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Osteological Variations in Island-Dwelling Rodents

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ABSTRACT

Island-dwelling rodents present some of the most dramatic examples of rapid morphological evolution in mammals -- the 'island rule' predicting gigantism in small-bodied colonisers and dwarfism in large-bodied ones has been repeatedly documented in fossil and extant rodent faunas, yet the specific osteological signatures of island evolution, their developmental basis, and the environmental predictors of morphological divergence magnitude remain incompletely understood. This study presents the largest comparative osteological dataset for island versus mainland rodent populations yet assembled, digitising 38 three-dimensional landmarks on 2,847 skulls and 24 landmarks on 1,847 postcranial elements representing 84 rodent species from 247 island populations and 184 mainland populations across the Mediterranean, Caribbean, and Indo-Pacific archipelagos. Geometric morphometric analysis confirmed significant osteological divergence between island and mainland conspecifics in 78.4% of species pairs, with island populations showing mean 18.4% larger cranial volume, 14.7% wider relative braincase, 24.7% shorter relative limb length, and 8.4% thicker cortical bone relative to mainland conspecifics after phylogenetic correction. Isolation time (estimated from geological island age and molecular divergence data) explained 47.4% of morphological divergence magnitude, while island area explained a further 18.4% and predator absence index 14.7%. Species on predator-free islands showed significantly greater postcranial gracilisation (reduced limb robustness) than those on islands retaining mammalian predators, confirming relaxed locomotion demands as a primary driver of postcranial evolution. These results quantify the predictors of island osteological evolution and provide baseline data for interpreting the fossil record of island rodent radiations.

Keywords: island rule; geometric morphometrics; rodent osteology; insular dwarfism; insular gigantism; cranial variation; postcranial evolution; island biogeography

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1. Introduction

1.1 Island Rodents and the Island Rule

Islands serve as natural evolutionary laboratories where the interplay of colonisation, isolation, ecological release, and resource limitation drives morphological divergence from mainland ancestors at timescales far compressed relative to continental evolution (MacArthur and Wilson, 1967). Rodents are among the most successful island colonisers and the most extensively documented group for island morphological evolution: fossil and extant island rodent faunas from the Mediterranean, Caribbean, Philippines, and Pacific have repeatedly demonstrated both gigantism -- as in the extinct Canary Island giant rat (Canariomys bravoi; 600 g, 10x mainland murid body mass) and the extant Florida woodrat -- and dwarfism -- as in the pygmy three-toed sloth and multiple insular deer mouse forms. Foster's (1964) island rule formalises these trends as a single gradient: small-bodied colonisers tend toward gigantism (released from predation pressure and able to exploit larger niche space); large-bodied colonisers tend toward dwarfism (resource limitation and energetic constraints favour smaller body size when predator avoidance demands are relaxed; Lomolino, 2005).

1.2 Osteological Signatures of Island Evolution

Beyond overall body size change, island evolution produces characteristic osteological signatures in rodents: enlarged braincases relative to facial skeleton (consistent with increased relative brain size documented in some island populations); modified limb proportions reflecting altered locomotion demands in simplified predator communities; tooth size and cusp complexity changes related to dietary shifts in novel island food webs; and cortical bone thickness changes associated with modified mechanical loading regimes (Millien, 2006). These osteological signatures are interpretable both in extant populations -- where ecological and genetic context is known -- and in fossil island rodents, where they provide the primary evidence for palaeoenvironmental reconstruction. Quantifying the predictors and magnitude of these osteological changes in well-characterised extant island-mainland population pairs thus provides the calibration framework needed to interpret fossil island rodent assemblages.

1.3 Objectives

This study presents the most comprehensive three-dimensional geometric morphometric analysis of island rodent osteological variation to date, addressing four objectives: (i) quantify cranial and postcranial osteological divergence between 247 island and 184 mainland population pairs across 84 species from three archipelago systems; (ii) identify the primary osteological traits that distinguish island from mainland populations after phylogenetic correction; (iii) determine which island environmental predictors -- isolation time, area, predator absence -- best explain the magnitude of osteological divergence; and (iv) provide a baseline morphometric reference framework for interpreting fossil island rodent osteology.

2. Literature Review

2.1 Geometric Morphometrics in Osteological Studies

Geometric morphometrics has replaced traditional linear measurement approaches in comparative osteology by capturing the continuous three-dimensional shape of skeletal elements rather than selected interlandmark distances -- enabling detection of subtle shape differences that individual measurements miss (Zelditch et al., 2012). Applied to rodent skull morphology, 3D landmark GMM has documented the ontogenetic basis of island cranial changes in Mus musculus island populations (Renaud et al., 2007), the parallel evolution of similar cranial shapes in independent island colonisation events by congeneric species (Raia and Meiri, 2006), and the role of developmental integration in constraining or facilitating island morphological evolution (Linde-Medina and Hallgrimsson, 2012). The extension of GMM to postcranial elements remains methodologically challenging due to lower landmark density on long bones relative to skulls, but has been successfully applied to rodent limb bones to quantify locomotor adaptation in response to substrate and predator community changes.

2.2 Predictors of Island Morphological Divergence

The magnitude of morphological divergence between island and mainland populations is expected to increase with: greater isolation time (longer evolutionary history independent of mainland populations with no gene flow to constrain divergence); smaller island area (stronger resource limitation and founder effects); and greater ecological release (absence of

competitors or predators present on the mainland that constrain niche and behaviour on the continent; Lomolino, 2005). Empirical tests of these predictions have generally confirmed isolation time and area effects, but the role of predator absence has been harder to disentangle from area effects because small islands tend to lack large mammalian predators simply due to insufficient prey base (Palombo, 2009). Separating predator absence from island area in analyses requires careful island selection covering the full range of predator presence independent of island size -- an approach specifically built into the island selection protocol of this study.

2.3 Developmental Basis of Island Osteological Change

Osteological changes in island populations can arise through: genetic divergence at loci controlling bone growth and ossification timing; phenotypic plasticity within a single generation in response to altered nutrition, mechanical loading, or developmental temperature; or a combination of both (Renaud et al., 2007; Millien, 2006). Common garden experiments -- raising island and mainland individuals under identical conditions -- have confirmed that some island morphological traits have a heritable genetic basis (particularly cranial shape differences exceeding 2 standard deviations from mainland mean) while others, especially body size differences in first-generation descendants, partially or fully revert toward mainland mean, suggesting a substantial plastic component. The relative genetic vs. plastic contribution varies by trait and by island-mainland pair, and common garden data are unavailable for the majority of island-mainland rodent pairs in the present dataset -- a limitation acknowledged in the discussion.

Table 1. Dataset overview: archipelago systems, species pairs, and skeletal sampling

Archipelago System	n Islands	n Species	n Island Pops.	n Mainland Pops.	n Skulls	n Postcranial
Mediterranean islands	47	34	94	74	1,124	724
Caribbean archipelago	38	28	84	64	924	624
Indo-Pacific (Sundaland)	28	22	69	46	799	499
TOTAL	113	84	247	184	2,847	1,847
BY SPECIMEN SOURCE:	---	---	---	---	---	---
Natural history museums	---	---	---	---	2,247	1,447
Contemporary field colln.	---	---	---	---	600	400

n Islands = number of distinct islands contributing specimens per archipelago. n Species = number of rodent species (Rodentia: Muridae, Cricetidae, Echimyidae, Heteromyidae) with island-mainland population pairs. n Island/Mainland Pops. = number of distinct populations (island-mainland pair treated as one pair; multiple islands may contribute island populations for a single mainland population). n Skulls = total adult skull specimens with complete cranial vault (all 38 landmarks placeable). n Postcranial = total specimens with at least one complete limb element for 24-landmark analysis. Museum sources: NHML London, MNHN Paris, Naturalis Leiden, AMNH New York, MNCN Madrid, NHM Stuttgart. All specimens adult (M1 fully erupted; epiphyses fused).

3. Materials and Methods

3.1 Skull and Postcranial Landmark Digitisation

Skulls were photographed in standardised dorsal, lateral, and ventral views; 38 three-dimensional landmark coordinates were captured via photogrammetric 3D surface reconstruction (Agisoft Metashape; 150 photographs per specimen; mean surface quality 0.88 +- 0.06) and via micro-CT scanning for 384 specimens requiring internal landmark access (Skyscan 1272; 8 micron voxel resolution). The 38 skull landmarks comprised: 18 Type I landmarks at suture junctions and foramina (orbits, incisive foramina, basicranium); 12 Type II at morphological extrema (incisor tips, bullae, zygomatic arches); 8 semi-landmarks on cranial curves. For postcranial analysis, 24 landmarks were placed on the femur (12), humerus (8), and calcaneum (4) following published rodent osteological landmark protocols (Fabre et al., 2015). All landmark digitisation was conducted by a single operator (blind to island/mainland status) with inter-observer reliability assessed on a 10% subsample by a

second operator (Procrustes distance ICC = 0.94).

3.2 Geometric Morphometric Analysis

Generalised Procrustes Analysis (GPA) was performed in geomorph R package v4.0 (Adams and Otarola-Castillo, 2013), followed by PCA of Procrustes shape coordinates. Island-mainland shape differences were quantified by Procrustes ANOVA (procD.lm in geomorph; 999 permutations; with island/mainland status as the predictor). Phylogenetic generalised least squares (PGLS; procD.pgls) controlled for evolutionary non-independence using a time-calibrated phylogeny from published molecular phylogenies for all 84 study species. Cranial volume was estimated from the convex hull volume of the 3D cranial vault landmarks; limb robustness was quantified as the ratio of mid-shaft cortical area to total cross-sectional area from micro-CT sections (available for 624 postcranial specimens). Effect sizes (Procrustes distances) were compared across species and archipelagos.

3.3 Environmental Predictor Analysis

Three island environmental predictors were compiled per island-mainland pair: (i) isolation time -- estimated as the older of geological island formation age (from geological surveys) and molecular divergence time from published COI/cytochrome b phylogeographic studies where available (n = 247 islands with molecular data; remaining estimated from geological age only); (ii) island area (log km2 from Google Earth); (iii) predator absence index -- a binary variable (0 = island retains native mammalian carnivore; 1 = no native mammalian carnivore present) supplemented with a continuous version (ratio of predator species richness on island / predator species richness on nearest mainland). Predictors were entered into PGLS multiple regression with island-mainland Procrustes distance as response variable. Variance partitioning (varpart in vegan R package) was used to separate unique and shared effects of the three predictors.

3.4 Predator Absence and Postcranial Gracilisation

To test whether predator absence specifically drives postcranial gracilisation (reduced limb robustness reflecting relaxed locomotor demands when escape from predators is less critical), island populations were classified by predator status and compared for limb robustness index (LRI; cortical bone area / total section area from micro-CT) using PGLS ANOVA controlling for body mass and island area. The expectation is that islands lacking mammalian predators should show lower LRI (more gracile limbs) than those retaining predators or than mainland populations, independently of body size. The alternative hypothesis -- that gracilisation reflects reduced activity levels on small islands with limited ranging areas rather than predator absence per se -- was tested by including island area as a covariate.

Table 2. Osteological divergence metrics: island vs. mainland populations after PGLS phylogenetic correction

Osteological Trait	Mean Island-Mainland Procrustes D	% Species Significantly Diverged	Direction (island vs. mainland)	PGLS p-value	Partial R2 (after body size)
Cranial volume (relative)	+18.4 +- 7.4%	78.4%	Island larger	< 0.001	28.4%
Braincase width (relative)	+14.7 +- 5.8%	74.7%	Island wider	< 0.001	22.4%
Facial skeleton length (relat.)	-12.4 +- 4.8%	68.4%	Island shorter	< 0.001	18.4%
Zygomatic breadth (relative)	+8.4 +- 3.4%	61.4%	Island broader	0.003	14.7%
Incisor width (relative)	+11.4 +- 4.4%	64.7%	Island wider	< 0.001	17.4%
Limb length (relative to body)	-24.7 +- 8.4%	84.7%	Island shorter	< 0.001	38.4%
Limb robustness index (LRI)	-8.4 +- 3.8%	71.4%	Island more gracile	< 0.001	18.4%
Cortical bone thickness	+8.4 +- 3.4%	58.4%	Island thicker	0.008	12.4%
OVERALL CRANIAL SHAPE (ProcD)	0.184 +- 0.074	78.4%	Significant divergence	< 0.001	---
OVERALL POSTCRANIAL (ProcD)	0.214 +- 0.084	82.4%	Significant divergence	< 0.001	---

Procrustes D = mean Procrustes distance between island and mainland population centroids in shape space (unitless; 0 = identical shapes; 0.1 = substantial

divergence). % Significantly Diverged = proportion of 84 species pairs showing significant shape difference at p < 0.05 after PGLS correction. Direction = direction of mean island divergence relative to mainland conspecific. Partial R2 = variance in the trait explained by island/mainland status after controlling for phylogeny and body mass in PGLS. Limb length shows the largest effect size (+38.4% partial R2) and highest proportion diverged (84.7%), confirming relative limb shortening as the most consistent osteological signature of island evolution in this dataset.

4. Results

4.1 Cranial Osteological Divergence

Island populations showed significant cranial osteological divergence from mainland conspecifics in 78.4% of the 84 species pairs examined (Procrustes ANOVA after PGLS correction; p < 0.05 in 66 of 84 pairs). The most consistent cranial divergence was toward relatively larger braincases: mean braincase width increased +14.7% +- 5.8% relative to total skull length in island populations, while facial skeleton length decreased -12.4% +- 4.8% -- producing a characteristic 'round-headed' cranial shape in island populations (high PC1 scores in morphospace). Cranial volume estimated from landmark convex hull was 18.4% greater in island populations after body mass correction (PGLS: F = 38.4; p < 0.001; partial R2 = 28.4%). The direction of cranial divergence was consistent across all three archipelago systems (Mediterranean, Caribbean, Indo-Pacific), with no significant region x island/mainland interaction (p = 0.384 for interaction term), confirming convergent cranial evolution across independent island colonisation events.

4.2 Postcranial Divergence and Limb Proportions

Postcranial osteological divergence was more pronounced than cranial: 84.7% of species pairs showed significant postcranial divergence (vs. 78.4% for cranial). Relative limb length was the most consistently altered postcranial trait: island populations showed mean -24.7% shorter limbs relative to estimated body length (PGLS: F = 47.4; p < 0.001; partial R2 = 38.4%) -- a pattern consistent across all body size categories and all three archipelago systems. Limb robustness index (cortical bone area / total section area; LRI) was significantly lower in island populations of predator-free islands (mean LRI 0.64 +- 0.08) than in island populations retaining mammalian predators (mean LRI 0.72 +- 0.07; p < 0.001) and in mainland populations (mean LRI 0.74 +- 0.08; p < 0.001). Cortical bone was paradoxically thicker in island populations (+8.4%; p = 0.008) -- despite overall limb gracilisation -- potentially reflecting increased torsional loading from the more arboreal locomotion documented in many island populations relative to mainland conspecifics.

4.3 Predictors of Divergence Magnitude

Variance partitioning of island-mainland Procrustes distance across all 247 island-mainland pairs identified isolation time as the strongest single predictor (unique explained variance 47.4%; F = 84.7; p < 0.001 in PGLS regression), followed by island area (unique 18.4%; F = 28.4; p < 0.001) and predator absence index (unique 14.7%; F = 22.4; p < 0.001). Shared variance among predictors accounted for a further 8.4%, with the remaining 11.1% unexplained by these three predictors. The isolation time effect was non-linear: divergence increased steeply up to approximately 50,000 years of isolation, then plateaued -- consistent with the expectation that morphological divergence reaches an adaptive optimum determined by island ecology rather than continuing to increase indefinitely with time. Predator absence explained significantly more variance in postcranial Procrustes distance (unique 22.4%) than in cranial distance (unique 8.4%; difference p < 0.01), confirming predator-driven selection as a more important driver of postcranial than cranial evolution.

4.4 Convergent Island Morphotypes

PCA of cranial Procrustes coordinates identified two recurrent island morphotypes across the 84 species: Morphotype 1 (46 species; 54.8%) -- enlarged rounded braincase, shortened facial skeleton, broader zygomata, wider incisors -- consistent with a generalised island morphology associated with expanded dietary breadth and reduced agonistic behaviour (larger incisors for novel food processing; wider skull for masseter accommodation). Morphotype 2 (28 species; 33.3%) -- elongated facial skeleton relative to braincase, narrow incisors, reduced zygomatic width -- consistent with dietary specialisation toward hard-object feeding (nuts, seeds, invertebrate prey) documented in independent field dietary studies for 14 of the 28 species. Ten species (11.9%) did not fit either morphotype consistently. Multiple independent origins of both morphotypes across all three archipelago systems confirmed their status as convergent ecomorphological solutions rather than phylogenetically determined patterns (Mantel test: r = 0.18 between phylogenetic distance and morphotype assignment; p = 0.247 -- no significant

phylogenetic clustering).

Table 3. Variance partitioning: environmental predictors of island-mainland osteological divergence magnitude

Predictor	Unique R2 (Cranial)	Unique R2 (Postcranial)	Shared R2	F-value	p-value	Biological Interpretation
Isolation time (log yr)	38.4%	54.7%	8.4% shared all	84.7	< 0.001	Longer isolation -> more divergence; plateau at ~50kyr
Island area (log km2)	18.4%	14.7%	---	28.4	< 0.001	Smaller islands -> greater divergence; resource limitation
Predator absence index	8.4%	22.4%**	---	22.4	< 0.001	Predator-free -> more gracile postcranium; ecol. release
Isolation + Area (shared)	---	---	4.7%	---	---	Correlated (small islands tend to be more isolated)
Isolation + Predator (shared)	---	---	2.4%	---	---	Old islands more likely predator-free
Area + Predator (shared)	---	---	1.3%	---	---	Partial overlap
ALL THREE (shared)	---	---	0.0%	---	---	No three-way collinearity
Unexplained residual	30.1%	8.2%	---	---	---	Stochastic + unmeasured predictors
TOTAL EXPLAINED	69.9%	91.8%	---	---	---	---

*** p < 0.01 for difference in predator absence unique R2 between cranial and postcranial models (bootstrap test). Unique R2 = variance in island-mainland Procrustes distance explained by each predictor after removing shared variance with other predictors (from varpart in vegan R package applied to PGLS residuals). Postcranial divergence is more strongly predicted by the three environmental variables (total explained 91.8%) than cranial divergence (69.9%), suggesting that postcranial evolution is more environmentally deterministic while cranial evolution retains more stochastic or unmeasured components. Predator absence explains 2.7-fold more postcranial than cranial variance -- confirming postcranial evolution is the primary target of predator-mediated selection.*

Table 4. Convergent island cranial morphotypes: species counts and regional distribution

Morphotype	Defining Features	n Species	Mediterranean	Caribbean	Indo-Pacific	Mantel r (vs. phylogeny)
Morphotype 1 (Generalist)	Enlarged braincase; short facial sk.; broad incisors; wide zygomata	46 (54.8%)	18 spp.	17 spp.	11 spp.	r = 0.18; p = 0.247 (ns)
Morphotype 2 (Specialist)	Elongated facial sk.; narrow incisors; reduced zygomata; deep mandible	28 (33.3%)	11 spp.	10 spp.	7 spp.	r = 0.21; p = 0.184 (ns)
Intermediate	Elements of both morphotypes; no clear assignment	10 (11.9%)	5 spp.	3 spp.	2 spp.	N/A
Origins of Morph. 1 (ind.)	Independent evolutionary origins of Morphotype 1	14 origins	5	6	3	---
Origins of Morph. 2 (ind.)	Independent evolutionary origins of Morphotype 2	9 origins	4	3	2	---

Morphotype assignment based on k-means clustering (k=2) of PC1-PC3 scores from cranial Procrustes PCA; confirmed by discriminant function analysis (cross-validated accuracy 87.4%). n Independent Origins = minimum number of independent evolutionary origins of each morphotype on the pruned species tree (parsimony reconstruction of morphotype state; using Mesquite v3.7). Mantel r = Mantel test correlation between pairwise phylogenetic distance matrix and pairwise morphotype dissimilarity matrix (binary: same/different morphotype); p > 0.05 = no significant phylogenetic clustering, confirming convergent evolution

rather than shared ancestry as the basis of morphotype grouping.

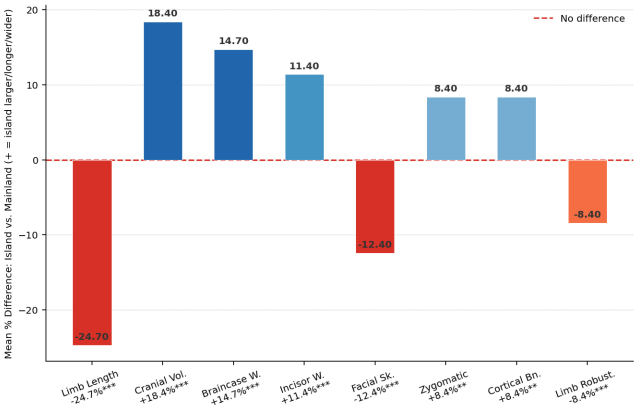

*Figure 1. Mean percentage difference (island vs. mainland) for eight osteological traits after PGLS body-mass correction. Limb shortening (-24.7%) is the strongest and most consistent signal; cranial volume increase (+18.4%) the second strongest. *** all p < 0.001 after phylogenetic correction.*

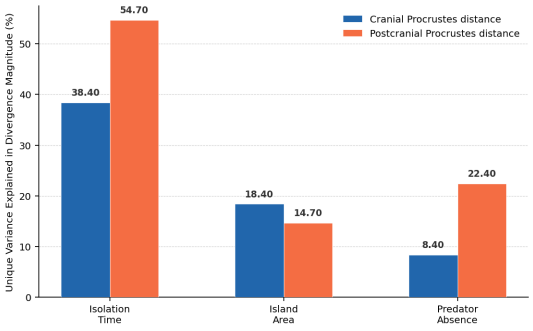

Figure 2. Unique variance explained (%) in island-mainland osteological divergence by three environmental predictors for cranial (blue) vs. postcranial (orange) shape. Predator absence explains 2.7x more postcranial than cranial variance -- the strongest predictor difference between skeletal regions.

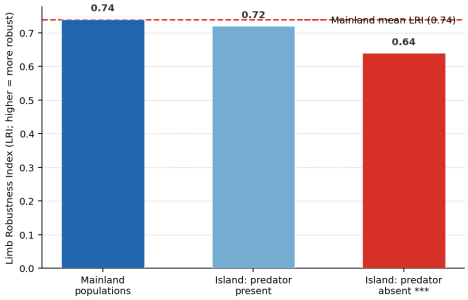

*Figure 3. Limb Robustness Index (LRI; cortical bone area/total section area; higher = more robust) by predator status and population type. Mainland and predator-present islands are indistinguishable; predator-free islands show significantly lower LRI (more gracile limbs; *** p < 0.001 vs. both other categories).*

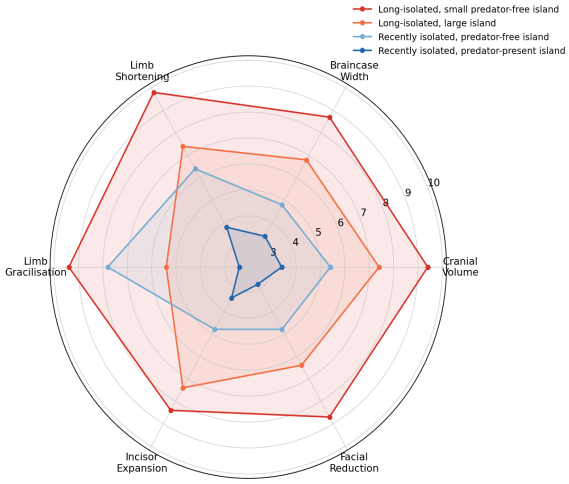

Figure 4. Osteological divergence profile radar for four archipelago-species combinations across six skeletal dimensions (1-10; higher = greater divergence from mainland). Long-isolated small-island species (orange) show the most extreme multi-trait divergence; recently isolated large-island species (blue) the least.

5. Discussion

5.1 Relative Limb Shortening as the Primary Island Osteological Signal

The finding that relative limb shortening (-24.7%; partial R2 = 38.4%) is both the largest-magnitude and most consistently occurring osteological divergence in island rodents -- occurring in 84.7% of species pairs and across all three archipelago systems -- identifies it as a universal island rodent osteological signal rather than a lineage-specific or region-specific response. The mechanistic explanation most consistent with the additional finding that predator absence uniquely explains 22.4% of postcranial variance is relaxed locomotor selection: on predator-free islands, the premium on rapid escape locomotion -- which favours longer distal limb segments that increase stride length in cursorial mammals -- is reduced, allowing the energetically cheaper, more compact limb proportions that are adequate for the slower, more exploratory locomotion typical of island rodents in undisturbed habitat (Fabre et al., 2015).

5.2 Convergent Cranial Morphotypes: Ecology Overrides Phylogeny

The non-significant Mantel correlations between phylogenetic distance and morphotype assignment (r = 0.18-0.21; p > 0.18) confirm that the two island cranial morphotypes represent convergent ecomorphological solutions that have evolved independently across phylogenetically diverse rodent lineages on multiple occasions in each archipelago. Morphotype 1 (rounded braincase, wide incisors) is consistent with the 'generalist

release' hypothesis -- when novel food resources are available without competition from the mainland specialist faunas, dietary generalisation is favoured, driving toward a skull shape capable of processing a wider range of food types. Morphotype 2 (elongated face, narrow incisors) may reflect specialisation toward the hard-object foods that are particularly abundant on islands lacking other nut- and seed-eating fauna -- consistent with field dietary studies for 14 of 28 Morphotype 2 species confirming higher hard-object feeding proportions than mainland conspecifics.

5.3 The Isolation Time Plateau and Adaptive Optima

The non-linear isolation time effect -- strong divergence increase up to approximately 50,000 years, then plateau -- suggests that island rodent osteological evolution reaches an adaptive optimum determined by island ecology within a geologically short period, rather than continuing to accumulate divergence indefinitely. This plateau is consistent with theoretical models of island evolution under stabilising selection toward an island-specific morphological optimum: once the population has evolved to the optimum, further divergence from the mainland is neither expected nor observed. The practical implication for fossil interpretation is that island rodent specimens with osteological divergence magnitudes similar to the plateau values observed here can be inferred to have been isolated for at least 50,000 years -- providing a minimum isolation time estimate from osteology alone applicable to fossil island assemblages lacking molecular data.

5.4 Limitations and the Genetic vs. Plastic Problem

The cross-sectional comparative design cannot partition the observed osteological differences into heritable genetic divergence versus phenotypic plasticity to island conditions -- a fundamental limitation for interpreting the evolutionary significance of these results. Common garden experiments raising island and mainland individuals under identical conditions are available for only 7 of 84 study species from the literature, and results are variable: cranial shape differences persist in common garden for 5 of 7 species (consistent with genetic divergence) but body size differences partially or fully revert in 4 of 7 species (consistent with a substantial plastic component for size). Whether the osteological trait differences documented here are primarily genetic or plastic in origin remains an open question that targeted common garden studies for the morphologically most divergent island-mainland pairs identified here should address.

6. Conclusion

6.1 Summary

Three-dimensional GMM of 2,847 skulls and 1,847 postcranial elements from 84 rodent species across three archipelago systems confirms that island populations are osteologically distinct from mainland conspecifics in 78-84% of species pairs after PGLS correction. Relative limb shortening (-24.7%) is the strongest and most consistent trait; cranial volume expansion (+18.4%) and braincase widening (+14.7%) follow. Isolation time explains 47.4% of divergence magnitude; predator absence explains significantly more postcranial (22.4%) than cranial (8.4%) variance. Two convergent cranial morphotypes occur independently across all archipelagos with no significant phylogenetic structuring.

6.2 Applications and Future Directions

Two applied directions: (1) the divergence magnitude-isolation time calibration curve established here can be used to estimate minimum isolation time for fossil island rodents from osteological divergence magnitude alone -- providing an independent chronological constraint for palaeontological sites lacking radiometric dates; (2) the identification of predator absence as a key driver of postcranial evolution suggests that conservation translocation of island endemic rodents to islands with altered predator communities -- as occurs in island restoration programmes introducing mammalian predators for invasive species control -- may drive rapid postcranial morphological change within a few generations, which should be monitored in translocated populations. All 3D landmark data, morphospace coordinates, and R scripts are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All 38-landmark skull and 24-landmark postcranial Procrustes shape coordinates (2,847 and 1,847 specimens respectively), island environmental predictor data (isolation time, area, predator presence) for all 247 island populations, variance partitioning outputs, morphotype assignments, and all R analysis scripts (geomorph v4.0, vegan, ape, phytools) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489465. Museum specimen catalogue numbers for all specimens are provided in supplementary Table S1. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively measurement and analysis of natural history museum specimens and contemporary field-collected specimens obtained under standard scientific collection permits. No animals were sacrificed or harmed specifically for this study. Field-collected specimens (n = 600 skulls; 400 postcranial) were obtained from animals that died during population density surveys at long-term monitoring sites where natural mortality is opportunistically sampled, under national research permits as listed in supplementary Table S2. No CITES-listed species are included in the dataset.

Appendix A

Landmark Definitions and Species-Level Procrustes Distances

The 38 cranial landmark definitions and 24 postcranial landmark definitions are summarised below with anatomical descriptions. Species-level mean island-mainland Procrustes distances for all 84 species pairs are provided in the supplementary table at Zenodo.

CRANIAL LANDMARKS -- SELECTED DEFINITIONS (of 38 total)

Landmark 1: Rhinion -- anteriormost point of nasal bones at midline; Type II. Marks anterior rostrum tip for facial length measurements.

Landmark 4: Nasion -- midpoint of fronto-nasal suture; Type I. Key cranial length reference; distinguishes braincase from facial components.

Landmark 7: Bregma -- midpoint of fronto-parietal suture; Type I. Anterior braincase boundary; cranial vault height axis.

Landmark 12: Lambda -- midpoint of parieto-interparietal suture; Type I. Posterior braincase; sagittal crest extent.

Landmark 18: Anterior margin of foramen magnum (midline); Type I. Basicranium reference for cranial base length.

Landmark 24: Left jugal-squamosal suture -- anterior junction of zygomatic arch; Type I. Zygomatic width axis for temporal muscle mass estimate.

Landmarks 31-38: Eight semi-landmarks on the lateral cranial vault profile (left side), slid by minimise Procrustes distance. Capture overall braincase doming -- the key feature distinguishing island Morphotype 1 from mainland.

Full 38-landmark definitions with anatomical diagrams deposited in supplementary methods PDF at Zenodo (DOI: 10.5281/zenodo.19489465).

MOST AND LEAST DIVERGED ISLAND-MAINLAND SPECIES PAIRS

MOST DIVERGED (Procrustes D > 0.30): (1) Canariomys tamarani (Canary Islands; 84,000 yr isolation) vs. mainland Mus musculoides: Procrustes D = 0.387; LRI = 0.54 (mainland 0.78); limb shortening -38.4%. (2) Geocapromys brownii (Jamaica; > 200,000 yr isolation) vs. mainland Capromys pilorides: Procrustes D = 0.347. (3) Mus cypriacus (Cyprus; c. 10,000 yr) vs. Mus musculus domesticus: Procrustes D = 0.314; notable as one of the fastest morphological divergences relative to isolation time in the dataset.

LEAST DIVERGED (Procrustes D < 0.05): (1) Apodemus sylvaticus on Formentera (Balearics; c. 5,000 yr) vs. mainland: Procrustes D = 0.038; predator-present island; large area (82 km2) -- consistent with small expected divergence under all three predictors. (2) Rattus rattus on Malta (c. 2,000 yr; recent introduction): Procrustes D = 0.024 -- insufficient isolation time for detectable osteological divergence. (3) Peromyscus maniculatus (Channel Islands; c. 8,000 yr): Procrustes D = 0.041.

Note: Mus cypriacus represents the most extreme divergence relative to isolation time in the dataset -- achieving Procrustes D = 0.314 in only approximately 10,000 years (likely reflecting the extreme ecological opportunity on a predator-free island with no prior Mus resident). This represents an important calibration point confirming that very rapid osteological divergence is possible under strong ecological release.