

Title: Morphological divergence in giant fossil dormice

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1 **Abstract**

2 Insular gigantism – evolutionary increases in body size from small-bodied mainland ancestors - is a
3 conceptually significant, but poorly studied, evolutionary phenomenon. Gigantism is widespread on
4 Mediterranean islands, particularly among fossil and extant dormice. These include an extant giant
5 population of *Eliomys quercinus* on Formentera, the giant Balearic genus †*Hypnomys* and the
6 exceptionally large †*Leithia melitensis* of Pleistocene Sicily. We quantified patterns of cranial and
7 mandibular shape and their relationships to head size (allometry) among mainland and insular
8 dormouse populations, asking to what extent the morphology of island giants is explained by
9 allometry. We find that gigantism in dormice is not simply an extrapolation of the allometric trajectory
10 of their mainland relatives. Instead, a large portion of their distinctive cranial and mandibular
11 morphology resulted from population- or species-specific evolutionary shape changes. Our findings
12 suggest that body size increases in insular giant dormice were accompanied by evolutionary divergence
13 of feeding adaptations. This complements other evidence of ecological divergence in these taxa, which
14 span predominantly faunivorous to herbivorous diets. Our findings suggest that insular gigantism
15 involves context-dependent phenotypic modifications, underscoring the highly distinctive nature of
16 island faunas.

17

18 **Keywords**

19 Insular Gigantism; Geometric morphometrics; Allometry; Island rule; *Leithia*; *Hypnomys*

20

21 **Introduction**

22 Insular gigantism is a widespread macroevolutionary pattern [1,2]. It occurred on many Mediterranean
23 islands throughout the Neogene and Quaternary, and is known among small mammals including
24 dormice, hamsters, murids, lagomorphs, shrews and moonrats [3-10]. Despite its prevalence, the
25 ecological drivers of insular gigantism are rather complex, with climate, island area, availability of

26 resources, and the presence of competitors and predators all proposed to play a part [2, 11-18].
27 Similarly, the morphological consequences of gigantism are not well understood, and it is not clear
28 whether giant island species have attained large size via similar evolutionary pathways. This raises the
29 possibility that insular gigantism does not represent a single well-defined process, but in fact reflects
30 the outcomes of evolution in a broad set of distinct ecological contexts.

31 Shape changes associated with increasing body size (allometry) are suggested to either result
32 from optimised functionality based on natural selection, or from constraints that impose fixed or
33 slowly-evolving allometric trajectories [19]. Allometric constraints will result in shared allometric
34 patterns ('common allometry') among related species, and provide an expectation that evolution will
35 proceed along lines of least evolutionary resistance (or "genetic lines of least evolutionary resistance")
36 [20], represented by a multivariate factor of the genetic or phenotypic variation [21] (but see [22]).
37 Deviation from these lines might be expected during adaptation to distinct ecological niches, resulting
38 in functional modification in shape and size. However, the evolvability of allometric relationships, and
39 therefore the ability of ecological adaptation to cause divergent patterns of phenotypic evolution, is
40 variable [23,24]: divergence from allometric trajectories may be common on long macroevolutionary
41 timescales but are rare on shorter timescales.

42 The Island Rule describes extensive variation in both shape and size [1], and suggests a graded
43 trend from gigantism in small mammals to dwarfism in larger species [13]. The evolutionary timescales
44 of adaptation to insularity are generally short [25], meaning that divergence from an ancestral
45 allometric trajectory may be difficult to realise [24]. Nevertheless, the exceptional increase in body size
46 associated with insular gigantism can result in unexpected morphologies, and evolutionary shifts to
47 novel ecologies in context of the island setting might also be a powerful driver of evolutionary changes
48 in morphology via functional adaptation.

49 Dormice (Gliridae) are potent exemplars of the evolutionary 'island effect' of body size
50 increase, having evolved extraordinary large sizes more frequently than other mammals –and on at
51 least eight different islands since the beginning of the Miocene [26,27]. Furthermore, giant dormice

52 are known from both the fossil record (e.g. *Hypnomys* spp. from the Balearic Islands and *Leithia* spp.
53 from Sicily and Malta) and an extant population of *Eliomys quercinus* on the island of Formentera [28].
54 Dormice therefore provide an ideal study system for addressing key questions regarding insular
55 gigantism.

56 The fossil giants *Hypnomys* and *Leithia* most likely evolved from a mainland ancestor related
57 to the genus *Eliomys* (Leithiinae) [29,30,31]. Previous studies uncovered craniomandibular differences
58 between extant *Eliomys* populations and fossil island genera [31-34]. The possibility that they were
59 more than simply enlarged forms of their mainland relatives is further supported by the change in
60 ecological niche displayed by the extant giant population on Formentera, which shows increased
61 faunivory in its diet [28]. Furthermore, the morphological features of the extinct island giants imply
62 alternative lifestyles such as increased terrestriality in *Hypnomys* [31] and herbivory in *Leithia* [32].

63 Here, the cranial and mandibular morphology in the extant giant *Eliomys quercinus* from
64 Formentera and the extinct giant genera *Leithia* and *Hypnomys* are investigated in the context of a
65 large dataset of non-giant dormouse skulls. *Eliomys quercinus* has a large geographic distribution
66 across Europe, including several populations on Mediterranean islands. Alongside fossil giants and the
67 extant giant population on Formentera, non-giant *E. quercinus* still display significant intraspecific size
68 variations. We aim to understand the transformation of cranial and mandibular form (size and shape)
69 in giant dormice by investigating the allometric trajectory of non-giant dormice. Characterisation of
70 the common allometric trajectory within *E. quercinus* populations enables us to distinguish between
71 morphological differences occurring due to size variations and those potentially related to other
72 factors. We ask to what extent the cranial and mandibular morphologies of island giant dormice are
73 predicted by extrapolation of the allometric trajectory for extant non-giant dormice, or whether
74 additional morphological variation occurs during evolution of giant size – possibly driven by island-
75 specific shifts in ecology.

76

77 **Material and Methods**

78 *Sample*

79 We analysed the skulls and mandibles of 63 adult specimens (fully erupted third molar) of the extant
80 species *Eliomys quercinus*. Specimens were from the collections of the Senckenberg Museum,
81 Frankfurt (SMF), the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Natural History
82 Museum, London (NHMUK). Table S1 includes a full list of all extant specimens used in this study and
83 details of our μ CT scanning methods are given in Appendix S1. Because only adult individuals were
84 analysed, our analyses (see below) describe patterns of static allometry.

85 Size variation in *Eliomys* was characterised among geographically separated extant
86 populations and in fossil giants. We used centroid size (the square root of the summed squared
87 distances between landmarks and the centroid [35]) derived from our landmark configurations as a
88 size proxy. Our subsequent analyses focused on quantifying allometry within a single species, *Eliomys*
89 *quercinus*, the closest living relative of insular giant dormice lineages [29,30,31]. Ideally, we would
90 compare extinct giant dormice with their specific mainland ancestor populations. However,
91 phylogenetic relationships among populations of *E. quercinus* are not currently known, let alone the
92 relationships of mainland populations with extinct island giants.

93 Fossil specimens of the insular species *Hypnomys onicensis*, *H. morpheus* and *Leithia melitensis*
94 were included in the analyses based on μ CT models (Appendix S1), with small missing portions
95 reconstructed from photogrammetric models of other specimens. The fossil specimens include: a
96 composite reconstruction of the skull of *L. melitensis* based on specimens present at the Museo
97 Geologico Gemmellaro (mgupPS 78: 1-5)[32]; the reconstruction of an *L. melitensis* mandible located
98 at the Museo Universitario di Scienze Della Terra, Rome (MUST R2s26); a well preserved skull of *H.*
99 *morpheus* from Cova des Coral-loides (unnumbered specimen, under the responsibility of the Heritage
100 Authorities of the Consell Insular de Mallorca, Palma); and a mostly complete skull of the giant Balearic
101 dormouse *H. onicensis* in the collection of the Institut Mediterrani d'Estudis Avançats, Esporles,
102 Mallorca (IMEDEA 106855). Although this specimen is likely a sub-adult, based on size, dental wear
103 and the unfused skull sutures, it is the most complete skull available of this species.

104

105 *Shape analyses of extant dormice*

106 Anatomical landmarks were recorded from each cranium (42 landmarks) and mandible (19 landmarks)
107 using Avizo Lite v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). The *Arothron* package [36] was
108 used to import the landmarks into R v3.5.3 [37]. We used 3D geometric morphometrics to characterize
109 shape variation among extant populations of *E. quercinus* and extinct giants. Generalized Procrustes
110 Analysis (GPA) was performed, translating the landmark coordinates to the origin, scaling to unit
111 centroid size, and rotating them to a shared orientation, using a least squares criterion [38,39]. This
112 analysis separates variation in size (centroid sizes) from variation in shape (Procrustes coordinates) so
113 they can be treated as individual variables. A Principal Component Analysis (PCA) was performed using
114 the geometric morphometric R package *Morpho* v2.6 [40], in order to evaluate the data in a lower
115 dimensional space and identify the largest variances in shape within the dataset.

116

117 *Allometry*

118 Analysis of variance (ANOVA) was used to test the effect of size on adult shape variation (i.e. static
119 allometry) in *E. quercinus* and the fossil giants. Using the `procD.lm()` function with 999 iterations in the
120 R package *geomorph* v3.2.0 [41], the following linear model formula was evaluated:
121 $shape \sim \log_{10}(size)$, in which size is represented by centroid size. This analysis asks what changes in
122 cranial or mandibular shape are associated with changes in cranial or mandibular size. Our initial
123 analyses included a categorical variable differentiating between non-giant and giant dormice for both
124 the extant dataset (including the extant Formentera giants), as well as the complete dataset (including
125 the fossil giants). When used as a covariate, $shape \sim \log_{10}(size) + giant$, this variable asks whether
126 giant dormice show specific differences in skull shape compared to non-giant dormice; when used as
127 an interaction term, $shape \sim \log_{10}(size) * giant$, it asks whether the relationship between shape
128 and size (i.e. its slope) differs between giant and non-giant dormice.

129 Subsequent analyses aimed to quantify the allometric signal among non-giant populations and
130 therefore used a more restricted sample, excluding giants. The independent effects of population
131 (defined by geographic location) and sex on shape were evaluated for non-giant *Eliomys* specimens
132 using the model: $shape \sim \log_{10}(size) + population + sex$ (Tables S2 and S3). We also asked
133 whether the effect of allometry varies among populations (Table S1) using the model formula:
134 $shape \sim \log_{10}(size) * population$. The significance of coefficients and interaction terms in these
135 models was assessed using ANOVA with permutation procedures.

136

137 *Predicted Shape Model*

138 The allometric relationship defined above can be used to evaluate the extent to which the morphology
139 of (giant) specimens is explained by their size. A multivariate regression for allometry $shape \sim size$
140 can be expressed as $Y = C + BX + E$ [42], in which Y is the shape vector, C is the intercept, B is
141 the vector of the regression coefficients for size and represents the angle of the slope of the
142 multivariate regression line, X represents centroid size, and E explains the error term. When using
143 Procrustes coordinates, the size component X can be evaluated as the difference between the centroid
144 size of each specimen and mean centroid size across all specimens. This procedure renders the
145 intercept term C redundant with the mean shape from Procrustes superimposition.

146 Our analyses of allometry among non-giant dormice demonstrated a small, but significant,
147 contribution of population (i.e. geographic location) to cranial and mandibular shape variation (Tables
148 S2 and S3). Therefore, we used the allometric relationships derived from the model
149 $shape \sim \log_{10}(size) + population$ among non-giant dormice for the allometric base model in the
150 subsequent analyses.

151

152 *Predicting shape from size.*

153 The base allometric model provides a predicted shape for each specimen based on its size. The
154 Procrustes coordinates of individual specimens can be projected on to an axis described by the vector

155 of size coefficients, B , from the multivariate regression [43]. This vector defines an axis in multivariate
156 space and is equivalent to the common allometric component (CAC) [44]. The orthogonal projection
157 of specimens onto this axis gives a regression (or CAC) score. The plot of regression score against size
158 provides a 2D representation of the allometric model. Shape residuals describe how the true shape of
159 each specimen differs from its predicted shape and are represented in the plot as the vertical (i.e.
160 shape) deviation of each specimen from the regression line.

161

162 *Predicting size from shape.*

163 The base allometric model can also be used to infer a 'predicted size' for each specimen based
164 on its shape (Procrustes coordinates). Predicted sizes identify whether the shape of a specific specimen
165 resembles that of a smaller or a larger specimen. They also allow us to infer a best-fit shape based on
166 predicted size, representing the shape a specimen would have if it only deviated from allometric
167 expectations by modification of the position on the allometry line (under the assumption that all shape
168 variation between specimens is associated with allometry).

169 Predicted sizes were inferred using a custom-written R function: `predict.size()` (Appendix S2).
170 This function uses the regression vector from the base allometric model to generate a series of
171 predicted shapes representing individuals of different sizes. These predicted shapes are calculated
172 using a $2 \times n$ matrix in which the first row comprises the vector of intercept values and the second row
173 comprises the coefficients of size in the base allometric model. This was multiplied by an $m \times 2$ matrix,
174 in which the first column consists solely of ones and the second column contains an ascending
175 sequence of size values of length m . Our `predict.size()` function by default sets the upper size limit to
176 1.5 times the size of the largest individual within the dataset. The resulting matrix is transformed to an
177 array based on the number of landmarks within the configuration and its dimensionality, creating a
178 dataset comprising a sequence of shape coordinate data associated with the allometric trajectory per
179 increment of size. This approach can be used to generate predicted sizes of external specimens that

180 were not included in the base allometric model, provided they are superimposed on the consensus
181 shape of this model.

182 The extent to which specimen shapes differ from the shapes predicted by allometry, given
183 their predicted sizes, provides a measure of the amount of shape difference between specimen shapes
184 and their deviation from allometric expectations (given actual sizes) that cannot be explained simply
185 by modification of position on the allometry line. It therefore allows us to quantify the amount of non-
186 allometric shape deviation exhibited by a specimen, which might, for example, reflect individual-,
187 population- or species-specific variation. This is calculated as the orthogonal projection of specimen
188 shapes on the regression vector. Our `predict.size()` function estimates this by evaluating the Procrustes
189 distances between the actual specimen shape and every proposed shape on the regression vector. The
190 proposed shape with the shortest Procrustes distances is the indicator for predicted size.

191 The relationship between predicted and actual size for each specimen was displayed
192 graphically via a 'predicted size versus actual size', or PSvAS, plot. This method is complementary to
193 existing allometric methods, and allows for the evaluation of the shape of individual specimens with
194 respect to the base allometric model. A line with intercept = 0 and slope = 1 on this plot represents
195 shapes with predicted sizes that match their actual sizes. This identity line divides the graph into two
196 sections, the lower-right indicating specimens with a centroid size exceeding the predicted centroid
197 size based on shape, and the upper-left including specimens with larger predicted sizes than the actual
198 centroid size.

199

200 *Application of PSvAS to the dormouse dataset*

201 The PSvAS method was used for analysing the shape of giant dormice, based on an allometric base
202 model including non-giant, extant *Eliomys quercinus* specimens. The fit of the fossil and extant giants
203 within the model was analysed to determine whether certain morphological features are in line with
204 the allometric predictions, or can be considered distinct characteristics for giants. Because the giant
205 dormice are considerably different in size and shape compared to non-giant *Eliomys*, including such

206 specimens will affect the GPA and therefore influence the inferred allometric component. Instead,
207 these specimens were superimposed to the consensus shape of the base model rather than being
208 included in the original GPA.

209

210 **Results**

211 *Shape variation in dormice.*

212 Principal component ordinations for both the cranial and mandibular dataset depict a clear signal
213 related to the distinctive morphology of giant species (Figure 1A,D). The first principal component is
214 correlated with size variation of extant, non-giant populations, with more positive values being
215 associated with larger individuals. The second principal component appears to distinguish between
216 extant (negative values) and fossil (positive values) giants. Overall, these patterns are more defined in
217 the cranial analyses.

218

219 *Size-shape relationships*

220 Our initial analyses of allometry demonstrate statistical significance for an independent variable
221 distinguishing between giant and non-giant dormice both when including only extant populations, and
222 for the complete dataset including fossil specimens (Tables S4 and S5). This indicates a role for non-
223 allometric shape variation during the origin of giant dormouse cranial and mandibular morphology.
224 The interaction term of this variable is non-significant for the extant dataset, but significant for the
225 complete dataset including fossil specimens. This indicates that the relationship between shape and
226 size among living and extinct giants from multiple islands is different to that among non-giant
227 populations (Figure 1B,E). Our subsequent analyses further interrogate and characterize these
228 differences.

229

230 *Allometric base model*

231 ANOVAs demonstrate statistically significant effects of size and population on the allometric
232 base models for both mandibular and cranial shape (Tables S2 and S3). The effect of sex (21 females;
233 24 males; 1 unknown) on mandibular and cranial shape is non-significant and sex was therefore was
234 excluded from further analyses ($p = 0.188$; $p = 0.271$). The interaction term between size and
235 population is also non-significant (mandible: $p = 0.548$; skull: $p = 0.346$), indicating that there is no
236 evidence for population-specific allometric effects in non-giant dormice. Thus, the best model is:
237 $shape \sim \log_{10}(size) + population$; which explains 53% of the total variation in both the
238 mandibular and cranial datasets (Tables S2 and S3). The PSvAS model was used to evaluate the shape
239 of giant dormice crania and mandibles with respect to this allometric model, based solely on non-giant
240 dormice (Figure 1C,F).

241

242 *Predicted Size versus Actual Size*

243 The PSvAS plots describe the relationship between the size of each specimen and its predicted
244 size based on shape in context of the allometric model (Figures 1C,F and 2). Giant specimens in these
245 graphs are located firmly below the identity line, indicating that their shapes resemble the crania and
246 mandibles of smaller individuals (Table S6). This effect is generally more pronounced for mandibles
247 than for crania (Figure 1). Furthermore, the larger fossil specimens deviate more from the identity line
248 compared to the extant giants from Formentera.

249

250 *Predicted and actual morphology of giant dormice*

251 Procrustes distances quantify the difference between the actual shape of giants and the
252 predicted shapes based on the allometric model (Table S6). Differences between giant shapes and
253 expectations under the allometric base model are relatively large (cranium: 0.07 – 0.18, mandible: 0.08
254 – 0.22), especially within the fossil genera *Hypnomys* and *Leithia*. These differences remain large even
255 when using the predicted (best fit) size given shape (Table S6; cranium: 0.07 – 0.13, mandible: 0.06 –
256 0.12), indicating that the actual morphology of giants is rather poorly predicted by the allometric

257 model, suggesting that giant dormouse cranial and mandibular morphologies originated via largely
258 non-allometric evolutionary processes.

259 Based on both their actual and predicted sizes, the crania of larger dormice are expected to
260 have upper incisors that curve more posteriorly, an inferiorly angled rostrum, an increased maximum
261 width of the zygomatic arch, and a relative narrowing of the auditory meatus (Figure 2). The predicted
262 relative narrowing of the auditory meatus is seen in the fossil taxa, but other aspects of the actual
263 shapes of the giants deviate from these predicted shapes: none show the predicted curvature in the
264 incisors, and the proposed inferior angle of the rostrum is only evident in *Leithia melitensis*. The
265 widening of the zygomatic arch is present within fossil giants, but is absent in the extant Formentera
266 giants. Furthermore, the zygomatic widening in the fossil giants is located much more anteriorly than
267 predicted.

268 Predicted mandibular morphology of giant dormice is also very different from their actual
269 shapes. The predicted shapes show a very narrow and antero-posteriorly elongated structure, whereas
270 the actual giants have robust mandibles, with the posterior part being greatly enlarged dorsoventrally.
271 Although the PSvAS graph implies a best-fit for giant mandibular shapes similar to that of non-giant
272 dormice, the large Procrustes distances between the fitted shape and the actual shape (Table S6)
273 indicate this is not the result of isometric scaling. Instead, the giants exhibit some unique
274 morphologies; e.g. distinct features in *L. melitensis* include a foreshortened and relatively straight
275 lower incisor, an exceptionally large and unperforated angular process, a posteriorly located anterior
276 margin of the masseteric ridge, and a vertically oriented coronoid process.

277 As the cranial and mandibular warps were created using the respective landmark
278 configurations, features not included in the configuration, such as the shape of the auditory bullae,
279 cannot be reliably assessed using the warped images. Figure S2 shows the positioning of the landmarks
280 on the giants with regards to their predicted shapes. The width of the zygomatic plate, visible in lateral
281 view, seems to increase with size in the fossil specimens. Furthermore, all giants appear to have a

282 sharply angled cranial vault. Lastly, we noticed a peculiar enlargement of the occipital condyle when
283 observing the μ CT scan of *H. morpheus*, not seen in other specimens.

284

285 **Discussion**

286 Extant giant Formentera dormice and fossil giant specimens of Sicily and Mallorca show substantial
287 craniomandibular differences from their non-giant relatives (*Eliomys quercinus*; Figures 1 and S3). Only
288 a small portion of these morphological differences can be explained by the allometric trajectories of
289 non-giant populations. Insular giant dormice therefore diverge substantially from allometric
290 expectations. Additionally, we recognized that different species of giant dormice show distinctive
291 deviations from their predicted shapes.

292

293 *Predicting giant size and shape*

294 The cranial and mandibular morphologies of living and extinct island giants are different from those
295 expected under an allometric model. Allometry-related aspects of the shapes of these giants are
296 generally more similar to those of smaller dormice (although they also show substantial non-allometric
297 shape differences), and this effect is more pronounced for the mandible than for the cranium (Figure
298 1C,F). Although the craniomandibular shapes of giant dormice are more similar to smaller dormice
299 than expected, this does not imply isometric scaling; the actual fit of the giants within the model is
300 rather poor, and is worse for larger specimens (see Procrustes distances Table S6). Phylogenetically,
301 the fossil specimens are more separated from the base model, potentially explaining the poor fit of
302 these shapes within the model. The biologically implausible geometries that result from extrapolation
303 of the allometric model to giant sizes provide an alternative explanation. For example, the predicted
304 skull shape based on the cranial size of *L. melitensis* (log centroid size = 5.02) has an unrealistically
305 flexed cranial vault and occipital region, including a highly constricted foramen magnum. A similarly
306 unlikely morphology is evident for mandibular geometry, with the expected shape at the size of *L.*
307 *melitensis* (log centroid size = 4.11) being implausible owing to the very thin mediolateral width of the

308 bone. Interestingly, the morphologies of smaller giants (Formentera population and *Hypnomys*) are
309 not correctly predicted by the allometric base model either. These observations suggest that flattening
310 or truncation of the allometric trajectory occurs at large size in order to maintain biological
311 functionality.

312 Only part of the morphology of giant dormice can be explained by flattening of the allometric
313 trajectory — large differences are also evident in comparison to their expected shapes based on
314 (smaller) ‘best fit’ centroid sizes (Table S6; Figure 2). This indicates the presence of population-specific
315 morphological features within island giants, potentially reflecting adaptive variation due to island-
316 specific environmental conditions or ecological shifts. For example, the extant giant population of
317 Formentera is noticeably more faunivorous compared to other populations [28]. This suggests either
318 that insular body size increases have resulted in a dietary niche shift, or that a shift towards carnivory
319 reflects insular selective pressures on Formentera and is the driver of evolutionary increases in body
320 size. Although this is not the classic explanation of large body size in small mammals on islands [1], it
321 indicates that morphological variation among dormouse populations could represent allometry and
322 dietary (or other ecological) adaptations.

323

324 *Morphological traits of giant dormice*

325 Cranial morphology of island giants clearly deviates from the allometric expectations, even when
326 compared to their ‘predicted sizes’ (i.e. best-fit sizes to the line of allometry; Figure 2). The robust
327 rostrum and narrowing of the infraorbital foramen within all fossil giants are not predicted by the
328 allometric model at any cranial size. The model predicts the zygomatic arch in giants to become more
329 enlarged posteriorly. In reality, the arch does get more robust, but its maximum width is located much
330 more anteriorly. Larger dormice show a dorso-ventral flattening of the skull and changes to the
331 posterior part of the mandible, such as an elongated coronoid process and enlarged condylar and
332 angular processes. These are areas associated with masticatory muscle attachment [45], and their
333 modification suggests relative increases in molar bite force [46,47] or gape [48,49]. Multiple studies

334 have already shown that small changes in cranial and mandibular size and shape can affect mechanical
335 advantage and gape, both of which will impact the range of dietary items that can be processed. This
336 effect has been shown in a number of mammalian groups [50-53] but is particularly well-studied in
337 rodents [54-60]. The flattening of the skull is commonly seen in more rupicolous dormice [61],
338 although it may also be product of enlarged body size owing to negatively allometric scaling of brain
339 size [62] and craniofacial evolutionary allometry (CREA)[63]. This pattern, which is seen in many
340 mammalian groups, predicts relatively smaller braincases and longer rostra in larger species [64,65].

341

342 *Unique features of giant dormouse species*

343 Significant modifications to shape and size can result from evolutionary adaptation to novel ecologies,
344 including new diets [22]. We therefore interpret the unique morphological features identified in the
345 giant dormouse populations as reflecting specific ecological adaptations to insular settings. As well as
346 diverging from the non-giant allometric trajectory, giant dormice also differ morphologically from one
347 another. Such differences can be the result of various factors, including variation in ecosystem
348 composition, ecological niche occupation, as well as duration of isolation on islands. The introduction
349 of *Eliomys quercinus* to Formentera is thought to have occurred roughly 4000 years ago, whereas both
350 *Hypnomys* and *Leithia* were isolated for millions of years. Even though the morphology of Formentera
351 dormice does not resemble an intermediate shape between an average-sized *E. quercinus* and the
352 fossil giants, the differences in duration of isolation are substantial. Many population-specific aspects
353 of giant dormouse cranial, and especially mandibular, structure complement previous evidence of
354 divergent dietary and other ecological traits in these taxa.

355

356 *Formentera*

357 The Formentera dormice are the only extant giants and are morphologically different from the fossil
358 giants. It is the only giant population retaining a large infraorbital foramen. Furthermore, the
359 mandibular morphology of this population is characterised by a deep angular notch and relatively large

360 coronoid process, in contrast to the fossil giants. This enlarged coronoid results in a larger attachment
361 area for the temporalis muscle, suggesting an increased incisor bite force, which would be
362 advantageous for the extensive faunivorous behaviour observed within the Formentera population
363 [28]. Previous research has suggested that faunivory, more than other diets, places unique pressures
364 on rodents, driving greater morphological change [59,66]. However, this is not the case in the dormice
365 studied here, with the Formentera population resembling non-giant dormice more than the other
366 giants, based on the relatively short Procrustes distances of the best-fit in the PSvAS model (cranium
367 0.07; mandible 0.06) (Table S6).

368

369 *Hypnomys*

370 The *Hypnomys* material in our dataset is much more robust than other dormice, with the exception
371 of *Leithia melitensis*. The PSvAS model indicates that the morphology of this genus is substantially
372 different from extant dormice (cranium 0.10; mandible 0.08). The *H. onicensis* specimen examined
373 here is considered a subadult and is less robust than *H. morpheus*. The latter is characterised by
374 exceptionally pronounced occipital condyles. The robust morphology of the zygomatic area and
375 mandible in the two *Hypnomys* specimens indicates well developed masseteric musculature, which
376 suggests a diet including tough foods for this genus. A more abrasive plant-based diet has also been
377 suggested based on molar microwear [67].

378

379 *Leithia*

380 *Leithia melitensis* is the largest and most robust dormouse. *Hypnomys* and *Leithia* show similar
381 morphological modifications, although these are often more pronounced within *Leithia* [32]. This also
382 explains the relatively large Procrustes distances seen in the PSvAS model for this species (cranium
383 0.13; mandible 0.12). In particular, the width of the rostrum and the zygomatic plate is exceptional.
384 The mandible within this giant has very large angular and condylar processes. It is the only giant in
385 which there appears to be no fenestration of the angular process. However, the functional significance

386 of this fenestra is unknown. The coronoid is deflected less posteriorly, resulting in a more upright
387 position. The anterior margin of the masseteric ridge is positioned more posteriorly than in other
388 dormice and the incisor is relatively short and curves less superiorly. The cranial and mandibular
389 features seen in *L. melitensis*, in particular the exceptionally robust mandible, likely represent
390 adaptations to a herbivorous diet [68], possibly explaining its extraordinary size. In addition,
391 considerable variability in wear of the molar row is seen within the analysed fossil material of *L.*
392 *melitensis* (Figure S4), indicating a relatively abrasive diet against which the molars were used
393 extensively, also consistent with herbivory.

394

395 *Conclusion*

396 Multiple, independent dormice lineages achieved exceptional large size in insular habitats since the
397 end of the Messinian Salinity Crisis (5.33 Ma [69]). Extrapolation of common allometry as an
398 evolutionary line of least resistance on short timescales predicts that island giants could have highly
399 similar craniomandibular morphologies. Moreover, a graded trend to gigantism as proposed by the
400 island rule suggests that the importance of selective pressures within an ecosystem varies in a
401 predictable manner [13,14]. However, we find that the morphologies of giant dormice are not an
402 extrapolation along the allometric gradient of non-giant populations. This indicates that insular
403 gigantism may lead to a deviation from the otherwise strong allometric conservatism suggested to
404 exist in rodents [70]. Furthermore, the cranial and mandibular features of giant dormice contain a
405 prominent population-specific component, illustrating divergence and inherently non-predictable
406 adaptations to various different ecological niches, on different islands. These differences in the
407 evolutionary pathways of island giants may reflect differences in ecosystem composition among
408 islands and through geological time. Our findings have implications that extend beyond the study of
409 giant dormice, suggesting that island adaptation may commonly involve ecological shifts that are
410 unique and context-dependent, resulting in a high diversity of evolutionary responses to insular
411 habitats in mammals.

412

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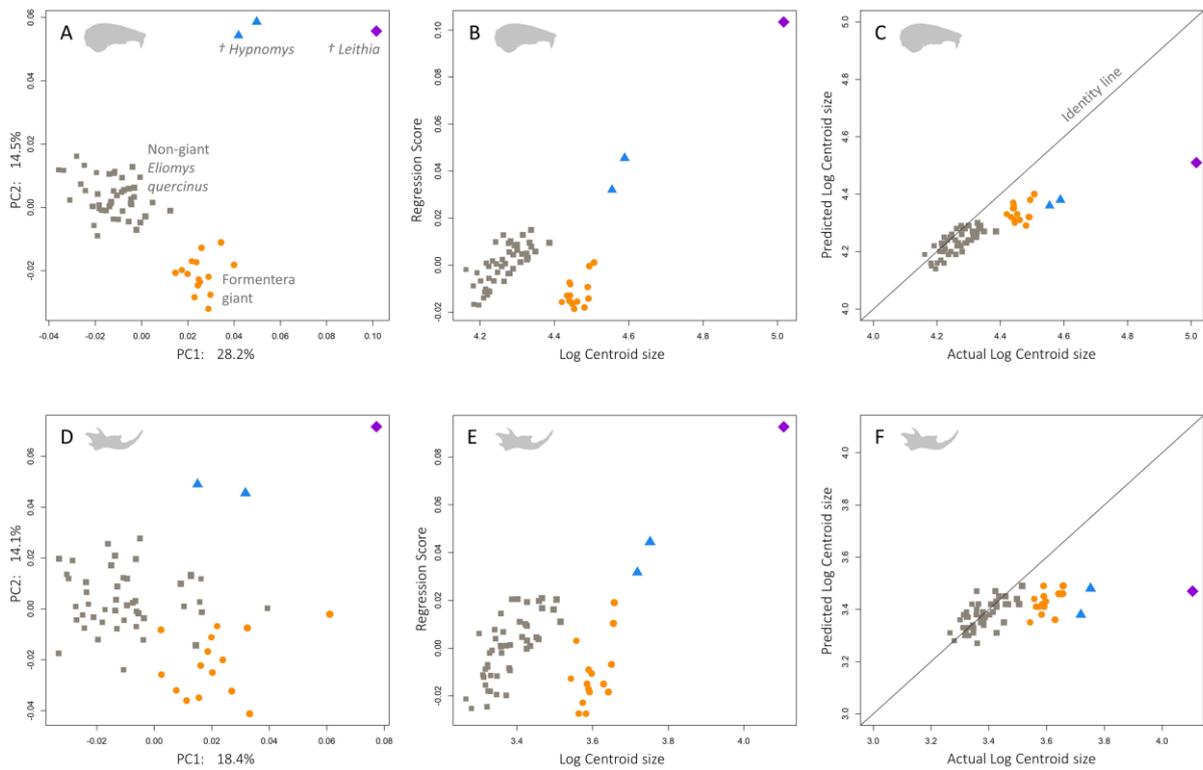
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596 Figure 1: Cranial (top) and mandibular (bottom) shape differentiation in extant *Eliomys quercinus*
 597 specimens and fossil giants on the first two principal components (A,D); the common allometric
 598 component versus log centroid size with grouping (B,E); and the predicted size versus actual size
 599 analyses based on a non-giant base model including the predicted sizes for the giant Formentera
 600 population and fossil giants (C,F).

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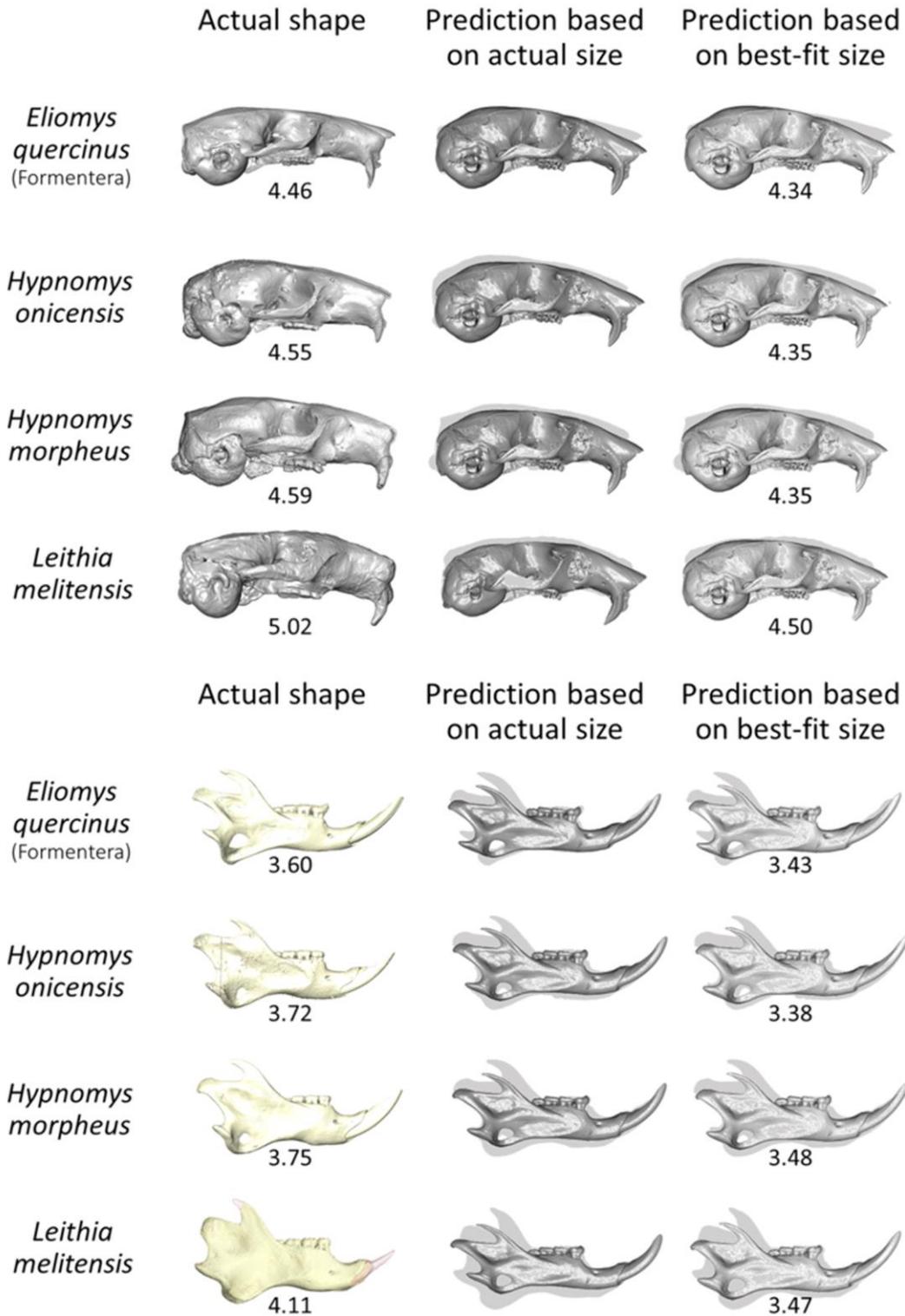
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611 Figure 2: Predicted shapes of the fossil giants derived from the PSvAS model, using the shape

612 predicted by the actual centroid size of the specimen and the shape presumed to be the best fit with

613 the actual shape of the specimen.