



Skull evolution in Canary Island mice reflects responses to geography and environment shaped by morphological integration

Francesc Muñoz-Muñoz¹ · S. Tulloch¹ · J. Martínez-Vargas² · C. Feliu³ · J. Ventura⁴

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Abstract

Islands provide powerful systems for studying morphological evolution, and although body size evolution in insular mammals is well documented, less is known about how integrated cranio-mandibular traits respond to the combined effects of environmental variation and geographic isolation. Here, we examine cranial and mandibular variation in house mice (*Mus musculus domesticus*) from the Canary Islands, a system characterised by repeated colonisation events and marked ecological heterogeneity. Using geometric morphometrics, we assess cranio-mandibular shape across the archipelago within an integrated morphological framework. Cranio-mandibular integration is evaluated using partial least squares, while the relative contributions of environmental and geographic factors are quantified using variation partitioning analyses. Body size varied significantly among islands but showed no clear geographic pattern. In contrast, cranial and mandibular shape exhibited strong population differentiation largely independent of size, with pronounced geographic structuring. Despite a strong signal of integration, localised shape changes were also evident, most notably affecting the coronoid process. Variation partitioning analyses revealed that both geographic structure and environmental heterogeneity contributed significantly to cranial and mandibular shape variation, although geographic factors consistently accounted for a larger proportion of morphological differentiation. These findings indicate that cranio-mandibular evolution in insular mice reflects responses to environmental variation and geographic structure, with morphological integration modulating these effects, and suggest a potential role for localised functional adaptation, phenotypic plasticity, and colonisation history. Overall, our results highlight the importance of jointly considering spatial and environmental drivers within an integrated framework to understand morphological evolution in island systems.

Keywords Adaptation · Cranio-mandibular shape · Geometric morphometrics · Insular evolution · *Mus musculus* · Phenotypic covariation

Introduction

The house mouse (Linnaeus 1758) is a well-established model organism in evolutionary, ecological, genetic, and biomedical research, and one of the most widely distributed mammal species. It is thought to have originated in the northern part of the Indian subcontinent, where it diverged into three widely recognised subspecies (*Mus musculus musculus*, *Mus musculus domesticus*, and *Mus musculus castaneus*) approximately 226,000–187,000 years ago (Guénét and Bonhomme 2003; Fujiwara et al. 2022). Owing to its ancient commensal relationship with humans, the house mouse dispersed from its ancestral range and established populations across nearly all continents and many island systems worldwide (Guénét and Bonhomme 2003; Fujiwara et al. 2022). Specifically, *M. musculus domesticus*

✉ Francesc Muñoz-Muñoz
francesc.munozm@uab.cat

¹ Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma de Barcelona, Edifici C, C1/121, Campus de la UAB, Cerdanyola del Vallès, Barcelona 08193, Spain

² Museu de Ciències Naturals de Barcelona, Barcelona, Spain

³ Departament de Biologia, Sanitat i Medi Ambient, Universitat de Barcelona, Barcelona, Spain

⁴ Museu de Ciències Naturals de Granollers, Granollers, Barcelona, Spain

dispersed westward through the Near East into Western Europe and North Africa, later reaching the Americas and Australia (Guénet and Bonhomme 2003; Li et al. 2021; Fujiwara et al. 2022). The colonisation of distant continents and remote archipelagos was largely mediated by human maritime transport, with mice travelling as stowaways on ships (Gabriel et al. 2024).

Among the numerous island systems colonised by *M. musculus domesticus* are the Canary Islands, a volcanic archipelago located approximately 95 km off the north-western coast of Africa. This archipelago comprises seven major islands and several islets, which have remained isolated from the continent since their sequential formation between 20.6 and 1.12 million years ago (Pagès et al. 2012). Archaeological evidence indicates that *M. musculus* was already present in the Canary Islands between at least 756 BCE (Before Common Era) and 313 CE (Common Era), coinciding with the earliest known human settlement in the archipelago. This temporal overlap supports the hypothesis that mice arrived on the islands accompanying humans, rather than via natural oceanic dispersal (Alcover et al. 2009). Phylogeographic studies, however, have identified three distinct mitochondrial D-loop clades in the Canary Islands to date, each originating from a different geographic region, thus supporting the hypothesis of a complex colonisation history characterised by multiple independent introduction events over time (Bonhomme et al. 2011; Gabriel et al. 2015, 2024). Following their introduction, populations of house mice became established across all the main islands and associated islets of the Canary archipelago, except for Montaña Clara (Nogales et al. 2006), and adapted to a wide range of ecological conditions, from arid coastal zones to humid high-altitude habitats. These environmental differences are largely structured along strong altitudinal gradients, resulting in well-defined vegetation belts ranging from xeric coastal scrub and thermophilus woodlands to laurel forests and high-elevation pine forests in the wetter islands (Fig. 1).

Islands are typically characterised by ecological simplification, including reduced species richness, relaxed interspecific competition, and lower predation pressure relative to mainland systems (Adler and Levins 1994). Such conditions can foster distinctive evolutionary trajectories, often resulting in recurrent and predictable changes in morphology, behaviour, and life-history traits across diverse taxa, a pattern collectively referred to as the “island syndrome” (Adler and Levins 1994; Lomolino 2005). Among the traits that commonly diverge in insular mammals, body size is one of the most consistent and well documented. This variation often conforms to the “island rule”, a general pattern whereby insular

populations exhibit shifts in body size relative to their mainland counterparts (Foster 1964; Lomolino 2005; Benítez-López et al. 2021). According to this rule, small species tend to evolve larger sizes, whereas large species typically become smaller. Increases in body size consistent with the “island rule” have been reported for several insular populations of small mammals (Adler and Levins 1994; Michaux et al. 2002; Sánchez-Chardi et al. 2018), including the house mouse, *Mus musculus* (Rowe-Rowe and Crafford 1992; Renaud and Auffray 2010; Wilches et al. 2021). Mice populations of the Canary Islands therefore provide an exceptional natural framework for investigating how isolation and contrasting ecological conditions shape morphological variation.

Because the function of biological structures depends on their form (Gans 1988), the study of morphological variation is fundamental to elucidating the mechanisms underlying adaptation and diversification in natural populations. Although some studies have previously examined morphological variation in Canarian mice (Carrascosa and López-Martínez 1988; Michaux et al. 2007), to our knowledge, a detailed analysis of skull shape variation has not been conducted to date. Cranial and mandibular structures are closely associated with feeding ecology, bite performance, and functional efficiency (Ginot et al. 2018, 2019) and can therefore provide valuable insights into how populations respond to ecological pressures (Anderson et al. 2014; Renaud et al. 2017). Therefore, examining cranial and mandibular variation in *M. musculus* not only sheds light on patterns of adaptive evolution but also provides a framework for understanding how insularity drives morphological divergence through the combined effects of ecological and evolutionary mechanisms.

In this context, we analyse cranial and mandibular form variation in house mouse populations from several islands of the Canary archipelago to uncover patterns of morphological differentiation and determine potential signals of adaptation or evolutionary divergence. In addition, we compare the skull morphology of insular populations with that of samples from the Iberian Peninsula to assess the degree and pattern of insular differentiation and to explore whether these patterns are consistent with the expectations of an island syndrome. We also examine the covariation between cranial and mandibular shape to assess the degree of morphological integration of these structures and to evaluate whether coordinated changes in both structures are consistent with the observed geographical pattern. Finally, we explore the influence of geographical and environmental factors on shape divergence, providing insight into the microevolutionary processes shaping introduced populations in insular environments.

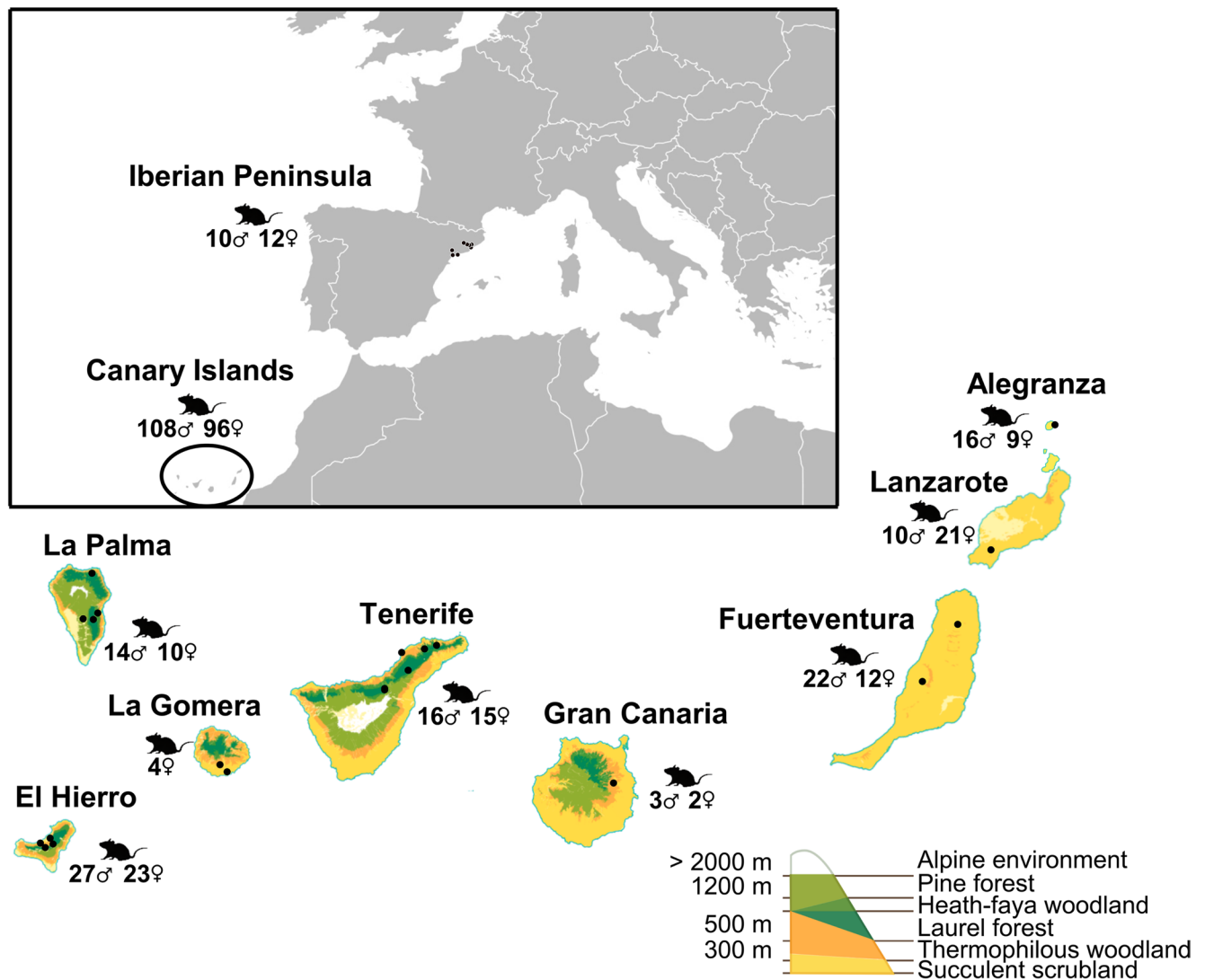


Fig. 1 Geographic origin of the sampled mice. Vegetation belts according to altitude are displayed in each island; variations are chiefly due to thermal gradient (adapted from the open educational resource “Pisos

de vegetación” by the TSP project (IECI-EFC) of the Government of the Canary Islands; <https://www3.gobiernodecanarias.org/medusa/ecoescola/recursosdigitales/2015/06/10/html5-pisos-de-vegetacion/>)

Materials and methods

Sample composition

The sample consisted of skulls from 226 adult individuals of wild *Mus musculus domesticus*, preserved in zoological collections at the Universitat de Barcelona and Universitat Autònoma de Barcelona. Of these, 204 were from the seven main islands of the Canary archipelago (Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Palma, La Gomera, and El Hierro) as well as from the nearby islet of Alegranza. The remaining 22 specimens originated from various locations in the northeastern Iberian Peninsula (Fig. 1, Online Resource 1: Table S1). Individuals included in this study originated from previous

research projects in which specimens were sexed and weighed to the nearest 0.1 g after removal of the visceral organs. Eviscerated body mass was used as a proxy for body size in all analyses because it reduces variation unrelated to structural body size, such as differences in gut contents or pregnancy status.

Morphological data acquisition

Cranial morphology was studied using 3D models obtained through photogrammetric techniques according to the protocol established by Durão et al. (2018). Each 3D model was built from a set of 36 photos obtained using a Canon EOS 750D DSLR camera mounted on a tripod and equipped with a Tamron 60 mm f/2.0 Di II

LD macro lens and a polarising filter. A complete photo set was captured for each cranium using the ‘turntable method’, where the camera remained fixed while the specimen was rotated in 10° increments. All images were taken inside a light box to homogenise the light and avoid shadows and flares. Each photo was taken using a remote trigger to reduce camera vibration and obtain photos that were as focused and sharp as possible. Model quality was assessed using internal software parameters, including total error, residuals, and precision values. The 3D form of the cranium was characterised by a set of 40 landmarks (Fig. 2, Online Resource 1: Table S2) digitised using the PhotoModeler software v.2015.1.1 (EOS Systems Inc., 2015). All the models were scaled using the linear distance between the rhinion (landmark 1) and opisthion (landmark 30) (Fig. 2, Online Resource 1: Table S2), measured directly on each cranium, to assign a metric scale to the photogrammetric models.

Given the relatively flat structure of the mouse mandible, its form was studied by means of 2D landmarks. To this end, the two hemimandibles of each individual were photographed in a mesial view along with a scale bar using the same camera, lens and filter as for the cranium, mounted on a copy stand. Afterwards, a set of 12 landmarks were digitised (Fig. 2, Online Resource 1: Table S3) on each scaled hemimandible using tpsDig2 v. 2.26 (Rohlf 2010).

Geometric morphometric analyses

All geometric morphometric analyses were performed using the packages geomorph version 4.0.6 (Baken et al. 2021; Adams et al. 2023) and RRPP version 1.4.0 (Collyer and Adams 2018, 2023) within the R software environment, version 4.3.1 (R Core Team 2023). The morphology defined by each set of landmarks was decomposed into size and shape, which were analysed separately. Size was quantified as centroid size (CS), calculated as the square root of the sum of squared distances from each landmark to the centroid of the landmark configuration (Bookstein 1991). Therefore, CS was calculated separately for each cranium and each hemimandible. Shape information was extracted from landmark configurations by performing, separately for each structure, a generalised Procrustes analysis (GPA) and a projection onto the tangent space (Rohlf and Slice 1990). In the cranium, given that it is a symmetric structure (object symmetry), the GPA was conducted using both original and reflected configurations of landmarks (Klingenberg et al. 2002). Since the two hemimandibles were photographed separately (matching symmetry), prior to the GPA reflected configurations of the left hemimandibles were generated by multiplying their x coordinates by -1 (Adams et al. 2023). This approach enabled the partitioning of shape variation of both structures into the symmetric and asymmetric components

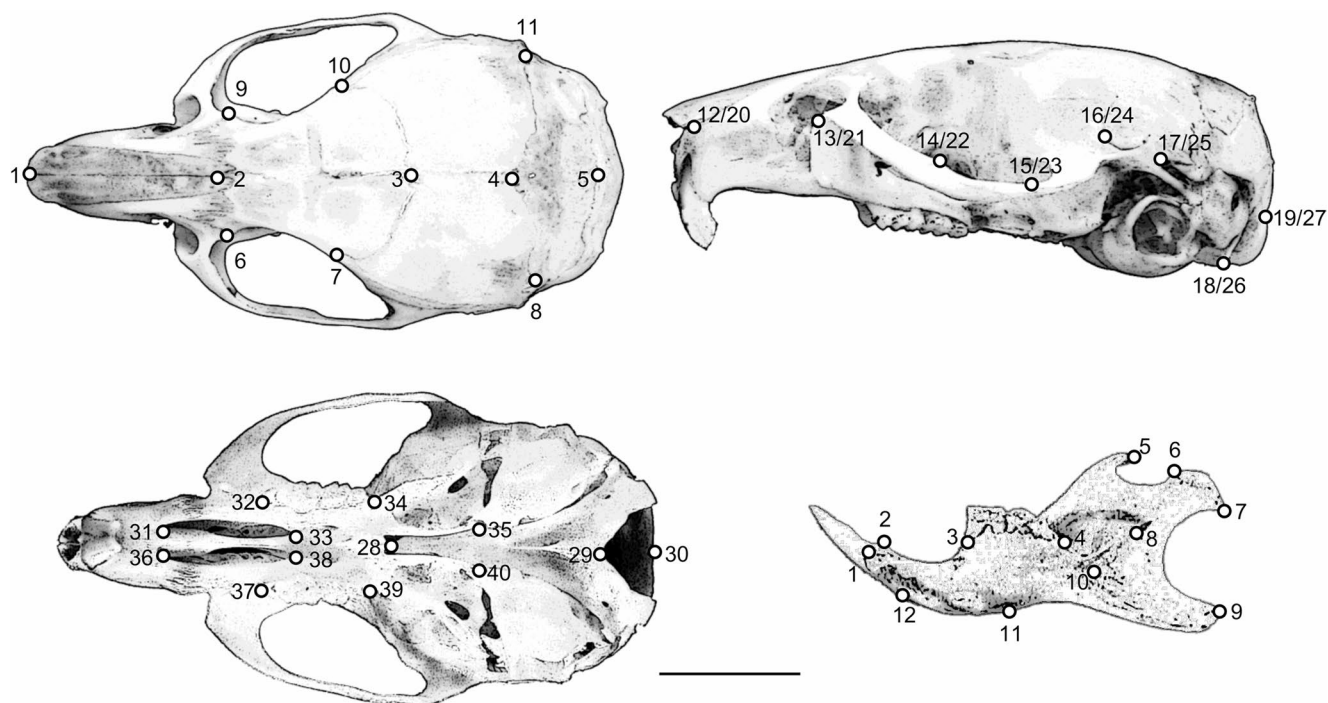


Fig. 2 Location of the forty 3D landmarks digitised on the cranium and the twelve 2D landmarks digitised on the mesial side of the mandible. In the lateral view of the cranium (upper right), pairs of landmarks

refer to the left and right sides, respectively. Illustrations are of *Mus musculus domesticus* UZUAB_99063006. Scale bar equals 5 mm

(Klingenberg et al. 2002). The symmetric component of shape of each structure was used in subsequent analyses.

Size variation

Before testing for differences in mandibular and cranial size, variation in body size (estimated as eviscerated body mass) was first assessed using the *lm.rpp* function in the RRPP package (Collyer and Adams 2023). An initial model was fitted including population, sex, and their interaction as predictors, and eviscerated body mass as the dependent variable. As sex and the interaction term were not significant (see Results), the model was simplified to include only population as a predictor. Post-hoc differences among populations were then evaluated using the *pairwise* function, with significance determined via permutation tests (1,000 iterations).

Prior to evaluating variation among populations in mandible and cranium size, bilateral symmetry in mandible size was examined using the *bilat.symmetry* function from the geomorph package (Adams et al. 2023). Since the cranium exhibits object symmetry, and a single CS was calculated for it, bilateral symmetry in cranial size was not tested. Differences in cranium and mandible size were assessed using analyses of variance (ANOVAs) based on a residual randomisation procedure, implemented via the *procD.lm* function (Adams et al. 2023). For each structure, an initial model was fitted including eviscerated body mass, sex, population, and all pairwise interactions as predictors. Type III sum of squares was used to account for unbalanced group sizes. Models were subsequently simplified by removing non-significant predictors. When interaction terms were not supported by the data or lost significance during model simplification, reduced models excluding interactions were fitted using Type II sum of squares to obtain more robust estimates of main effects. As only eviscerated body mass and population showed significant effects for both structures (see Results), post-hoc pairwise comparisons were conducted following Type II ANOVAs with eviscerated body mass and population as factors, in order to assess size differences among islands while statistically controlling for body size. Post-hoc tests were performed using the *pairwise* function implemented in the RRPP package, and significance was evaluated via permutation tests with 1,000 iterations. Given that the tests rely on permutation procedures and were guided by a priori biological hypotheses, *p*-values were not further adjusted for multiple comparisons.

Shape variation

Bilateral symmetry in mandibular and cranial shape was assessed separately ahead of shape variation analyses,

using the *bilat.symmetry* function from the geomorph package (Adams et al. 2023). Differences in cranium and mandible shape were also examined separately using analyses of variance with residual randomisation, implemented via the *procD.lm* function (Adams et al. 2023). Significance was determined via permutation tests with 1,000 iterations. Prior to testing for shape differences among populations, simple allometry was evaluated for each structure by fitting a linear model with CS as the predictor and the symmetric component of shape as the dependent variable. Afterwards, for each structure, a model including CS, sex, population, and their pairwise interactions was fitted using Type III sum of squares to account for unbalanced group sizes. Since sex showed no significant effect on shape in either the cranium or the mandible (see Results), males and females were pooled in all subsequent analyses. In contrast, a significant effect of size was detected in both structures (see Results). Therefore, to evaluate the role of allometry in morphological differentiation at the population level, two sets of analyses were conducted for each structure: one based on raw shape data (total shape variation) and another based on size-corrected data (non-allometric shape variation). Size correction was performed by extracting residuals from a simple allometric model. For both datasets, linear models were fitted, with population as the predictor and shape as the response variable. Post-hoc tests were then conducted to examine pairwise differences among populations. Because the tests rely on permutation procedures and were driven by a priori biological hypotheses, *p*-values were not further adjusted for multiple comparisons.

Additionally, to further explore patterns of shape variation, a principal component analysis (PCA) was performed on both datasets (Klingenberg et al. 2002).

Covariation between cranial and mandibular shape

Morphological integration refers to the degree of covariation between anatomical structures (Olson and Miller 1958). To quantify integration between mandible and cranium shape, a two-block partial least squares (2B-PLS) analysis was performed using the *two.b.pls* function implemented in the geomorph package (Adams et al. 2023). This method identifies pairs of linear combinations of variables that maximise covariance between datasets and is widely used to assess morphological integration in geometric morphometrics. To evaluate the effect of allometry on covariation patterns, analyses were conducted on both total shape variation and non-allometric shape variation. The statistical significance of these covariations was tested using permutation tests with 1,000 iterations.

Variation factors

To evaluate the relative contributions of environmental and geographic factors to morphological differentiation, variation partitioning analyses were conducted separately for cranial and mandibular shape following Viacava et al. (2020). Analyses were performed using the *varpart* function in the *vegan* package (Oksanen et al. 2018), which allowed partitioning shape variation into pure and shared fractions attributable to environmental and spatial predictors. Because our goal was to disentangle the effect of geographic structure and environmental factors on morphological differentiation of insular populations, mice from the Iberian Peninsula were excluded from these analyses.

Environmental predictors were selected a priori to represent the main climatic and topographic gradients across the archipelago. Four variables were initially considered: elevation, annual mean temperature (BIO1), annual temperature range (BIO7), and annual precipitation (BIO12), with climatic data extracted from WorldClim v2.1 at 30 arc-second resolution for the period 1970–2000 (Fick and Hijmans 2017). To reduce collinearity among predictors and summarise major environmental gradients, a PCA was performed on standardised variables. The first two principal components were retained as composite environmental predictors for subsequent analyses.

Spatial structure was modelled using principal coordinates of neighbour matrices (PCNM) derived from the geographic coordinates of sampling localities (Borcard and Legendre 2002), providing orthogonal spatial variables that capture spatial patterns across multiple scales and help to account for spatial autocorrelation. Positive eigenvectors were retained and subjected to forward selection to identify significant spatial predictors while limiting model overfitting; selection was based on adjusted R^2 criteria. The significance of full and partial models in the variation partitioning framework was assessed using redundancy analyses (RDA) with 1,000 permutations.

All variables were standardised to zero mean and unit variance using the *scale* function in R (R Core Team 2023).

Analyses were performed on both total shape variation and non-allometric shape variation to evaluate the potential influence of allometry.

Results

Size variation

In the full model assessing eviscerated body mass differences, only the population factor had a significant effect ($R^2 = 0.157$, $F = 5.65$, $p = 0.001$), whereas neither sex nor the interaction term were significant. In the simplified model, population remained highly significant, explaining almost 25% of the variance ($R^2 = 0.249$, $F = 8.97$, $p = 0.001$). Significant differences in eviscerated body mass were detected among mice populations from the Canary Islands and the mainland (Table 1 and Online Resource 1: Table S4). Individuals from Lanzarote, the Iberian Peninsula, and Alegranza showed the highest body masses, whereas mice from Fuerteventura, La Gomera, and El Hierro were the lightest (Fig. 3). Populations from La Palma, Gran Canaria, and Tenerife exhibited intermediate body mass values. Pairwise comparisons confirmed these patterns, revealing significant contrasts among the specimens from several island pairs, particularly within the eastern group (Alegranza, Fuerteventura, Lanzarote) and between these islands and the mainland (Table 1 and Online Resource 1: Table S4). In contrast, most comparisons among the western islands were nonsignificant, indicating relatively homogeneous body sizes within that region.

The ANOVA assessing bilateral symmetry in mandible size revealed a significant effect of individual, but not of side. However, the p -value for the side effect was close to 0.05, suggesting a potential trend toward directional asymmetry of mandible size (Online Resource 1: Table S5).

The linear model testing the effects of body size, sex, and population on cranial and mandibular size revealed significant effects of body size and population on both structures, while sex had no significant influence (Online Resource 1:

Table 1 Significance values for post-hoc comparisons of population differences in eviscerated body mass

Populations	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerteventura	Lanzarote	Alegranza	Peninsula
El Hierro	–	0.067	0.711	0.102	0.970	0.218	0.001	0.002	0.001
La Palma		–	0.242	0.739	0.329	0.004	0.026	0.224	0.030
La Gomera			–	0.271	0.743	0.862	0.022	0.084	0.027
Tenerife				–	0.455	0.011	0.002	0.101	0.008
Gran Canaria					–	0.523	0.023	0.075	0.030
Fuerteventura						–	0.001	0.001	0.001
Lanzarote							–	0.318	0.958
Alegranza								–	0.370
Peninsula									–

p -values less than 0.05 are shown in bold

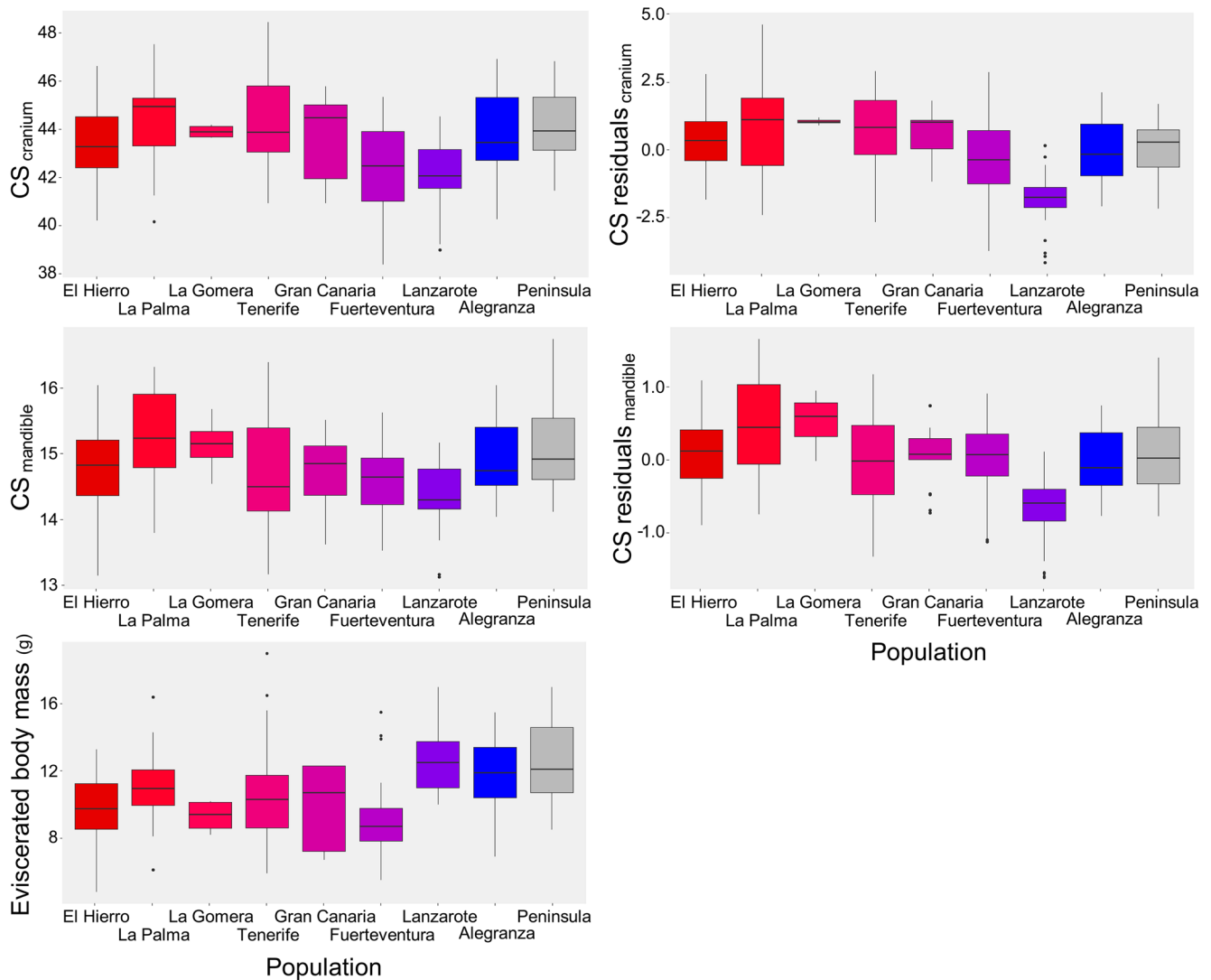


Fig. 3 Size differences between sampled populations of *Mus musculus*. Islands are ordered and coloured following a red-to-blue gradient according to a west-east longitudinal order. Boxplots show the distribution of CS values and eviscerated body mass across the sampled populations. Left-hand graphs show raw values, while right-hand

graphs show residuals from the regression of CS on eviscerated body mass. Each box represents the interquartile range (IQR), with the central line indicating the median. Whiskers extend up to 1.5 times the IQR, and black dots denote outliers

Table S6). A significant interaction between body size and population was detected for the mandible but not for the cranium. In simplified models excluding non-significant terms, both body size and population remained significant predictors of size in both structures, jointly explaining a substantial proportion of the observed variation (Table 2). Post-hoc comparisons identified 12 and 15 significant pairwise differences among populations for the cranium and mandible size, respectively (Table 3 and Online Resource 1: Table S7). For both structures, individuals from Lanzarote consistently exhibited the smallest size values after correcting for eviscerated body mass, differing significantly from all other localities. In contrast, individuals from La Palma displayed the largest sizes and differed significantly from

several populations, including Alegranza, Fuerteventura, the Iberian Peninsula, and in the case of the mandible, El Hierro and Tenerife. Additional significant contrasts involved La Gomera, El Hierro, and Tenerife, though with less consistency across structures. Overall, cranial and mandibular size variation showed broadly similar patterns across populations, particularly with respect to the marked divergence between the populations from Lanzarote and La Palma (Fig. 3).

Shape variation

The ANOVAs assessing bilateral symmetry in mandibular and cranial shape revealed significant effects of

Table 2 Results of the reduced lineal models assessing the effect of eviscerated body mass and population on cranial and mandibular size. Abbreviations: **df**, degrees of freedom; **MS**, mean square; **SS**, sum of squares

Cranium	df	SS	MS	R ²	F	Z	p-value
Body mass	1	231.660	231.661	0.320	138.976	6.749	0.001
Population	8	165.300	20.663	0.229	12.396	6.745	0.001
Residuals	216	360.060	1.667	0.498			
Total	225	722.980					
Mandible	df	SS	MS	R ²	F	Z	p-value
Body mass	1	34.688	34.688	0.327	138.011	6.568	0.001
Population	8	23.840	2.980	0.225	11.857	7.040	0.001
Residuals	216	54.290	0.251	0.512			
Total	225	106.008					

p-values less than 0.05 are shown in bold

Table 3 Significance values for post-hoc tests assessing differences in cranial (above the diagonal) and mandibular (below the diagonal) size between populations

Populations	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerteventura	Lanzarote	Alegranza	Peninsula
El Hierro	–	0.207	0.341	0.440	0.708	0.073	0.001	0.212	0.195
La Palma	0.045	–	0.734	0.614	0.713	0.009	0.001	0.025	0.028
La Gomera	0.136	0.656	–	0.555	0.614	0.105	0.001	0.140	0.142
Tenerife	0.099	0.001	0.032	–	0.960	0.023	0.001	0.078	0.063
Gran Canaria	0.776	0.190	0.193	0.605	–	0.237	0.002	0.336	0.304
Fuerteventura	0.655	0.031	0.093	0.264	0.943	–	0.001	0.798	0.868
Lanzarote	0.001	0.001	0.001	0.001	0.005	0.001	–	0.001	0.001
Alegranza	0.201	0.002	0.044	0.851	0.676	0.405	0.001	–	0.937
Peninsula	0.353	0.013	0.069	0.635	0.836	0.612	0.001	0.755	–

p-values less than 0.05 are shown in bold

both individual and side (Online Resource 1: Table S5), thereby indicating the presence of directional asymmetry. However, the magnitude of this effect was negligible, as evidenced by the low R² values. Linear models further detected a significant association between shape and size in both the cranium and mandible, consistent with simple allometry (cranium: R² = 0.063, $p < 0.001$; mandible: R² = 0.052, $p < 0.001$). Nonetheless, the low R² values suggest that size explains only a small fraction of the observed shape variation. Models including sex and population as additional predictors also identified a significant effect of size on cranial shape, though a marginally significant effect on mandibular shape, and significant effects of population as well as of the interaction between population and size in both structures (Online Resource 1: Table S8). Given the significant allometric effects, shape differences among populations were assessed using total and non-allometric shape variation. In both analyses, population had a significant and substantial effect on cranial and mandibular shape, revealing that shape variation among populations cannot be explained solely by allometry (Table 4). Post-hoc comparisons revealed widespread differences in cranial and mandibular shape among populations, with most pairwise comparisons being significant for both total and non-allometric shape variation (Tables 5 and 6, and Online Resource 1: Tables S9 and S10). Cranial shape

diverged most strongly between Alegranza and the Iberian Peninsula populations, although notable differences were also detected between the population from this islet and those from some of the western islands (La Gomera, La Palma and Tenerife). Mandibular shape differences were most pronounced between El Hierro and Lanzarote, Lanzarote and Tenerife, and several pairs involving Alegranza and the Iberian Peninsula populations. Non-significant comparisons were largely restricted to pairs including La Gomera and Gran Canaria, the two samples with lower sample sizes, suggesting limited statistical power. These patterns were further supported by the PCA results. The cranial PCA placed Alegranza and the Iberian Peninsula populations at opposite ends of the PC1 axis, with the remaining populations positioned between them in a pattern broadly consistent with their geographic distribution (Fig. 4a). A geographic pattern was also evident in the mandibular PCA, with Alegranza and Lanzarote at one end of the PC1 axis and El Hierro at the other (Fig. 4a). However, the mandibular pattern differed in its configuration from that observed for the cranium, notably due to the more central position of Iberian mice within the mandibular morphospace.

In the cranium, shape variation along PC1 was primarily expressed in the skull vault, nasal region, zygomatic arch and foramen magnum. Insular mice exhibited a dorsocaudally

Table 4 Results of the lineal models assessing the effect of population on cranial and mandibular shape. Abbreviations: **df**, degrees of freedom; **MS**, mean square; **SS**, sum of squares

Cranium _{total}	df	SS	MS	R ²	F	Z	p-value
Population	8	0.076	0.010	0.180	5.958	10.601	0.001
Residuals	217	0.347	0.002	0.820			
Total	225	0.423					
Mandible _{total}	df	SS	MS	R ²	F	Z	p-value
Population	8	0.070	0.009	0.197	6.654	10.619	0.001
Residuals	217	0.285	0.001	0.803			
Total	225	0.355					
Cranium _{non-allometric}	df	SS	MS	R ²	F	Z	p-value
Population	8	0.073	0.009	0.183	6.085	11.814	0.001
Residuals	217	0.324	0.001	0.817			
Total	225	0.396					
Mandible _{non-allometric}	df	SS	MS	R ²	F	Z	p-value
Population	8	0.068	0.009	0.202	6.887	11.775	0.001
Residuals	217	0.269	0.001	0.798			
Total	225	0.337					

p-values less than 0.05 are shown in bold

Table 5 Significance values for post-hoc comparisons of population differences in total cranial (above the diagonal) and mandibular (below the diagonal) shape

Populations	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerteventura	Lanzarote	Alegranza	Peninsula
El Hierro	–	0.002	0.100	0.001	0.049	0.001	0.001	0.001	0.001
La Palma	0.001	–	0.389	0.001	0.138	0.001	0.001	0.001	0.001
La Gomera	0.361	0.495	–	0.012	0.426	0.082	0.116	0.001	0.019
Tenerife	0.001	0.001	0.132	–	0.037	0.001	0.001	0.001	0.001
Gran Canaria	0.002	0.060	0.028	0.024	–	0.086	0.279	0.003	0.001
Fuerteventura	0.001	0.001	0.369	0.001	0.011	–	0.001	0.001	0.001
Lanzarote	0.001	0.001	0.005	0.001	0.182	0.001	–	0.001	0.001
Alegranza	0.001	0.001	0.008	0.001	0.493	0.001	0.002	–	0.001
Peninsula	0.001	0.001	0.140	0.001	0.032	0.001	0.001	0.001	–

p-values less than 0.05 are shown in bold

Table 6 Significance values for post-hoc comparisons of population differences in non-allometric shape of the cranium (above the diagonal) and mandible (below the diagonal)

Populations	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerteventura	Lanzarote	Alegranza	Peninsula
El Hierro	–	0.001	0.084	0.001	0.027	0.001	0.001	0.001	0.001
La Palma	0.001	–	0.315	0.001	0.131	0.001	0.001	0.001	0.001
La Gomera	0.196	0.413	–	0.008	0.373	0.147	0.152	0.001	0.013
Tenerife	0.001	0.001	0.087	–	0.013	0.001	0.001	0.001	0.001
Gran Canaria	0.002	0.040	0.025	0.011	–	0.074	0.196	0.003	0.001
Fuerteventura	0.001	0.001	0.482	0.001	0.007	–	0.001	0.001	0.001
Lanzarote	0.001	0.001	0.010	0.001	0.160	0.001	–	0.001	0.001
Alegranza	0.001	0.001	0.005	0.001	0.446	0.001	0.002	–	0.001
Peninsula	0.001	0.001	0.113	0.001	0.046	0.001	0.001	0.001	–

p-values less than 0.05 are shown in bold

expanded neurocranium, a dorsoventrally flattened nasal region, an anterodorsal expansion of the jugal and a foramen magnum shifted to a more ventral and anterior position (Fig. 4b). In the mandible, variation associated with PC1 was concentrated in the processes, particularly the coronoid, which in mice from Lanzarote, Alegranza, and Gran Canaria showed a marked anterior displacement (Fig. 4c).

Covariation between cranial and mandibular shape

As expected, 2B-PLS analyses revealed significant covariation between cranial and mandibular shape when considering total shape variation (r -PLS = 0.661, Z = 6.876, p < 0.001) and non-allometric shape variation (r -PLS = 0.486, Z = 3.793, p < 0.001). Distribution of populations in the integrated

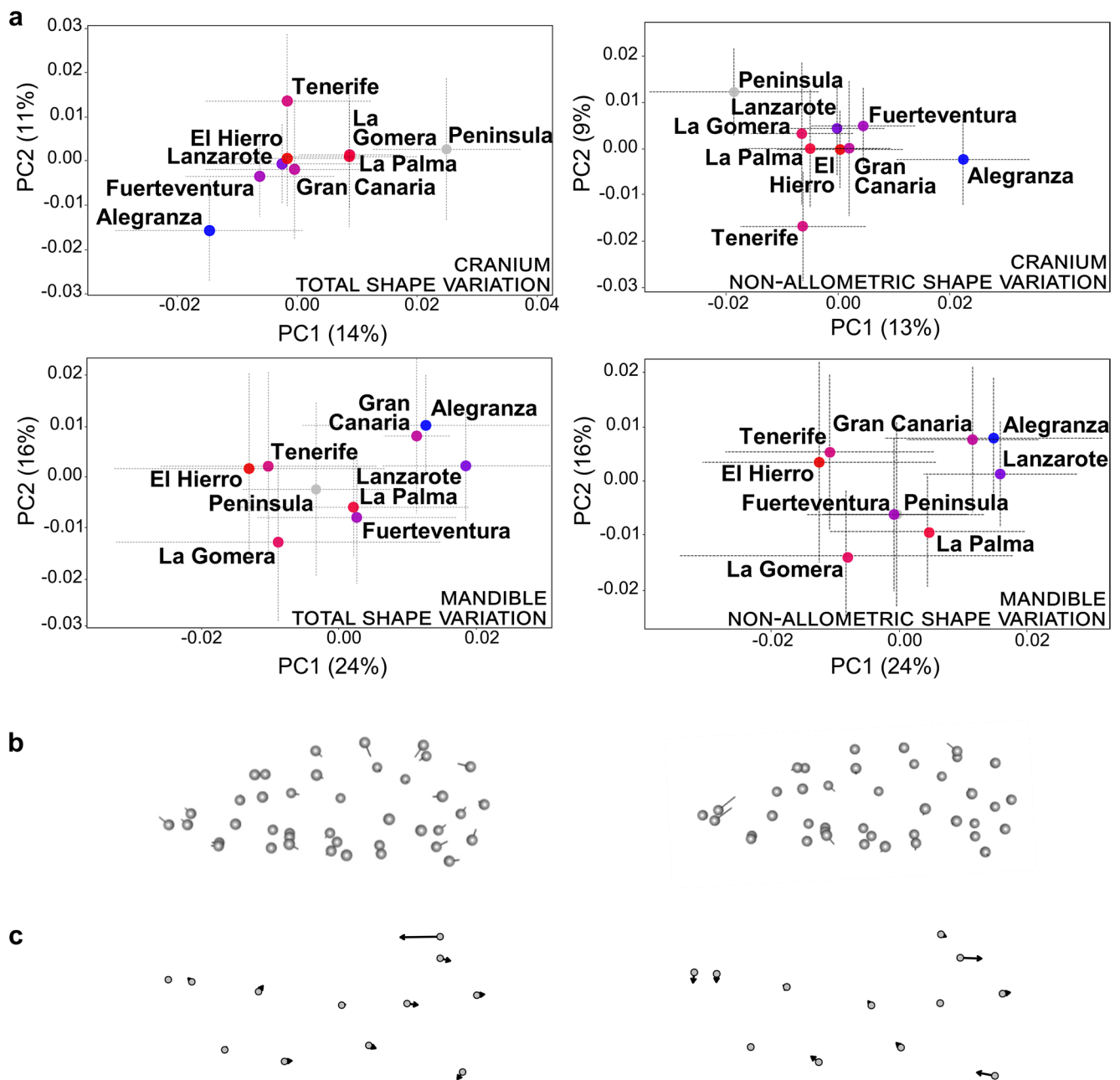


Fig. 4 Shape differences between sampled populations of *Mus musculus domesticus*. **a**. PC1 versus PC2 scores from PCAs of the cranium (top) and the mandible (bottom). Left panels show total shape variation; right panels show non-allometric shape variation. Coloured points represent population means and bars indicate standard deviation.

tions. Island colours follow a red-to-blue gradient from the western to the eastern islands; **b**. cranium shape changes (magnitude=1) along PC1 (left) and PC2 (right); **c**. mandible shape changes (magnitude=1) along PC1 (left) and PC2 (right)

shape space closely mirrored the patterns observed in the cranial PCA, also revealing a clear geographic structure (Fig. 5a). Alegranza and the Iberian Peninsula consistently occupied opposite extremes of the variation, whereas Tenerife displayed a marked positional shift when comparing total and non-allometric shape variation (even surpassing the Iberian Peninsula in non-allometric data). The remaining populations (El Hierro, La Palma, La Gomera, Gran

Canaria, Lanzarote, and Fuerteventura) occupied intermediate positions, still displaying a defined geographic structure (Fig. 5a). Integrated shape differences closely paralleled those displayed by the PCA results, with island mice characterised by a dorsocaudally elongated neurocranium, dorsoventrally compressed nasal region, anteroventrally displaced foramen magnum, elongated molar row, and anteriorly shifted condylar and angular processes (Fig. 5b).

Variation factors

The PCA revealed strong covariation among environmental variables and summarised environmental variation into two main axes. The first principal component primarily reflected an altitudinal and climatic gradient, contrasting high-elevation sites characterised by higher precipitation and lower temperatures with low-elevation sites with warmer and drier conditions. The second principal component was mainly associated with annual temperature range, capturing an independent gradient of thermal variability. Together, the first two PCs accounted for 95.3% of the total environmental variation and were retained as synthetic predictors for subsequent analyses.

Variation partitioning analyses revealed significant effects of both geographic structure and environmental variation on cranial and mandibular shape, regardless of whether allometric effects were included or removed. In all cases, the pure geographic component explained the largest proportion of shape variation. A substantial fraction of variation was also shared between geographic and environmental predictors, whereas the pure environmental component accounted for a comparatively smaller proportion of variation (Table 7). For cranial shape, the relative contributions of geographic and environmental factors remained virtually unchanged after correcting for allometry, with the pure geographic fraction accounting for approximately twice as much variation as the pure environmental fraction. In contrast, mandibular shape

showed a stronger spatial signal, with the pure geographic component explaining substantially more variation than the environmental component, particularly after size correction. The shared spatial-environmental fraction was consistently moderate in magnitude, indicating that part of the environmental variation across the archipelago was geographically structured. Partial redundancy analyses further showed that the pure geographic and pure environmental fractions were significant in all cases, and that the full models combining both predictor sets were also significant for both cranial and mandibular shape, irrespective of allometric correction (Table 7).

Discussion

A specific manifestation of the “island syndrome” is the “island rule”, which predicts that small mammals living on islands often tend to become larger than their mainland conspecifics (Adler and Levins 1994; Lomolino 2005; Benítez-López et al. 2021). In Canarian mice, we observed significant variation in cranial, mandibular, and overall body size among populations; however, size differences did not follow the general predictions of the island rule. None of the studied island populations showed an increase in overall body size relative to continental mice, as opposed to what was previously reported for several insular rodent populations (Adler and Levins 1994; Michaux et al. 2002),

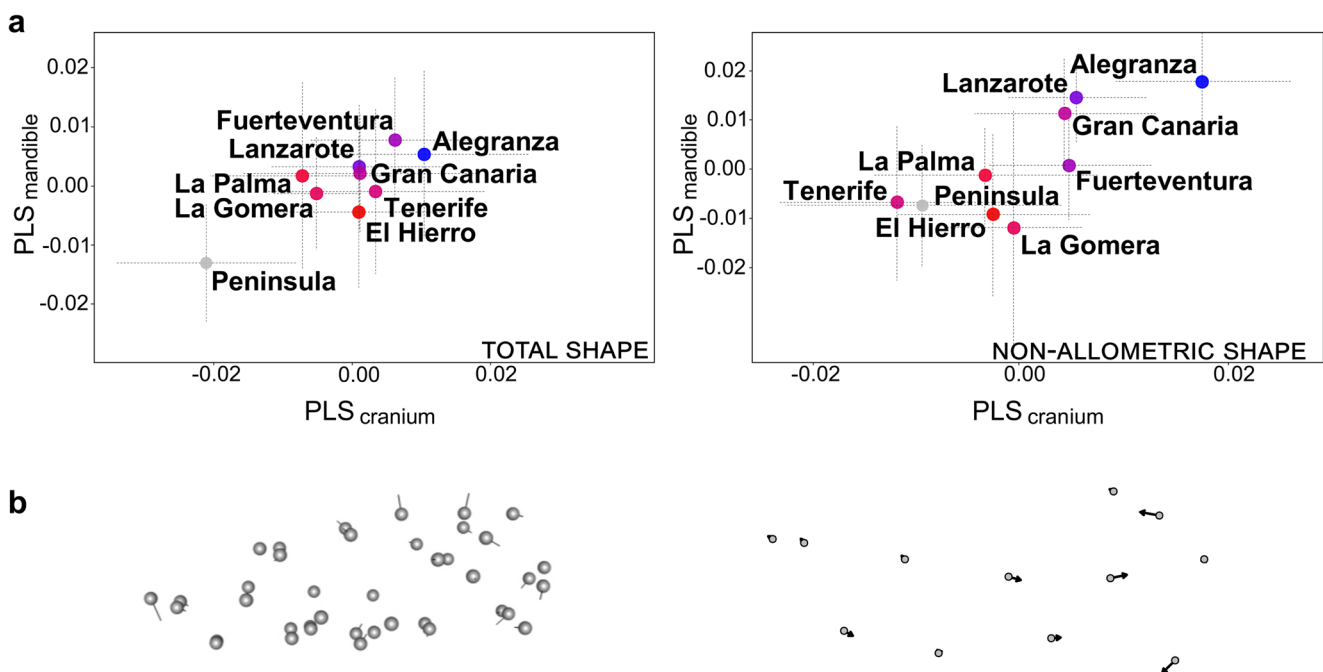


Fig. 5 Covariation between mandible and cranium shapes in sampled populations of *Mus musculus domesticus*. **a.** scatterplots of PLS1 scores obtained from 2B-PLSs analyses using total shape (left) and non-allometric shape (right). Coloured points represent population

means and bars indicate standard deviations. Island colours follow a red-to-blue gradient from the western to the eastern islands; **b.** integrated shape changes of the cranium (left) and mandible (right) along PLS1 (magnitude=1)

Table 7 Results of variation partitioning analyses for cranial and mandibular shape. Adjusted R^2 values indicate the proportion of variation explained by each component. F and p -values correspond to significance tests of the geographic, environmental, and full models. The shared fraction cannot be tested directly. Abbreviations: **Adj. R^2** , adjusted R^2

Dataset	Fraction	Adj. R^2	F	p -value
Cranium _{total}	Geographic	0.058	2.900	0.001
	Environmental	0.027	3.585	0.001
	Shared	0.031	-	-
	Full Model	0.116	3.897	0.001
Cranium _{non-allometric}	Geographic	0.055	3.727	0.001
	Environmental	0.031	4.057	0.001
	Shared	0.025	-	-
	Full Model	0.112	4.718	0.001
Mandible _{total}	Geographic	0.113	4.451	0.001
	Environmental	0.015	2.603	0.005
	Shared	0.054	-	-
	Full Model	0.182	5.389	0.001
Mandible _{non-allometric}	Geographic	0.122	4.706	0.001
	Environmental	0.015	2.540	0.001
	Shared	0.041	-	-
	Full Model	0.178	5.249	0.001

p -values less than 0.05 are shown in bold

including some populations of *Mus musculus* (Rowe-Rowe and Crafford 1992; Renaud and Auffray 2010; Wilches et al. 2021). Instead, most Canarian populations showed significantly smaller body sizes than Iberian mice, except for individuals from Lanzarote and Alegranza, which did not differ significantly from the continental population. Body size evolution in insular mammals reflects the combined influence of factors such as island area, isolation, resource availability, and the presence of competitors and predators (Michaux et al. 2002; Lister and Hall 2014; Berg and Nietlisbach 2025). These effects are interrelated and strongly context-dependent. For example, *Mus musculus* from Scottish and Faroese islands display a positive relationship between island area and body size, likely reflecting resource scarcity on very small islands (Lister and Hall 2014), whereas *Apodemus sylvaticus* from Mediterranean islands and *Peromyscus maniculatus* from the Gulf Islands show the opposite trend, linked to increased predator richness (Michaux et al. 2002; Berg and Nietlisbach 2025). Although neither Michaux et al. (2002) nor Berg and Nietlisbach (2025) explicitly tested a parabolic model, their data suggest a parabolic relationship between island area and body size, consistent with Lister and Hall's (2014) model, in which islands of intermediate size favour body size expansion. The Canary Islands, with areas ranging from ~10 to ~2,000 km², fall within this range; however, no comparable pattern was detected, suggesting that other ecological or historical factors may influence body size evolution in these populations. Interestingly, when controlling for overall body size, most insular populations tended to have relatively larger skulls, particularly mandibles, than continental mice, although only those from La Palma

exhibited significantly larger cranial and mandibular sizes. In this sense, it is important to note that studies addressing insular size evolution differ in the traits they measure: some focus on overall body size (Michaux et al. 2002), while others consider correlated traits such as cranial, dental or appendicular dimensions as proxies of size (Lister and Hall 2014). Analysing different traits may therefore influence observed patterns, since traits under distinct selective pressures can display divergent trends even when correlated with body size.

Beyond size variation, cranial and mandibular shape showed pronounced differentiation between populations from the Canary Islands and the Iberian Peninsula, as well as among island populations. Most pairwise comparisons remained significant after accounting for allometric effects, and patterns of differentiation were largely consistent between total and non-allometric data. Together with the low proportion of shape variation attributable to size, these results suggest that differentiation reflects factors acting directly on shape rather than being merely a by-product of size variation, in line with observations from other insular rodent populations (Pergams and Ashley 2001; Ledevin et al. 2016). Overall, both cranial and mandibular shape showed patterns of variation consistent with geographic structuring. However, the degree of differentiation between Iberian and Canarian populations varied markedly between the two skeletal structures. Cranial shape clearly separated Iberian mice from all Canarian populations, consistent with previous observations for molar shape (Michaux et al. 2007). In contrast, this distinction was far less pronounced for the mandible. Indeed, in the morphospace defined by the first two principal components of mandibular shape,

Iberian mice occupied a central position and overlapped with several Canary populations.

If morphological differentiation were driven primarily by neutral genetic drift under isolation, broadly concordant patterns of divergence between cranial and mandibular shape would be expected, particularly given their significant morphological integration. Covariation analyses, indeed, revealed an intermediate degree of integration, indicating that despite sharing common axes of variation, the two structures retain sufficient capacity to vary independently. The higher *r*-PLS value obtained for total shape variation relative to non-allometric shape variation confirms the role of size as a major contributor to cranio-mandibular integration (Klingenberg 2008, 2009; Martínez-Vargas et al. 2014), even when allometric effects on shape are modest. Integrated shape changes mainly involved the neurocranium, as well as the articular condyle and angular process of the mandible, underscoring the role of the masticatory musculature as an important integrating factor (Cornette et al. 2013). Notably, the distribution of populations along the PLS axes exhibited a clear geographic structure, suggesting that integrated shape variation captures a spatial signal consistent with processes such as isolation and shared evolutionary history.

Beyond the integrated component of shape variation, the contrasting differentiation observed between the two structures suggests that additional mechanisms, including localised functional selection and phenotypic plasticity, have contributed to cranio-mandibular variation across the archipelago (Renaud and Auffray 2010; Merilä and Hendry 2014). Indeed, one of the clearest localised shape changes not captured by the integrated patterns revealed by PLS analyses is the anterior displacement of the coronoid process in mice from islands such as Alegranza or Lanzarote. This shift reflects a reorganisation of the temporalis lever system, potentially altering the trade-off between bite force and jaw closing speed (Souquet et al. 2019). This reorganisation is particularly relevant because Canary Island populations, unlike Iberian mice, are feral and have transitioned from a commensal lifestyle to living in natural environments. Previous studies on feral mice indicate that mandibular shape is especially responsive to ecological conditions and dietary variation and can change rapidly through postnatal remodeling and phenotypic plasticity (Anderson et al. 2014; Renaud et al. 2017). In contrast, because the cranium is involved in multiple functions, it may be more constrained than the mandible in its capacity to evolve in response to dietary demands (Law et al. 2022).

Analyses of differentiation factors restricted to the Canary Islands further support the view that cranio-mandibular variation reflects the combined influence of spatial and environmental processes. Variation partitioning analyses revealed significant effects of both geographic structure

and environmental heterogeneity on shape variation in the cranium and mandible, and these relationships remained significant after removing allometric effects. A substantial fraction of shape variation was jointly explained by geographic and environmental predictors, indicating that environmental gradients are closely linked to spatial structure. Nevertheless, after accounting for this shared component, the pure geographic fraction consistently explained a larger proportion of shape variation than the pure environmental fraction in both structures, particularly in the mandible. Environmental variables nevertheless retained a significant independent association with shape after controlling for geography, indicating that environmental heterogeneity contributes to morphological differentiation beyond the effects of spatial structure alone. Together, these results suggest that morphological differentiation among islands is not solely the outcome of neutral divergence under isolation but also reflects responses to environmental heterogeneity operating across the archipelago. The environmental variables considered (altitude, temperature means and seasonality, and annual precipitation) capture major climatic gradients that are closely associated with variation in vegetation and resource availability among islands, providing a plausible ecological basis for the environmentally structured shape variation. Interestingly, the relative contribution of environmental factors was consistently greater in the cranium than in the mandible, whereas mandibular variation showed a stronger geographic component. This pattern suggests that, although localised functional responses and phenotypic plasticity may contribute to mandibular diversification, part of these differences may remain embedded within the spatial structure of the archipelago. Moreover, since the environmental variables included in the analyses represent broad-scale climatic gradients, it may not fully capture the local ecological factors most directly related to mandibular function, such as diet composition or food mechanical properties.

A study analysing the factors influencing molar shape in insular mice, including some Canarian populations, identified phylogenetic history as a major determinant of morphological variation (Ledevin et al. 2016). Colonisation history has clearly shaped the genetic background of Canary Island mouse populations (Bonhomme et al. 2011; Gabriel et al. 2015, 2024) and may therefore also have contributed to the observed cranio-mandibular differentiation. Notably, the marked cranial differentiation of mice from Tenerife coincides with the predominance of a distinct mitochondrial haplogroup on this island, in contrast to other islands such as La Palma, El Hierro or Gran Canaria (Gabriel et al. 2015). However, the role of phylogenetic history in shaping cranio-mandibular variation could not be explicitly addressed in the present study. Although several phylogeographic studies

of house mice in Macaronesia have included Canarian samples (Bonhomme et al. 2011; Gabriel et al. 2015, 2024), none has yet provided a detailed molecular characterisation of phylogenetic relationships across the entire archipelago. Available evidence nonetheless points to a complex colonisation history involving multiple introduction events from different source regions, likely linked to successive phases of human settlement and maritime connectivity (Alcover et al. 2009; Bonhomme et al. 2011; Mitchell 2024). Such a scenario implies that founder effects, admixture, and asynchronous colonisation may have contributed to the geographic structuring of cranio-mandibular shape, potentially interacting with environmentally driven differentiation.

Overall, our results suggest that insular cranio-mandibular differentiation in house mice arises from the interplay of shared developmental and allometric constraints, local adaptive and plastic responses to insular environments, geographic isolation, and colonisation history. In this context, morphological integration modulates the capacity of the cranium and mandible to evolve with a degree of independence in response to ecological and historical pressures. Disentangling the relative contributions of these processes will require detailed phylogenetic analyses across the archipelago, together with comparative data on diet and trophic ecology among islands, which would provide a more comprehensive framework for understanding the evolution of cranio-mandibular shape in insular mouse populations.

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Author contributions Francesc Muñoz conceived the study, and contributed to the experimental design, acquisition of 3D models, statistical analyses, and manuscript writing. Sergi Tulloch was involved in landmark digitisation and verification, statistical analyses, and preparation of an early version of the manuscript. Jessica Martínez contributed to acquisition of 3D models, statistical analyses, and manuscript writing. Carles Feliu participated in providing data and securing funding. Jacint Ventura conceived the study and contributed to experimental design, statistical analyses, manuscript revision and securing funding. All authors read and approved the final manuscript.

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Data availability The data that support the findings of this study are available at CORA RDR (<https://dataverse.csuc.cat/>).

Declarations

Competing interests The authors declare no competing interests.

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