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Morphological divergence in giant fossil dormice

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

1. Introduction

Insular gigantism is a widespread macroevolutionary pattern [1,2]. It occurred on many Mediterranean islands throughout the Neogene and Quaternary, and is known among small mammals including dormice, hamsters, murids, lagomorphs, shrews and moonrats [3–10]. Despite its prevalence, the ecological drivers of insular gigantism are rather complex, with climate, island area, availability of resources, and the presence of competitors and predators all proposed to play a part [2,11–18]. Similarly, the morphological consequences of gigantism are not well understood, and it is not clear whether giant island species have attained large size via similar evolutionary pathways. This raises the possibility that insular gigantism does not represent a single well-defined process, but in fact reflects the outcomes of evolution in a broad set of distinct ecological contexts.

Shape changes associated with increasing body size (allometry) are suggested to either result from optimized functionality based on natural selection, or from constraints that impose fixed or slowly evolving allometric trajectories [19]. Allometric constraints will result in shared allometric patterns (common allometry) among related species, and provide an expectation that evolution will

proceed along lines of least evolutionary resistance (or ‘genetic lines of least evolutionary resistance’) [20], represented by a multivariate factor of the genetic or phenotypic variation [21] (but see [22]). Deviation from these lines might be expected during adaptation to distinct ecological niches, resulting in functional modification in shape and size. However, the evolvability of allometric relationships, and therefore the ability of ecological adaptation to cause divergent patterns of phenotypic evolution, is variable [23,24]: divergence from allometric trajectories may be common on long macroevolutionary time scales but are rare on shorter time scales.

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

Dormice (Gliridae) are potent exemplars of the evolutionary ‘island effect’ of body size increase, having evolved extraordinary large sizes more frequently than other mammals—and on at least eight different islands since the beginning of the Miocene [26,27]. Furthermore, giant dormice are known from both the fossil record (e.g. *Hypnomys* spp. from the Balearic Islands and *Leithia* spp. from Sicily and Malta) and an extant population of *Eliomys quercinus* on the island of Formentera [28]. Dormice therefore provide an ideal study system for addressing key questions regarding insular gigantism.

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

Here, the cranial and mandibular morphology in the extant giant *E. quercinus* from Formentera and the extinct giant genera *Leithia* and *Hypnomys* are investigated in the context of a large dataset of non-giant dormouse skulls. *E. quercinus* has a large geographical distribution across Europe, including several populations on Mediterranean islands. Alongside fossil giants and the extant giant population on Formentera, non-giant *E. quercinus* still display significant intraspecific size variations. We aim to understand the transformation of the cranial and mandibular form (size and shape) in giant dormice by investigating the allometric trajectory of non-giant dormice. Characterization of the common allometric trajectory within *E. quercinus* populations enables us to distinguish between morphological differences occurring due to size variations and those potentially related to other factors. We ask to what extent the cranial and mandibular morphologies of island giant dormice are predicted by extrapolation of the allometric trajectory for extant non-giant dormice, or whether additional morphological

variation occurs during evolution of giant size—possibly driven by island-specific shifts in ecology.

2. Material and methods

(a) Sample

We analysed the skulls and mandibles of 63 adult specimens (fully erupted third molar) of the extant species *E. quercinus*. Specimens were from the collections of the Senckenberg Museum, Frankfurt (SMF), the Muséum National d’Histoire Naturelle, Paris (MNHN) and the Natural History Museum, London (NHMUK). Electronic supplementary material, table S1 includes a full list of all extant specimens used in this study and details of our μ CT scanning methods are given in electronic supplementary material, appendix S1. Because only adult individuals were analysed, our analyses (see below) describe patterns of static allometry.

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

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

(b) Shape analyses of extant dormice

Anatomical landmarks were recorded from each cranium (42 landmarks) and mandible (19 landmarks) using Avizo Lite v. 9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). The Arothron package [36] was used to import the landmarks into R v. 3.5.3 [37]. We used three-dimensional geometric morphometrics to characterize shape variation among extant populations of *E. quercinus* and extinct giants. Generalized procrustes analysis (GPA) was performed, translating the landmark coordinates to the origin, scaling to unit centroid size and rotating them to a shared orientation, using a least-squares criterion [38,39]. This analysis separates variation in size (centroid sizes) from variation in shape (Procrustes coordinates) so they can be treated as individual variables. A principal component analysis (PCA) was performed using the geometric morphometric R package Morpho v. 2.6 [40], in order to evaluate the data in a lower-dimensional space and identify the largest variances in shape within the dataset.

(c) Allometry

Analysis of variance (ANOVA) was used to test the effect of size on adult shape variation (i.e. static allometry) in *E. quercinus* and the fossil giants. Using the `procD.lm()` function with 999 iterations in the R package `geomorph` v. 3.2.0 [41], the following linear model formula was evaluated: $\text{shape} \sim \log_{10}(\text{size})$, in which size is represented by centroid size. This analysis asks what changes in cranial or mandibular shape are associated with changes in cranial or mandibular size. Our initial analyses included a categorical variable differentiating between non-giant and giant dormice for both the extant dataset (including the extant Formentera giants), as well as the complete dataset (including the fossil giants). When used as a covariate, $\text{shape} \sim \log_{10}(\text{size}) + \text{giant}$, this variable asks whether giant dormice show specific differences in skull shape compared to non-giant dormice; when used as an interaction term, $\text{shape} \sim \log_{10}(\text{size}) \times \text{giant}$, it asks whether the relationship between shape and size (i.e. its slope) differs between giant and non-giant dormice.

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

(d) Predicted shape model

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

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

(e) Predicting shape from size

The base allometric model provides a predicted shape for each specimen based on its size. The Procrustes coordinates of individual specimens can be projected on to an axis described by the vector of size coefficients, B , from the multivariate regression [43]. This vector defines an axis in multivariate space and is equivalent to the common allometric component (CAC) [44]. The orthogonal projection of specimens onto this axis gives a regression (or CAC) score. The plot of the regression score against size provides a two-dimensional representation of the allometric model. Shape residuals describe how the true shape of each specimen differs from its predicted shape and are represented in the plot as the vertical (i.e. shape) deviation of each specimen from the regression line.

(f) Predicting size from the shape

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

Predicted sizes were inferred using a custom-written R function: `predict.size()` (electronic supplementary material, appendix S2). This function uses the regression vector from the base allometric model to generate a series of predicted shapes representing individuals of different sizes. These predicted shapes are calculated using a $2 \times n$ matrix in which the first row comprises the vector of intercept values and the second row comprises the coefficients of size in the base allometric model. This was multiplied by an $m \times 2$ matrix, in which the first column consists solely of ones and the second column contains an ascending sequence of size values of length m . Our `predict.size()` function by default sets the upper size limit to 1.5 times the size of the largest individual within the dataset. The resulting matrix is transformed to an array based on the number of landmarks within the configuration and its dimensionality, creating a dataset comprising a sequence of shape coordinate data associated with the allometric trajectory per increment of size. This approach can be used to generate predicted sizes of external specimens that were not included in the base allometric model, provided they are superimposed on the consensus shape of this model.

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

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

(g) Application of PSvAS to the dormouse dataset

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

Figure 1. Cranial (top) and mandibular (bottom) shape differentiation in extant *Eliomys quercinus* specimens and fossil giants on the first two principal components (*a,d*); the common allometric component versus log centroid size with grouping (*b,e*); and the predicted size versus actual size analyses based on a non-giant base model including the predicted sizes for the giant Formentera population and fossil giants (*c,f*). (Online version in colour.)

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

3. Results

(a) Shape variation in dormice

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

(b) Size-shape relationships

Our initial analyses of allometry demonstrate statistical significance for an independent variable distinguishing between giant and non-giant dormice both when including only extant populations, and for the complete dataset including fossil specimens (electronic supplementary material, tables S4 and S5). This indicates a role for non-allometric shape variation during the origin of giant dormouse cranial and mandibular morphology. The interaction term of this variable is non-significant for the extant dataset, but significant for the complete dataset including fossil specimens. This indicates that the relationship between shape and size among the living and extinct giants from multiple islands is different to that among non-giant populations (figure 1*b,e*). Our subsequent analyses further interrogate and characterize these differences.

(c) Allometric base model

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

(d) Predicted size versus actual size

The PSvAS plots describe the relationship between the size of each specimen and its predicted size based on shape in the context of the allometric model (figures 1*c,f* and 2). Giant specimens in these graphs are located firmly below the identity line, indicating that their shapes resemble the crania and mandibles of smaller individuals (table 1). This effect is generally more pronounced for mandibles than for crania (figure 1). Furthermore, the larger fossil specimens deviate more from the identity line compared to the extant giants from Formentera.

(e) Predicted and actual morphology of giant dormice

Procrustes distances quantify the difference between the actual shape of giants and the predicted shapes based

Figure 2. Predicted shapes of the fossil giants derived from the PSvAS model, using the shape predicted by the actual centroid size of the specimen and the shape presumed to be the best-fit with the actual shape of the specimen. (Online version in colour.)

on the allometric model (table 1). Differences between giant shapes and expectations under the allometric base model are relatively large (cranium: 0.07–0.18, mandible: 0.08–0.22), especially within the fossil genera *Hypnomys* and *Leithia*. These differences remain large even when using the predicted (best-fit) size given shape (table 1; cranium: 0.07–0.13, mandible: 0.06–0.12), indicating that the actual morphology of giants is rather poorly predicted by the allometric model, suggesting that giant dormouse cranial and mandibular morphologies originated via largely non-allometric evolutionary processes.

Based on both their actual and predicted sizes, the crania of larger dormice are expected to have upper incisors that curve more posteriorly, an inferiorly angled rostrum, an increased maximum width of the zygomatic arch and a relative narrowing of the auditory meatus (figure 2). The

predicted relative narrowing of the auditory meatus is seen in the fossil taxa, but other aspects of the actual shapes of the giants deviate from these predicted shapes: none show the predicted curvature in the incisors, and the proposed inferior angle of the rostrum is only evident in *L. melitensis*. The widening of the zygomatic arch is present within fossil giants, but is absent in the extant Formentera giants. Furthermore, the zygomatic widening in the fossil giants is located much more anteriorly than predicted.

The predicted mandibular morphology of giant dormice is also very different from their actual shapes. The predicted shapes show a very narrow and antero-posteriorly elongated structure, whereas the actual giants have robust mandibles, with the posterior part being greatly enlarged dorsoventrally. Although the PSvAS graph implies a best-fit for giant mandibular shapes similar to that of non-giant dormice, the large

Table 1. Fit of extant and fossil specimens within the PSvAS model for the cranial (top) and mandibular (bottom) dataset, including Procrustes fits of shapes compared with predicted shape based on both centroid size and shape. The values for the extant *Eliomys* specimens are average values for all *E. quercinus* (non-giant) and all *E. quercinus* (Formentera), respectively.

	species	centroid size	Procrustes distance from predicted shape based on actual size	predicted (best fit) centroid size	Procrustes distance from predicted shape based on predicted size
<i>Eliomys quercinus</i> (non-giant)	4.26	0.0485	4.23	0.0476
	<i>Eliomys quercinus</i> (Formentera)	4.60	0.0725	4.34	0.0670
	† <i>Hypnomys onicensis</i>	4.55	0.1105	4.35	0.1002
	† <i>Hypnomys morpheus</i>	4.59	0.1159	4.35	0.1035
	† <i>Leithia melitensis</i>	5.02	0.1754	4.50	0.1312
<i>Eliomys quercinus</i> (non-giant)	3.38	0.0549	3.37	0.0533
	<i>Eliomys quercinus</i> (Formentera)	3.60	0.0763	3.43	0.0582
	† <i>Hypnomys onicensis</i>	3.72	0.1221	3.38	0.0783
	† <i>Hypnomys morpheus</i>	3.75	0.1128	3.48	0.0825
	† <i>Leithia melitensis</i>	4.11	0.2178	3.47	0.1223

Procrustes distances between the fitted shape and the actual shape (table 1) indicate this is not the result of isometric scaling. Instead, the giants exhibit some unique morphologies; for example, distinct features in *L. melitensis* include a foreshortened and relatively straight lower incisor, an exceptionally large and unperforated angular process, a posteriorly located anterior margin of the masseteric ridge and a vertically oriented coronoid process.

As the cranial and mandibular warps were created using the respective landmark configurations, features not included in the configuration, such as the shape of the auditory bullae, cannot be reliably assessed using the warped images. Electronic supplementary material, figure S2 shows the positioning of the landmarks on the giants with regards to their predicted shapes. The width of the zygomatic plate, visible in lateral view, seems to increase with size in the fossil specimens. Furthermore, all giants appear to have a sharply angled cranial vault. Lastly, we noted a peculiar enlargement of the occipital condyle when observing the μ CT scan of *H. morpheus*, not seen in other specimens.

4. Discussion

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

(a) Predicting giant size and shape

The cranial and mandibular morphologies of living and extinct island giants are different from those expected under an allometric model. Allometry-related aspects of the shapes of these giants are generally more similar to those of smaller dormice (although they also show substantial non-allometric

shape differences), and this effect is more pronounced for the mandible than for the cranium (figure 1c,f). Although the craniomandibular shapes of giant dormice are more similar to smaller dormice than expected, this does not imply isometric scaling; the actual fit of the giants within the model is rather poor, and is worse for larger specimens (see Procrustes distances in table 1). Phylogenetically, the fossil specimens are more separated from the base model, potentially explaining the poor fit of these shapes within the model. The biologically implausible geometries that result from the extrapolation of the allometric model to giant sizes provide an alternative explanation. For example, the predicted skull shape based on the cranial size of *L. melitensis* (log centroid size = 5.02) has an unrealistically flexed cranial vault and occipital region, including a highly constricted foramen magnum. A similarly unlikely morphology is evident for mandibular geometry, with the expected shape at the size of *L. melitensis* (log centroid size = 4.11) being implausible owing to the very thin mediolateral width of the bone. Interestingly, the morphologies of smaller giants (Formentera population and *Hypnomys*) are not correctly predicted by the allometric base model either. These observations suggest that flattening or truncation of the allometric trajectory occurs at large size in order to maintain biological functionality.

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

(b) Morphological traits of giant dormice

Cranial morphology of island giants clearly deviates from the allometric expectations, even when compared to their 'predicted sizes' (i.e. best-fit sizes to the line of allometry; figure 2). The robust rostrum and narrowing of the infraorbital foramen within all fossil giants are not predicted by the allometric model at any cranial size. The model predicts the zygomatic arch in giants to become more enlarged posteriorly. In reality, the arch does get more robust, but its maximum width is located much more anteriorly. Larger dormice show a dorsoventral flattening of the skull and changes to the posterior part of the mandible, such as an elongated coronoid process and enlarged condylar and angular processes. These are areas associated with masticatory muscle attachment [45], and their modification suggests relative increases in molar bite force [46,47] or gape [48,49]. Multiple studies have already shown that small changes in cranial and mandibular size and shape can affect mechanical advantage and gape, both of which will impact the range of dietary items that can be processed. This effect has been shown in a number of mammalian groups [50–53] but is particularly well studied in rodents [54–59]. The flattening of the skull is commonly seen in more rupicolous dormice [60], although it may also be a product of enlarged body size owing to negatively allometric scaling of brain size [61] and craniofacial evolutionary allometry (CREA) [62]. This pattern, which is seen in many mammalian groups, predicts relatively smaller braincases and longer rostra in larger species [63,64].

(c) Unique features of giant dormouse species

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

(d) Formentera

The Formentera dormice are the only extant giants and are morphologically different from the fossil giants. It is the only giant population retaining a large infraorbital foramen. Furthermore, the mandibular morphology of this population is characterized by a deep angular notch and relatively large coronoid process, in contrast to the fossil giants. This enlarged coronoid results in a larger attachment area for the temporalis muscle, suggesting an increased incisor bite force, which would be advantageous for the extensive faunivorous

behaviour observed within the Formentera population [28]. Previous research has suggested that faunivory, more than other diets, places unique pressures on rodents, driving greater morphological change [58,65]. However, this is not the case in the dormice studied here, with the Formentera population resembling non-giant dormice more than the other giants, based on the relatively short Procrustes distances of the best-fit in the PSvAS model (cranium 0.07; mandible 0.06) (electronic supplementary material, table S6).

(e) *Hypnomys*

The *Hypnomys* material in our dataset is much more robust than other dormice, with the exception of *L. melitensis*. The PSvAS model indicates that the morphology of this genus is substantially different from extant dormice (cranium 0.10; mandible 0.08). The *H. onicensis* specimen examined here is considered a sub-adult and is less robust than *H. morpheus*. The latter is characterized by exceptionally pronounced occipital condyles. The robust morphology of the zygomatic area and mandible in the two *Hypnomys* specimens indicates well developed masseteric musculature, which suggests a diet including tough foods for this genus. A more abrasive plant-based diet has also been suggested based on molar microwear [66].

(f) *Leithia*

Leithia melitensis is the largest and most robust dormouse. *Hypnomys* and *Leithia* show similar morphological modifications, although these are often more pronounced within *Leithia* [32]. This also explains the relatively large Procrustes distances seen in the PSvAS model for this species (cranium 0.13; mandible 0.12). In particular, the width of the rostrum and the zygomatic plate is exceptional. The mandible within this giant has very large angular and condylar processes. It is the only giant in which there appears to be no fenestration of the angular process. However, the functional significance of this fenestra is unknown. The coronoid is deflected less posteriorly, resulting in a more upright position. The anterior margin of the masseteric ridge is positioned more posteriorly than in other dormice and the incisor is relatively short and curves less superiorly. The cranial and mandibular features seen in *L. melitensis*, in particular the exceptionally robust mandible, likely represent adaptations to a herbivorous diet [67], possibly explaining its extraordinary size. In addition, considerable variability in wear of the molar row is seen within the analysed fossil material of *L. melitensis* (electronic supplementary material, figure S4), indicating a relatively abrasive diet against which the molars were used extensively, also consistent with herbivory.

5. Conclusion

Multiple, independent dormice lineages achieved an exceptional large size in insular habitats since the end of the Messinian Salinity Crisis (5.33 Ma) [68]. Extrapolation of common allometry as an evolutionary line of least resistance on short time scales predicts that island giants could have highly similar craniomandibular morphologies. Moreover, a graded trend to gigantism as proposed by the island rule suggests that the importance of selective pressures within an ecosystem varies in a predictable manner [13,14]. However, we find that the morphologies of giant dormice are not an

extrapolation along the allometric gradient of non-giant populations. This indicates that insular gigantism may lead to a deviation from the otherwise strong allometric conservatism suggested to exist in rodents [69]. Furthermore, the cranial and mandibular features of giant dormice contain a prominent population-specific component, illustrating divergence and inherently non-predictable adaptations to various different ecological niches, on different islands. These differences in the evolutionary pathways of island giants may reflect differences in ecosystem composition among islands and through geological time. Our findings have implications that extend beyond the study of giant dormice, suggesting that island adaptation may commonly involve ecological shifts that are unique and context-dependent, resulting in a high diversity of evolutionary responses to insular habitats in mammals.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material. MicroCT scans are uploaded to the MorphoSource project 'Dormice (Gliridae)' (https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/941)

Authors' contributions. J.J.H. and P.G.C. conceived the study. R.B.J.B., N.J. and J.J.H. scanned the extant specimens. V.L.H., J.A.A., E.T.-R. and J.J.H. provided scans of fossil material. J.J.H. reconstructed and land-marked the dataset, and developed the applied methodology with

R.B.J.B. J.J.H. drafted the manuscript. All authors contributed to the editing of the final manuscript and gave final approval before submission.

Competing interests. We declare we have no competing interests.

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