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Feeding biomechanics reveals niche differentiation related to insular gigantism

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Abstract

Insular gigantism is an evolutionary phenomenon whereby small animals become bigger on islands compared to their mainland relatives. The abundance of insular giant taxa in the fossil record suggests the presence of a universal “giant niche” present on islands, with resource limitation as a potential driver for this process. However, insular habitats are ecologically diverse, suggesting that island taxa adopt different survival strategies, including adaptations for foraging behaviors. Here, we used finite element analysis to evaluate insular feeding niche adaptations in some of the most extreme examples of insular gigantism: Mediterranean giant dormice. We calculated stress, strain, and mechanical advantage during incisor and molar biting for 3 extinct insular giant species (*Leithia melitensis*, *Hypnomys morpheus*, and *H. onicensis*), an extant giant (*Eliomys quercinus ophiusae*), and their extant non-giant mainland relative, the generalist-feeder *Eliomys quercinus*. Our results show that dietary adaptations vary between giant taxa on different islands, and can occur relatively rapidly. Furthermore, the functional mandibular morphology in some insular taxa indicate adaptations moving away from a generalist feeding strategy toward greater trophic specialization. We show that the “insular giant niche” varies between islands and across time periods, arguing against a universal ecological driver for insular gigantism in small mammals.

Keywords: insular gigantism, finite element analysis, Island evolution, dormice, *Leithia*, *Hypnomys*

Insular gigantism is an evolutionary phenomenon whereby small-sized species, notably mammals, achieve large body size on islands compared to their mainland relatives (Foster, 1964; Van Valen, 1973). Treated as one half of the “Island Rule” (alongside insular dwarfism of large mammals, sensu Van Valen, 1973), or as part of a wider Island Syndrome (sensu Adler & Levins, 1994), the causes of insular gigantism—and the validity of these ecophenotypic rules—continue to elicit much debate, in particular the interlinked role of diet and resource limitation (Case, 1978; Lawlor, 1982; Lomolino, 2005). Resource limitation is thought to be a key driver for insular gigantism in small mammals (Case, 1978; Grant, 1965; Hennekam et al., 2020a; Lawlor, 1982; Van Valen, 1973), with an increase in body size enabling exploitation of a wider dietary niche in an otherwise resource-limited island setting (Orlandi-Oliveras et al., 2016). Ecological release from predation, and the resultant reduction in extrinsic mortality, may also select for larger body size (and slower life history) via intraspecific competition (Angerbjörn, 1986; Melton, 1982; Palkovacs, 2003), making it difficult to unpick causal vs correlative factors in insular body size trends, particularly over short timescales.

Insular gigantism is particularly well known in the Gliridae (Hennekam et al., 2020a; Palombo, 2018; van der Geer et al.,

2010), with dramatic examples of insular gigantism known from the fossil record of dormice from the Mediterranean, most notably the ca. 200 g anagenetic *Hypnomys* lineage from the Plio-Pleistocene of Mallorca and Menorca (Moncunill-Solé et al., 2014; Orlandi-Oliveras et al., 2016), and ca. 1,000 to 1,500 g *Leithia melitensis* from the Middle Pleistocene of Sicily (Adams, 1863; estimated body mass based on *Canariomys bravoii* which has a similar skull size [Hennekam et al., 2020b; Michaux et al., 2012; Moncunill-Solé et al., 2014]). While the mainland ancestry of these fossil taxa is unknown, their closest living relative is the 75–80 g mainland garden dormouse, *Eliomys quercinus* (Bertolino & Cordero di Montezemolo, 2007; Bover et al., 2019; Daams & de Bruijn, 1995; Freudenthal & Martínez-Suárez, 2013), an omnivorous generalist feeder found across Europe and the Maghreb (Holden-Musser et al., 2016). *E. quercinus* is also the phyletic ancestor of the only extant insular giant dormouse, *Eliomys quercinus ophiusae* from the Balearic island of Formentera. At 130 g, *E. q. ophiusae* is roughly 1.5 times larger, than mainland *E. quercinus* (Hennekam et al., 2020a; Kahmann & Lau, 1972), and descended from an Iberian population of *E. quercinus* that arrived in Formentera following human colonization of the Balearics 4,000 years ago (Bover et al., 2008; Hautier et al., 2009). In contrast, both *Hypnomys*

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and *Leithia* lineages are thought to be Miocene relicts, evolving in isolation on their respective palaeoislands from the end of the Messinian Salinity Crisis, implying isolation times of up to 5 million years.

Dormice therefore provide a study system to evaluate feeding adaptation in a generalist colonizer across different timescales and degrees of size change, and thus explore the role of dietary niche in insular gigantism. With a diverse diet (encompassing seeds, fruits, leaves, invertebrates, small vertebrates, and eggs; [Kuipers et al., 2012]), mainland dormice are morphologically and behaviorally pre-adapted to consume a wide range of foodstuffs, and selection for further morphological adaptations might therefore be expected to be weak. Body size change alone would increase the potential dietary breadth owing to biomechanical scaling of bite force and gape, allowing larger and tougher foods to be consumed. Hennekam et al. (2020a) showed, however, that the shapes of the mandibles of insular giant dormice diverge from the extrapolated linear allometric trajectory seen in mainland-sized dormice in different ways, with each insular species instead showing a unique morphology that cannot be explained by size change (allometric or isometric) alone. Given that morphological differences between rodent mandibles have been shown to correlate with dietary ecology (Hennekam, 2022; Maestri et al., 2016; Michaux et al., 2007), with highly specialized adaptations in the attachment of masseteric muscles reflecting a clear distinction between the two feeding modes characteristic for Rodentia (gnawing at the incisor, and chewing at the molar row [Becht, 1953; Cox et al., 2012; Wood, 1965]), it is possible that these divergent morphologies reflect adaptations to disparate dietary niches. Intriguingly, while the diets of fossil taxa remain unknown, observational studies have shown increased faunivory in Formentera relative to mainland *E. quercinus* (Kahmann & Lau, 1972), although it is unclear whether this simply reflects behavioral plasticity in a generalist taxon.

Here, we tackle the issue of functional morphology directly in insular giant dormice for the first time, using finite element analysis (Rayfield, 2007) to evaluate the impact of mandibular shape variation on masticatory abilities. We compare the performance of mandibles from extant “mainland-sized” dormice with extant and extinct insular giant dormice, under different loading conditions, to assess the variation in stresses, strains, and elastic deformation during feeding. We use the biomechanical data as a proxy for feeding ecology, ground-truthed by observational data on the feeding ecologies of extant mainland and island taxa, and assess whether there is good evidence that previously observed morphological changes (Hennekam et al., 2020a) had a functional significance. If so, this would suggest that (a) the giant insular dormice shifted dietary niche compared to their mainland sister-taxa, and (b) the “island giant niche” varies between islands and across time periods, with implications for the generality of the island syndrome.

Material and methods

Institutional abbreviations

IGUP, Museo Di Geologia e Paleontologia, Padova; IMEDEA, Institut Mediterrani d'Estudis Avançats, Esporles, Mallorca; MUST, Museo Universitario di Scienze Della Terra, Rome; NHMUK, the Natural History Museum, London; SMF, Senckenberg Museum, Frankfurt.

Sample and scanning

Five dormouse specimens were microCT scanned for use in this study (Figure 1). Three belonged to extinct island species from the Mediterranean (*Leithia melitensis*, *Hypnomys morpheus*, and *H. onicensis*) and varied in size significantly. None of the fossil material was dated, and the chronology of the caves in which most material was found is not resolved. The fossil skull and left hemimandibles of *Hypnomys morpheus* (unnumbered specimen from Cova des Coral·loides, under the responsibility of the Heritage Authorities of the Consell Insular de Mallorca, Palma) and *H. onicensis* (IMEDEA 106855: Cova des Pas de Vallgorner) from Mallorca were scanned at the Centro Nacional de Investigación sobre la Evolución Humana (Burgos, a microCT VITomeX s240, GE Sensing & Inspections Technologies), with voxel dimensions of 34 μm . The left hemimandible of the giant *Leithia melitensis* from Sicily was reconstructed using a relatively complete specimen from Spinagallo Cave (MUST-r2s26), scanned at the Natural History Museum, London with a resolution of 38 μm , combined with photogrammetry models of two similarly sized *L. melitensis* specimens (MUST-r1d1 from Spinagallo Cave for the incisor; and IGUP: unnumbered specimen [our ID: Imm19-gm] found in Grotta Marasà, for the distal end of the coronoid). The *L. melitensis* specimens from Grotta di Marasà and Spinagallo Cave are considered to be of the same size group (Hennekam et al., 2020b). As the additions to specimen MUST-r2s26 constituted a very small proportion of the whole mandible (only a small portion of the coronoid and the protruding part of the incisor), their inclusion is not expected to have impacted our FEA results significantly. For the skull of *Leithia melitensis*, a composite model created from skulls at the Museo Geologico Gemmellaro (mgupPS 78: 1–5 from Poggio Schinaldo, Sicily) was used (Hennekam et al., 2020b). More details of the scanning and reconstruction of all the fossil material used in this study can be found in the supplementary information in Hennekam et al. (2020a). Alongside the fossil specimens was included the skull and left hemimandible of an extant giant dormouse from Formentera, Balearic Islands, Spain (*Eliomys quercinus ophiusae*, NHMUK 73–164), as well as an average-sized *Eliomys quercinus* specimen from Baden-Württemberg, Germany (SMF 18895, skull and left hemimandible). Respectively, these specimens were scanned at the University of Liverpool (SKYSCAN 1272) and the University of Bristol (Nikon XT H 225 ST CT scanner), with isometric voxel dimensions of 10 and 24 μm . All specimens belong to, or are considered to be closely related to, the extant genus *Eliomys* (Bover et al., 2019; Daams & de Bruijn, 1995).

Feeding strategies have been shown to correlate with mandibular morphology and its associated mechanical performance (i.e., resistance to stress and strain, mechanical advantage). For instance, species that habitually process hard food items will have more robust jaws (and will thus have lower levels of bone stress during biting simulations) than those with softer diets (Fu et al., 2022; Marcé-Nogué et al., 2017). Therefore, insectivorous species will generally exhibit higher stresses and lower mechanical advantage at all bites compared to herbivores and omnivores (Maestri et al., 2016; Serrano-Fochs et al., 2015), because jaw-closing speed and rostral length are more important adaptations for a faunivorous diet. Within herbivores, FE analyses have shown that the mandibles of browsers tend to show lower stresses than those of grazing species during incisor bites

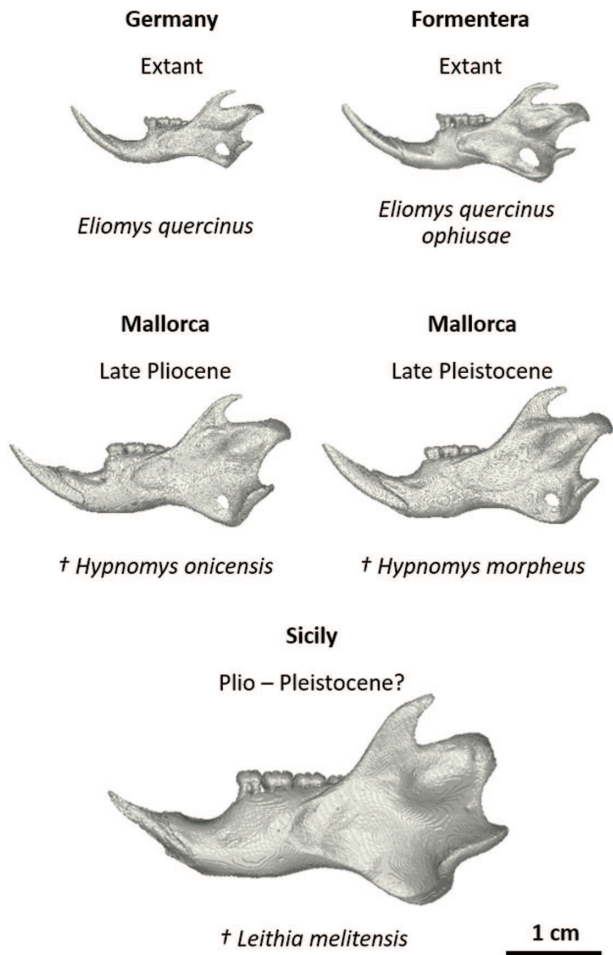


Figure 1. Lateral view of the dormouse hemimandibles analyzed in this study.

(Mitchell & Wroe, 2019), as grazers can pluck grass from the ground by pulling back with their cervical muscles (which does not require a high bite force), whereas browsers must bite through plant matter to ingest it (Mitchell et al., 2018). In general, browsers also perform better than grazers during molar bites, with FE simulations of chewing predicting lower stresses in browser mandibles (Fletcher et al., 2010; Zhou et al., 2019). The exception to this trend occurs if a browsing species is feeding on easily processed vegetation such as soft foliage, in which case its mandible will show higher stresses than the mandible of a grazer during molar biting (Fu et al., 2022). Omnivores and generalists are also expected to have mandibles that perform well in both incisor and molar biting owing to their need to be able to process a wide variety of food items (Marcé-Nogué et al., 2017). These expectations of relative biomechanical performance of the mandible during different bites are summarized in Figure 2.

Model creation

Avizo v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA) was used to create volume reconstructions of the mandibular material and to separate them into three materials: bone, molars and incisor. The preservation of the fossil mandibles did not allow for the separation of trabecular bone from cortical bone; instead, the internal structure of bone was reconstructed to be solid (one material). This follows previous

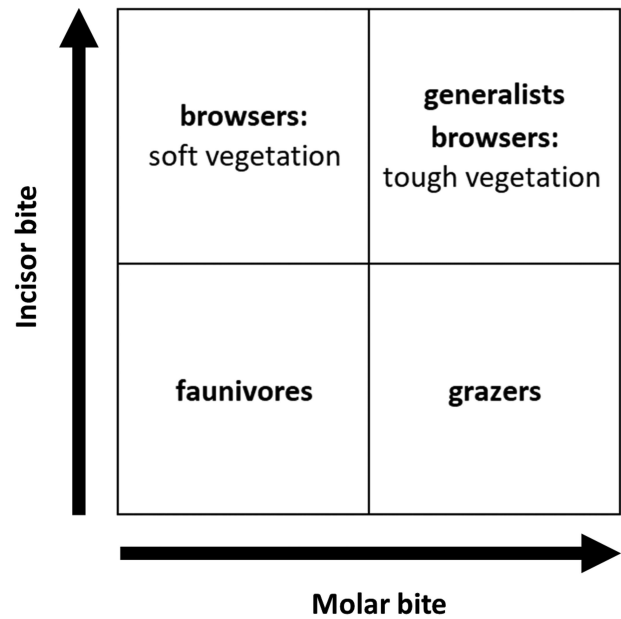


Figure 2. Schematic of presumed performance during incisor and molar biting for various feeding strategies. Arrows indicate increasing masticatory performance, based on a combination of minimized stresses and strains and maximized mechanical advantage.

finite element studies on fossil material (e.g., Cox et al., 2015; Morales-García et al., 2019) and rodent mandibles (Cox & Jeffery, 2015), and is supported by sensitivity analyses (Fitton et al., 2015; Stansfield et al., 2018; Toro-Ibacache et al., 2016) demonstrating that solid models show very similar strain patterns to models that distinguish trabecular and cortical bone (although strain magnitudes are substantially lower in the stiffer, solid models). Small foramina were filled, whereas the larger angular fenestra present in some mandibles was left open. *Leithia melitensis* is the only specimen completely lacking a fenestra in the angular process, although the fenestra in the *Hypnomys* specimens is reduced in size. In preparation for constraining the models, each specimen was oriented such that the symphysis was aligned with y-axis and the occlusal surface and condyle with the z-axis.

Model inputs

Finite element analyses were performed using the VOX-FE software (Liu et al., 2012). All specimens were converted to eight-noded cubic element meshes, using direct voxel conversion (Table 1). To check for discretization error, the model with the smallest number of elements (*Leithia melitensis*) was recreated with voxels that were three-quarters and half as long in all three dimensions. The results (Supplementary Information) were not substantially different between the three models and thus the smallest model was used for all subsequent analyses to minimize solution times. Bone, molars and incisors were assigned specific material properties. No significant variation in material properties was modeled between specimens. Although material properties will vary within the bony parts of the mandible, we expected this variation to have a relatively minor impact on the results of the finite element analyses compared to variation in shape (Cox et al., 2011). Young’s modulus for the bone material was set at 17 GPa, at 30 GPa for the molars, and at 60 GPa for the incisors (Cox et al., 2012). Poisson’s ratio for all materials was set at 0.3 (Williams & Edmundson, 1984).

Each model was constrained in three areas to avoid translation during loading. The hemimandibles were constrained at the condyle in all three axes, at the symphysis in the medio-lateral axis due to the assumption of symmetry, and at the biting tooth in an axis perpendicular to the occlusal plane (following Adams et al., 2019). The constraint at the biting tooth simulates the vertical resistance of a food item against the tooth as the mandible is brought into occlusion with the upper jaw. The symphyseal constraint takes the place of the missing right hemimandible, which would otherwise resist translational movements of the left hemimandible in the lateral plane. Two loading scenarios were modeled, representing biting at the incisor and at the first molar.

The skulls of the specimens were used in order to ascertain the correct orientation of the masticatory muscle vectors. As the corresponding skull for the *L. melitensis* mandible was missing, a reconstruction of a *L. melitensis* skull originating from another cave was slightly scaled to the correct size based

on the molar row to create the best representation of the missing skull possible (Hennekam et al., 2020b). Although using a different skull with the modeled mandible could, in theory, impact the orientation of the muscle force vectors, the difference is likely to be of the order of a few degrees—well within the margin of error that results from representing muscles single vectors running between the centroids of their attachment sites. Moreover, it should be noted that this composite skull model is the only known complete representation of the cranium of *L. melitensis* (Hennekam et al., 2020b). As the fossil hemimandibles are no longer fused at the symphysis, the fused mandible of the mainland *E. quercinus* was used to assess the relative positioning of specimens to their respective crania.

Data on the jaw adductor musculature within dormice are scarce and unknown for fossil species. A diceCT scan (Gignac et al., 2016) of *Eliomys quercinus* was used to reconstruct the masticatory muscles, defining muscle attachment sites on the mandible and skull (Figure 3). As no data on dormouse muscle forces have been published, relative muscle forces of a closely related rodent, the eastern grey squirrel (*Sciurus carolinensis*), were used instead (Cox et al., 2012). The squirrel skull length was similar to that of the dormouse from Formentera (*Eliomys quercinus ophiusae*). Muscle forces are derived from their physiological cross-sectional area and thus scale in proportion to the volume of the mandible to the 2/3 power (Fortuny et al., 2015). The mainland *E. quercinus* and the fossil giant specimens muscle forces were scaled accordingly, based on the difference in mandibular volume from the Formentera dormouse:

Table 1. Number and dimensions of elements in each mandibular finite element model.

Model	No. cubic elements	Voxel dimensions (μm)
<i>E. quercinus</i>	905452	40
<i>E. q. ophiusae</i>	1698965	40
<i>H. onicensis</i>	776484	67
<i>H. morpheus</i>	274613	100
<i>L. melitensis</i>	245969	150

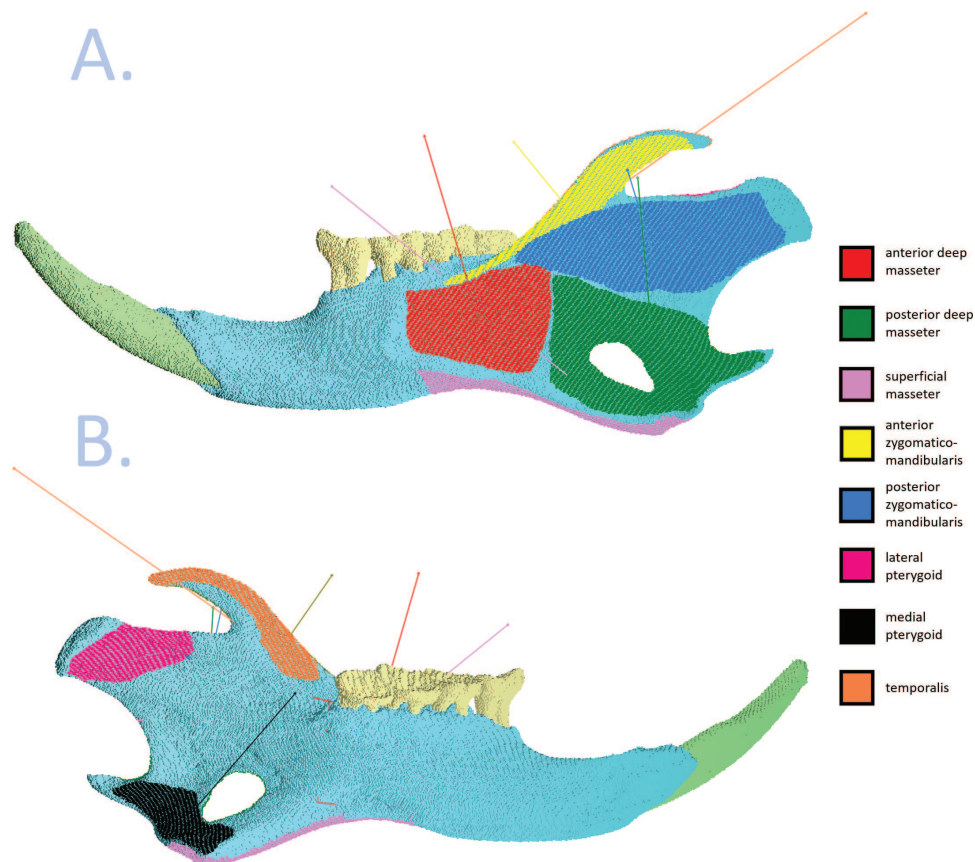


Figure 3. Mandibular muscle attachment sites for *Eliomys quercinus ophiusae* in VOX-FE in (A) lateral and (B) medial orientation.

$$\text{Muscle Force B} = \text{Muscle Force A} \times \left(\sqrt[3]{\frac{\text{Mandibular Volume A}}{\text{Mandibular Volume B}}} \right)^2$$

The orientation of the muscle vectors was determined by the centroids of muscle attachment on the mandible, and by placing landmarks on the estimated centroids of the muscle attachment sites of the respective skulls. Although morphology suggests variation in musculature to be apparent, applying the same relative forces for all specimens scaled to size enabled us to directly compare stress and strain values between models (Marcé-Nogué et al., 2017). Thus, in this analysis, we were evaluating the effects of shape variation between the specimens in their overall response to loading. However, the absolute values of bite force, strain and stress should not be interpreted as reflecting biological reality, as these could be impacted by changes in muscle size, orientation, and internal architecture.

Sensitivity

To investigate the effect of errors in muscle force orientation in the models, a sensitivity analysis was conducted in which the force vectors of each of the four largest muscles were varied over 20° in the antero-posterior axis. After determining which direction produced increases and decreases in stress for each muscle, all four muscles were reoriented together to induce the largest possible changes in results in both incisor and molar biting. Further details of the sensitivity analysis methods are given in the Supplementary Information. The numerical range generated by the sensitivity analysis is reported for both von Mises stress and mechanical advantage in Tables 2 and 3 respectively. While not a formal statistical analysis, where the distributions of numerical outputs from different species overlapped, these were determined to be

Table 2. Median von Mises stress per model during incisor and molar biting.

Model	Median element von Mises stress (MPa)	
	Incisor	Molar
<i>E. quercinus</i>	11.68 (11.06–11.70)	5.62 (5.26–5.90)
<i>E. q. ophiusae</i>	11.38 (10.82–12.08)	4.17 (3.99–4.27)
<i>H. onicensis</i>	8.72 (8.28–8.99)	4.46 (4.16–4.73)
<i>H. morpheus</i>	8.61 (8.03–9.04)	4.60 (4.27–4.88)
<i>L. melitensis</i>	17.80 (16.57–18.68)	8.77 (7.94–9.43)

Note. Range of median stress generated by reorientation of muscle force vectors over 20° given in brackets.

Table 3. Bite force, total muscle force, and mechanical advantage in all five dormice for incisor and molar biting scenarios.

Model	Bite force (N)		Total muscle force (N)	Mechanical advantage	
	Incisor	Molar		Incisor	Molar
<i>E. quercinus</i>	10	17	33	29.7 (28.1–30.5)	50.5 (48.0–52.0)
<i>E. q. ophiusae</i>	13	22	50	25.0 (23.6–25.8)	44.1 (41.5–45.5)
<i>H. onicensis</i>	26	41	83	31.2 (29.6–32.0)	48.9 (46.4–50.2)
<i>H. morpheus</i>	29	45	94	30.7 (28.7–31.9)	47.8 (44.7–49.9)
<i>L. melitensis</i>	59	98	196	30.1 (28.1–31.5)	49.8 (46.4–52.1)

Note. Range of mechanical advantages generated by reorientation of muscle force vectors over 20° given in brackets.

indistinguishable from modeling error and thus not meaningfully different from one another.

Analysis

The mechanical performance of the five structurally different dormouse mandibles was compared using von Mises stress, principal strains and mechanical advantage. As all muscles were scaled proportionally, differences in performance between specimens related strictly to variation in mandibular morphology. Von Mises stress is a measure of structural strength and can predict failure in biological structures. By predicting the distribution of von Mises stress across the loaded mandibles, we assess which areas of the bony mandible have the lowest safety factors for structural failure. We assume it is selectively advantageous to reduce von Mises stress relative to safety factor. Thus, a model showing low von Mises stress can be said to be performing better than a model with higher stresses under the same load. As well as examining von Mises distributions across the whole mandible, the median element stress for each model during incisor and molar biting was calculated. The median, rather than mean, was preferred as an average to minimize the effect of artificially high stresses at constrained elements or elements directly attached to loads.

How efficiently energy is transmitted from muscle input into biting output is dependent on the energy lost in deformation as forces are transmitted through the structure. Stiffer models are less susceptible to elastic deformation and consequently more efficient in converting muscle input into bite force. Principal strains 1 and 3 indicate maximum and minimum values of strain, with higher values approximating tensile strain in the structure, and minimum values approximating compression. However, principal strains are in order, with principal strain 1 always being higher than principal strain 3. Therefore, negative values of principal strain 1 (and thus also of principal strains 2 and 3) indicate compressive strain and positive values of principal strain 3 (and thus also of principal strains 1 and 2) indicate tensile strain. Here, we make a standard (if sometimes implicit) assumption of FEA that morphology will be optimized to its most frequently experienced loading conditions via adaptive bone remodeling (Huiskes et al., 2000; Rayfield, 2007). Thus, we assume that both tensile and compressive strain will be minimized in the mandible during the most common feeding behavior of each species.

The forces measured at the incisor and the molar constraints perpendicular to the occlusal plane represent the respective bite forces. By combining forces on all the nodes, the total bite force can be estimated for each biting scenario.

The mechanical efficiency of biting (Dumont et al., 2011), or mechanical advantage, is calculated by dividing the bite force by the total muscle input and represents the proportion of muscle force converted to bite force. Because our muscle inputs were derived from the masticatory system of *Sciurus carolinensis*, and scaled accordingly, the muscle forces are not biologically realistic. However, mechanical advantage is a ratio and therefore dimensionless, resulting in it being consistent irrespective of the force values. The differences between specimens in stress, strain and bite force are relative rather than absolute and should be evaluated accordingly.

Results

Stress and strain

The two biting scenarios (incisor and molar bite; Figure 4) show similar patterns of stress and strain, with especially the posterior part of the mandible being highly affected. High tension (approximated by high values of principal strain 1) is seen around the coronoid, condyle, and angular region in all dormice. High compressive strain (approximated by the most negative values of principal strain 3) is evident at the condyle and at the angular process, surrounding the angular fenestra where present. Additional stresses and strains located at the diastema are seen during incisor biting but are absent during molar biting. All areas associated with high values of von Mises stress seem also to be highly strained in every specimen and during both loading conditions. The areas affected by the two loading conditions are relatively similar between specimens, but the relative magnitudes of stress and strain clearly vary.

Both extant *Eliomys* specimens are highly strained at the coronoid process and the condylar region during both biting scenarios. The posterior part of the lateral flaring of the angular process is highly strained in *Eliomys quercinus ophiusae*. The degree of flaring in the fossil giants like *Hypnomys* is less pronounced and, consequently, this region experiences lower strains. Overall, the fossil *Hypnomys* specimens experience less stress and strain during both biting conditions with respect to the other dormice, with only the condylar region significantly affected. In general, strains in these specimens are more evenly distributed across the mandibular surface. *Leithia* experiences relatively similar stresses and strains to the extant *Eliomys* specimens, mostly affecting the posterior part of the mandible. However, the condylar and angular regions appear to have slightly lower stresses and strains than the extant dormice. During incisor biting, *Leithia* seems more strained at the diastema. Compressive strain is evident at the location of the angular fenestra, which was to be expected, but to a lesser extent than seen in *Eliomys quercinus* specimens. The median element stress during incisor biting is highest in *Leithia*, and lowest in the two *Hypnomys* species (Table 2). Sensitivity analyses suggest that there is no substantial difference in stress level between *E. quercinus* and *E. q. ophiusae*, nor between *H. morpheus* and *H. onicensis*. The pattern is slightly different in molar biting, such that *Leithia* has the highest median von Mises stress, then *E. quercinus*, then the two *Hypnomys* species, and the Formentera dormouse has the lowest median stress. It should be noted, however, that the sensitivity analysis showed the distributions of median von Mises stress of *E. q. ophiusae* and *H. onicensis* to overlap (Table 2).

Mechanical advantage

The mechanical advantage of each specimen for both biting scenarios was derived from the output at the molar and incisor constraint relative to the total muscle input (Table 3). The most notable difference is seen in the Formentera dormouse which has a substantially lower mechanical advantage in both incisor gnawing and molar chewing compared to all other specimens. The differences between the other four dormice are relatively small. Sensitivity analyses in which the orientation of the largest muscles of mastication were varied over 20° suggests that the differences in mechanical advantage between the non-Formentera dormice are within the margin of error and should not be treated as meaningful. Additionally the ranges of mechanical advantage calculated for molar biting in *E. q. ophiusae* and *H. morpheus* slightly overlap.

Discussion

The mandibles of insular giant dormice modeled in this study showed a diversity of responses to mechanical loading. Where some giants are more robust and experience less strain and stress (*Hypnomys*), other giant shapes cope less well with the forces generated during mastication (*E. quercinus ophiusae*). To explore the implications of these variations in biomechanical performance and the degree to which they match the known or hypothesized dietary ecology of each species, we compared the finite element outputs of the four giant specimens with the one non-giant reference specimen. More faunivorous dormice are expected to invest less in increasing their biting efficiency, while instead focusing on extended gape or increasing jaw-closing speed (Maestri et al., 2016). High performance (low stresses and strains alongside high mechanical advantage) is expected during molar biting for more herbivorous dormice (Serrano-Fochs et al., 2015). Increased performance during chewing at the molar row is correlated with grazing behavior, while browsing would benefit from an efficient incisor bite as well (Mitchell & Wroe, 2019). It should be noted that, in the following discussion, consideration of biomechanical performance is relative. As muscle force data were estimated and scaled between models, absolute values for bite force and stress and strain should be approached with caution. Nonetheless, the results are able to shed light on the impact of changing mandibular morphology when other factors are held constant.

Eliomys quercinus (mainland)

Dormice are considered to be opportunistic feeders and omnivorous to some extent (Holden-Musser et al., 2016). The garden dormouse, *Eliomys quercinus*, has a generalist feeding strategy, with a diet varying from seeds, fruits to insects, snails, and occasionally eggs and lizards (Gigirey & Rey, 1999; Gil-Delgado et al., 2010; Gosálbez, 1987; Holden-Musser et al., 2016; Palacios, 1974). Thus, it will use both incisor gnawing and molar chewing regularly when feeding. The biomechanical results support this known feeding behavior, showing similar results for both incisor and molar bites. Stresses and strains are moderately high in both biting scenarios for this specimen (Figure 4), with higher strain and stress around the mandibular notch and posterior mandibular margin. The mechanical advantages indicate *E. quercinus* has good gnawing and chewing efficiency (Table 3). As this is the specimen in our analysis for which the diet is best understood,

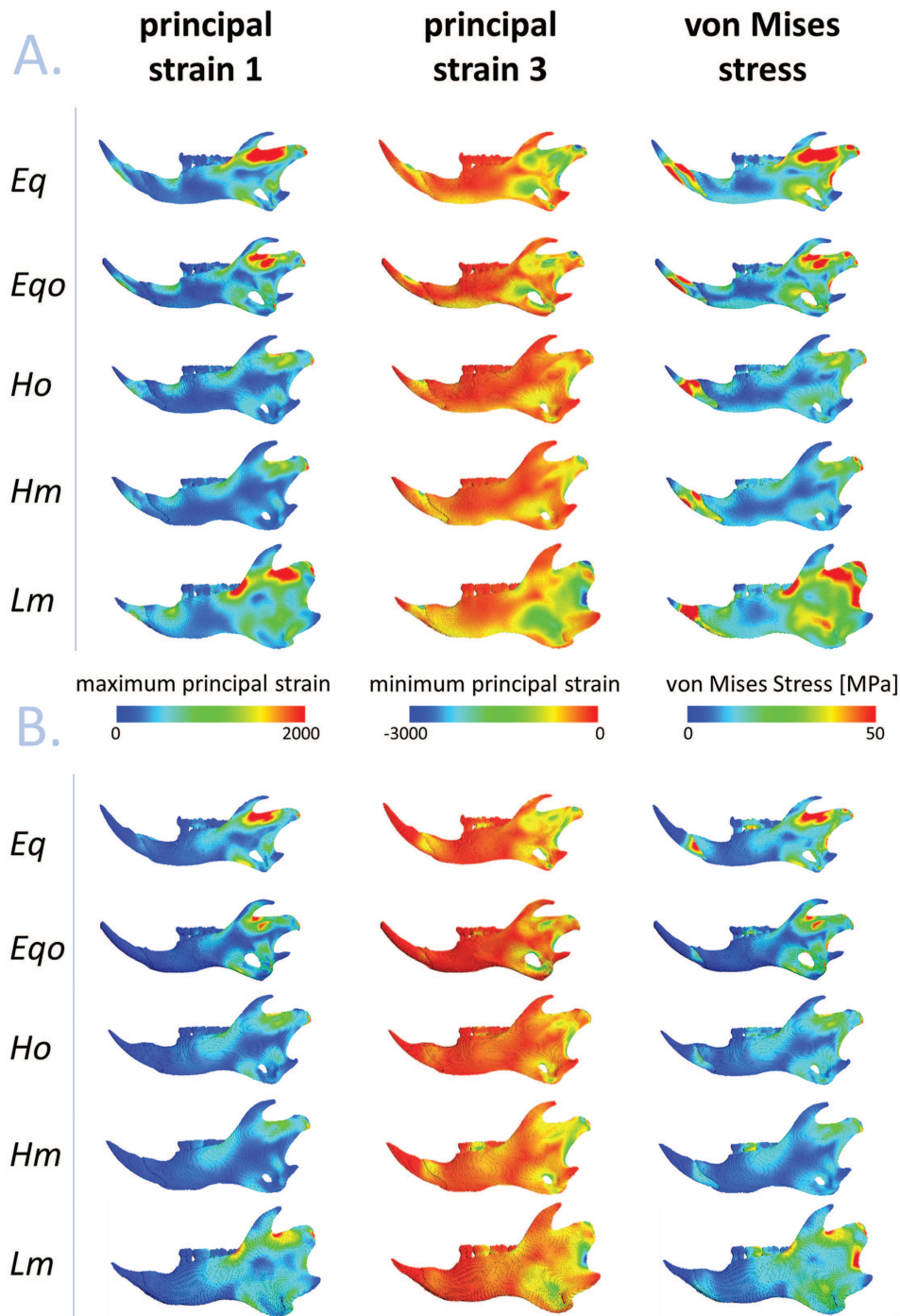


Figure 4. Predicted distributions of principal strains 1 and 3 (in microstrains) and von Mises stress (MPa) across the mandibles of five dormouse specimens during incisor (A) and molar biting scenarios (B). Abbreviations represent the five different dormice: *Eq*, *Eliomys quercinus*; *Eqo*, *Eliomys quercinus ophiusae*; *Ho*, *Hypnomys onicensis*; *Hm*, *Hypnomys morpheus*; *Lm*, *Leithia melitensis*.

the results for the other four specimens will be interpreted in relation to *E. quercinus*.

***Eliomys quercinus ophiusae* (Formentera)**

The dormice on the island of Formentera belong to the only extant giant population of *Eliomys*. The mandible of this dormouse is roughly 80% greater in volume than that of its mainland relative. Furthermore, these insular dormice are considered to be the most faunivorous population of *Eliomys*, and are suggested to compete with the black rat (Kahmann &

Lau, 1972). Morphologically, the mandible is relatively similar to that of the non-giant *Eliomys*, with small variations in the coronoid process (slightly longer and orientated more posteriorly), more lateral flaring of the angular process and a pronounced notch at the posterior margin of the mandible. All these areas are associated with elevated values of stress and strain (Figure 4). However, in molar biting, the anterior half of the mandible in this species has very low von Mises stresses leading to the lowest median element stress of the five models. The specimen has the lowest mechanical advantage

in both incisor and molar biting, indicating that the morphological changes associated with this giant dormouse result in a decreased performance of the masticatory apparatus compared to its mainland relatives. [Maestri et al. \(2016\)](#) showed that specialized insectivorous rodents have weak bites with respect to their body size. It is therefore unsurprising to find the relatively low mechanical advantage in the faunivorous Formentera giant. Instead, the morphological changes within the mandible (an elongated mandibular body and more procumbent incisor; [Figure 1](#)) are associated with an elongated skull and a longer rostrum, which consequently result in a larger out-lever and increased jaw-closing velocity ([Samuels, 2009](#)), as seen in many other insectivorous rodents ([Maestri et al., 2016](#)). Thus it appears that, in just 4,000 years, *E. q. ophiusae* has evolved a morphology that prioritizes speed of jaw closure over bite force, suited to feeding on fast-moving, but not highly mechanically resistant prey.

Hypnomys onicensis and *Hypnomys morpheus*

The ecosystem of Mallorca and Menorca is thought to have become fairly depauperate after the initial colonization by mainland species during the Messinian. The giant dormouse *Hypnomys* was one of the few surviving taxa and is believed to have persisted on the island up to the arrival of humans during the Holocene ([Bover & Alcover, 2008](#)). These two species are slightly larger than the extant Formentera giant but have a significantly more robust mandibular morphology. The loading of the two specimens in this study resulted in low levels of deformation with respect to the other dormice. The pattern within *Hypnomys* is very consistent, with the mandible of *H. morpheus* being slightly less affected during loading than *H. onicensis*. Compared to other dormice, strain is more evenly distributed across the mandible in this genus. Given the low stresses and strains, and similar mechanical advantage, during both molar and incisor biting compared to the generalist *E. quercinus*, it is clear that both gnawing and chewing could have been accomplished very efficiently, and both likely formed an important component of the feeding habits of these two taxa.

The above hypothesis is substantiated by work on the post-crania of *Hypnomys*. The morphology and proportions of the long bones and terminal phalanges of *H. morpheus* indicate this species to have had a less arboreal lifestyle than *Eliomys* ([Quintana Cardona & Moncunill-Solé, 2014](#)). Furthermore, morphological adaptations such as broadened epicondyles of the humerus, and a relatively long radius and ulna, suggest potential digging behavior ([Bover et al., 2010](#); [Mills, 1976](#); [Quintana Cardona & Moncunill-Solé, 2014](#)). These adaptations may be related to the foraging of subterranean resources, such as tubers and bulbs, which can be relatively large and tough. Such food items would require efficient incisor bites for acquisition and efficient molar bites for processing. Exploitation of such underground resources is also in line with previous studies on microwear on the molars of *Hypnomys*, which indicate a relatively abrasive diet ([Hautier et al., 2009](#)).

Leithia melitensis

The giant dormouse of Sicily and Malta is considered one of the largest dormice ever to have existed. *Leithia* has not been as thoroughly studied as *Hypnomys*, but its cranial morphology seems to indicate a terrestrial existence and relatively herbivorous diet ([Hennekam et al., 2020a,b](#)). Its mandible is more than five times larger than that of the mainland *Eliomys*

quercinus and is twice the size of the second largest giant in our dataset, *H. morpheus*. The ecosystem in which *Leithia* thrived was not as faunally depauperate as the Balearic Islands, presumably due to the occurrence of multiple invasion events from the mainland over the preceding six million years ([Marra, 2013](#)). The mandible of this giant is more affected by loading than the smaller *Hypnomys* species. Especially during incisor biting the morphology of *Leithia* results in the mandible enduring relatively large strain magnitudes, even larger than those seen in extant *Eliomys* species (both mainland and insular taxa). Additionally, extensive strain at the diastema is present during incisor loading, whereas it is not as prevalent in other dormice. Differences in von Mises stresses between the two biting scenarios show that the mandibular structure of *L. melitensis* is more suitable for chewing, and less so for gnawing at the incisors. This is in comparison to the mainland *E. quercinus*, which is a generalist and shows similar performance in incisor and molar bites. Due to its large body size, *Leithia* had a relatively large bite force at the molars, roughly six times larger than that of a mainland dormouse ([Table 3](#)). Animals with a larger bite force are expected to have a larger range of food items in their diet, as they are capable of consuming a more resistant diet ([Anderson et al., 2008](#)). The increase in size enables the consumption of larger food items without the need to increase gape angle or reduce food size by gnawing. Alongside enabling the consumption of a wide range of food resources, we expect other factors to be associated with the exceptional size of *Leithia* as well; these include the potential to digest plant material or to outgrow avian predation ([Hennekam et al., 2020b](#); [Pavia, 2004](#)).

Isolation and evolutionary adaptation

Phenotypic variation can result from evolutionary adaptations to new ecological conditions ([Marroig & Cheverud, 2001](#)). We interpret the morphological variation seen within the insular giant dormice as specific, and disparate, ecological adaptations to each taxon's isolated habitat. Various drivers, including competition, isolation, predation, and diet, have been hypothesized to impact body size in insular mammals (e.g., [Carlquist, 1974](#); [Case, 1978](#); [Foster, 1964](#); [Lawlor, 1982](#); [Lomolino, 1985, 2005](#); [McNab, 1980](#); [Sondaar, 1991](#); [van der Geer et al., 2013](#); [Van Valen, 1973](#)). Lack of predation increases population densities of rodents, resulting in food limitation becoming a strong evolutionary driver ([Van Valen, 1973](#)). Alternatively, [Lomolino \(1985\)](#) suggests the increase in size is correlated with competitive release, enabling niche expansion to incorporate larger food items ([Grant, 1965](#)). However, our finite element analyses indicate that the morphological changes associated with increased body size point toward different responses in different taxa. The extant Formentera dormouse shows clear niche narrowing toward an insectivorous diet. This could potentially relate to the presence of a competitor species (black rat; [Kahmann & Lau, 1972](#)) or even humans on Formentera, although this scenario is highly speculative at the moment. In contrast, the two *Hypnomys* species do not show evidence of niche narrowing; they show compared to *E. quercinus*, in both incisor and molar biting, indicate that they were able to use a wide range of bites very efficiently. This suggests that they had a similarly general diet to their mainland relative, or indeed may have expanded their niche even further given their increase in body size. Whether or not niche broadening occurred would be

dependent on the available resources and whether any competitors were present. Lastly, *Leithia* shows a more complex story. The finite element analyses show less efficient incisor bites compared to molar bites, which suggests more frequent molar chewing and a more herbivorous diet. However, this does not necessarily equate to niche narrowing as the enormous body size increase in this species will, in and of itself, greatly expand the range of available food items.

The differences between giants seen here can be explained by various factors, including island ecosystem composition, niche occupation, duration of isolation (Hennekam et al., 2020a), or life history shift (Köhler et al., 2021). *E. q. ophi-usae* colonized Formentera around 4,000 years ago (Hautier et al., 2009), and over this short period of time this species has altered its shape and size significantly compared to mainland *Eliomys* populations, developing highly adaptive traits to its novel faunivorous feeding strategy. This suggests that selection for these new functional adaptations must have been quite strong and quick. Similarly rapid morphological change related to dietary change has also been described in insular house mice (Renaud et al., 2013, 2015). This contrasts with the widely accepted idea that morphological adaptations to new island niches arise secondarily to the primary response of body size change, and thus may not be observable in the neontological record or over ecological time scales (Lister, 1996; Lomolino et al., 2013): e.g., insular dwarfism is suggested to occur in phases starting with changes in body size and locomotion, followed by alteration of the feeding apparatus (Alcover et al., 1981; Lister 1989, 1996; Lomolino et al., 2013).

The fossil giants *Hypnomys* and *Leithia* were both isolated for millions of years, but their respective island habitats differed both in terms of their paleogeography and ecosystem composition. The finite element analyses indicate almost no functional morphological differences within the anagenetic *Hypnomys* lineage, suggesting adaptation to the insular habitat had already occurred by the end of Late Pliocene (before 2.6 Ma) (Bover et al., 2008). These functional niche adaptations apparently then remained stable over 2 million years, during the transition from the Late Pliocene taxon *H. onicensis* to the larger Pleistocene/Late Holocene species *H. morpheus* (Alcover et al., 1981), despite the repeated climatic (interglacial-glacial) fluctuations of the Pleistocene. *H. morpheus* went extinct in the Balearics during the Holocene. Its demise, together with the extinction of the dwarfed goat *Myotragus*, is linked with the arrival of human settlers and a coinciding introduction of various mainland species, including the dormouse *Eliomys* (Bover & Alcover, 2008). Our FEA results strengthen the argument, that the arrival of mainland *Eliomys* did not cause the extinction of *Hypnomys* as a result of increased competition (Bover & Alcover, 2008): each are adapted to different dietary niches.

Animal populations frequently evolve different body sizes in insular habitats (Foster, 1964; Van Valen, 1973). Morphological variation linked with insular changes in size appears to deviate from the allometric trajectory of mainland relatives (Hennekam et al., 2020a). In addition, functional morphological differences are present between insular populations, indicating that the shape changes are not convergent. Instead, changes in shape and size linked to insularity seem to be island-specific and driven by various selective pressures, allowing for adaptation to different ecological niches. In this study, we have shown that three different

insular ecosystems resulted in three morphologically and functionally distinct groups of dormice. Phenotypic evolution is proposed to be directed along lines of least evolutionary resistance (Marroig & Cheverud, 2010; Renaud et al., 2011; Schluter, 1996), which represent a clade-wide relationship between size and shape. However, environmental changes can result in selective gradients, allowing divergence from such trajectories (e.g., Renaud et al., 2006). It is becoming more and more evident that insular gigantism is linked with specific niche occupation resulting in optimized functionality, rather than simply following an allometric trajectory. While insular gigantism is a widespread phenomenon, both taxonomically and geographically, its occurrence does not appear to imply the convergent evolution of a standard suite of morphological or functional characters, nor a shift into a specific ecological niche. This is likely because the “insular giant niche” varies widely between islands and across time periods, arguing against a universal ecological driver for island gigantism.

Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut/qqad041>)

Data availability

The datasets supporting this article are 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). Finite Element models, projects and results are uploaded to figshare (https://figshare.com/articles/dataset/Dormouse_FEA/22201882).

Author contributions

J.J.H. and P.G.C. conceived the study. J.J.H. created the finite element models, analyzed the results, and drafted the manuscript. P.G.C. and V.L.H. contributed to the editing of the final manuscript and gave final approval before submission.

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