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Systematics of the insular giant fossil dormice (Rodentia: Gliridae) of the Mediterranean

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The dormice (Gliridae) are a family of rodents currently represented by 29 extant species, but with a greater fossil diversity stretching back to the early Eocene. The extant forms are generally small, but some fossil species on islands evolved larger body size through the phenomenon of insular gigantism. The phylogeny of dormice has historically been unstable, with between three and five subfamilies recognized and considerable movement of species between them. Recent molecular work has led to greater consensus on the systematics of the extant forms, but there remains some uncertainty about the placement of some giant fossil species, especially the Siculo-Maltese genus *Leithia*. Here we review our understanding of the phylogeny of dormice, explore some of the important outstanding questions regarding the systematics of the giant fossil forms, and propose future directions for research on this family of rodents.

Keywords: dormouse; Gliridae; insular gigantism; island rule; skull morphology

Current understanding of dormouse systematics

The dormice are a family of small- to medium-sized rodents found across Europe, Asia and Africa. The current extant diversity is represented by 29 species across nine genera (Holden-Musser et al., 2016): *Chaetocauda* Wang, 1985 (a single species from Sichuan, China); *Dryomys* Thomas, 1905 (three species from Eastern Europe and Asia); *Eliomys* Wagner, 1840 (three species distributed across Europe, North Africa and the Middle East); *Glirulus* Thomas, 1905 (one species, endemic to Japan); *Glis* Brisson, 1762 (one species distributed across Europe and western and Central Asia); *Graphiurus* Smuts, 1832 (15 species in sub-Saharan Africa); *Muscardinus* Kaup, 1829 (one species found widely across Europe); *Myomimus* Ognev, 1924 (three species from Eastern Europe and Central Asia); and *Selevinia* Belosludov and Bazhanov, 1939 (one species, endemic to Kazakhstan). Both *Chaetocauda* and *Selevinia* are very rare, with only a few specimens of each being known to exist in museum collections.

The name of the family has been subject to some controversy in the past, with both Gliridae and Myoxidae being used. Whilst the earliest named dormouse genus is *Glis* (Brisson, 1762), it has been argued (e.g. Holden, 1993; Wahlert et al., 1993) that this name is invalid as Brisson's nomenclature is not binomial, and that the oldest valid generic name for dormice is *Myoxus* (Zimmermann, 1780). However, Gliridae already had wide acceptance owing to its use in Simpson's 1945 classification of mammals and, arguments of invalidity notwithstanding, the International Commission on Zoological Nomenclature ruled in favour of Gliridae (ICZN, 1998).

Phylogenetic relationships within the Gliridae have been inferred by various means over the last few decades, including dental morphology (Daams, 1981; Daams & de Bruijn, 1995), cranial and mandibular morphology (Wahlert et al., 1993), overall body morphology (Storch, 1995), and genetics (Bover et al., 2020; Montgelard et al., 2003; Nunome et al., 2007; Petrova et al., 2024). These have often led to conflicting views of the relationships among some dormouse genera (Fig. 1). In one of the earliest classifications of the Gliridae, de Bruijn (1967) partitioned the dormice among five subfamilies, four of which contained extant genera: Graphiurinae (*Graphiurus*); Glirinae (*Glis* and *Muscardinus*); Dryomyinae (*Dryomys* and *Myomimus*); and Glirulinae (*Glirulus*). The classification of Daams (1981) was very similar to de Bruijn (1967) but Daams moved *Glirulus* into the Dryomyinae (thus dispensing with Glirulinae) and placed *Myomimus* in a new subfamily, Myomiminae. Daams (1981) also added *Eliomys* to the Dryominae. As

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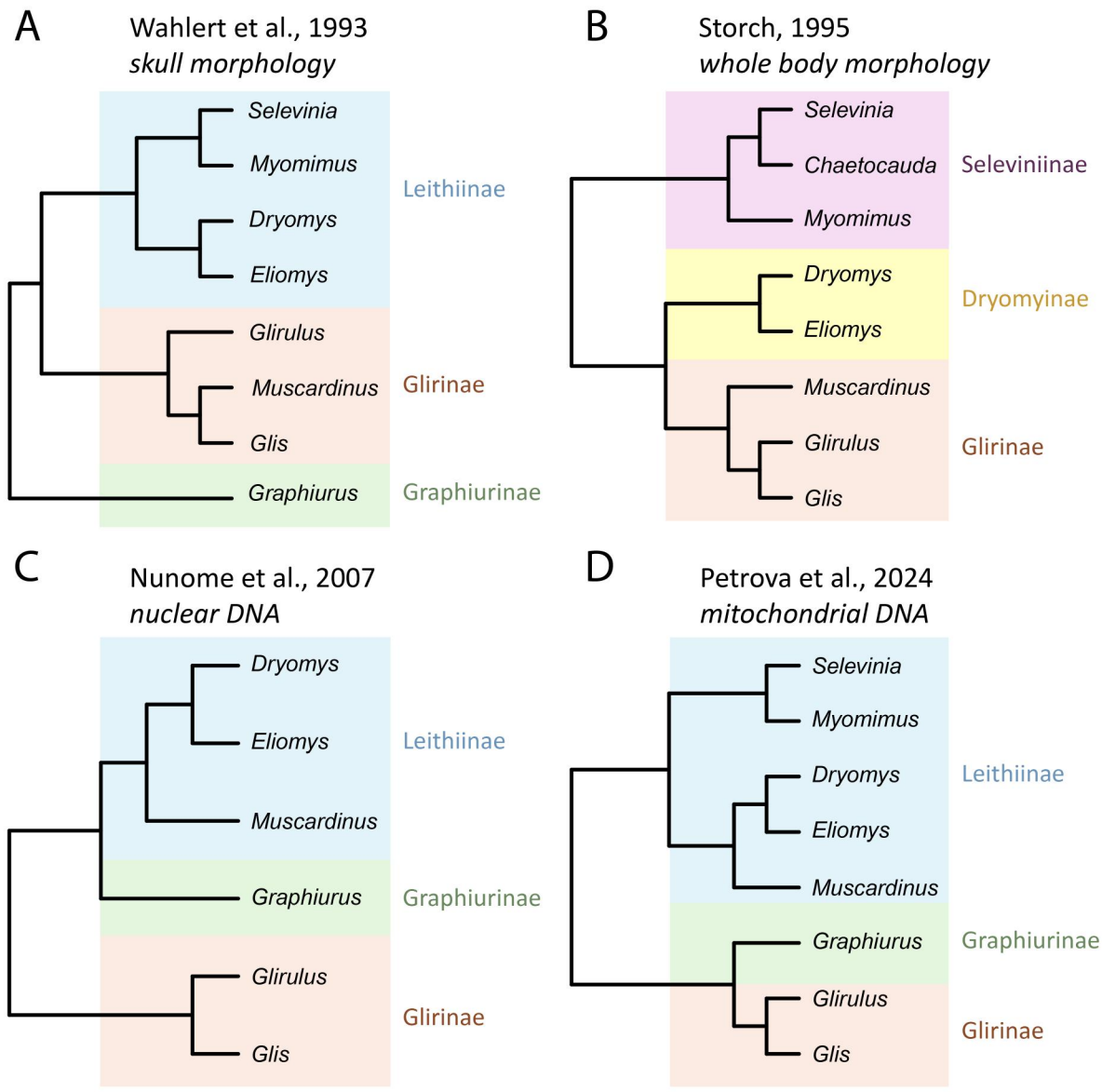


Figure 1. Phylogenetic relationships of extant dormouse genera as retrieved by: **A,** skull morphology (including cranium, mandible and dentition); **B,** whole body morphology (including skeleton, dentition and soft tissues); **C,** nuclear DNA; and **D,** mitochondrial DNA.

might be expected, Daams and de Bruijn (1995) differs little from the earlier work of Daams (1981), except for the unusual inclusion of *Graphiurus* in the Dryominae. This is the only classification or phylogeny in which *Graphiurus* is not assigned to its own subfamily. Additionally, Daams and de Bruijn (1995) include the relatively newly described *Chaetocauda* (Wang, 1985), placing it in the Dryominae. In contrast, Wahlert et al. (1993) erected just three subfamilies: Graphiurinae (*Graphiurus*); Myoxinae (*Myoxus* [*Glis*], *Muscardinus* and *Glirulus*); and Leithiinae (*Dryomys*, *Eliomys*, *Myomimus* and *Selevinia*). Storch (1995) also included *Glirulus* in the Glirinae/Myoxinae but split the Leithiinae into Dryomyinae (*Dryomys* and *Eliomys*) and Seleviniinae (*Myomimus*, *Selevinia* and *Chaetocauda*).

More recent phylogenies based on molecular data (Bover et al., 2020; Montgelard et al., 2003; Nunome et al., 2007; Petrova et al., 2024) have settled on a topology most similar to that of Wahlert et al. (1993). However, there is one major difference between the morphology-based and molecular-based phylogenies – the position of *Muscardinus* (see Table 1 and Fig. 1). Morphology alone suggested a close relationship between *Glis* and *Muscardinus*, but molecular data tends

to place *Muscardinus* in the Leithiinae (albeit often as the most basal member of the subfamily). Recent classifications of all mammals (Holden-Musser et al., 2016; Wilson & Reeder, 2005) have followed the results of the molecular phylogenetic analyses and split the Gliridae into three subfamilies: Graphiurinae, Glirinae (*Glis* and *Glirulus*) and Leithiinae (all other genera). The most recent analysis (Petrova et al., 2024), based on mitochondrial genomes, was the first to include data from the rare species *Selevinia betpakdalaensis*. In line with the conclusions of Ognev (1947), Storch (1995) and Wahlert et al. (1993), *Selevinia* was shown to have a close relationship with *Myomimus*. The even rarer *Chaetocauda* has yet to have any of its genome sequenced but is currently assumed to belong to the Leithiinae based on dental morphology (Storch, 1995). The evidence for the inclusion of each genus within the three glirid subfamilies is summarized in Table 1.

The phylogenetic relationship among the three subfamilies is somewhat unclear, with all three possible topologies having been proposed (Fig. 1), probably as a result of all three subfamilies having originated within a short time period around the Eocene–Oligocene boundary. The two most recent phylogenies (Bover et al., 2020; Petrova et al., 2024) favour a sister-group relationship between the Graphiurinae and Glirinae to the exclusion of Leithiinae.

In contrast to the relatively restricted extant diversity, the fossil record of dormice is extensive, with over 30 named extinct genera, the oldest of which (*Eogliravus*) dates to the early Eocene (Daams & de Bruijn, 1995). Peak glirid diversity was in the early Miocene when 18 genera and 36 species of dormouse are known from Europe alone (Daams, 1999; Lu et al., 2021). Amongst fossil dormice, the island taxa from the Mediterranean are of particular interest as all have undergone the process of insular gigantism to a greater or lesser degree. These extinct giant insular genera include: *Carbomys*, *Microdyromys*, *Hypnomys* and *Eivissia* from the Balearic Islands (Agustí, Furió et al., 2026; Agustí, Torres-Roig et al., 2026; Alcover & Agustí, 1985; Bate, 1918; Mein & Adrover, 1982); *Tyrrhenoglis* from Sardinia (Engesser, 1976); *Leithia* and *Maltamys* from Sicily and Malta (Lydekker, 1895; Zammit Maempel & de Bruijn, 1982); and *Stertomys* from the palaeo-island of Gargano (Daams & Freudenthal, 1985). In addition to the fossil genera, two extant genera are known to have, or have had, enlarged island forms: *Muscardinus cyclopeus* (Agustí et al., 1982), an extinct relative of the extant hazel dormouse (*M. avellanarius*) from Menorca; and *Eliomys quercinus ophiusae*, an extant subspecies of the garden dormouse, endemic to the island of Formentera (Kahmann & Lau, 1972). The distribution of fossil giant dormice across Mediterranean islands is summarized in Figure 2.

Hypnomys, *Eivissia*, *Tyrrhenoglis*, *Leithia* and *Maltamys* are known from the Pliocene, Pleistocene and/or Holocene, and are generally thought to have become isolated on their respective islands following the rapid rise in sea level during the Zanclean flood. The ancestor of these genera that dispersed to the islands from the mainland during the Messinian Salinity Crisis has often been suggested to be *Eliomys* (Alcover et al., 1981; Alcover & Agustí, 1985; Daams & de Bruijn, 1995; Lomolino et al., 2013; Zammit Maempel & de Bruijn, 1982). The phylogenetic placement of *Hypnomys morpheus* was tested using ancient mitochondrial DNA (Bover et al., 2020) and a close relationship with *Eliomys* was supported. However, this scenario has been challenged by the recent discovery of dental material of *Microdyromys boveri* from the very early Pliocene of Mallorca (Agustí, Furió et al., 2026). This species is larger than its mainland congeners, but smaller than later Mallorcan dormice. Analysis of the molar morphology has suggested that *Microdyromys* could be the ancestor of *Hypnomys*, *Tyrrhenoglis* and *Maltamys*, and that *Microdyromys* may have dispersed to Europe and Mediterranean islands from north Africa (Agustí, Torres-Roig et al., 2026).

Muscardinus cyclopeus was present on Menorca from the late Miocene to the late Pliocene or Early Pleistocene (Moncunill-Solé et al., 2014), again suggesting an arrival during the Messinian Salinity Crisis. *E. q. ophiusae* is the only extant giant glirid and appears to

Table 1. Proposed genera in each subfamily of Gliridae and the evidence on which this is based.

Subfamily	Glirinae	Graphiurinae	Leithiinae
Genera	*Glirulus*^{D,M} *Glis*^{D,M} *Muscardinus*^{M}	*Graphiurus*^{D,M}	*Chaetocauda*^{M} *Dryomys*^{D,M} *Eliomys*^{D,M} *Muscardinus*^{D} *Myomimus*^{D,M} *Selevinia*^{D,M}

Note: D, nuclear and/or mitochondrial DNA (Bover et al., 2020; Montgelard et al., 2003; Nunome et al., 2007; Petrova et al., 2024); M, morphology (Storch, 1995; Wahlert et al., 1993).

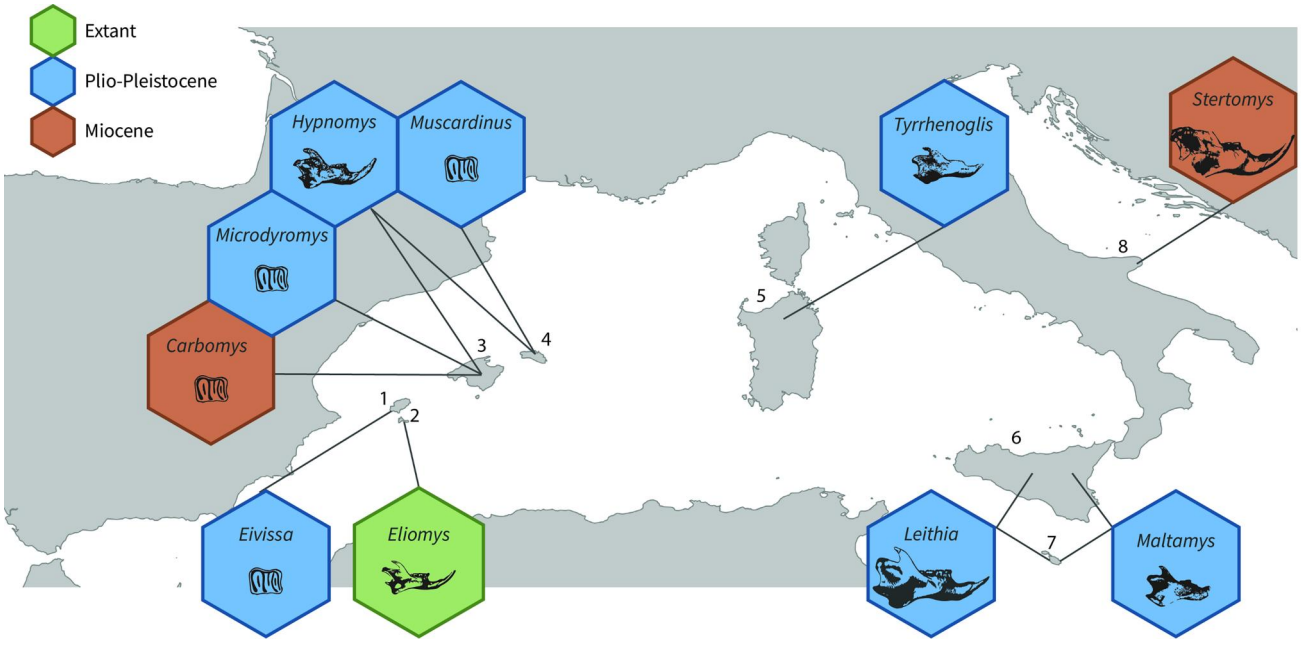


Figure 2. Map of the western Mediterranean showing geographical and temporal distribution of fossil insular giant dormice. Genera known from skeletal material are illustrated with the mandible of that genus (not to scale). Genera known only from isolated teeth are illustrated with a tooth icon (not specific to the genus; redrawn from figure 1 of Daams & de Bruijn, 1995). Key to (palaeo-)islands: **1,** Ibiza; **2,** Formentera; **3,** Mallorca; **4,** Menorca; **5,** Sardinia; **6,** Sicily; **7,** Malta; **8,** Gargano.

have arrived in the Balearic Islands after human colonization approximately 4000 years ago (Hautier et al., 2009).

Carbomys and *Stertomys* are older taxa, dating back to the early and late Miocene respectively (Daams & Freudenthal, 1985; Mein & Adrover, 1982). There has been very little research on *Carbomys* as it is only known from isolated teeth, and thus its 'giant' status is still provisional, but it appears to be most closely related to *Myomimus* (Lu et al., 2021). *Stertomys* was originally included in the Glirinae by Daams and de Bruijn (1995) alongside *Glis* and *Muscardinus*. However, later analyses (Rinaldi & Masini, 2009) refer to *Stertomys* species as belonging to the Myomiminae, which, as noted above, was a subfamily erected by Daams (1981) containing the extant genus *Myomimus*. Recently, *Stertomys* has been moved back to the Glirinae, albeit with that subfamily now understood to contain *Glis* and *Glirulus* but not *Muscardinus* (Lu et al., 2021).

It should be noted that, although gigantism has occurred many times in insular dormice, it is not a given for island glirids. Extant populations of *Eliomys quercinus* are known from several Mediterranean islands, including Mallorca, Menorca, Formentera, Corsica, Sardinia and Sicily, but only the Formentera subspecies shows an increased body size compared to the mainland population (Bover et al., 2020; Hennekam et al., 2020). Conversely, enlarged body size is also found on the mainland in 'habitat islands', e.g. Doñana National Park in the south of Spain.

Outstanding questions

In our opinion, one of the most pressing unanswered questions with regard to dormouse systematics is the phylogenetic placement of *Leithia melitensis* and its sister species *L. cartei*. Both species of *Leithia* are insular giants from the Pleistocene of Sicily and Malta. *Leithia melitensis* is the largest known species of dormouse, with an estimated body mass of approximately 1–1.5 kg (Hennekam et al., 2023), around 10 times the size of its presumed ancestor (Lomolino et al., 2013). It therefore represents an extreme increase in body size compared to extant forms which range between 15 and 180 g. Understanding where *Leithia* fits into the phylogeny of dormice is thus key for studying the phenomenon of insular gigantism, as it will enable the estimation of the degree and rate of body size change during the evolution of *L. melitensis*.

Leithia melitensis was first described from material from Ghar Dalam cave, Malta, by Leith Adams, and was given the name *Myoxus miletensis* (Adams, 1863). Four years later, Adams named a second

species from the same cave, *Myoxus cartei*, which was similar but had lower jaws that were "comparatively more slender" (Adams, 1867, p. 307). It was in this second paper that the specific name of the larger species was written as '*melitensis*', a spelling that has persisted ever since. In 1895, Lydekker examined the material and proposed that these two species did not belong to the dormouse family (then named Myoxidae) on the basis of cranial and dental morphology. At that time, the Myoxidae were included as part of the Myomorpha, based in part on the enlarged infraorbital foramen through which part of the masseter extended on to the rostrum. However, Lydekker noted that the skull of *Leithia* was sciuromorphous, i.e. the infraorbital foramen was small and slit-like, as seen in squirrels. Lydekker (1895) thus proposed the generic name *Leithia* in honour of Leith Adams and also suggested that this genus should be placed in its own family, Leithiidae, within the Sciuromorpha. Forsyth Major (1899) agreed that the fossils warranted their own genus but disagreed that they should be removed from the Myoxidae completely as he believed the small infraorbital foramen was due to crushing of the fossil material.

Subsequent analyses have all retained the genus name *Leithia* and no-one other than Lydekker (1895) has seriously suggested that *Leithia* species are not dormice. However, their position within the Gliridae is not certain and often based on misreadings of prior literature. Wahlert et al. (1993, p. 5) stated that "Both Bruijn (1966, 1967) and Daams included *Leithia* in the Dryominae". It is assumed that 'Daams' in this sentence refers to Daams (1981, p. 101) as that is the only reference by this author in the bibliography. However, Daams (1981) clearly states that "*Leithia*, *Hypnomys* and *Tyrrhenoglis* have not been assigned to a subfamily". Similarly, Daams and de Bruijn (1995, p. 19) stated that "The insular dormice *Leithia*, *Hypnomys*, *Tyrrhenoglis*, *Maltamys* and *Eivissia* […] are considered to have descended from *Eliomys* (Zammit Maempel & de Bruijn, 1982; Alcover & Agustí, 1985)". But Zammit Maempel and de Bruijn (1982) only stated this clearly for *Hypnomys*, *Tyrrhenoglis* and *Maltamys*. They were much more cautious about *Leithia*, noting that its phylogenetic relationships were still uncertain, although they did believe it to belong to the subfamily Dryominae alongside the extant genera *Dryomys*, *Eliomys* and *Glirulus*. Similarly, Alcover and Agustí (1985) stated that all endemic glirids of the western Mediterranean islands from the Plio–Pleistocene were descended from *Eliomys*, with the exception of *Leithia* and *Muscardinus cyclopeus*, and Petruso (2004, p. 206) suggested that *Maltamys* evolved from *Eliomys*, but that *Leithia* "derived from an unknown ancestor". Thus, the phylogenetic relationships of *Leithia* within the Gliridae are still unclear. The recent suggestion that the ancestor of *Hypnomys, Tyrrhenoglis* and *Maltamys* may be *Microdyromys* rather than *Eliomys* (Agustí, Furió et al., 2026) only adds to the uncertainty.

Wahlert et al. (1993) did not use the name Dryominae in their study of extant dormice, instead noting that Leithiinae had priority, following Holden (1993). The use of Leithiinae has persisted in most subsequent mammalian classifications (e.g. Holden-Musser et al., 2016; McKenna & Bell, 1997; Wilson & Reeder, 2005). However, Daams and de Bruijn (1995) disagreed with the use of Leithiinae on the basis that *Leithia* did not seem to fit the characters that Wahlert et al. (1993) used to characterize the subfamily. At that time, there was only limited cranial material of *Leithia* available to examine, but recent scanning and reconstruction of material from Poggio Schinaldo cave, Sicily, by the present authors (Hennekam, Herridge et al., 2020) allows us to interrogate in greater detail whether *Leithia* fits the characters used to define Leithiinae.

Wahlert et al. (1993) noted four characters of the cranium and mandible uniting the extant members of the Leithiinae:

1. a fenestra or posterior emargination in the squamosal bone;
2. a fenestra in the mandibular angle;
3. a low inclination of the leading edge of the coronoid process (less than 60° relative to the occlusal plane);
4. a complete transverse valley across the occlusal surface of the lower second molar.

From the composite skull reconstructed in Hennekam, Herridge et al. (2020), it does not appear that *L. melitensis* had a fenestrated or emarginated squamosal. The mandibular angle is also not fenestrated (Hennekam et al., 2023) and the anterior edge of the coronoid process forms an angle of greater than 60° relative to the occlusal plane. The only one of the four characters we have unequivocally found in *L. melitensis* is the transverse valley of the lower second molar, which can be seen in the figures of Adams (1863).

The working hypothesis in the literature appears to be that *Leithia* descends from, or is the sister genus to, *Eliomys* (Lomolino et al., 2013). We contend that this is currently just an assumption based on analogy with *Hypnomys* (Bover et al., 2020), and that the precise origins of *Leithia* have not been rigorously investigated. Furthermore, it is also assumed that *Leithia* belongs to a subfamily of dormice also including *Dryomys*, *Muscardinus*, *Myomimus* and *Selevinia*, but *Leithia*

bears very few of the morphological characters said to underpin this group (Wahlert et al., 1993). This may not be surprising as the process of gigantism experienced by *Leithia* could have led to many changes in cranio-mandibular morphology. However, the phylogenetic placement of *Leithia* has yet to be tested. If *Leithia* were found to belong to a different part of the dormouse phylogeny, this would of course lead to further nomenclatural changes to the glirid subfamilies.

A second, related unanswered question is how many species of dormice there are on Sicily and Malta. As noted above, Adams (1863) named one genus and two species (as *Myoxus*): *L. melitensis* and *L. cartei*. However, Lydekker (1895) believed these to be synonyms and even Adams himself (1867) was uncertain whether they represented two separate species. A century after the original discovery, a third Maltese dormouse species was found and assigned to the Balearic genus *Hypnomys* by de Bruijn (1966) as the new species *H. gollcheri*. Petronio (1970) and Storch (1974) both synonymized *H. gollcheri* with *L. cartei*, but Zammit Maempel and de Bruijn (1982) disagreed and instead erected the new genus *Maltamys* (originally as a subgenus of *Eliomys*). The diagnosis of *Maltamys* was based on dental characters and the presence of a fenestra in the angular process of the mandible (which is lacking in *Leithia*). These authors split the genus into two species (*M. gollcheri* and *M. wiedincitensis*) and noted them to be present on Sicily as well as Malta. Petruso (2004) states that 'most' material formerly identified as *L. cartei* from both islands is in fact *Maltamys*. Nonetheless, *L. cartei* currently remains a valid taxon, largely distinguished from *L. melitensis* by size (although Petruso, 2004, notes that the precise size boundary is unclear). Both species of *Leithia* are known from both Sicily and Malta (Hunt & Schembri, 1999; Marra, 2013; Palombo, 2009). However, from our own research (Hennekam, Herridge et al., 2020), we have begun to suspect that the Sicilian and Maltese populations of *L. melitensis* may in fact be separate species. The holotype from Maghlak cave, Malta (Adams, 1863; National Museum of Ireland, F 19835) and the specimen described by Lydekker in 1895 (Natural History Museum, London, PV OR 49344), also from Malta, are both significantly smaller than the specimens described by the current authors from Poggio Schinaldo, Sicily (Hennekam, Herridge et al., 2020), and have very different proportions. This is currently just speculation as no formal morphological analysis has taken place, and comparisons are hampered by the fragmentary nature of the Maltese specimens. Furthermore, we have noted considerable differences between the *Leithia* populations from the north and south of Sicily, but again this requires more in-depth analysis to confirm.

Future work

In our opinion, a detailed analysis of the Siculo-Maltese dormice specimens needs to be undertaken in order to determine the extent to which *Leithia* and *Maltamys* differ from one another, and similarly what, if anything, distinguishes the species within those genera. In particular, we would like to be able to assess whether *Leithia cartei* differs at all from *Maltamys*, and whether the Sicilian and Maltese populations of *L. melitensis* are indeed separate species (or subspecies) as we have speculated above. Geometric morphometrics has been previously used to assess shape change in the skull and mandible of giant insular dormice relative to non-giant mainland relatives (Hennekam, Benson et al., 2020), and thus could also be of use to assess morphological differences within and between *Leithia* and *Maltamys* species. However, this would require sufficient intact skeletal elements from each species under study. Currently, much of the material is fragmentary, so fieldwork to locate more complete specimens is important. However, it should also be noted that there is a great deal of postcranial material already in collections that has had little research attention compared to skulls, mandibles and teeth. This underutilized resource may shed light on the taxonomic questions around *Leithia* and *Maltamys*. Additionally, new techniques applied to existing material can also play a vital role. The skulls of *L. melitensis* analysed in Hennekam, Herridge et al. (2020) were found in a slab of material that had already been excavated and was present in the Museo Geologico Gemmellaro, Palermo. By scanning this conglomerate with micro-computed tomography, we revealed five skulls in much better condition than most others known in museum collections at that time.

Further fieldwork would also be valuable to look for more specimens of the other giant fossil dormice (*Tyrrhenoglis*, *Microdyromys*, *Eivissa*, *Carbomys* and *Stertomys*). Previous morphometric and biomechanical studies (Hennekam, Benson et al., 2020; Hennekam et al., 2023) have shown that gigantism has evolved in noticeably different ways in *Leithia*, *Hypnomys* and *Eliomys quercinus ophiusae* when compared to their putative mainland ancestor. It would provide a more complete understanding of insular gigantism to subject the remaining giant dormice to such analyses. However, there are many fewer specimens of *Tyrrhenoglis*, *Eivissa*, *Carbomys* and *Stertomys*, and they are generally quite fragmentary. *Microdyromys* is known from a

larger number of specimens, but they are all isolated teeth. Thus, new and more complete specimens are needed before we can really begin to understand how varied the process of gigantism is in the Gliridae. In particular, more specimens of *Stertomys laticrestatus* would be very welcome, as our own preliminary analyses have led us to suspect that it may rival *Leithia melitensis* for the title of the largest species of dormouse. A third very large species (although smaller than *Stertomys* and *Leithia*) is known from a single first lower molar from Ibiza. Originally referred to *Hypnomys* (Moyà-Solà et al., 1984) this molar may actually represent an unknown endemic Ibizan lineage (Agustí et al., 2021). Either way, more information about this intriguing species would add greatly to our understanding of glirid evolution and dispersal in the Balearic Islands.

Better knowledge of the masticatory musculature of the modern dormouse genera is also greatly needed. This could be obtained via traditional dissection and/or digital methods such as diceCT (Gignac et al., 2016). Dormice are unusually varied amongst rodents in their zygomasseteric structure. Most of the genera are considered to be myomorphous (or 'pseudo-myomorphous'; Vianey-Liaud, 1985) as they show both expansion of the deep masseter onto a zygomatic plate and extension of the zygomatico-mandibularis through an enlarged infra-orbital foramen (Cox & Jeffery, 2011; Hautier et al., 2015; Wood, 1965). However, the African dormice (*Graphiurus*) are hystricomorphous, exhibiting an even more enlarged infraorbital foramen and no zygomatic plate (Hautier et al., 2008). As mentioned above, *Leithia* appears to be sciuromorphous (Lydekker, 1895) owing to its small infraorbital foramen, although this was later dismissed as a taphonomic artefact (Forsyth Major, 1899). More recent work on *Leithia* skulls from Sicily (Hennekam, Herridge et al., 2020) has indicated that Lydekker's original assessment of sciuromorphy was likely correct. Furthermore, preliminary dissections of *Myomimus roachi* by the current authors have suggested that sciuromorphy may also exist in this extant species in line with its small infraorbital foramen (Wahlert et al., 1993). Thus, a deeper analysis of masseteric morphology in extant dormice may provide clues to the evolutionary relationships of the extant taxa.

Ancient DNA should also play a role in future analyses. Mitochondrial DNA has been successfully extracted and sequenced from *Hypnomys morpheus* (Bover et al., 2020), which provided confirmation of its close evolutionary relationship with *Eliomys*. *Leithia*, *Maltamys*, *Tyrrhenoglis* and *Eivissia* are all of a similar age and should also be amenable to DNA extraction. This would be especially interesting for *Leithia* whose phylogenetic placement is considerably less certain than that of the others. *Stertomys* also has uncertainty in its relationship with other dormouse genera that it would be very helpful to resolve, but unfortunately its age (late Miocene) is far beyond the current limit for DNA sequencing.

In conclusion, although our understanding of relationships between extant dormice appears to be approaching some kind of consensus, there is still considerable uncertainty on the phylogenetic placement of a number of fossil glirid taxa. Renewed research effort on existing specimens in museum collections as well as newly excavated material not only would help us to reveal more detail of the evolutionary history and radiation of the Gliridae but also would shed light on the fascinating but poorly understood evolutionary phenomenon of insular gigantism.

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Author contributions

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Disclosure statement

The authors report there are no competing interests to declare.

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Data availability statement

There is no new data associated with this review.

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