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RESEARCH PAPER

Virtual Cranial Reconstruction of the Endemic Gigantic Dormouse *Leithia melitensis* (Rodentia, Gliridae) from Poggio Schinaldo, Sicily

Jesse J. Hennekam*, Victoria L. Herridge†, Loïc Costeur‡, Carolina Di Patti§ and Philip G. Cox*||

The endemic dormouse *Leithia melitensis* from the Pleistocene of Sicily is considered an insular giant, whose body size is exceptionally large in comparison to that of any extant dormouse species. However, knowledge of the skull morphology of this giant glirid species is limited as cranial material is rare and mostly fragmentary. A fossil conglomerate representing a cave floor segment from Poggio Schinaldo, Sicily, presented an exceptional opportunity to reconstruct the cranium of *Leithia melitensis*. Following microCT scanning, five partial crania were digitally extracted from the conglomerate. A composite skull of the partial crania was then reconstructed with the use of merging and warping techniques, resulting in the best approximation to the complete skull morphology of this species thus far. All major structures except for the nasal bone are present in the composite model, indicating very robust morphology, especially in the zygomatic area and the pterygoid flange. This model could potentially be very important for our understanding of the morphology and ecology of this gigantic dormouse, as well as for providing valuable data for understanding the phenomenon of insular gigantism more generally.

Keywords: Insular Gigantism; Dormice; Pleistocene; Skull Morphology; Virtual Reconstruction

Introduction

The Late to Middle Pleistocene faunas on Sicily are characterised by the presence of endemic animals such as the dwarf elephants *Palaeoloxodon* (alternatively: *Elephas*) *falconeri* and *P. (E.) mnaidriensis*, resulting in eponymous Faunal Complexes (Accordi & Colacicchi, 1962; Accordi, 1963; Bonfiglio, Marra & Masini, 2000; Bonfiglio et al., 2002; Burgio et al., 2002). During this time, the dwarf elephants were accompanied by the presence of the endemic dormouse genera *Maltamys* and *Leithia* (Adams, 1863). These dormice were already present in the older “Monte Pellegrino” Faunal Complex and presumably constituted a remnant of an unknown Messinian-aged population phase (Azzaroli & Guazzone, 1979; Daams & de Bruijn, 1995). *Leithia melitensis* is by far the largest known dormouse species, being at least twice the size of other insular species both extant and extinct.

Variations in body size caused by insularity frequently coincide with changes in cranial morphology. Various comparative studies on insular *Apodemus* species in the Mediterranean area indicate clear variations in both shape and size within the cranial morphology (e.g. Libois and

Fons, 1990; Michaux et al. 1996; Renaud and Michaux, 2003). Parmenter et al. (2020) describes morphological changes in the largest wild house mouse, *Mus musculus*, on Gough Island correlated with enhancing masticatory processes. Furthermore, both size and cranial morphological variations are present between mainland and insular populations of *Rattus rattus* (e.g. Ibrahim et al., 2017). This correlation between cranial morphology and size is not limited to rodents, but apparent in various insular mammals; especially during the Plio-Pleistocene on Mediterranean islands, when highly endemic terrestrial mammals showcased rather extreme examples. Besides unique variations in antler and horn morphology seen in various ungulates, including *Hoplitomeryx* and *Candiacervus* (De Vos, 1979; Leinders, 1984; Van der Geer et al., 2006), skull morphology changes are known in various insular mammalian genera, unrelated to suprapostorbital appendages. *Deinogalearix*, a gigantic moonrat (Galericinae) from the palaeo-island of Gargano shows a proportional elongation of its rostrum, and is characterized by multiple diastemata between its teeth, as well as a clear flattening of the skull (Freudenthal, 1972). *Myotragus*, a dwarf goat genus from the Balearic Islands, exhibits a change in the size and orientation of the orbits resulting in a more binocular vision, as well as the development of ever-growing incisors and a relatively reduced endocranial volume (Bate, 1909; Alcover et al., 1981; Moyà-Solà & Pons-Moyà, 1982; Köhler & Moyà-Solà, 2004). The Balearic Islands were also the home of the large dormouse genus *Hypnomys* (Bate, 1918; Bover et al., 2019),

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which modified its cranium by varying the relative size of the braincase and the position of the zygomatic arches (Bover et al., 2010). *Leithia melitensis*, the subject of this study, is another insular Mediterranean species from the Plio-Pleistocene that has undergone a significant shift in body size. However, whilst mandibular material of *Leithia melitensis* is well represented in museum collections, e.g. Museo di Geologia G.G. Gemmellaro (MGPalermo), Museo Universitario di Scienze Della Terra (MUST, Rome), Museo di Geologia e Paleontologia (IGUP, Padova), Naturhistorisches Museum Basel (NMBA, Basel) and the Senckenberg-Forschungsinstitute und Naturmuseum (Frankfurt), cranial fragments are rather scarce. Most material originates from either fissure or cave deposits, excavated in the last two centuries (Adams, 1867; Petronio, 1970; Esu, Kotsakis & Burgio, 1986; Bonfiglio et al., 2002). Even though this species is exceptionally large and a striking example of

insular gigantism, only dental characteristics of this gigantic dormouse have been thoroughly investigated (Zammit Maempel & de Bruijn, 1982; Daams & de Bruijn, 1995; Petruso, 2004).

Given the prevalence of cranial shape-change associated with changes in body size in insular rodents (De Bruijn, 1966), including the dormouse genus *Hypnomys* (Bate, 1918; Mills, 1976), changes in the cranial morphology of the gigantic dormouse species *L. melitensis* are to be expected. However, complete *Leithia* skulls are rare and their 3D morphology has yet to be characterised. In this work a *L. melitensis*-rich conglomerate slab from the Sicilian cave locality of Poggio Schinaldo was analysed (Figure 1). The aim of this study was to evaluate the cranial morphology of *Leithia melitensis* by creating a composite digital model from a number of partial crania present within the conglomerate. This model is the best

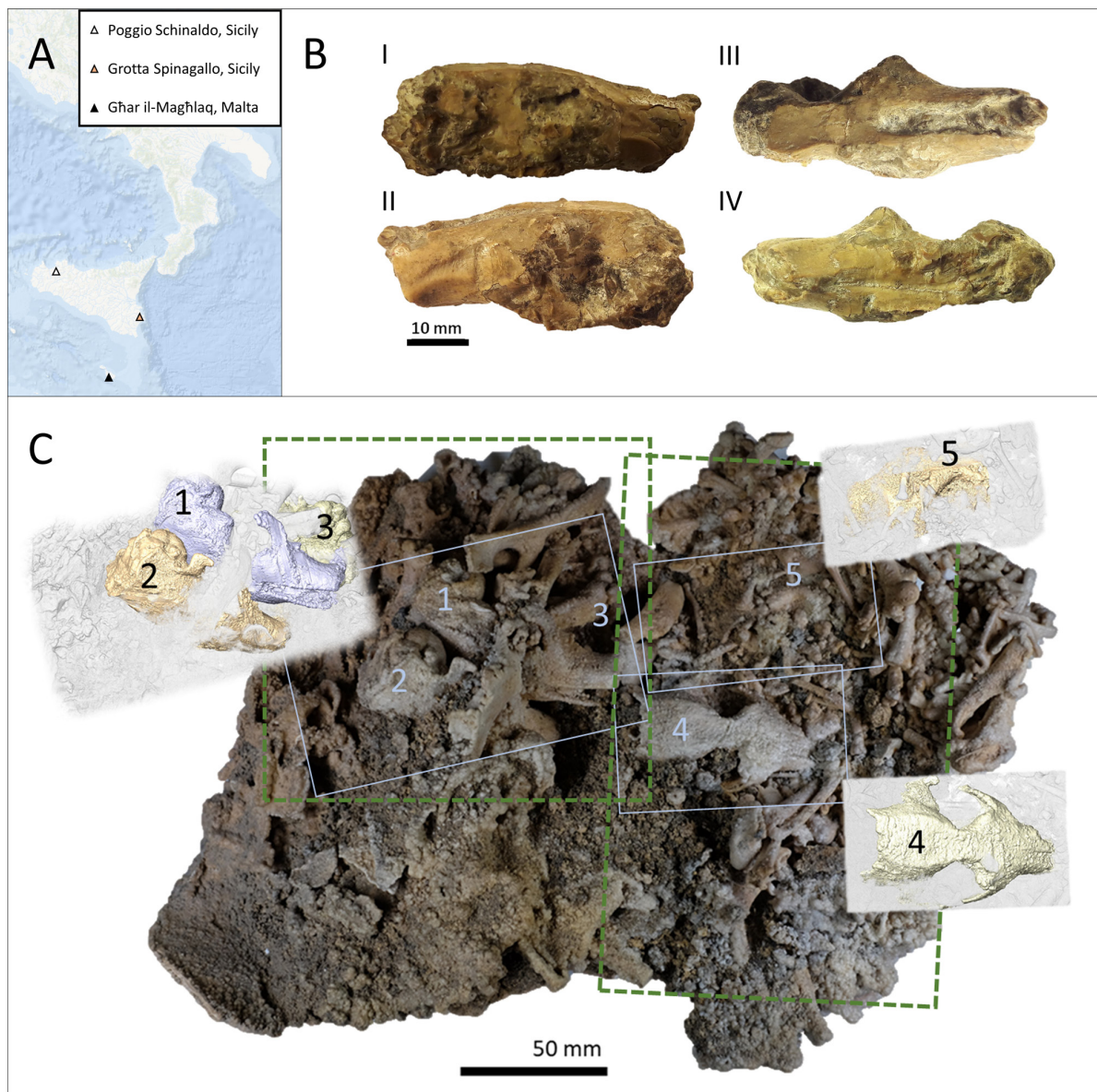


Figure 1: A) Location of cave deposits including *Leithia melitensis* material on Sicily and Malta. B) Holotype of *Leithia melitensis* (previously *Myoxus miletensis* Adams, 1863) from Maghlak cave, Malta. I right lateral view, II left lateral view, III dorsal view, IV ventral view. C) Cave floor segment (mgupPS 78) containing fossil material of the gigantic dormouse *Leithia melitensis*. Numbers 1–5 show the position of the five skulls selected for reconstruction. The green dashed boxes depict the boundaries of scan 1 (left) and scan 2 (right).

reconstruction of a fully intact cranium of *L. melitensis* currently known and reveals hitherto unseen cranial characteristics of the largest glirid known in the fossil record. In addition, the composition of the slab itself, including the matrix of the conglomerate and the presence of avian bones, can be used to understand the palaeoecology of this fossil giant. Together, this information will provide the basis for future studies, which will help us better understand modifications in cranial morphology correlated with the phenomenon of insular gigantism.

Introduction to *Leithia melitensis*

Leithia melitensis, the giant dormouse that is the focus of this study, was first described by Adams (1863), who erected a new species for it, *Myoxus miletensis (nobis)*. Lydekker (1895) created the family Leithiidae after Leith Adams, in order to distinguish between this giant and other dormice, and reassigned the species as *Leithia melitensis*. Later, Major (1899) re-evaluated the species and determined *Leithia* to be a dormouse, but retained the subfamily Leithiinae, which now contains the extant genera *Chaetocauda*, *Dryomys*, *Eliomys*, *Muscardinus*, *Myomimus* and *Selevinia*, as well *Leithia* and other insular fossil genera (Holden-Musser et al., 2016). The insular fossil dormice were classified as *incertae sedis* for an extended period of time, but are now presumed descendants of the genus *Eliomys* (Zammit Maempel and de Bruijn, 1982; Alcover & Agustí, 1985; Daams and de Bruijn, 1995). The holotype of *Leithia melitensis* originates from Maghlaq Cave, Malta, and is currently located in the collection of the National Museum of Ireland (NMI F19835; **Figure 1B**).

Geological Setting

Poggio Schinaldo is a small, low-ceilinged cave approximately 15 m in diameter, located south of the town of Terrasini in northwest Sicily (Esu, Kotsakis & Burgio, 1986) (**Figure 1A**). It was discovered during the construction of the Palermo-Mazara del Vallo motorway in 1976, and a rescue excavation was carried out before the entrance was resealed. Excavated segments of the cave floor are currently on display at Museo Geologico Gemmellaro, Palermo.

The entrance to the cave is located roughly 2.5 km away from the coast at an altitude of 125 m above current sea level, in a brecciated Upper Thitonian-Lower Cretaceous Limestone (Catalano, Abate & Renda, 1978). Owing to the unstable condition of the cave, stratigraphical observations and specimen provenance information were limited, however the cave stratigraphy can be summarised as follows: [1]. A deposit of grey sand with pebbles, and containing marine mollusc remains (depth unknown – excavations were limited to the top section of this layer only), underlies [2]. A layer of fine red soil “*terra rossa*”, up to 30 cm thick, the upper portion of which contained fossil mammal material dominated by *Leithia*, and capped by [3]. a stalagmitic calcite layer of varying thickness, encrusting the fossil material and cementing the red soil (**Figure 1C**) (Esu et al., 1986). Constraining the age of the fossil material is difficult in the absence of direct dates, but the fossil mammal assemblage derived from the calcite-encrusted red soil layer is consistent with attribution to

the Middle Pleistocene *Elephas falconeri* Faunal Complex (FC), with *Leithia melitensis*, *L. carteri*, *Crocidura esuae* and *Palaeloxodon falconeri* co-occurring here. The presence of *Dama* (alternatively: *Praemegaceros*) *carburangelensis* is at odds with the *Elephas falconeri* FC attribution, but Esu et al. (1986) note that this was a surface find, and so may not be stratigraphically associated with the assemblage in the red soil layer. The underlying marine layer potential provides a maximum age for the mammal material; however, the marine molluscs are biostratigraphically undiagnostic. Their presence, as well as encrustations of *Chthalamus* barnacles, indicate that the cave was once at sea level (Esu et al., 1986), with regional uplift indicating a post-Pliocene origin for the cave, although marine terrace correlations in NW Sicily are difficult (e.g. Marine Isotope Stage 5 terraces in NW Sicily range from –20 m to +35 m, Antonioli et al., 2006).

Faunal assemblage

The faunal assemblage in the cave was first described in an anonymous note in *Il Naturalist Siciliano* (Anon, 1978) and later by Esu et al. (1986). The fauna is dominated by the presence of two species of the glirid genus *Leithia*. Unique for this assemblage and the focus of this study is the presence of a multitude of well-preserved skulls of the gigantic dormouse *Leithia melitensis*, as well as cranial material of *Leithia carteri*, being smaller in size and less abundant in the deposit. Besides the large amount of dormouse material, other mammalian fossils within the deposit include the scapula and tibia of the dwarf Sicilian elephant *Elephas falconeri*, and the mandible and fragmented post-cranial material of the soricid genus *Crocidura*. The cave deposit further includes the distal end of a humerus of a cervid *Dama* (*Notomegaceros*) *cfr. carburangelensis* (Esu et al., 1986), although this is a surface deposit and may not be from the same context as *Leithia*. The cranium and post-cranial material from the mustelid *Nesolutra* (alternatively: *Lutra*) *trinacriae* (Burgio et al., 1988; Willemsen, 1992) are also present, but it is unclear if these are in the same layer as *Leithia*, *C. esuae* and *P. falconeri* (calcite-capped red soil, layer 2). Squamate fossil material in the deposit includes vertebrae of the giant lizard *Lacerta siculimelitensis* (although the provenance of this material is not recorded by Esu et al., 1986), while vertebrae of a snake belonging to the group Colubrinae was also found cemented by calcite, presumably to the surface of layer 2 (Esu et al., 1986). Many remains of small to medium-sized birds are present in the deposit, including a number of owls, although the stratigraphical provenance for these was not recorded (Esu et al., 1986; Pavia and Mourer-Chauviré, 2002). Given the large number of small mammal remains, the presence of bird bones and even a bird egg, the cave appears to have been the nesting ground of birds of prey (Esu et al., 1986).

Material and methods

Sample

The fossil conglomerate analysed in this study is located at the Museo Geologico Gemmellaro (mgupPS 78), and has a high concentration of relatively complete skull fragments of a large-sized glirid species. The fossil conglom-

erate was part of the cave floor, containing a mixture of cranial and postcranial material of rodents and birds. The slab is roughly 27 cm long and 22 cm wide. The thickness varies between 4 cm up to roughly 10 cm, with osteological material being stacked from top to bottom. The matrix consists of a very grainy, dense sandstone with calcareous concretions encrusting the top layer. Esu et al. (1986) mentions the presence of the glirids *Leithia cartei* and the larger *Leithia melitensis* in Poggio Schinaldo. The skull fragments within this slab appear to be larger compared to the holotype of *L. melitensis* (Maghlak cave, Malta), but relatively similar in size and shape of *L. melitensis* cranial material originating from Grotta di Marasà (Sicily). In order to confirm the identity of the specimens within the conglomerate, their dental morphology and dimensions were compared with those of known specimens of *Leithia melitensis*. Mandibular material of this species is well represented in museum collections, whereas only a very small number of skull fragments appear to have been collected. The slab includes multiple fragmented skulls that appear to be in a more complete condition than any of the cranial material investigated at previously visited collections (Museo di Geologia G.G. Gemmellaro (Palermo), Museo di Paleontologia (Catania), Museo Universitario di Scienze Della Terra (Rome), Museo di Geologia e Paleontologia (Padova), Naturhistorisches Museum Basel (Basel), the Senckenberg-Forschungsinstitute und Naturmuseum (Frankfurt), University of Utrecht (Utrecht), Natural History Museum (London) and the National Museum of Ireland (Dublin)). Three mounted skeletons of *L. melitensis* are located in Palermo, Rome and Padova. However, the Palermo mount appears to be a cast of the Padova mount. These specimens all include skulls that are reconstructed to some extent (Appendix A), including all the zygomatic arches. Aside from these mounted skeletons, the best preserved skulls are located at the Senckenberg Institute (SMF 71-1303), the Natural History Museum London (NHMUK PV OR 49344), and the Naturhistorisches Museum Basel (NMBA: G.2128, G.2129 and G.2132).

CT-scanning and 3D virtual reconstruction

Two areas of interest were selected on the basis of the fragmented skulls visible on the surface (**Figure 1C**). 3D X-ray imaging was performed at a scanning facility in Basel, Switzerland, using a nanoCT® system nanotom® m (phoenix X-ray, GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany) to produce two micro-computed tomography (μ CT) scans with a pixel size of 50 μ m and 55 μ m respectively. In order to image the specimens an accelerating voltage of 180 kV and a beam current of 30 μ A were used where the mean photon energy was increased by adding a 0.25 mm copper filter. The field of view of each scan was 3052 \times 3052 and contained a total of 2400 slides for scan 1 and 1796 slides for scan 2. Imaging software Avizo v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA) was used for the segmentation of the scan.

The scans indicated the presence of five fragmented skulls of *L. melitensis* within the scanned windows. Three additional skulls were revealed by the scans, but only part of them was scanned and segmented, so they are not

considered in this study. The orientation of the slab as displayed in **Figure 1C** shows the relative positions of the five skull fragments selected for reconstruction.

Taphonomic processes resulted in encrusting of calcareous nodules, severely affecting the condition of the fossil material. This calcification process mainly affected the surface of the slab and became less apparent at lower levels. Due to the high density of this crust, it was frequently difficult to identify differences between bones, teeth and sediment within the slab. Besides the calcareous layer, the material with the highest density properties is expected to be the enamel on teeth. However, due to the presence of the much more dense concretions, distinguishing between the density of enamel and bone in the scans proved very difficult, if not impossible (**Figure 2**). Furthermore, the encrusting of the exposed surfaces of the specimens obscures the morphology of the material. Part of the taphonomic process included calcification of the actual bone material, making it impossible to separate the calcareous nodules from the affected bony surfaces. Instead, manual segmentation based on the overall thickness of the bone material in less affected areas was used to estimate the correct bone thickness in affected regions. This manual smoothing of the fossil material is only an estimation of the bone thickness and results in the absence of visible sutures in the affected areas.

The matrix of the conglomerate appeared to contain a large amount of bone material sharing the same material density as the skulls embedded in the slab. This bony matrix in conjunction with the effects of calcification resulted in it being impractical to use density differences for segmentation purposes (**Figure 2**). Instead, segmentation was based on the continuation of contours and interpolation between more distinctly discernible bony margins. This method of segmentation is much more time consuming, as well as more prone to mistakes. This is especially the case for cranial fragments of specimens fully submerged within the slab. However, by combining the best segmented areas of multiple skulls to create the composite model, the potential error is minimised.

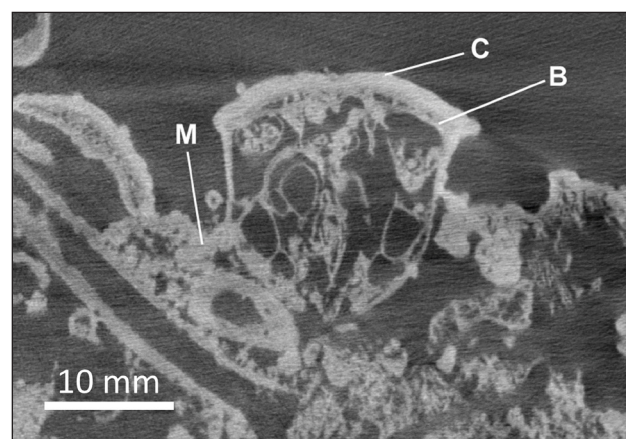


Figure 2: MicroCT slice from scan 2. Skull 4 (mgupPS 78-4) is visible, half submerged in the matrix. Note the similar density of the surrounding matrix (M) and the bone material (B) of this specimen, as well as the more dense layer of calcite (C) encrusting the vault of this specimen.

In order to create a composite model, well preserved features of the segmented skulls were isolated and merged together using both rigid and Bookstein warping (Bookstein, 1989) in Avizo. Before warping, all material was scaled to a similar consensus size. Rigid warping was preferred over Bookstein warping as it preserves the morphology of the material. Assuming cranial symmetry, features used for the composite model were solely placed on either the left or right side of the skull. A mirrored image of these features was then created and rigidly warped onto the original, completing the composite model. The specimen was then smoothed using manual segmentation and constrained smoothing. Furthermore, imperfections were removed using the engineering software Geomagic Studio (Geomagic Inc., Morrisville, USA). An unsmoothed model was uploaded to the MorphoSource repository.

Morphological comparisons

The morphology of the composite model was compared with other known cranial material of *Leithia melitensis*, including the holotype, as well as an average-sized cranium of *Eliomys quercinus* (ID 60534, locality: Germany: Rheinland-Pfalz (Senckenberg Institute)), its presumed nearest living relative based on dental characters (Zammit Maempel & de Bruijn, 1982). In addition we briefly compare the composite model to published descriptions of another enlarged insular glirid, *Hypnomys morpheus* (Hautier et al., 2009).

Results

Comparative dental characteristics of *Leithia melitensis*

Dental characteristics for the crania within the slab are best preserved in the right molar row of Skull 5 (mgupPS 78-5). The entire molar row is visible, however, the effects of calcification have made clear description of the molar morphology in P4 and M1 limited. M2 and M3 are better preserved. However, the taphonomic process have resulted in ridges appearing widened and potentially connecting with one another, where they were originally detached. The upper dentition of *Leithia* has previously been documented by Adams (1863), Lydekker (1895), Petronio (1970) and Zammit-Maempel & de Bruijn (1982). Given the well preserved state of the fossil (NHMUK PV OR 49344, Malak Cave, Malta) described by Lydekker (1895), this specimen was scanned in order to compare cranial features including dental characteristics with the composite from Poggio Schinaldo. Images by other authors were also incorporated, in order to show variation and commonalities in dentition for this giant dormouse species (Figure 3). We follow the nomenclature for glirid molar morphology as described in Daams (1981).

The multitude of blunt ridges present in a comb-like manner extending labially for both M2 and M3 in our specimen, and correspond with descriptions and figures of *Leithia melitensis* by Adams (1863), Lydekker (1895) and Petronio (1970). The outlines of all molars do not include distinct outer columns, as is the case within *Eliomys* and *Glis*. The morphology of M2 in the Poggio Schinaldo specimen resembles that of the molars depicted in Adams (1863), Lydekker (1895) and Petronio

(1970), although slight variations between the four exist. Specimen F19838 at the National Museum of Ireland (Adams, 1863) is used in the comparison, as the molars present in the holotype are in very poor condition. It should be noted that Adams mentioned this to be a relatively young individual, something which potentially affects patterns within tooth morphology. In all specimens, the M2 endoloph extends anteriorly. Only within the Petronio molar does the endoloph include a furrow on the lingual side. The posteroloph is disconnected from the endoloph, as also mentioned by Zammit-Maempel & de Bruijn (1982). Interestingly, this feature is not clearly present in the drawing by Adams (1863). Although this furrow is difficult to distinguish in the drawing in Lydekker (1895), it is unmistakably present when observing the scanned image of the right molar row in this specimen (Figure 3C–D). A shared base for the protoloph and metaloph is present in the Petronio specimen and connects with the endoloph. In Adams and the Poggio Schinaldo specimen, both protoloph and metaloph connect to the endoloph separately, whereas the metaloph in the Lydekker specimen connects to the posteroloph. The positioning and shape of the base and protoloph within Petronio is similar to that of the protoloph in Lydekker, Adams and Poggio Schinaldo, whereas the base and the metaloph are similar in position to the metaloph within the specimens from Adams and Poggio Schinaldo, but originates on the posteroloph in Lydekker. The positioning and shape of the anterior centroloph is similar in all four specimens, and a posterior centroloph is absent in all specimens. Zammit Maempel and de Bruijn (1982) also mention the absence of a posterior centroloph. Furthermore, they describe the protoloph and metaloph reaching the endoloph separately, a characteristic also seen in our specimen and in the molars described by Adams, Petronio and Lydekker. The M3 appears more variable in dental characteristics, even within specimens (see posterior part M3 in Figure 3C–D). However, all specimens show a similar comb like structure, resulting in a continuous ridge going along the anterior, lingual and posterior margins of the third molar. The protoloph is detached from the endoloph in Lydekker, whereas they are connected in Petronio and in our specimen. The anterior centroloph in Petronio and in our specimen is attached to the protoloph, whereas they are detached in the Lydekker specimen. The anterior centroloph appears to be longer and folded in the Poggio Schinaldo specimen, resulting in its distal end being orientated labially. We would like to note that this could be the result of calcification, merging the anterior centroloph with part of the posterior centroloph. Unfortunately, the microCT scan could not provide more detail due to similarities in the density of the calcite and enamel. If this connection is caused by taphonomy, this morphology would most resemble that of Adams, in which three disconnected parallel ridges are placed posterior to the anterior centroloph. The metaloph in our specimen attaches to the endoloph at a similar position as in Adams and Petronio, albeit being more sharply angled. Furthermore, this ridge is longer in the Poggio Schinaldo specimen, stretching

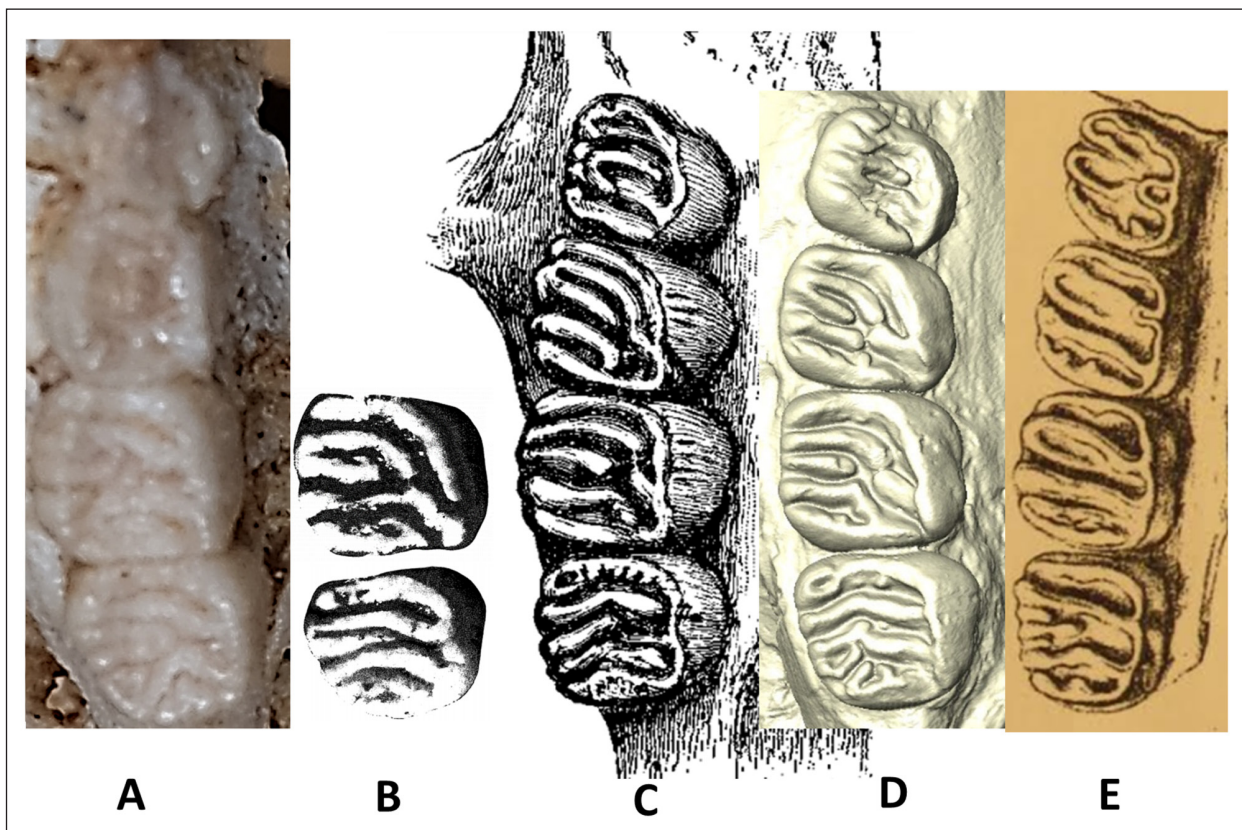


Figure 3: Molar row of various specimens of *L. melitensis*. **A.** Skull 5 within the slab (mgupPS 78-5); **B.** M2 and M3 from Petronio (1970); **C.** Mirrored drawing of NHMUK PV OR 49344 (Lydekker, 1895); **D.** Scan of NHMUK PV OR 49344; **E.** Drawing of F19838 (Adams, 1863).

Table 1: Upper molar lengths of Poggio Schinaldo specimen and other *Leithia melitensis* specimens from Sicily and Malta.

| | Specimen number | P ⁴ | M ¹ | M ² | M ³ | Source |
|--------------------|-------------------|----------------|----------------|----------------|----------------|----------------------------------|
| Spinagallo (min) | n°1–20 | 2.3 | 2.7 | 2.9 | 2.8 | Petronio, 1970 |
| Spinagallo (max) | | 3 | 3.5 | 3.8 | 3.4 | Petronio, 1970 |
| Spinagallo (mean) | | 2.6 | 3.1 | 3.3 | 2.8 | Petronio, 1970 |
| Malta | n°266 | 3.2 | 3.6 | 4 | 3.6 | Petronio, 1970 |
| Wied incita, Malta | | | 3.4 | | | Zammit Maempel & de Bruijn, 1982 |
| Ghar Dalam, Malta | NMI F19838 | 2.2 | 2.8 | 3.0 | 2.9 | Figure in Adams, 1863 |
| Malak Cave, Malta | NHMUK PV OR 49344 | 2.9 | 3.1 | 3.4 | 3.3 | Figure in Lydekker, 1895 |
| Poggio Schinaldo | mgupPS 78-5 | 2.9 | 3.5 | 3.6 | 3.4 | |

anteriorly along the labial margin. However, this could be a misinterpretation due to calcification. This feature is not seen in the other specimens, that all have a different morphology of the metaloph and more posterior features. These variations are also present in the molar rows within specimens (**Figure 3C–D**). It is evident the dental characteristics of the third molar within *Leithia melitensis* are more variable than those within the second molar. Dental characteristics between specimens are similar, but show small differences within the morphology of the protoloph and metaloph. This could be the result of variations in phylogeny, ontogeny and/or wear.

Previously documented dimensions of the various upper molars belonging to *Leithia melitensis* from both Sicily and Malta are compared with the specimen from Poggio Schinaldo (**Table 1**). The mean from Spinagallo is derived from the measurements of 20 different specimens (Petronio, 1970). The molar row from Poggio Schinaldo has similar molar lengths compared to the largest specimens from Spinagallo Cave. The specimen from Malta (referred to as n°266 in Petronio, 1970) appears to be slightly larger than the Schinaldo specimen. Given the resemblance in both dimensions and molar characteristics with recognized specimens of the giant dormouse *Leithia melitensis*, the specimen used in this study is considered a member of this species.

Description

Scan 1

Three skulls are present within the first scan (mgupPS 78-1:3), two of which are clearly visible from the surface and strongly affected by small calcite nodules encrusting the surface of the exposed bony material. Another relatively complete skull is located directly underneath the most centrally positioned cranium (**Figure 1C**). The left part of the scan includes the posterior portion of an additional skull fragment. This area of the slab, including its fossil contents, appears to be more weathered and the fossil material more fragmented. Another skull fragment is partially included in the bottom part of the scan, just below the surface. Considering its only partial inclusion within the scanned area, this specimen was not further analysed. The top part of the scan includes the frontal bone of a dormouse. This skull fragment is clearly smaller than the other skulls. Esu et al. (1986) mentions the presence of the smaller dormouse species *L. cartei* in the cave. However, the lack of molars and the preservation state of the skull make it difficult to determine whether it is a juvenile *L. melitensis* or an adult specimen of *L. cartei*. Considering the fragmented state and partial presence of fragments in the scan, the latter three individuals were excluded from further analyses.

Skull 1 (mgupPS 78-1)

This skull is the most centrally positioned skull in scan 1 and the most complete specimen present (**Figure 1C**). The fossil is embedded in the slab on its right side, leaving the left side exposed and highly affected by the process of calcification. The anterior parts of both zygomatic arches are intact as are the zygomatic plates (**Figure 4**). The right squamosal is well preserved, but missing on the left side. However, segmentation of the infraorbital foramen was only possible for the inferior part of this foramen on the right side of the specimen. The glenoid fossa is present on

the right side, whereas it is partially missing on the left. A long bone of presumably avian origin is located in the left orbit, making segmentation of the temporal orbital wall difficult on this side of the skull. Both the right auditory bulla and the posterior part of the cranium were difficult to segment because of the fusion with the bony matrix. The rostral margin of the foramen magnum and the pterygoid flanges are incomplete. The hard palate seems to be intact, as are the premaxillae and the molar and incisor alveoli. The right incisor alveolus is better preserved than the left one. Incisors were fully embedded in the matrix and, due to the calcification of the material, very difficult to identify. Based on analysing the shape rather than the density differences, the shape of the incisors was estimated. The right third molar is the only molar present in this specimen. The location of the incisive foramina is not clearly visible, but can be roughly estimated. The cranial vault is greatly affected by calcification and thus was subjected to significant manual smoothing.

Skull 2 (mgupPS 78-2)

Only the posterior part of this specimen was clearly visible before scanning and it had clearly been affected by the calcification process. The skull is oriented on its right side, dipping anteriorly into the matrix (**Figure 1C**). A very fragmented frontal bone of another individual overlaps the left zygomatic arch of this specimen. The midsection of this arch is missing, whereas the squamosal appears to be well preserved. The scan indicated that the complete skull is preserved within the slab, including molars and incisors. The bony composition of the matrix resulted in complications during segmenting, resulting in only a rough estimation of the incisor shape. Considering the shape and length of the incisors present in skull 1, as well as the orientation of the incisors in this specimen (**Figure 4**), we suspect that some movement of the incisors relative to the alveoli took place post-mortem. The left side of the

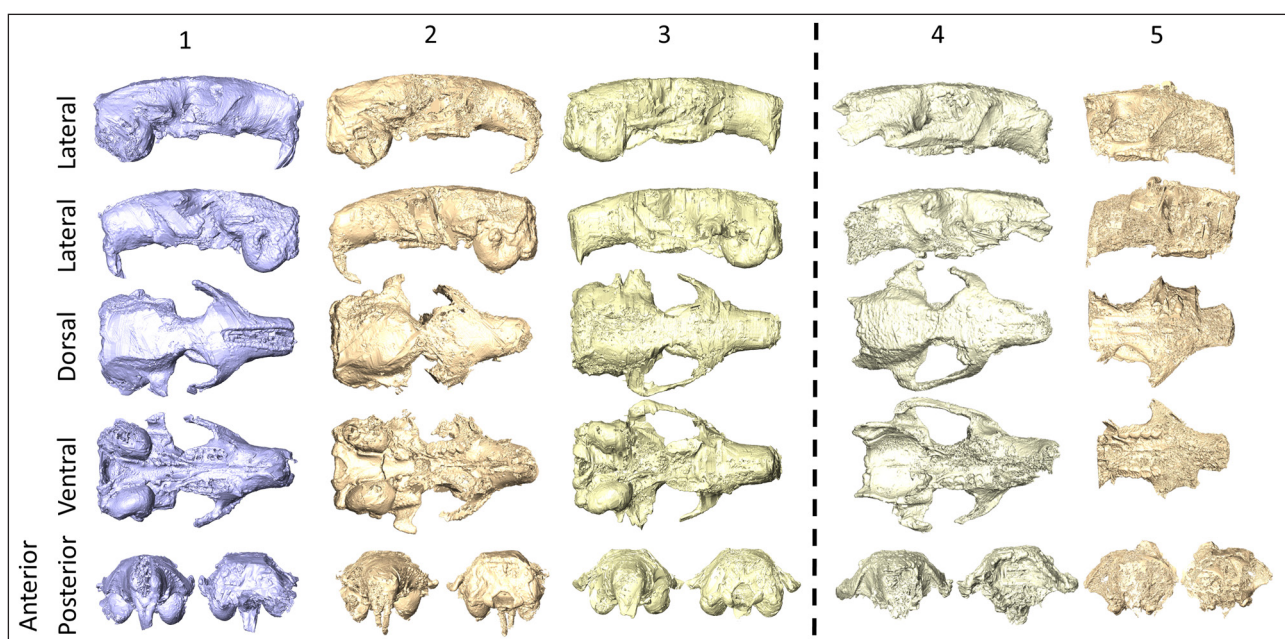


Figure 4: Segmented skulls in numerical order from left to right. Dotted line separates skulls originating from scan 1 (left) and scan 2 (right).

skull is more affected by calcification than the right side, whereas segmenting of the right side was difficult due to connections with the bony matrix. The left auditory bulla was better segmented, but highly affected by calcification, as the rest of the left side of the specimen. The basisphenoid-basioccipital suture is open (**Figure 4**) and shows slight displacement of the basisphenoid. The foramen magnum and the occipital condyles are well preserved, but the shape and position of the remaining part of the occipital bone are difficult to analyse due to the high concentration of calcite. The pterygoid flanges are broken in this specimen. The hard palate seems to be intact. The nasal bone of this specimen is present; however it proved very difficult to segment, and is partly broken anteriorly. A small undetermined rib was found within the braincase of this specimen.

Skull 3 (mgupPS 78-3)

This specimen is almost fully included within the slab and located directly under skull 1 (**Figure 1C**). Segmentation was very difficult due to the large amount of bony matrix connected with the specimen. The right zygomatic arch seems to be intact, but it is almost impossible to identify within the bony matrix. The left zygomatic arch is less embedded, but broken in the middle part. The zygomatic plates, the posterior parts of the zygomatic arches, the nasal bone and the vault are all preserved, but were difficult to extract. Segmentation of the incisors was only partially possible so that the incisor tips could not be identified (**Figure 4**). The occipital area was well preserved and less embedded in the bony matrix. Furthermore, the left pterygoid flange was well preserved and segmented. Segmentation of the left auditory bulla was exceptionally good considering the conditions. Segmentation of the remainder of the ventral part of this specimen was highly affected by the presence of the bony matrix.

Scan 2

Only one relatively complete cranium is visible on the surface of the slab within the window of the second scan (**Figure 1C**). Another skull is visible on the other side of the slab and appears to be less affected by the calcification process. The scanned area is densely packed with bone material, but cranial and intact long bone material is less apparent than in the first scan. The top part is more affected by calcification than the lower part and more saturated with bony material. Some smaller postcranial material is present that does not seem to belong to the adult dormouse specimens.

Skull 4 (mgupPS 78-4)

The dorsal side of this specimen is clearly visible and highly affected by weathering and calcification (**Figures 1C and 2**). The skull is slightly embedded in the slab, with matrix covering the zygomatic arches, but not the vault. The scan showed that significant parts of the ventral side are missing, including the basioccipital, auditory bullae and occipital area. The anterior part of the skull is highly weathered and incomplete. The segmentation of the incisors was not possible due to similar density of the surrounding bony matrix. The P4, M2 and M3 are present on

the left side of the maxilla (**Figure 4**). The hard palate and pterygoid flanges are broken, as well as the midsection of the left zygomatic arch. The right zygomatic arch is complete and was segmented with special care as this feature is often broken in other specimens.

Skull 5 (mgupPS 78-5)

This highly fragmented skull is visible to the naked eye on the reverse surface of the slab and appears to have been less affected by taphonomic processes than the other fossils; calcification does not seem to have affected this part of the slab at all. Unfortunately, the presence of surrounding matrix on the dorsal side still made segmentation of this specimen difficult. Furthermore, the posterior part of the skull seems to be missing. The clearly segmented parts of this specimen include the complete molar rows and the posterior part of the right orbital wall, which were not attached to the surrounding matrix.

Skull 1 appears to be the best preserved skull within the slab (**Figure 4**), although it is still very much affected by the encrusting of calcareous material. Segmentation of the other skulls was less successful, but often included features missing in specimen 1. Using mirroring and warping techniques in Avizo, well-preserved elements from the various crania with specimen 1 were merged in order to create a composite skull (**Figure 5**). Various elements of cranial morphology were studied in all the skull material segmented from the slab. The best preserved parts were assigned to be part of the composite model, and wherever possible elements of specimen 1 were preferred, resulting in a more accurate representation of that particular individual. All skulls were merged rigidly to correspond with the size of specimen 1. No material from skull 2 was used. Skull 3 provided the left pterygoid flange and the posterior part of the cranium, including the occipital, condyles and foramen magnum. The right zygomatic arch of skull 4 was used to reconstruct this part of the composite model. Here, the arch was warped rigidly and the overall shape locked using landmarks. A Bookstein warp (Bookstein, 1989) of the distal ends merged the arch to the zygomatic plate and squamosal of specimen 1. Lastly, the molar row segmented from skull 5 was warped to complete the dentition of the composite cranium. Attempts to include either the nasal bone of skull 2 and skull 3 were unsuccessful due to the broken condition of this feature in both specimens. All other features originate from either the left or right side of specimen 1. Eventually, the merged model was mirrored and merged with the original orientation, resulting in a complete composite model of *L. melitensis* (**Figure 6**).

Description and comparison of the composite skull of *Leithia melitensis*

The presumed nearest living relatives of *Leithia melitensis* are the garden dormice of the genus *Eliomys* (Daams & De Bruijn, 1995). A skull belonging to an adult specimen of *Eliomys quercinus* was used for a comparative anatomical analysis between *Eliomys* and the composite model (**Figure 7**) (SMF 60534, Senckenberg Institute). As *L. melitensis* is considered a giant form, all cranial characteristics were evaluated relatively, rather than absolutely. The composite model represents an adult specimen including

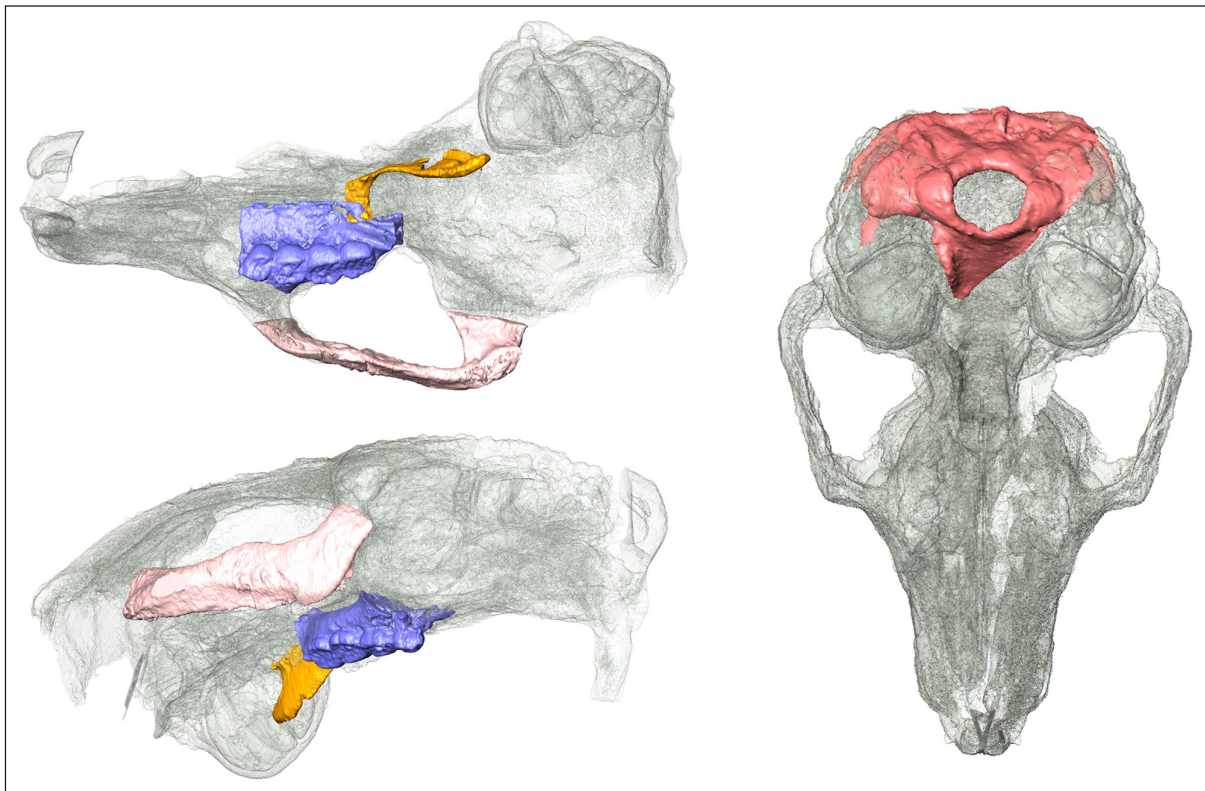


Figure 5: Partial composite skull of *Leithia melitensis*. Skull 1 (transparent) was used as the base model. The various other colours represent well preserved elements from different skulls merged onto skull 1: orange, left pterygoid flange (skull 3); red, posterior portion of the cranium (skull 3); pink, right zygomatic arch (skull 4); purple, right molar row (skull 5). Orientation: top left; ventral, bottom left; lateroventral, right; ventral.

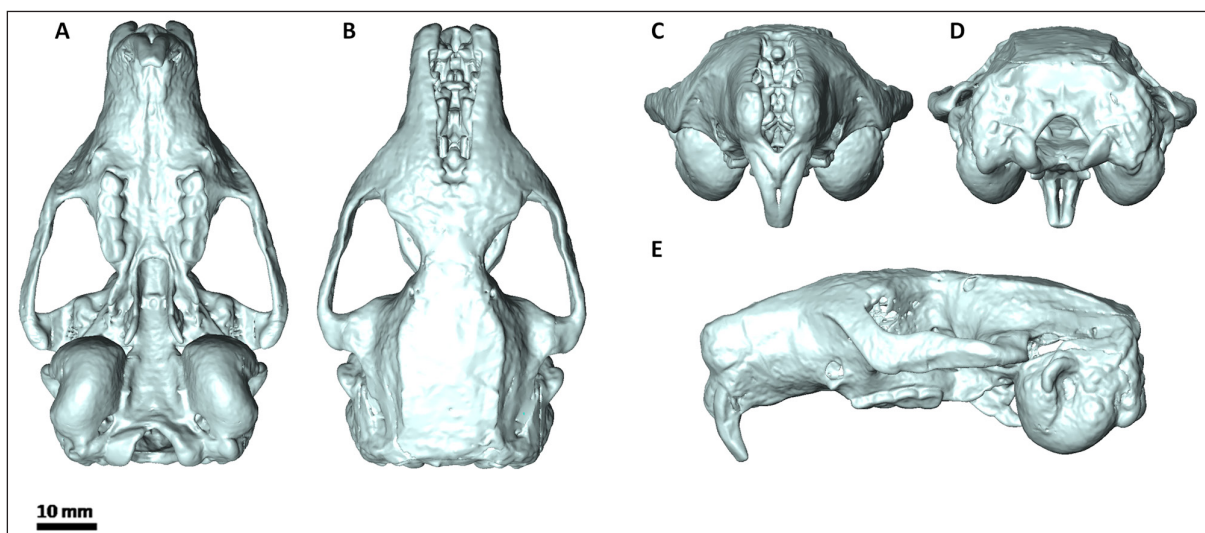


Figure 6: Composite skull of *Leithia melitensis*: **A.** dorsal view, **B.** ventral view, **C.** anterior view, **D.** posterior view, **E.** left lateral view.

all molars (P4-M3) and the two incisors. The incisors are slightly more curved posteriorly than those of *E. quercinus* and of similar relative size. The distal part of the incisors is narrower, but this could be the result of the segmentation process. The molars and especially premolars are more robust, enlarged and more concave. The area for superficial masseter attachment between the molar row and the incisive foramen is more pronounced and extends in a more posteromedial direction. The angulation of the molar row is similar to that of *Eliomys quercinus*. The ros-

trum is shortened and very robust. The incisive foramina are not well preserved in the composite model, but appear to be significantly narrower and of similar relative length as *Eliomys*. This is confirmed when compared with other fragmentary specimens of *L. melitensis* (e.g. SMF 71-1303 and NHMUK PV OR 49344). The infraorbital foramina in the composite model are not very pronounced and it is unclear whether this is due to the segmentation process, taphonomy or an actual reduction of this characteristic. The most anterior part of the infraorbital foramen is

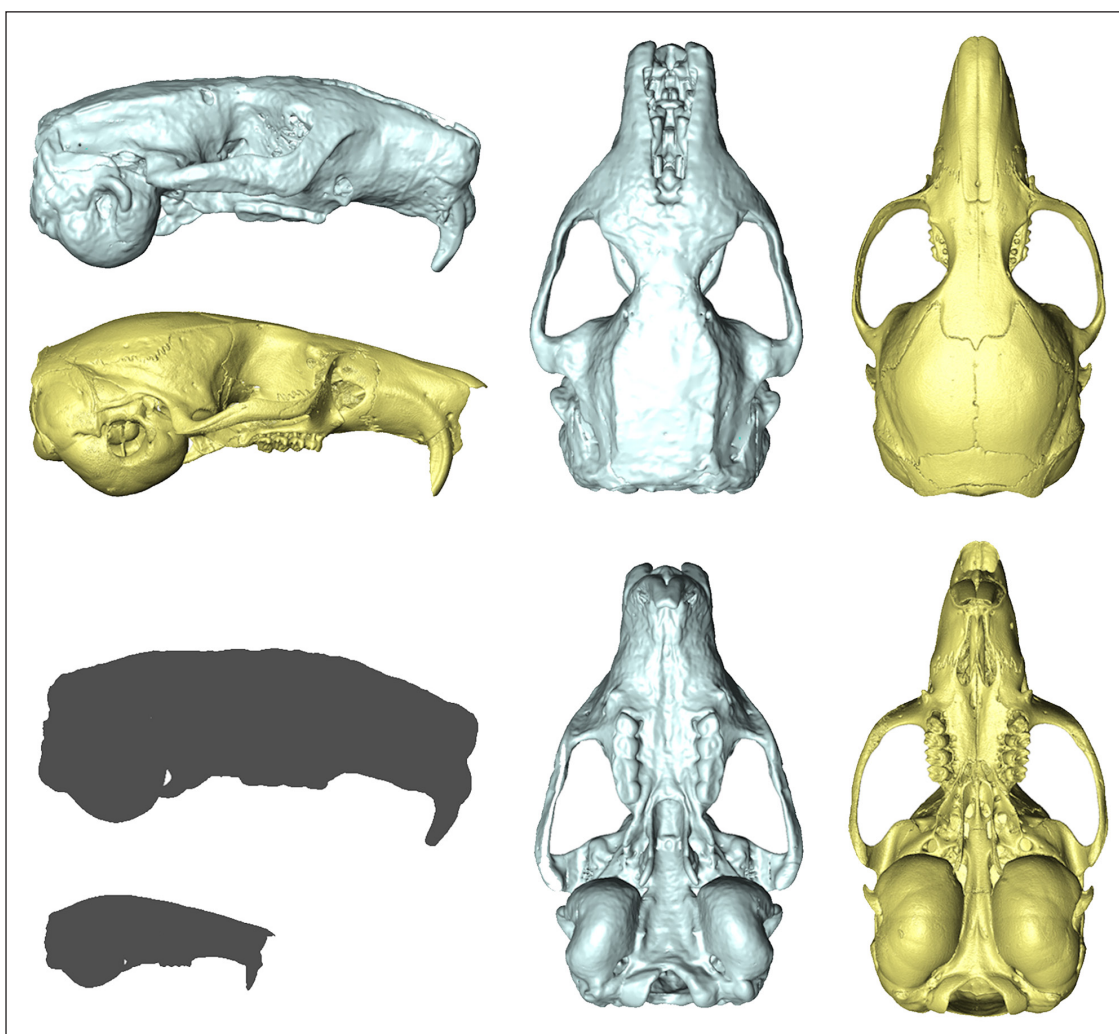


Figure 7: Comparison of *Leithia melitensis* (silver) and a consensus specimen of *Eliomys quercinus* (gold) (ID 60534). Shaded specimens in the lower left corner are scaled to represent the relative size difference (top *L. melitensis*, bottom *E. quercinus*).

located inferior to the superior part of the zygomatic plate, whereas it protrudes more anteriorly in extant dormice. The posterior margin of the hard palate is situated at a similar position i.e. the posterior end of the M3. The pterygoid flange is slightly enlarged and of similar length, but much more robust than the consensus *E. quercinus* skull. The lateral wall of the pterygoid fossa is slightly longer in the fossil specimen. The zygomatic area is less rounded, resulting in a triangular shaped orbital fossa when viewed dorsally, in contrast to the circular or elliptical shape present in *Eliomys*. The zygomatic plate is therefore narrower, extending less laterally, whereas the squamosal is more robust and extends laterally in a similar fashion. In lateral view, the zygomatic arch is more robust and its posterior part less curved ventrally. The maximum elevation of the arch is located roughly in the middle of the arch in both species. The anterior part of the zygomatic arch, including the zygomatic plate is much more robust. The upper part of the zygomatic plate is tilted anteriorly and located relatively ventrally. Furthermore, the anteroposterior depth of the zygomatic plate is much greater when viewed dorsally and laterally. The glenoid fossa for the articulation of the mandibular condyle is aligned parasagittally and is parallel to the occlusal plane, whereas the glenoid fossa of

Eliomys runs antero-medially and is tilted ventrally in lateral view (**Figure 7**). The frontal bone is of similar shape, although slightly broadened anteriorly in *Leithia*. Both genera show a post-orbital constriction of the frontal in dorsal view. As information on the position of the sutures is not available, the exact location of the occipital and parietal bone was impossible to determine in the composite model. The posterior part of the cranium displays sharply angled temporal crests in comparison to the more smoothly curved vault in *Eliomys*, and indeed these crests are more pronounced than in any other extant dormouse (Wahlert et al., 1993). It appears that the area where the parietal bones are to be expected is less inflated, resulting in a relatively narrow part of the vault in this region. The auditory bullae are less inflated. The occipital condyles are slightly wider ventrally, and the foramen magnum is significantly narrower than in *Eliomys*.

Discussion

The CT scanning and segmentation of the fossil conglomerate from the cave floor of Poggio Schinaldo resulted in the discovery of hitherto unknown features in the cranium of the gigantic dormouse, *Leithia melitensis*. Petronio (1970) described an individual of this species containing

a complete zygomatic arch; however, the current whereabouts of this particular specimen are unknown. Therefore, the only accessible information on this feature until now has been a dorsally oriented black and white photograph (Petronio, 1970). The 3D reconstruction of the zygomatic arch clearly reveals the attachment site of the masseter muscle, which will facilitate future biomechanical analysis of feeding in *L. melitensis*. The incisors present in the slab were difficult to segment. Nevertheless, as rodent incisors are often missing in fossil specimens, the upper incisors revealed here, and their orientation with respect to the skull, will provide clues to the gnawing behaviour of *L. melitensis* and how they would have occluded with the relatively foreshortened lower incisors.

The unique composition of the slab, including the large number of cranial fragments of *L. melitensis*, enabled the creation of an almost complete composite model of this rare species. Additional skull fragments from different

cave localities would complement the composite model further by including information on e.g. the position of sutures or the shape of the nasal bone. However, due to the difficult nature of dating cave deposits, it would be impossible to assure that these specimens are of the same age. Furthermore, the locations of the various Sicilian fossil sites are scattered significantly across the island. Grotta Spinagallo, a well-known site including *L. melitensis* specimens, is over 200 km south-east of Poggio Schinaldo. Material from this site could indicate a separated population, both temporally and geographically, with associated morphological variation. The composition of the cranial fragments within the slab suggests that the animals were deposited at the same time. The shared location and geological age contributes to the accuracy of our composite model, especially as this species is considered to have inhabited the island of Sicily for a prolonged period of time during the Pleistocene.

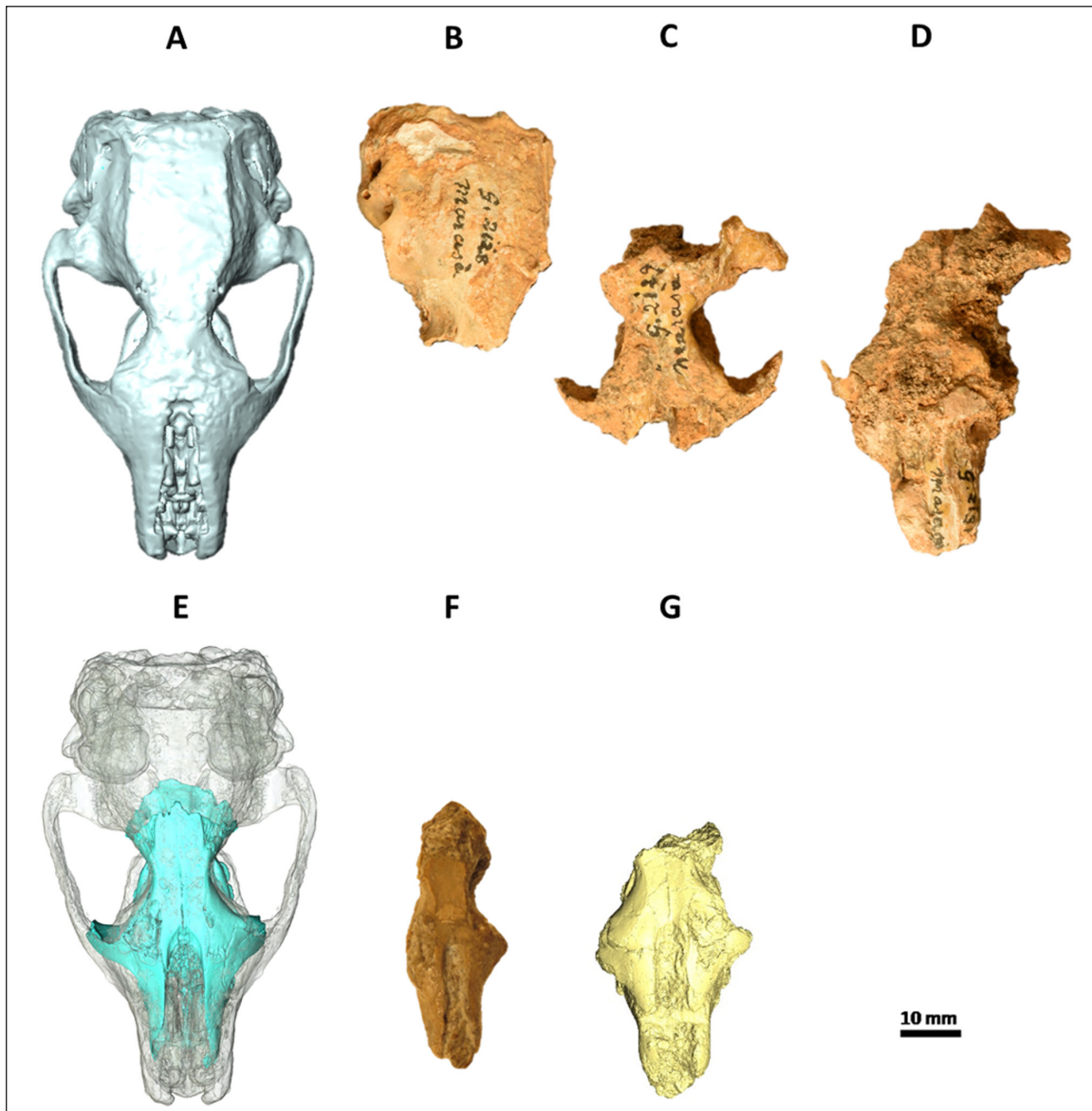


Figure 8: Various skull fragments of *L. melitensis* and the composite skull in dorsal view: **A.** composite skull, Poggio Schinaldo (Sicily); **B.** NMBA G.2128, Marasà cave (Sicily); **C.** NMBA G.2129, Marasà cave (Sicily); **D.** NMBA G.2132, Marasà cave (Sicily); **E.** SMF 71-1303, Spinagallo cave (Sicily) overlapping the composite model (transparent) **F.** NMI F 19835, Holotype, Maghlaq cave (Malta); **G.** NHMUK PV OR 49344 (Malta).

Comparison of the composite skull with other cranial fragments

Interestingly, all the *L. melitensis* skulls within the floor segment are significantly larger than the holotype from Malta (**Figure 8**). The holotype includes the molars of the left molar row (M1–M3) and the maxillofrontal, premaxillofrontal, and nasofrontal sutures (**Figure 1B**). Dental characteristics within the holotype could not be evaluated because of the poor preservation of the molars. Most of the anterior part of the cranium is present, with the exception of the nasal bone and the incisors. The rostrum appears to be slightly crushed laterally. The frontal bone is mostly complete and only the most posterior part of this feature is missing (**Figure 1B**). The posterior part of the skull is not preserved in the holotype. The entire specimen is only slightly deformed by taphonomic processes, resulting in the rostrum deflecting to the left when examined dorsally (**Figure 1B**). The internal structure of the specimen appears to be filled with sediment, indicating that internal features are presumably broken or absent. As no CT data of the holotype is available, its internal structure has not been analysed. Due to the incomplete state of the holotype, it proved rather difficult comparing the composite model with the holotype in detail. The rostrum appears to be relatively more elongated in the holotype. Furthermore, the composite model appears to be also larger when compared with a fairly complete cranial fragment from Malta, described by Lydekker (1895) (NHMUK PV OR 49344; **Figure 8G**), and a skull fragment from Spinagallo cave, near Siracusa, Sicily (Senckenberg Institute 71–1303; **Figure 8F**). These skulls are in a better state than the holotype. Also, they provide valuable information on certain cranial characteristics within *L. melitensis* that are absent or not well-defined in the composite model, especially regarding the location of premaxillary-maxillary suture and the incisive foramen. Although clearly smaller than the composite model, both specimens and the holotype are considered adults based on the eruption of the third molar and the lack of deciduous premolars. Material of *L. melitensis* was extracted from Marasà cave, in the north of Sicily and relatively near Poggio Schinaldo. Cranial fragments from this cave have the same proportions as the composite model. It appears that *L. melitensis* fluctuated in size geographically, and possibly over time as well. It would be interesting to compare fossil material from various localities in more detail in order to determine the extent of morphological and size variation within this endemic species.

Evaluating the condition of the segmented material, no apparent deformation appears to have occurred during the fossilisation process. The presence of the calcareous nodules and the bony matrix did result in difficulties with the segmentation. Furthermore, the warping and merging of various specimens might have added additional errors to the model. However, we consider these issues inevitable regarding the state of the material and the quality of the scans. The composite model created by segmenting this slab enables us to analyse the cranial morphology of this gigantic dormouse more accurately than before.

The composite model was compared with its presumed nearest living relative, *Eliomys quercinus*, in

order to evaluate morphological alterations that could consequently be linked to gigantism. Overall, the giant dormouse appears to be more robust in its cranial structure; with a relatively shortened rostrum, a very robust zygomatic plate and arch as well as relatively enlarged molars and premolars. These morphological changes can be linked either with the ecological niche *Leithia melitensis* occupied or a structural adaptation for coping with the actual size increase it has undergone. The sturdy zygomatic arch and thickened zygomatic plate suggest a highly developed deep masseter muscle, indicating modifications within the masticatory system. *Hypnomys*, the giant dormouse from the Balearic, is smaller than *Leithia melitensis* (Skull length *H. morpheus* \approx 46 mm, *L. melitensis* \approx 69 mm), but shows similar cranial modifications. The zygomatic arch of *Hypnomys* is more robust than *Eliomys*, although not as robust as that of *Leithia*. The infraorbital foramen through which the zygomaticomandibularis protrudes is relatively small in *H. morpheus*. This is very unusual in dormice, resulting in a more sciuromorphic condition (Hautier et al., 2009). This foramen is small in the composite of *L. melitensis* (**Figure 6C**), although it is unclear whether this is the result of taphonomy or an actual characteristic. The cranial morphology of *Hypnomys* is suggested to be connected with a widened ecological niche, including harder food objects in their diet (Hautier et al., 2009). Differences between the two giants besides size are present in the morphology of the braincase, with *Hypnomys* appearing to have less sharply defined temporal crests than *Leithia*. This could suggest an enlarged temporalis muscle, resulting in relatively increased bite forces in this species compared to other dormice. Furthermore, the rostrum of *Hypnomys* is more slender than that of *Leithia*, although clearly more robust than that of *Eliomys*. Both giant fossil dormouse genera show similar cranial modifications compared to *Eliomys*, but with less pronounced modifications in *Hypnomys*. Considering *Leithia* is larger than *Hypnomys*, it would be interesting to investigate whether this path to gigantism is allometric. Furthermore, if similar cranial modifications evolved in both insular populations, what drove *Leithia* to continue to grow and change morphologically whereas *Hypnomys* stopped? One potential explanation for size increases in insular dormice is a lack of predators on Mediterranean islands in the Pleistocene, although it should be noted that the extinct otter *Nesolutra* has been found within Poggio Schinaldo (Esu et al., 1986) and elsewhere on Sicily (Chilardi, 1996). However, given the diet of modern European otters, it is unlikely that *Nesolutra* preyed on rodents. The cranial morphology may also be a reflection of diet in this species. The robust zygomatic arch is likely an indication of large masseter muscles, which could suggest increased herbivory in the feeding ecology in *Leithia melitensis*.

Alongside skull fragments, several long bones and smaller elements are present within the scan. Although some of this material presumably belongs to *Leithia* sp., the hollow structure of certain bones indicates an avian origin. Considering the large quantity of bone material, the cave could potentially have been the refuge of a terrestrial or avian predator. In addition, the presence of an

unidentified egg in the cave indicates that at least some nesting behaviour occurred at a point in time at this locality. The avifauna during the Pleistocene on Sicily is distinctly modified (Pavia, 1999), with endemic owls morphologically modified to a terrestrial life style (Pavia and Mourer-Chauviré, 2002). Barn owl pellets are characterized by their high concentration of intact bone material in comparison to other owls and birds of prey (Dodson & Wexlar, 1979). Thus, the number of well-preserved skulls in the fossil slab leads us to speculate that this cave may have been the nesting site of a barn owl. Pavia & Mourer-Chauviré (2002) described the presence of *Athene trinacriae* remains in the cave (MGUP PS 77, MGUP PS 78), but this species has previously been considered too small to prey on gigantic rodents like *L. melitensis*. In contrast, the larger *Tyto mourerchauvireae*, known from other cave deposits from the Middle Pleistocene of Sicily, has been suggested by other authors to have preyed on *L. melitensis* (Pavia, 2004). Putting all the evidence above together, we hypothesise this cave to have been a nesting site of the giant barn owl, *T. mourerchauvireae*.

The lack of mandibular material in the slab is peculiar, especially as it is usually the most abundant bone present in barn owl pellets (Dodson & Wexlar, 1979). Esu et al. (1986) described the presence of mandibles belonging to *Leithia* sp., whereas not a single mandible was identified within the analysed conglomerate. Extraction of the material manually from the slab by previous researchers seems unlikely, due to the brittleness of the conglomerate's structure. Moreover, this fails to explain the absence of mandibular material more deeply embedded within the slab. A more likely scenario involves separation of the cranium and mandible material by water before fossilization (Levinson, 1982), which would explain the documentation of mandibles on site, but absence of the material within the slab.

Conclusions

The composite model of the insular gigantic dormouse *Leithia melitensis* clarifies some of cranial features of this endemic species. Comparison with its nearest living relative indicates distinct morphological features to be present in this animal, some of which are linked with the development of more powerful masticatory muscles. Due to the scarce and fragmented condition of the fossil record, this approach to creating composite morphologies is extremely valuable in cases such as *L. melitensis*. After digitally merging cranial elements of various skulls, we made an accurate approximation of cranial shape in this gigantic dormouse. This composite reconstruction is likely to play an important role in future research to improve our understanding of the causes and means by which some small animals evolve larger body sizes on islands.

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Competing Interests

VLH is an editor at Open Quaternary, but was removed from all editorial duties and had no access to the journal management system for the duration of paper handling (submission to acceptance). All other authors have no competing interests.

Author Contributions

JJH, VLH and PGC conceived the study. JJH segmented the data and reconstructed the composite model. CdP provided the slab and its transport to Basel, Switzerland. LC scanned the slab and organised the return of the slab to Palermo, Sicily. JJH drafted the manuscript. All authors contributed to the editing of drafts and the final manuscript, and gave final approval before submission.

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Appendix



Appendix A: Mounts.

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