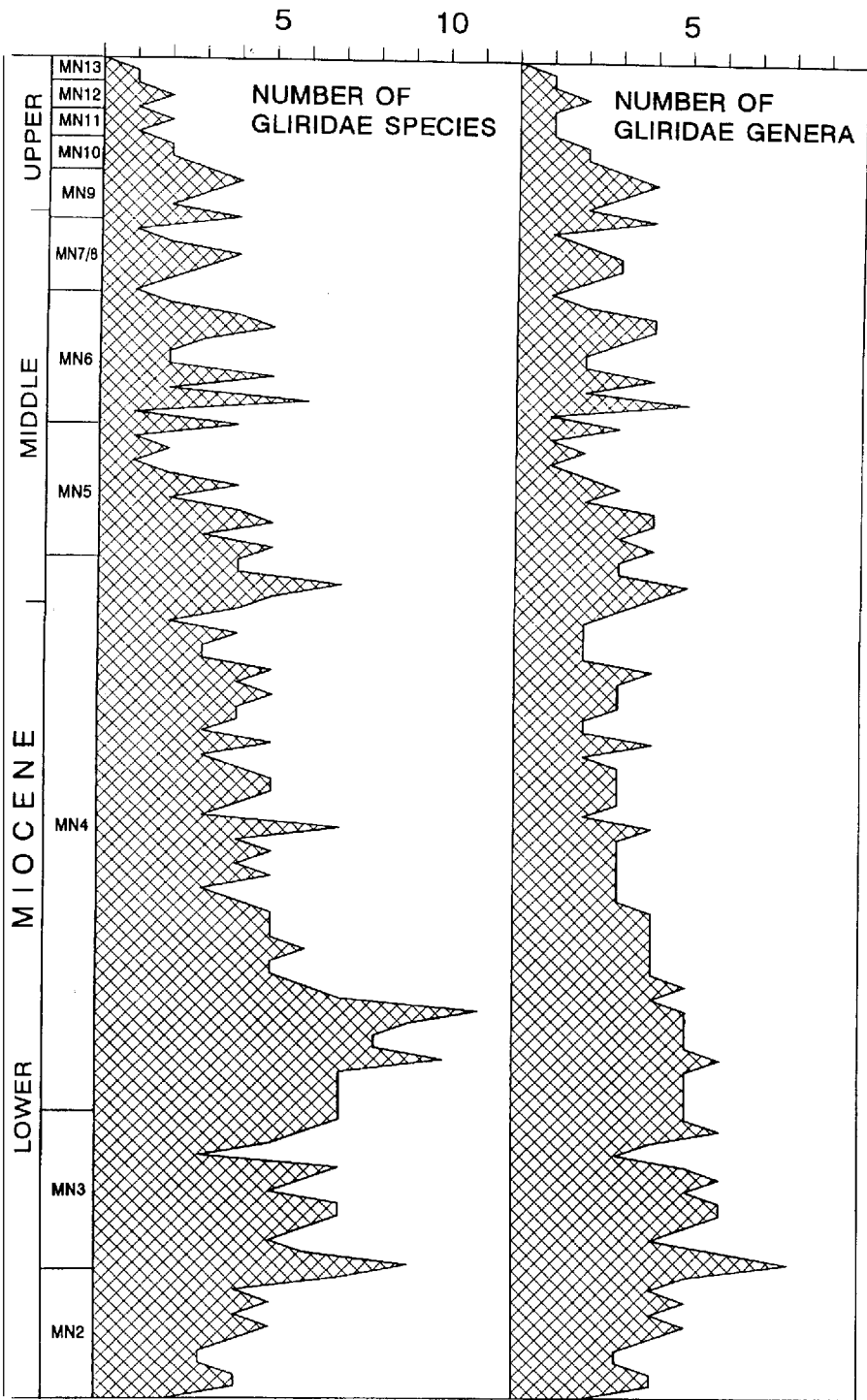


Fig. 9 – Relative abundance of Gliridae in 111 rodent assemblages from the Miocene in eastern central Spain.



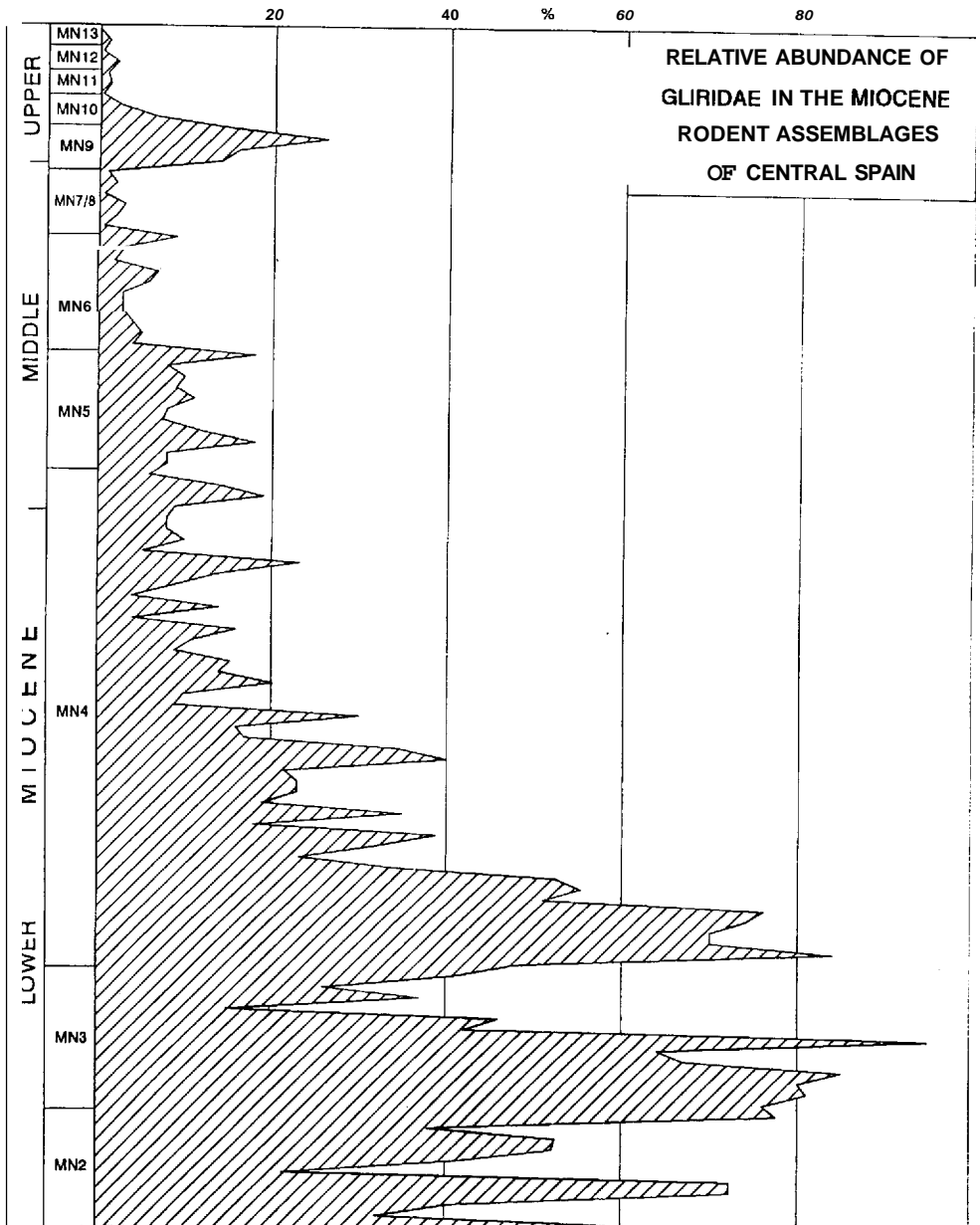


Fig. 10 – Number of Gliridae genera and species in 111 rodent faunas from the Miocene in eastern central Spain.

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## APPENDIX WITH ALPHABETICALLY ARRANGED GLIKIDAE GENERA, AND THEIR SPECIES

*AL TOMIRAMYS* DIAZ & LOPEZ. 1979

Original diagnosis, p. 158 (translated from Spanish): "A glirid of larger size than *Pseudodryomys ibericus*. Upper molars with subrounded outline, a low crown and concave occlusal surface. The ridges are thin and well-separated, with the anterior centroloph only, which joins the anteroloph in an arch-shaped ridge. The labial end of the posteroloph ends free. There is no continuous endoloph."

Type species, type locality and type level – *Altomiramys daamsi* Diaz & López, 1979; Loranca, Cuenca. Spain; MN2B, Early Miocene.

*ANTHRACOG LIS* ENGESSER. 1983

Original diagnosis, p. 766 (translated from German): "Glirid of the same size as the extant *Glis glis* with very concave, massive cheek teeth; dental pattern is like that of *Microdryomys*; the upper and lower premolar are considerably molarized; M sup.: the anterior centroloph is longer than the posterior one, the anteroloph is lingually connected to the endoloph; the lingual border shows "ornamentation". M. inf.: the endolophid is generally interrupted, and the centrolophid is very long: the anterior and posterior valley each have an extra ridge; the metalophid, mesolophid and centrolophid join the endolophid.

Type species, type locality and type level: *Anthraco glis marinoi* Engesser, 1983; Baccinello V1, Italy; MN11 or MN12, Late Miocene

*ARMANTOMYS* DE BRUIJN 1966 a

Synonymy: *Quercomys* Lacomba & Martínez-Salanova, 1988

Original diagnosis, p. 5: "Large Gliridae with simple dental pattern consisting of ridges which are high relative to the crown basis. Occlusal surfaces concave. Metaloph and protoloph separated. M1 larger than M2".

Type species, type locality and type level – *Armantomys aragonensis*, de Bruijn, 1966 a; Villafeliche 2A, Zaragoza, Spain; MN4A, Early Miocene

Synonymy: *Armantomys aragonensis giganteus* de Bruijn, 1967 from Valdemoros 1A

Other species of the genus:

*Armantomys bijmai* (Lacomba & Martínez-Salanova, 1988)

Type locality and type level – Quel 1, La Rioja, Spain; MN1, Early Miocene

*Armantomys daamsi* (De Visser, 1990 in Alvarez et al., 1990)

Type locality and type level – San Juan, Huesca, Spain; MN2B, Early Miocene

*Armantomys jasperi* Daams, 1990

Type locality and type level – Corcoles, Province of Guadalajara, Spain; MN4A, Early Miocene

*Armantomys parsani* Daams, 1990

Type-locality and type level – Ramblar 1, Teruel, Spain; MN2B, Early Miocene

*Armantomys triceristatus* Lopez, 1977 in López et al., 1977

Type locality and type level – Escobosa de Calatañazor, Soria, Spain; MN7/8, Middle Miocene

Synonymy: *Armantomys aragonensis giganteus* de Bruijn, 1967 from Las Planas 4A, Las Planas 4B and Manchones 1 in de Bruijn, 1967

*BRANSATOGLIS* HUGUENEY, 1967

Synonymy: *Paraglis* Baudelot, 1970; *Oligodyromys* Bahlo, 1975

Original diagnosis, p. 92 (translated from French): "Large-sized glirid resembling *Glis glis* Linné by the blunt aspect of its dental ridges, which are separated by narrow valleys, and by the higher lingual and labial borders. It differs from *Glis glis* by the strong concavity of the tooth, and the low and numerous ridges. The upper molars show a tendency to form a continuous endoloph and in the lower

molars the metalophid-metaconid connection is situated in an anterior position."

Emended diagnosis (Bosma & de Bruijn, 1982; p. 373): "The characteristic features of the dentition of *Bransatoglis* are:

1) the relatively large, rounded premolars

2) the strongly concave occlusal surfaces

3) the first and second molars which are long relative to the width

4) the presence of long extra ridges outside the trigone in the  $M^{1-2}$ , and the tendency to form a continuous endoloph in these teeth

5) the rounded shape of the  $M^3$ , and the short, curving metaloph of that tooth."

Type species, type locality and type level – *Bransatoglis concavidens* Hugueney, 1967; Coderet-Bransat, Allier, France; MP30, Late Oligocene

Synonymy: *Bransatoglis fugax* in Aguilar, 1974

Other species of the genus:

*Bransatoglis astaracensis* (Baudelot, 1970)

Type locality and type level – Sansan, France; MN6, Middle Miocene

*Bransatoglis attenuatus* Peláez-Campomanes, 1993

Type locality and type level – Aguaton, Teruel, Spain; MP21, Early Oligocene

Synonymy: *Bransatoglis* aff. *planus* in Anadón et al., 1983

*Bransatoglis bahloi* Bosma & de Bruijn, 1982

Type locality and type level – Headon Hill 3, Island of Wight, England; MP17, Late Eocene

*Bransatoglis cadeoti* Bulot, 1978

Type locality and type level – Bézian, France; MN4A, Early Miocene

Synonymy: *Bransatoglis astaracensis* in Mayr, 1979

*Bransatoglis complicatus* Ünay, 1994.

Type locality and type level – Harami 1, Turkey; MN2, Early Miocene

*Bransatoglis fugax* (Hugueney, 1967)

Type locality and type level – Coderet, Allier, France; MP30, Late Oligocene.

*Bransatoglis infralactorensis* (Baudelot & Collier, 1982)

Type locality and type level – Estrepouy, France; MN3, Early Miocene

*Bransatoglis* cf. *fugax* in Van der Meulen & de Bruijn, 1982

*Bransatoglis moyai* (Hugueney & Adrover, 1990)

Type locality and type level – Sineu, Mallorca, Spain; MP25, Late Oligocene

*Bransatoglis parvus* Peláez-Campomanes, 1993

Type locality and type level – Olalla 4, Teruel, Spain; MP21, Early Oligocene

*Bransatoglis planus* (Bahlo, 1975)

Type locality and type level – Heimersheim, Germany; MP24, Early Oligocene

*Bransatoglis rimosus* Peláez-Campomanes, 1993

Type locality and type level – Olalla 4, Teruel, Spain; MP21, Early Oligocene

*Bransatoglis sjeni* Ünay, 1990

Type locality and type level – Kocayarma, Turkey; Middle Oligocene

*Bransatoglis spectabilis* (Dehm, 1950)

Type locality and type level – Wintershof-West, Germany; MN3, Early Miocene

Synonymy: *Glis* ? *spectabilis* in Dehm, 1950

CARBOMYSMEIN & ADROVER, 1982

Original diagnosis, p. 456 (translated from French): "Giant Myomiminae with low crowns and molars with six ridges. The centrolophid joins the protoconid. Mesolophid and posterolophid are isolated

ridges. In the upper molars, the anteroloph and posteroloph are isolated. The P<sup>4</sup> is very large compared to the molars."

Type species, type locality and type level – *Carbomys sacaresi* Mein & Adrover, 1982; Santa Margarita, Mallorca, Spain; Middle Miocene

#### CHAETOCAUDA WANG, 1985

Original diagnosis, p. 74: "There is a dark chestnut around the eyes. Ears large, overing when lid forward to the eye. The terminal of tail is club shape, cover **with** dense hairs, and can not see the scale ring in external texture. The interorbited width is about one fifth of the greatest length of skull. incisive foramina is long, its posterior edge extend back beyond half of alveolar of M<sup>1</sup>. The mesopterygoid fossa extend forward beyond the posterior half of of alveolar of M<sup>3</sup>, so the palate bone is pressed in square shape. The mandible gracile in appearance, coronoid process arc long and slender and the upper margin at the same plane as occlusal of the cheektooth. The upper incisors are deeply grooved in the center of surface and the cutting edge with a "V" shape notch. The upper molar has an endoloph which connect with the anteroloph and situate in the inner side of the first upper molar."

Type species and type locality – *Chaetocauda sichuanensis* Wang, 1985: Wang-lang Natural reserve? Pinwu County, Northern Sichuan, China; Recent

#### DRYOMIMUS KRETZOI, 1959

Original diagnosis, p. 240 (translated from German): "P<sup>4</sup> rather little reduced, upper molars with - *Miodryomys* like - lingually separated protoloph, and uncomplicated dental pattern as in *Dryonzys*. On the other hand, the lower molars have features that are between *Dryomys*, *Myomimus* and *Peridyromys*.

Type species, type locality and type level: *Dryomimus eliomyoides* Kretzoi, 1959; Csarnota, Hungary: MN 15. Pliocene

#### DRYOMYSPALLAS. 1778

Synonymy: *Afrodryomys* Jacger, 1975

Diagnosis in Ellerman, 1941, p. 618, as far as the teeth are concerned: "Very closely related to *Elionzys*; upper cheek teeth less concave; the main cusps arranged as in *Elionzys*; five main transverse ridges in upper teeth, the main central depression with quite a well-marked ridge, this vestigial in *Elionzys*; premolar more reduced, not strongly cuspidate. Lower molars with four main ridges, and three rudimentary ones between them. Premolar reduced, and simple.

Type species and type locality: *Dryomys nitedula* (Pallas, 1778); Recent

Other species of the genus:

*Dryomys ambiguus* Lavocat, 1961

Type locality and type level – Beni Mellal, Morocco; MN7/8, Middle Miocene

*Dryomys chaabi* (Jacger, 1977)

Type locality and type level – Oued Zra, Algeria; MNIO, Late Miocene

*Dryomys laniger* Felten & Storch, 1968

Type locality – Bey Mountains, Turkey; Recent

#### EIVISSIA ALCOVER & AGUSTI. 1985

Original diagnosis, p. 52 (translated from Catalan): "Large-sized Dryomyinae. The upper molars have a continuous endoloph. Distinct paracone and metacone. The posterior centroloph is present."

Type-species, type locality and type level: *Eivissia canarreiensis* Alcover & Agusti, 1985; Cova dc Ca Na Reia, Island of Ibiza, Spain; Plio-Pleistocene

#### ELIOMYS WAGNER, 1840

Diagnosis in Ellerman, 1941, p. 615, as far as the teeth are concerned: "Cheektooth with crowns concave: in upper series, there are two high main cusps on the outer side, and one on the inner side;

and four main transverse ridges are present, separating three depressions, the general effect reminiscent of that of Sciuridae. P<sup>4</sup> slightly smaller than the molars, well cusped. M<sup>3</sup> slightly smaller than M<sup>2</sup>. Lower molars with three outer and two inner cusps; more basin shaped than the upper teeth; four main ridges present, the anterior and posterior of which form the terminal margins of the teeth. Premolars with three cusps, one each side, one anteriorly, and with one ridge."

Type species – *Elioniys quercinus* (Linnaeus, 1766)

Synonymy: *Elioniys melanurus* Wagner, 1843

Other species of the genus:

*Elioniys assimilis* Mayr, 1979

Type locality and type level – Hammerschmiede, Germany; MN9, Late Miocene

*Elionys intermedius* Friant, 1953

Type locality and type level – Sète, France; MN15, Pliocene

*Elionys reductus* Mayr, 1979

Type locality and type level – Hammerschmiede, Germany; MN9, Late Miocene

*Elionys truci* Mein & Michaux, 1970

Type locality and type level – Hautimagne, France; MN14, Pliocene

#### EOGLIRAVUS HARTENBERGEK, 1971

Original diagnosis, p. 112 (translated from French): "Primitive Gliravinae with a sinuous protoloph and metaloph."

Type species, type locality and type level – *Eogliravus hammeli* (Thaler, 1966); Bouxwiller, France; MP13, Middle Eocene

Other species included:

*Eogliravus moltzeri* Pelaez-Campomanes, 1995

Type locality and type level – Casa Ramón, Spain; MPI1, Middle Eocene

*Eogliravus wildi* Hartenberger, 1971

Type locality and type level – Mas de Gimel, France; MP10, Early Eocene

#### GLIRAVUS STEHLIN & SCHAUB, 1951

Synonymy: *Glanis*. Vianey-Liaud (1989) created *Glamys* on the basis of distinctive cranial features, although the teeth cannot be differentiated from *Gliravus*. We do not deny the importance of cranial features in taxonomy, but as our classification is exclusively based on the dental pattern, we cannot avoid that *Glanis* becomes a junior synonym of *Gliravus*.

Original diagnosis, p. 368 (translated from German): "Brachyodont, with two premolars in the maxilla. Upper molars trigonodont with simple and small mesostyl. Borders of trigone without intermediate cusps. Lower molars with four cusps and isolated mesoconid. Mesolophid is not yet developed. Paraconid separated from protoconid, like in *Sciurus vulgaris*."

Type species, type locality and type level – *Gliravus majori* Stehlin & Schaub, 1951; Quercy, France; Late ? Oligocene

Other species included:

*Gliravus alvarezae* Lacombe & Morales, 1987

Type locality and type level – Carrascosa del Campo, Cuenca, Spain; MP25, Late Oligocene

Synonymy: *Gliravtis* aff. *bruijni* in Agustí et al., 1985

*Gliravus bravoii* Huguéney, Adrover & Moissenet, 1985

Type locality and type level – Vivel del Rio, Teruel, Spain; MP28, Late Oligocene

*Gliravus bruijni* Huguéney, 1967

Type locality and type level – Coderet, France; MP30, Late Oligocene

*Gliravus caracensis* Daams, Freudenthal, Lacombe & Alvarez, 1989

Type locality and type level – Pareja, Guadalajara, Spain; MP25, Late Oligocene

*Gliravus daamsi* Bosma & de Bruijn, 1982

Type locality and type level – Headon Hill 2, Island of Wight, England; MP17, Late Eocene

*Gliravus devoogdi* Bosma & de Bruijn, 1979

Type locality and type level – Headon Hill 7, Island of Wight, England; MP19, Late Eocene

*Gliravus fordi* Bosma & de Bruijn, 1979

Type locality and type level – Bouldnor Cliff, Island of Wight, England; MP21, Early Oligocene

*Gliravus itardiensis* Vianey-Liaud, 1989

Type locality and type level – Itardies, France; MP23, Early Oligocene

*Gliravus meridionalis* Hartenberger, 1971

Type locality and type level – Fons 4, France; MP17, Late Eocene

*Gliravus micio* (Misonne, 1957)

Type locality and type level – Hoogbutscl, Belgium; MP21, Early Oligocene

*Gliravus minor* Bosma & de Bruijn, 1982

Type locality and type level – Headon Hill 2, Island of Wight, England; MP17, Late Eocene

*Gliravus priscus* Stehlin & Schaub, 1951

Type locality and type level – La Débruge, France; MP18, Late Eocene

*Gliravus robiacensis* Hartenberger, 1965

Type locality and type level – Robiac Sud, Gard, France; MP16, Late Eocene

*Gliravus tenuis* Bahlo, 1975

Type locality and type level – Heimersheim, Germany; MP23, Early Oligocene

*GLIRUDINUS* DE BRUIJN, 1966 a

Original diagnosis; p. 16: "Small Gliridae with extremely low-crowned cheek teeth. Occlusal surface slightly concave. Numerous low and narrow enamel ridges, that form an angle of approximately 45° with the longitudinal **axis** of the tooth."

Type species, type locality and type level – *Glirudinus gracilis* (Dehm, 1950); Wintershof-West, Bavaria, Germany; MN3, Early Miocene

Other species included:

*Glirudinus engesseri* Ünay, 1994.

Type locality and type level – Kilcak 0", Turkey; ? MN1, Early Miocene

*Glirudinus euryodon* Van der Meulen & de Bruijn, 1982

Type locality and type level – Aliveri, Island of Evia, Greece; MN4A, Early Miocene

*Glirudinus glirulus* (Dehnt, 1935)

Type locality and type level – Gunzenheim, Germany; MP30, Late Oligocene

*Glirudinus haramiensis* Ünay, 1994.

Type locality and type level – Harami 1, Turkey; MN2, Early Miocene

*Glirudinus minutus* Wu, 1993

Type locality and type level – Petersbuch 2, Germany; MN4A, Early Miocene.

*Glirudinus modestus* (Dehm, 1950)

Type locality and type level – Wintershof-West, Bavaria, Germany; MN3, Early Miocene

Synonymy: *Muscardinus* (*Muscardinulus*) *bouziguensis* in Thaler (1966)

*Glirudinus undosus* Mayr, 1979

Type locality and type level – Erkertshofen, Germany, MN4A, Early Miocene

Synonymy: *Glirudinus gracilis* in Daams, 1976; *Glirudinus gracilis* in Agusti, 1981c

### GLIRULUS THOMAS, 1906

Synonymy *Amphidyromys* Heller, 1936

Emended diagnosis (Van der Meulen & de Bruijn, 1982; p. 489): "Small to medium-sized Dryomyinae with usually 9 transverse ridges and an endoloph in their upper molars. The labial ends of anteroloph and posteroloph are as high as paracone and metacone. The anterior centroloph is connected to the endoloph in all but the earliest species. An endolophid may be present in the lower molars."

Type species and type locality – *Glirulus japonicus* (Schinz, 1845); Japan, Recent

Other species of the genus:

*Glirulus conjunctus* Mayr, 1979

Type locality and type level – Markt, Germany; MN9, Late Miocene

*Glirulus diremptus* (Mayr, 1979)

Type locality and type level – Erkerthshofen, Bavaria, Germany; MN4A, Early Miocene

*Glirulus ekremi* Ünay, 1994

Type locality and type level – Kcsekoy, Turkey; MN3, Early Miocene

*Glirulus gemmula* Kretzoi, 1962

Type locality and type level – Csarnota 2, level 15, Hungary; MNI 5, Pliocene

*Glirulus lissiensis* (Hugueney & Mein, 1965)

Type locality and type level – Lissicu, France; MN13, Late Miocene

*Glirulus minor* Wu, 1993

Type locality and type level – Petersbuch 2, Germany; MN4A, Early Miocene

*Glirulus pusillus* (Heller, 1936)

Type locality and type level – Gundersheim, Germany; MNI 5?, Pliocene

### GLIS BRISSON, 1762

Diagnosis in Ellerman, 1941, p. 622, as far as the teeth are concerned: "Cheek teeth simpler than in *Eliomys*, more flat; the outer side of upper series with five low cusps, the inner side with four. M<sup>1</sup> and M<sup>2</sup> with seven transverse ridges of which four are well developed, the three alternating between them weaker. P<sup>4</sup> considerably smaller than the other teeth, and with its elements reduced. Lower teeth like the upper series in general arrangement."

Type species and type locality: *Glis glis* (Linnaeus, 1766); Germany, Recent

Other species of the genus:

*Glis apertus* Mayr, 1979

Type locality and type level – Weissenburg 6, Germany; MN1, Early Miocene

*Glis galitopouli* Van der Meulen & de Bruijn, 1982

Type locality and type level – Aliveri, Island of Evia, Greece; MN4A, Early Miocene

*Glis guerbuezi* Ünay, 1989

Type locality and type level – Kocayarma, Thrace, Turkey; Middle Oligocene

*Glis major* de Bruijn & Rümke, 1974

Type locality and type level – Oschiri, Sardinia, Italy; MN2, Early Miocene

*Glis minor* Kowalski, 1956

Type locality and type level – Podlesicc, Poland; MN14, Pliocene

*Glis sackdillingensis* (Heller, 1930)

Type locality and type level – Cave of Sackdilling, Germany; Pleistocene

*Glis sussenbornensis* Soergel, 1919

Type locality and type level – Sussenborn, Germany; Pleistocene

*Glis transversus* Unay, 1994

Type locality and type level – Harami I, Turkey: MN2. Early Miocene

*Glis truyolsi* Daams, 1976

Type locality and type level – Cetina de Aragon, Zaragoza, Spain; MN2.4, Early Miocene

*Glis vallesiensis* Agustí, 1981a

Type locality and type level – Ballestar, Lérida, Spain; MN9. Late Miocene

*GRAPHIUROPS* BACHMAYER & WILSON, 1980

Original diagnosis, p. 367: "Size of cf. *Myomimus dehmi*, Bachmayer & Wilson, 1978. Protoconid and hypoconid cusps of M<sub>1</sub> and M<sub>2</sub> well-separated. Metalophid (?) crest well-developed, other basin structures variable and vestigial. Shape of lower molars as in most glirids, not decisively wider than long as in *Graphiurus*. M<sub>1</sub> two-rooted, M<sub>2</sub> three-rooted."

Type species: type locality and type level: *Graphiurops austriacus* Bachmayer & Wilson, 1980; Kohfidisch. Austria: MN10. Late Miocene

*GRAPHIURUS* SMUTS, 1832

Diagnosis in Ellerman, 1941, p. 604, as far as the teeth are concerned: "Crowns of cheek teeth concave. with low main external cusps; the general arrangement in pattern evidently near *Eliomys*, but the ridges in most indistinct, and a general tendency towards simplification. The premolars are usually only moderately reduced; but in the type species are strongly reduced."

Type species and type locality – *Graphiurus ocularis* (Smith, 1829); Recent

Other species included:

*Graphiurus parvus* (True, 1893)

Type locality – Tana River, Kenya; Recent

*Graphiurus murinus* (Desmarest, 1822)

Type locality – Cape Colony, South Africa; Recent

*Graphiurus platyops* Thomas, 1897

Type locality – Enkeldoorn, Mashonaland. Sout Africa; Recent

*HETEROMYOXUS* DEHM, 1938

Original diagnosis (translated from German): "Gliridae with low-crowned, large molars and longitudinal connections between the ridges in the lower molars."

Type species, type locality and type level: *Heteromyoxus wetzleri* (Schlosser, 1884); Eggingen, Germany; MN3, Early Miocene.

Other species of the genus:

*Heteromyoxus schlosseri* Dehm, 1950

Type locality and type level – Wintershof-West, Bavaria, Germany; MN3, Early Miocene

*HYPNOMYS* BATE, 1918

Original diagnosis, p 210-211: "Skull, mandible and limb-bones as in *Eliomys* but more robust; interorbital region wide and anterior portions of frontals greatly expanded. The infraorbital foramen opens anteriorly and the outer wall of the infraorbital canal is very robust with a wide base. The anterior palatine foramina penetrate for some distance the palatal plate of the maxillae which forms the greater portion of the palate. The angle of the mandible is perforated. Dental formula I 1 3 for both upper and lower tooth rows, molariform premolars and molar crowns sub-quadrate in shape with low transverse ridges. Upper molars with one large wide internal and two smaller external roots. In



the first and second lower molars the two posterior roots may be confluent for the greater part of, or for their entire length: the last molar has two anterior and one large posterior root. Tibia and fibula joined."

Type species: type locality and type level – *Hypnonzys mahonensis* Bate. 1918; Menorca, Spain; Pleistocene

Other species included:

*Hypnonzys eliomyoides* Agusti, 1980

Type locality and type level – Menorca, Spain; Pleistocene

*Hypnomys onicensis* Reumer, in press

Type locality and type level – Mallorca, Spain; Pleistocene

*Hypnonzys morpheus* Bate, 1918

Type locality and type level – Mallorca, Spain; Pleistocene

*Hypnomys waldreni* Reumer, 1979

Type locality and type level – Cap Farrutx, Mallorca, Spain; Early Pleistocene ?

#### LEITHIA LYDEKKER, 1895

Original diagnosis (p. 862): "specialized Sciuromorpha with squared upper molars bearing from four to five simple, low, parallel transverse ridges, three of which rise from the postero-internal angle or inner side of the crown, while the remainder are shorter and are formed by a single or double splitting of the more anterior of the two hind-most enamel folds. There is no trace of the presence of more than one pair of upper premolars. The palatine foramina are elongated, and the tibia and fibula united. Whether the skull had the well-developed postorbital processes characterizing existing Squirrels, I am unable to determine: but it was evidently constricted in the orbital region, like *Sciurus*, and thus unlike that of *Xerus*. The restoration of the lower jaw given by Leith Adams is probably incorrect. It is certain that *Leithia* does not belong to the Myomorpha, and I do not think the features in which it differs from other Sciuromorpha are sufficient to justify its reference to a suborder by itself."

Type species, type locality and type level – *Leithia melitensis* (Adams, 1863) Malta; Pleistocene

Other species included:

*Leithia carteri* (Adams, 1863)

Type locality and type level – Malta; Pleistocene

#### MALTAMYS ZAMMIT MAEMPEL & DE BRUIJN, 1982

Original diagnosis. p. 118: "Medium to large sized Dryomyinae, the occurrence of which is restricted to Malta and Sicily. The endolophid of the lower molars is almost always interrupted between the metaconid and entoconid. The M<sup>1-2</sup> always have two extra ridges outside the trigone and almost invariably have the posteroloph separate from the endoloph. The angular portion of the lower jaw is perforated."

Type species, type locality and type level: *Maltamys gollcheri* (de Bruijn, 1966c); Mnaidra Gap, Malta; Pleistocene

Other species included:

*Maltamys wiedincitensis* Zammit Maempel & de Bruijn, 1982

Type locality and type level – Wied Incita, Malta; Late Pleistocene ?

#### MARGARITAMYS MEIN & ADROVER, 1982

Original diagnosis. p. 457: "Large sized Myomiminae. Cheek teeth with unilateral high crowns (the maximum height is observed below the lingual part of the anteroloph, and not below the protocone as in *Armantomys*). Upper molars with 6 ridges, and lower molars with 5. The centrolophid joins the mesolophid."

Type species, type locality and type level – *Margaritامys lulli* Mein & Adrover, 1982; Santa Margarita, Mallorca, Spain; Middle Miocene

*MICRODYROMYS* DE BRUIJN, 1966 a

Synonymy: *Myolidus* Alvarez Sierra, 1986 in: Alvarez Sierra & Garcia Moreno, 1986  
 Original diagnosis. p. 11: "Small Gliridac with cheek teeth that have a concave occlusal surface. Lingual side of upper cheek teeth ornamented. The four main ridges of M<sup>1</sup>, M<sup>2</sup> and M<sup>3</sup> are connected to an endoloph. Anterior centroloph of M<sup>1</sup> and M<sup>2</sup> longer than the posterior centroloph. P<sup>4</sup> and M<sup>3</sup> relatively large compared to other genera. The accessory ridges are lower than the main ridges."  
 Type species, type locality and type level – *Microdyromys koenigswaldi* de Bruijn, 1966a; Valdemoros 3B, Zaragoza. Spain; MN4B. Middle Miocene  
 Synonymy: *M. praemurinus* in Legndrc. 1982  
 Other species included:

*Microdyromys complicatus* de Bruijn, 1966a

Type locality and type level – Armantes 7, Zaragoza. Spain; MN6, Middle Miocene  
 Synonymy: *Glirulus miocaenicus* Baudelot, 1965; *Paraglrirulus scalabicensis* Antunes & Mein, 1977 from Pero Filho. Portugal  
 Remarks: In 1965 Baudelot described *Glirulus miocaenicus* from Sansan (France), which is the same as *Microdyromys complicatus*. As Baudelot's paper is antedated and came out in 1966 and as de Bruijn's postdated paper came out in 1965, the name *complicatus* has priority.

*Microdyromys legidensis* Daams, 1981

Type locality and type level – Villafeliche 2A, Zaragoza, Spain; MN4A, Early Miocene  
 Synonymy: *M. aff. koenigswaldi* in Aguilar. 1974

*Microdyromys monspeliensis* Aguilar, 1977

Type locality and type level – Nouvelle Faculté Medicine, Hérault, France; MNI, Early Miocene

*Microdyromys orientalis* Wit, 1986

Type locality and type level – Xiacaowan. Jiangsu. China; Middle Miocene

*Microdyromys praemurinus* (Freudentberg, 1941)

Type locality and type level – Gaimersheim, Germany: MP28, Late Oligocene

*Microdyromys sinuosus* (Alvarez Sierra, 1986 in: Alvarez Sierra & Garcia Moreno, 1986)

Type locality and type level – Ampudia 3, Valladolid. Spain; MNIO, Late Miocene

*MIDYROMYS* KRETZOI, 1943

Original diagnosis absent in Kretzoi (1943).

Diagnosis (Baudelot, 1972, p. 328). translated from French: "*Miodyromys* differs from *Peridyromys* by the morphology of the upper molars in which the trigone has a U-shape, marked by the proto-loph and metaloph joining separately the lingual border. *Miodyromys* differs from *Pseudodryomys* de Bruijn, 1966 a by its more numerous ridges, by the metaloph and proto-loph joining the endoloph separately, whereas in *Pseudodryomys* these two ridges meet before reaching the lingual border."

Emended diagnosis of *Miodyromys* (Mayr, 1979, p. 151). Translated from German: "Medium-sized Gliridae with concave occlusal surface. M<sup>1-2</sup> with 6 main ridges. The anterior centroloph is longer than the posterior one. The anterior centroloph may fuse with the posterior one, or one or both of the centrolophs may fuse with extra ridge(s). But none of the centrolophs fuse with the middle part of the metaloph. Extra ridges are only present in the trigone, and they vary from zero to three. There is always one accessory ridge between the main ridges. The anteroloph and posteroloph are isolated at the labial border. Proto-loph and anterior centroloph are labially either connected or separated. Proto-loph generally connected to the lingual end of the posteroloph. M<sub>1-3</sub> two- or three-rooted. with 5 main ridges, and one to four extra ridges. The accessory ridge between mesolophid and posterolophid is stronger and longer than the other accessory ones."

The emended diagnosis of Mayr is not correct. He says that 6 main ridges are present, and that there is always one extra ridge between the main ridges. That implies that there are at least 5 extra ridges in every species of the genus, which is not the case. According to his diagnosis *Miodyromys* would differ from *Pseudodryomys* by the centrolophs never reaching the metaloph in the centre of the tooth. This feature, is highly variable in *Pseudodryomys ibericus*. In the older assemblages the centrolophs

do not generally join the metaloph whereas in younger ones this occurs more frequently.

Type species, type locality and type level – *Miodyromys hamadryas* (Forsyth Major, 1899); Grosslappen, Bavaria, Germany; MN7/8, Middle Miocene

Synonymy: *Eliomys* from La Grive in Major, 1899

Other species included:

*Miodyromys aegercii* (Baudelot, 1972)

Type locality and type level – Sansan, Gers, France; MN6, Middle Miocene

Synonymy: *Dryomys hamadryas* in Baudelot, 1965; *Miodyromys* cf. *ibericus* in Ginsburg & Sen, 1977

*Miodyronzys biradiculus* Mayr, 1979

Type locality and type level – Wintershof-West, Germany; MN3, Early Miocene

*Miodyroniys hugueneyae* Agusti & Arbiol, 1989

Type locality and type level – Fraga 11, Ebro Basin, Spain; MP30, Late Oligocene

*Miodyroniys praecox* Wu, 1993

Type locality and type level – Stubersheim 3, Germany; MN3, Early Miocene

*Miodyronzys prosper* (Thaler, 1966)

Type locality and type level – Bouzigues, Hérault, France; MN2B, Early Miocene

*Miodyroniys vagus* Mayr, 1979

Type locality and type level – Hesseloh, Germany; MN5, Middle Miocene

#### MUSCARDINUS KAUP, 1829

Synonymy: *Eomuscardinus* Hartenberger, 1966; *Pentaglis* Kretzoi, 1943

Diagnosis in Ellerman, 1941, p. 625, as far as the teeth are concerned: "P<sup>4</sup> very small indeed. M<sup>1</sup> conspicuously larger than M<sup>2</sup>, with five well-developed ridges, the depressions between them very broad; the ridges oblique, the tooth lengthened: M<sup>2</sup> with seven transverse ridges, the depressions between them narrow; M<sup>3</sup> like M<sup>2</sup> but smaller, with ridges less developed. P<sup>4</sup> usually with two ridges. In the lower cheekteeth there are six ridges extending across each tooth except the much reduced premolar; the lower first molar is less enlarged than the upper first molar, and its ridges less oblique." Hartenberger (1966) described *Eomuscardinus* as a new subgenus of *Muscardinus* and considered it the ancient stock of the genus. This new subgenus would have a relatively large P<sup>4</sup> compared to the more modern *Muscardinus* species, and *Muscardinus thaleri* was not included in it. As far as the complexity of the dental pattern is concerned no difference is observed between the Middle Miocene *M. thaleri* and *M. sansaniensis*. We do not think that the relative size of P<sup>4</sup> is sufficient to warrant subgeneric separation and consider *Eomuscardinus* a junior synonym of *Muscardinus*.

Type species and type locality – *Muscardinus avellanarius* (Linnaeus, 1758); Sweden, Recent

*Muscardinus cyclopeus* Agusti, Moya-Sola & Pons Moyá, 1982

Type locality and type level – Cala Es Pou, Menorca, Spain; Pleistocene

*Muscardinus dacicus* Kormos, 1930

Type locality and type level – Belfia (= Püspökföld), Hungary; Pleistocene

*Muscardinus davidi* Hugué & Mein, 1965

Type locality and type level – Lissieu, Rhône, France; MN13, Late Miocene

*Muscardinus heintzi* Aguilar, 1981

Type locality and type level – Montredon, Hérault, France; MN10, Late Miocene

*Muscardinus helleri* Fejfar & Storch, 1990

Type locality and type level – Gundersheim, Germany; MN15, Pliocene

*Muscardinus hispanicus* de Bruijn, 1966b

Type locality and type level – Pedregueras 2C, Zaragoza, Spain; MN9, Late Miocene

Synonymy: *Muscardinus crusafonti* Hartenberger: 1966 from Can Llobateres

*Muscardinus pliocaenicus* Kowalski, 1963

Type locality and type level – Weze, Poland; MN15, Pliocene

*Muscardinus sansaniensis* (Lartet, 1851)

Type locality and type level – Sansan, France; MN6, Middle Miocene

*Muscardinus thaleri* de Bruijn, 1966a

Type locality and type level – Manchones, Zaragoza, Spain; MN6, Middle Miocene

*Muscardinus vallesiensis* Hartenberger, 1966

Type locality and type level – Can Llobateres, Barcelona, Spain; MN9, Late Miocene

*Muscardinus vireti* Huguency & Mein, 1965

Type locality and type level – Lissieu, Rhône, France; MN13, Late Miocene

#### MYOGLIS BAUDELLOT, 1965

Original diagnosis, p. 761 (translated from French)(It is not clear if the diagnosis given by Baudelot refers to that of the genus or to the species *Myoglis lurteti*): "Large-sized Gliridae which resemble *Muscardinus* because of the flat occlusal surface, but from which it is different in the following features; the V-shape of the trigone, the incomplete mesoloph that converges towards the postero-lingual border, and the four isolated oblique ridges of the lower molars, separated from each other by deep valleys."

Type species, type locality and type level – *Myoglis nzeini* (de Bruijn, 1966a); Manchones, Zaragoza, Spain; MN6, Middle Miocene

Synonymy: *Myoglis lurteti* Baudelot, 1965. In 1965 Baudelot described *M. lurteti* from Sansan (France), which is the same as *M. nzeini*. As Baudelot's paper is antedated and came out in 1966 and as de Bruijn's postdated paper came out in 1965, the name *nzeini* has priority. Generally *Pentaglis Kretzoi*, 1943 was considered to be a synonym of *Myoglis*. However, the specimen figured (an M<sup>2</sup> instead of an M<sup>1</sup>) by Kretzoi (1943) does not show any resemblance to *Myoglis*. The small size of the only tooth, and the transverse ridges connecting separately to the endoloph, show that this tooth belongs to *Muscardinus*.

Other species included:

*Myoglis untecedens* Mayr, 1979

Type locality and type level – Erkertshofen, Germany; MN4A, Early Miocene

#### MYOMIMUS OGNEV, 1924

Synonymy: *Philistomys* Bate, 1937

Original diagnosis, p. 545-546: "No darkening around eyes and ears (neither stripe nor spot present). Tail thin, as in rats, covered with very short, even white hair growing thickly along tail shaft; rings on skin visible with lens. Skull elevated on line of upper profile, and markedly shortened rostrally. Occipital region rounded. Interorbital region somewhat compressed due to ovaly elongated depressions near basis of nasals, i.e., at the anterior part of infraorbital region. Auditory bullae large and inflated, much larger than in *Muscardinus*. Jugal bone forms sharp process protruding anteriorly and not quite reaching lateral contour of lacrimal. Infraorbital foramen very small and narrow, appreciably smaller than in *Muscardinus* (figs. 205-206). Angular process of lower jaw with small round aperture in wall.

Crowns of molars flat, inner and outer margins not elevated (fig. 254). Crowns of M<sup>1</sup> and M<sup>2</sup> of very similar structure, each with five transverse enamel folds: first two fairly long with inner margins pointing posteriorly; next two folds form deep bend reaching middle of tooth; last (fifth) fold extends along posterior margin of tooth, its inner tip bending somewhat anteriorly. This crown structure little resembles that of other dormice. Premolar of lower jaw small, its outer margin directed obliquely anteriorly. Four transverse ridges on surface, two internal ones forming closed arching protrusions directed posteriorly. Premolar of lower jaw small, below level of rest of toothrow (differing in this

from other dormice); three barely visible ridges on surface."

Description of the penis is outside the scope of this study.

Type species and type locality – *Myomimus personatus* Ognev, 1924; Kopet Dagh Mountains, U.S.S.R.. Recent

Synonymy: *M. setzeri* Rossolimo, 1976 a; *M. bulgaricus* Rossolimo, 1976 b

Other species included:

*Myomimus compositus* (Bachmayer & Wilson, 1970)

Type locality and type level – Kohfidisch, Austria; MNI 1, Late Miocene

*Myomimus dehmi* (de Bruijn, 1966 b)

Type locality and type level – Pedregucras 2C, Zaragoza, Spain; MN9, Late Miocene

Synonymy: *Peridyromys dehmi nombrevillae* de Bruijn, 1966 b *Peridyromys* sp. in Daxner-I lock, 1970

*Myomimus maritsensis* de Bruijn, Dawson & Mein, 1970

Type locality and type level – Maritsa, Island of Rhodes, Greece; MN 15, Pliocene

*Myomimus qafzensis* (Haas, 1973)

Type locality and type level – Qafzeh Cave. Israel; Pleistocene

*Myomimus roachi* (Batc, 1937)

Type locality and type level – Tabun Cave. Israel; Pleistocene

Synonymy: *Myomimus judaicus* Tchernov, 1968

*Myomimus sinensis* Wu, 1985

Type locality and type level – Ertemte 2. Inner Mongolia, China; Upper Turolian or Ruscianian

*Myomimus sumbalenwalicus* Munthe, 1980

Type locality and type level: H-GSP locality 18, upper Chinji Formation, Pakistan, Late Miocene

*NIEVELLA* DAAMS, 1976

Original diagnosis. p. 156: "Large glirids with high and wide ridges and an oblique V-shaped trigone in the upper molars."

Type species, type locality and type level – *Nievella mayri* Daams, 1976: Cetina de Aragon, Zaragoza, Spain; MN2A, Early Miocene

*PARAGLIRULUS* ENGESSER, 1972

Original diagnosis. p. 208 (translated from German): "Small to medium-sized Gliridae-genus. Concave occlusal surface and relatively simple dental pattern. Main ridges are higher than the extra ridges. Lower molars: two-rooted, without continuous endolophid, with strong main ridges; M<sub>2</sub> is generally wider than M<sub>1</sub>. Upper molars: three-rooted, subquadrate outline and continuous endoloph; anterior centroloph always connected to the endoloph; transverse ridges run parallel and at right angles to the endoloph, especially in M<sup>2</sup>. The lingual border has ornamentation."

Type species, type locality and type level – *Paraglrulus werenfelsi* Engesser, 1972; Anwil, Baselland, Switzerland; MN7/8, Middle Miocene

Other species included:

*Paraglrulus agelakisi* Van der Meulen & de Bruijn, 1982

Type locality and type level – Aliveri, Island of Evia, Greece; MN4A, Early Miocene

*PERIDYROMYS* STEHLIN & SCHAUB, 1951

Original diagnosis. p. 368 (translated from German): "M<sup>1</sup> and M<sup>2</sup> of which the anterior side of the trigone points obliquely backward. Lingual cusps and lingual ends of the posteroloph fused. In the trigone two small, accessory ridges (centrolophs) are present, of which the anterior one joins the paracone. Lower molars with well-developed mesoconid-entoconid ridge (=mesolophid). The

protoconid ridge (=metalophid) does not reach the metaconid. Paraconid, metaconid and mesolophid (=centrolophid) form a continuous ridge which curves twice at right angles."

Type species, type locality and type level – *Peridyromys murinus* (Pomel, 1853); Langy, France; MN2, Early Miocene

Synonymy: *Peridyromys occitanus* Baudelot & De Bonis, 1966; *Peridyromys murinus occitanus* in Flandrin et al., 1968; *Myomimus* sp. in de Bruijn & Rumke, 1974

Other species included:

*Peridyromys aquatilis* (de Bruijn & Moltzer, 1974)

Type locality and type level – Rubielos de Mora, Teruel, Spain; MN3, Early Miocene

*Peridyromys columbarii* Daams, 1989 h

Type locality and type level – Sayatón 6, Guadalajara, Spain; MP30, Late Oligocene

Synonyms: *Peridyromys murinus* in Brunet et al., 1981

*Peridyromys jaegeri* Aguilar, 1974

Type locality and type level – Les Cévennes, France; MNI, Early Miocene

Synonymy: *Peridyromys murinus* in Tobien, 1960

*Peridyromys ordinasi* Mein & Adrover, 1982

Type locality and type level – Santa Margarita, Mallorca, Spain; Middle Miocene

*Peridyromys turbatus* Alvarez et al., 1990

Type locality and type level – San Juan, Huesca, Spain; MN2B, Early Miocene

#### *PRAEARMANTOMYS* DE BRUIJN, 1966 a

Original diagnosis, p. 1: "Large Gliridac with simple dental pattern. The relatively thick ridges are as high as the basis of the crown. Occlusal surface of cheek teeth concave. Extra ridges absent. Anteroloph not connected to the protocone. M1 larger than M2."

Type species, type locality and type level – *Praearmantomys crusafonti* de Bruijn, 1966a; Ateca 1, Zaragoza, Spain; MN3, Early Miocene

Synonymy: *Praearmantomys ginsburgi* Antunes & Mein, 1971

#### *PRODRYOMYS* MAYR, 1979

Original diagnosis, p. 246 (translated from German): "Small-sized Gliridae with moderately concave occlusal surface and relatively **low** ridges, resembling those of the recent genus *Dryomys*. M<sup>1-2</sup> with labial ends of posterior centroloph and metaloph nearly at right angles. M<sup>2</sup> with long distance between protoloph and metaloph in the middle of the tooth, as in the recent species *Dryomys nitedula* (Pallas). M<sub>2</sub> distinctly larger than M<sub>1</sub>."

Type species, type locality and type level – *Prodryomys satus* Mayr, 1979; Sandelzhausen, Bavaria, Germany; MN6, Middle Miocene

Other species included:

*Prodryomys brailloni* (Thaler, 1966)

Type locality and type level – Bouzigues, Hérault, France; MN2B, Early Miocene

Synonymy: *Pseudodryomys aguirrei* Adrover, 1978

*Prodryomys gregarius* (Dohm, 1950)

Type locality and type level – Wintershof-West, Bavaria, Germany; MN3, Early Miocene

#### *PSEUDODRYOMYS* DE BRUIJN, 1966 A

Original diagnosis, p. 7: "Gliridae of intermediate size. Occlusal surface of cheek teeth concave. Crowns of cheek teeth low. P4 small relative to M1 and rounded; M1 smaller than M2. The Spanish representatives of the genus *Pseudodryomys* are characterized by a gradual simplification through time."

Type species, type locality and type level – *Pseudodryomys ibericus* de Bruijn, 1966a; Ateca 1,

Zaragoza, Spain: MN3, Early Miocene

Synonymy: *Peridyromys* cf. *hamadryas* in Antunes & McIn, 1971

Other species included:

*Pseudodryomys aljaphi* Huguenev et al., 1978

Type locality and type level – Montaigne-le-Blin, France; MN2A, Early Miocene

*Pseudodryomys julii* Daams, 1989 a

Type locality and type level – Artesilla, Zaragoza, Spain: MN4A, Early Miocene

*Pseudodryomys granatensis* Agustí, 1993 in Martin Suarez et al., 1993

Type locality and type level – Murchas, Granada, Spain; Latest Langhian – Early Serravalian

*Pseudodryomys rex* (Garcia Moreno 1986 in Alvarez Sierra & Garcia Moreno, 1986)

Type locality and type level – Torremormojón 6b, Palencia, Spain; MN7/8, Middle Miocene

*Pseudodryomys robustus* de Bruijn, 1967

Type locality and type level – Ateca 3, Zaragoza, Spain; MN3, Early Miocene

*Pseudodryomys simplicidens* de Bruijn, 1966 a

Type locality and type level – Valdemoros 3B, Zaragoza, Spain; MN4B, Early Miocene

Synonymy: *Pseudodryomys meini* Adrovcr, 1978

**RAMYS** GARCIA MORENO & LOPEZ MARTINEZ, 1986

Original diagnosis, p. 341: "Gliridae with brachyodont rectangular molars; somewhat irregular design of the ridges: centrolophs and extra ridges generally narrower than the main ridges; complex dental pattern, with frequently 3 or more extra ridges. The endoloph(id) may be present, and the labial ends of the ridges are curved anteriorly in the lower molars."

Type species, type locality and type level – *Ramys multicrestatus* (de Bruijn, 1966b); Pedregueras 2A, Zaragoza, Spain; MN9, Late Miocene

Other species included:

*Ramys perezii* Alvarez Sierra, 1986 in Alvarez Sierra & Garcia Moreno, 1986

Type locality and type level – Ampudia 9, Valladolid, Spain; MN9, Late Miocene

**STERTOMYS** DAAMS & FREUDENTHAL, 1985

Original diagnosis, p. 22: "Very large-sized Gliridae with a complicated dental pattern, low ridges and a slightly concave occlusal surface. The upper cheek teeth have flat, low and very wide ridges, and the anteroloph, protoloph and metaloph end freely at the lingual border.

Type species, type locality and type level – *Stertomyis laticrestatus* Daams & Freudenthal, 1985 San Giovanni. Gargano, Italy: Late Miocene ?.

**TEMPESTIA** VAN DE WEERD, 1976

Original diagnosis, p. 139: "Medium-sized Gliridae the molars of which have relatively high and broad ridges. The centroloph is short, high and isolated. The anteroloph is connected with the protocone in M<sup>1,2</sup>."

(The author made a mistake by forgetting the word "not". It should have been: The anteroloph is not connected with the protocone in M<sup>1,2</sup>.)

Type species, type locality and type level – *Tempestia hartenbergeri* (de Bruijn, 1966b); Masia del Barbo, Teruel, Spain; MN 10, Late Miocene

Other species included:

*Tempestia ovilis* Daams, 1989 a

Type locality and type level – Las Planas 5B, Zaragoza, Spain; MN6, Middle Miocene

Synonymy: *Pseudodryomys* cf. *ibericus-simplicidens* from Manchones I in de Bruijn, 1967

*TYRRHENOGLIS* ENGESSER, 1976

Original diagnosis, p. 784 (translated from German): "Very large glirid genus (of similar size as the recent *Glis glis* or larger) with concave, very massive cheek teeth. The dental pattern is *Microdyromys*-like: the upper molars have a complete endoloph, to which the anteroloph is connected at the lingual border. Proto-, meta- and posteroloph are more or less parallel to each other and join the endoloph at right angles and at similar distances. The anterior centroloph is longer than the posterior one, but it does not reach the endoloph. In the lower cheek teeth there is a tendency to form a continuous endolophid. The crown of the upper molars is lingually higher than labially."

Type species, type locality and type level: *Tyrrhenoglis majori* Engesser, 1976; Capo Figari, Sardinia, Italy; Pliocene ?

Other species included:

*Tyrrhenoglis figariensis* Zammit Maempel & de Bruijn, 1982

Type locality and type level – Capo Figari I; Pliocene ?

*VASSEUROMYS* BAUDELLOT & DE BONIS, 1966

Synonymy: *Szechenyia* Kretzoi, 1978; *Ebromys* Cuenca, 1985

Original diagnosis, p. 342 (translated from French): "Medium-sized Gliridae. Cheek teeth with concave occlusal surface. Lower molars characterized by a centrolophid reaching the labial border and by a longitudinal prolongation of the labial cusps, that form a nearly continuous ectolophid."

Type species, type locality and type level – *Vasseuromys rugosus* Raudelot & De Bonis, 1966; Laugnac, France; MN2B, Early Miocene

Other species included:

*Vasseuromys autolensis* (Cuenca, 1985)

Type locality and type level – Autol, La Rioja, Spain; MN1, Early Miocene

*Vasseuromys bacchius* (Martinez-Salanova, 1987)

Type locality and type level – Fuenmayor 2, La Rioja, Spain; MN2B, Early Miocene

*Vasseuromys duplex* Ünay, 1994

Type locality and type level – Harami I, Turkey; MN2, Early Miocene

*Vasseuromys elegans* Wu, 1993

Type locality and type level – Stubersheim 3, Germany; MN3, Early Miocene

*Vasseuromys pannonicus* (Kretzoi, 1978)

Type locality and type level – Budapest, Freshwater Limestone of the Széchenyi hill; MN10 ?, Late Miocene

Synonymy: *Vasseuromys thenii* Daxner-Hock & de Bruijn, 1981

*Vasseuromys priscus* De Bonis, 1973

Type locality and type level – Moissac 1, France; MN1, Early Miocene