



Mandible morphology, dental microwear, and diet of the extinct giant rats *Canariomys* (Rodentia: Murinae) of the Canary Islands (Spain)

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An ecomorphological approach of mandible shape through Fourier analyses combined with a paleodietary analysis of dental microwear patterns is used to reconstruct the diet of the extinct endemic *Canariomys bravoii* Crusafont, Pairó & Petter, 1964 and *Canariomys tamarani* López-Martínez & López-Jurado, 1987. These two large rodents, respectively, lived on Tenerife and Gran Canaria, the central islands of the Canary Archipelago. Mandible shape and dental microwear respectively inform us on the volume of vegetal matter and on the presence of grass in the diet. Both *Canariomys*, which are of similar size, possess relatively similar mandible outlines and microwear patterns. For each species, a diet based on plant materials except grass is the most likely. Such results chime with the similar environments offered by the islands in which the species lived. On the contrary, molar morphology suggests different feeding habits of the two *Canariomys*. Thus, this suggests a case of mosaic evolution between teeth and mandibles, as well as the likely sensitivity of mandible shape to a combination of ecological and allometric factors. These new data obtained from the fossil record underline the propensity of island endemic mammals to yield surprising examples of phenotypic evolution. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **101**, 28–40.

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INTRODUCTION

Endemic species from oceanic islands frequently represent unique biological types that are of great interest in ecological and evolutionary studies (Emerson, 2002). Among them, mammalian species provide many examples (e.g. Biknevicius, McFarlane & MacPhee, 1993; Van der Geer, 2008). However, their evolutionary histories are difficult to reconstruct. First, the quite often poor fossil record on islands very partially documents the evolutionary lineages from the colonization event up to their more recent forms (Millien, 2006). Secondly, because autochthonous insular mammals are prone to extinction (Alcover, Sans & Palmer, 1998), a large number of them have recently disappeared, leaving only bones and teeth. Amori, Gippoliti & Helgen (2008) showed that rodents, the most speciose group of mammals, fit this scenario, with more than 30

endemic species becoming extinct during the Late Pleistocene and Holocene periods or during historical times, and with at least 28 endemic genera threatened with extinction. This fall in biodiversity is associated with a loss of valuable phylogenetic, ecological, or behavioural data. Bones and teeth are the only available clues to determine the adaptive features of these extinct species.

The Canary Archipelago comprises seven main volcanic islands (Fig. 1A) that appeared successively between 24 and <2 Mya (Carracedo, 2008). Only four out of these seven islands had endemic terrestrial mammals that recently became extinct: *Malpaisomys insularis* Hutterer, López-Martínez & Michaux, 1988 from Lanzarote and Fuerteventura, *Canariomys bravoii* Crusafont-Pairó & Petter, 1964 from Tenerife and *Canariomys tamarani* López-Martínez & López-Jurado, 1987 from Gran

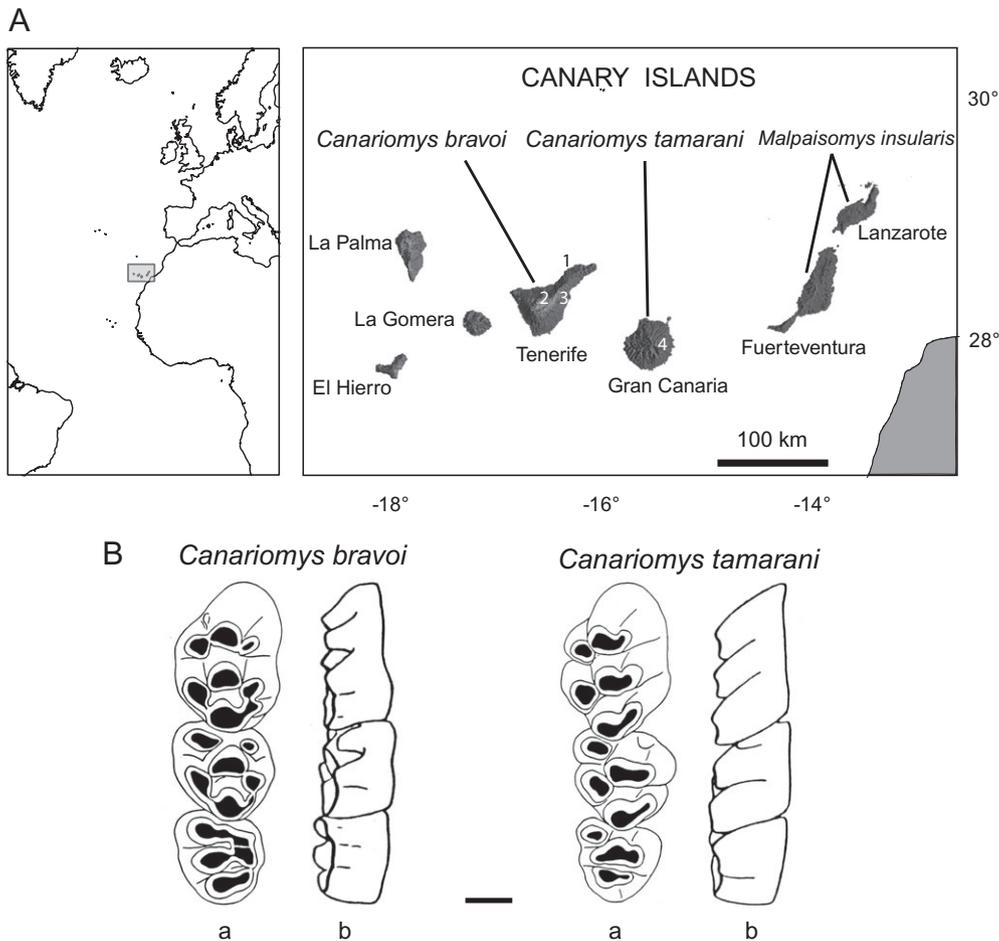


Figure 1. A, geographic location of the Canary Islands and distribution of the endemic rodents. The locations of the sites that yielded the fossil material are as follows: 1, Punta del Hidalgo (PDH); 2, Cueva del Viento (CDV) el Sobrado (GIS), San Marco (SM); 3, Barranco de Icod (CBI), Tenerife; 4, Ingenio (ING), Gran Canaria. B, upper tooth row of *Canariomys bravoii* and *Canariomys tamarani*: (a) apical view; (b) lateral view (from López-Martínez & López-Jurado, 1987: fig. 4). Scale bar: 1 mm.

Table 1. *Canariomys* samples for mandible outline and dental microwear analyses

Species	Site	Code	Age	Mandibles	Tooth
<i>Canariomys bravoii</i>	Cueva del Viento (Tenerife)	CDV	6000 years BP	2	10
	El Sobrado (Tenerife)	GIS	4000 years BP	2	–
	Punta del Hidalgo (Tenerife)	PDH	Holocene	3	–
	San Marcos (Tenerife)	SM	Holocene	–	4
	Barranco de Icod (Tenerife)	CBI	Holocene	1	–
<i>Canariomys tamarani</i>	Ingenio (Gran Canaria)	ING	4000 years BP	15	16

The last two columns indicate the respective numbers of individuals for each analysis.

Canaria. Whereas *M. insularis* is a middle-sized mouse, both *Canariomys* species are giant rats. This article focuses on *Canariomys*. Telesforo Bravo recovered the first *Canariomys* remains on Tenerife during the 1950s, later described as a new murine (*C. bravoii*) of enigmatic phylogenetic origin (Crusafont-Pairo & Petter, 1964). More than 20 years later, López-Martínez & López-Jurado (1987) described a second species, *C. tamarani*, from Holocene deposits of Gran Canaria. According to these authors, the high-crown molars of *C. tamarani* coupled with less individualized cusps at the expense of transversally oriented groups of cusps (Fig. 1B) could be interpreted as an adaptation to the consumption of abrasive material. By contrast, the low-crowned and bunodont molars of *C. bravoii* (Fig. 1B) would indicate an omnivorous diet based on softer materials. López-Martínez & López-Jurado (1987) also concluded from a cladistic analysis that both *Canariomys* represent sister species, themselves nested within arvicanthines, a group of Murinae that includes many vegetarian rats from Africa (Misonne, 1969; Ducroz, Volobouev & Granjon, 2001; Michaux, Chevret & Renaud, 2007; Lecompte *et al.*, 2008). However, the number of roots in *Canariomys* is rather primitive for Murinae: three or four on upper first molars, whereas the molar root pattern is more complex in modern arvicanthine (Bienvenu *et al.*, 2008). This could reveal an early divergence of the insular lineages from the arvicanthine continental stock, an interpretation already suggested by Misonne (1969), who referred *Canariomys* to the ‘*Parapodemus*’ group.

The paleoenvironmental context of *C. bravoii* has been investigated (Bocherens *et al.*, 2003) using carbon and nitrogen isotopic compositions of fossil bone collagen. The conclusion suggested a purely C3 environment on Tenerife in *Canariomys* times, and a plant-based diet for *C. bravoii* (see discussion in Bocherens *et al.*, 2003, 2006). In this paper we followed two different approaches for inferring the diet of both species. The first considers the mandible outline shape, which has already been shown to be correlated with dietary categories in Murinae (Michaux *et al.*, 2007).

The second approach is an analysis of dental microwear, which reflects the diet composition in murid rodents (Gomes Rodrigues, Merceron & Viriot, 2009). Two main questions will be tackled. Are predictions from tooth morphology, mandible outline, and dental microwear in agreement? How do these new analyses contribute to understanding the evolutionary history of *Canariomys*?

MATERIAL AND METHODS

MATERIAL

Six localities provided the studied fossils: five on Tenerife, and one on Gran Canaria. Specimens are housed in the Alexander Koenig Museum in Bonn (Germany), and in the Museo de la Naturaleza y el Hombre in Santa Cruz de Tenerife (Spain). The methods used in this study require a high quality of preservation: mandible processes must be preserved and, similarly, microwear patterns are very sensitive to taphonomic processes such as sedimentary abrasion or weathering (see King, Andrews & Boz, 1999), which can seriously alter the original signal resulting from the chewing of food during the last few days or weeks of an animal’s life (Teaford & Oyen, 1989). Thus, the number of specimens by site is consequently reduced in comparison with the original collections of specimens. The samples analysed for each species are listed in Table 1. The remains of *C. tamarani* are about 4000 years old, and those of *C. bravoii* range from the late Pleistocene to the late Holocene.

For palaeodietary inferences based on mandible morphology, we used part of the database described in Michaux *et al.* (2007). This database consists of the mean shape and size of mandibles for a set of living rodent species. To avoid a possible and uninformative variation arising from phylogeny, we only considered species belonging to the subfamily Murinae. As this study aims to determine whether the *Canariomys* species were either generalist feeders or mainly fed on plant material, only two diet categories were

retained from the database: omnivorous and herbivorous species, following the dietary classification of Michaux *et al.* (2007). The term ‘herbivorous’ previously used by Michaux *et al.* (2007) refers to species feeding on a wide variety of plant material, including grass, but also roots, leaves, fruits, and so on, but it can lead to confusion because of its narrower meaning associated with the word ‘herb’ that can also signify grass. To avoid this confusion we preferred to replace it by the less ambiguous adjective ‘vegetarian’. By contrast, ‘omnivorous’ refers to rodents feeding on both animal and vegetable items. Furthermore, we added to this subset the mean from a sample ($N = 35$) of the typically omnivorous species *Rattus exulans* Peale, 1848 (Nowak, 1999), leading to a final data set of 53 extant species. For inferences based on dental microwear analysis, we used the database of Gomes Rodrigues *et al.* (2009). This database provides mean values of the microwear variables measured on the dental facets for 17 Muridae. Dietary categories attributed to extant murids in the microwear sample correspond to those of Gomes Rodrigues *et al.* (2009): grass eaters, fruit–plant–insect eaters, and insect–plant eaters (the term ‘plants’ refers to a mixture of dicotyledon and monocotyledon vegetation, whereas ‘grass’ includes only monocots, i.e. grass and grass-like plant families such as Poaceae and Cyperaceae). Thus, although the outline analysis of the mandible should provide a distinction between omnivorous and vegetarian rodents, the microwear analysis should mainly reveal the presence of phytoliths associated with the consumption of grass, the material leaving the most distinctive patterns on wear facets in murids (Gomes Rodrigues *et al.*, 2009). The detailed composition of each of these databases is given in Appendices S1 and S2.

OUTLINE ANALYSIS

The rodent mandible can be described by morphometric methods either based on landmarks or outline analyses. The curved shape of the rodent mandible provides mostly type-2 landmarks (e.g. Duarte *et al.*, 2000) that are points of maximum curvature (Bookstein, 1991). As such landmarks are likely to be sensitive to measurement error, we chose to use outline analysis based on Fourier methods (see Rohlf & Archie, 1984). The mandible outline is defined as the two-dimensional projection of the mandible bone viewed from its buccal side (Renaud & Michaux, 2003). Thus, a digitalized mandible corresponds to the x and y coordinates of 64 points equally spaced along the dentary outline. We applied an elliptic Fourier transform (EFT) to these data using EFAwin software (Ferson, Rohlf & Koehn, 1985), extracting Fourier coefficients from the original outline and normalizing

these shape variables. This method considers the separate Fourier decomposition of the incremental change in the x and y coordinates as a function of the cumulative length along the outline (Kuhl & Giardina, 1982). Fourier methods allow the description of the complex outlines approximating them by a sum of trigonometric functions of decreasing wavelength (i.e. harmonics). For EFT, any harmonic N yields four Fourier coefficients (FCs): A_N and B_N for x , and C_N and D_N for y , which all contribute to describing the initial outline. The first three coefficients of the first harmonic (A_1 – C_1) are constant because of the standardization, and can be omitted in the subsequent analyses (Crampton, 1995; Renaud *et al.*, 1996). D_1 is often excluded because it is highly correlated to the orientation of the specimen under the stereomicroscope. However, Michaux *et al.* (2007) used the D_1 coefficient because it expresses the width : length ratio of the first ellipse, and hence of the object, an informative parameter for the analysis of the ecological signal contained in mandible shape. As we focus on this ecological signal, we retain the D_1 coefficient in this study. Following previous studies (e.g. Renaud & Michaux, 2003), we retain the first seven harmonics, which represents the best compromise between measurement error and information content for the murine mandible. Thus, we retain 25 FCs from the first seven harmonics, i.e. D_1 – D_7 . The use of Michaux *et al.*’s (2007) database implies the comparison of measurements taken by two observers. Measurement error on FCs is estimated following Yezerinac, Loogheed & Handford (1992). A preliminary analysis based on a sample of 31 *Apodemus sylvaticus* Linnaeus, 1758 measured twice indicated that the averaged intra- and interoperator measurement errors on FCs D_1 – D_7 reach, respectively, 6.0 and 8.8%. Moreover, interobserver measurement error is also shown to be negligible when compared with the interspecific shape differences of our data set, suggesting that it will not bias dietary predictions. Shape variation is visualized by reconstructing the outlines from estimated sets of FCs (Rohlf & Archie, 1984). This procedure is performed using R (R Development Core Team, 2008) and codes from Claude (2008) modified for EFAwin data.

MICROWEAR ANALYSIS

We used the the strategy of Gomes Rodrigues *et al.* (2009), adapted from Merceron *et al.* (2005). Translucent casts of the dental wear facets are observed with light stereomicroscopy at 100 \times magnification, and are photographed at high resolution. The analysis consists of counting several distinct features of the dental surface within a 0.01-mm² standardized square. Following Gomes Rodrigues *et al.* (2009), the counting

areas were firstly located on the lingual facet of the hypocone of the first upper molar. The degree of tooth wear does not significantly affect the microwear dietary signal in murine rodents (H. Gomes Rodrigues, unpubl. data). However, oldest and youngest specimens, respectively, exhibiting advanced wear stages and unworn molars were not considered in this study.

Gomes Rodrigues *et al.* (2009) quantified microwear patterns in rodents considering four features: wide and fine scratches, and large and small pits. Scratches are distinguished from pits as features possessing a minimum/maximum length ratio value higher than one-quarter (Grine, 1986). The distinction between large (or wide) from small (or fine) features is settled at a maximum width of 5 μm . Among these variables, small pits seem the most likely features to be sensitive to a non-dietary linked source of variation. In addition, Gomes Rodrigues *et al.* (2009) casted doubt on the relevance of small pits for dietary inferences in murid rodents. For these reasons, we chose to remove this variable from our analyses and to solely use the numbers of large pits (N_{lp}), wide scratches (N_{ws}), and fine scratches (N_{fs}).

STATISTICAL ANALYSES

Statistical analyses were performed with R v2.7.2 (R Development Core Team, 2008). Mandible size is estimated by the square root of the mandible area. This variable was preferred to classic linear measurements such as length or width because its variation integrates relevant aspects related to the weight of the mandible, and to the surface of attachment for the masticatory muscles. Size difference between *Canariomys* species was assessed using an analysis of variance (ANOVA). For shape variation, the first axes of a principal component analysis (PCA) on FCs D_1 – D_7 allows the visualization of the patterns associated with shape variation within the *Canariomys* genus. A multivariate analysis of variance (MANOVA) associated with a test of significance (Wilks' lambda test) was performed on the shape variables. However, the small size and heterogeneity of the *C. bravoii* sample (Table 1) prevented a detailed description of the between-species shape differences. As the number of specimens by group is lower than the number of FCs considered, we simplified the shape space using the first principal components (PCs) of the PCA, with the number of retained PCs being defined in order to keep at least 90% of the variance (a similar approach is described in Claude *et al.*, 2004).

A linear discriminant model based on FCs was used to predict the diets in extinct species based on mandible shape. Mandible shape in murine rodents is partly related to size because of the effect of

evolutionary allometry (Michaux *et al.*, 2007). As our database contains few species comparable in size with the giant *Canariomys*, and because these taxa exclusively had vegetarian diets (e.g. *Crateromys* and *Phloeomys*), the allometric effects may have hidden any dietary signal for large species. Therefore, we computed a second discriminant model based on evolutionary allometry-free shape variables, i.e. the residuals of the multivariate regression of FCs as dependent variables against size, and compared the results yielded by both approaches. We also tested for the correlation between diet and size using an ANOVA considering all the species of our database.

To reduce the dimensionality of the shape space, two preliminary PCAs were performed on the size-in and size-out FCs. Thereafter, successive discriminant models considering an increasing number of principal components were combined with leave-one-out cross-validation tests (see Stone, 1974). This procedure allowed us to select the number of PCs to include in the final model in order to maximize the cross-validation success (Baylac, Villemant & Simbolotti, 2003). This preliminary selection should optimize the probabilities of obtaining the correct dietary assignment for extinct species. The discriminant model considered two categories (omnivorous species and vegetarian ones), and consequently provided a single discriminant axis. Extinct species were projected onto this axis and their scores were compared with those of living ones. The model finally yielded a probability for the classification of the extinct species in both dietary categories considered.

Interspecific differences in microwear patterns were assessed with a MANOVA performed on the three retained microwear variables. ANOVAs were subsequently performed on each of these variables to estimate their respective involvement in the interspecific variation. For dietary predictions, microwear variables were also used in a linear discriminant analysis. However, the microwear data set was not substantial enough to obtain reliable quantitative predictions using a linear discriminant model associated with a cross-validation procedure. In consequence, diet was simply inferred by projecting the extinct species on the two obtained discriminant axes, and by comparing their positions relative to the three dietary groups of living species (grass eaters, fruit–plant–insect eaters, and insect–plant eaters).

RESULTS

MANDIBLE SIZE AND SHAPE

On one hand, mandible size is not significantly different between *Canariomys* species ($F = 2.846$; d.f. = 1, 21; $P = 0.106$). On the other hand, morpho-

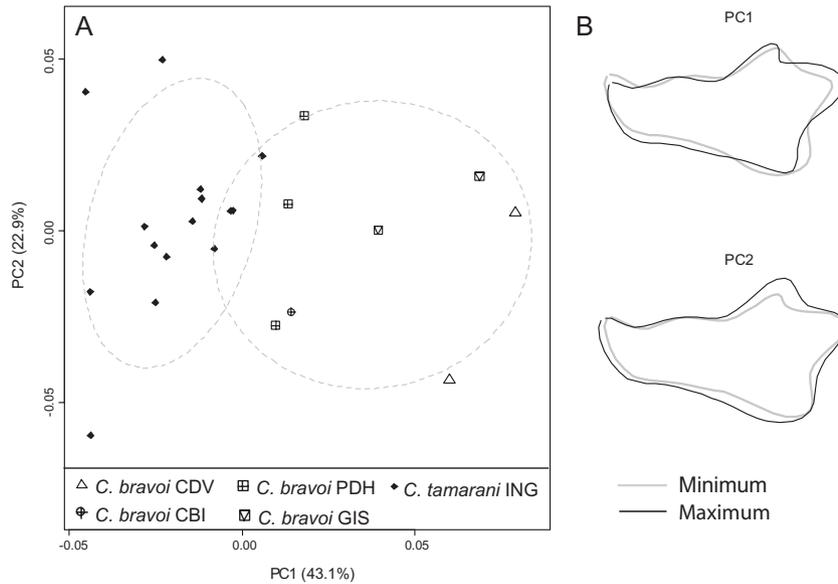


Figure 2. Mandible outline in *Canariomys*. A, shape variation on the first two axes of the principal components analysis (PCA) performed on the elliptic Fourier coefficients of mandibles D_1 – D_7 , with dotted ellipses corresponding to the 90% confidence interval for intraspecific variations. B, mandible shapes corresponding to the extreme values reconstructed along PC1 and PC2.

Table 2. Results for the cross-validation procedure illustrating the confidence in the predictions offered by the linear discriminant models based on mandible shape variables (Fourier coefficients) including the component related to evolutionary allometry (left values) and evolutionary allometry-free shape variables (right values)

Diet	Predicted diet		Right classifications (%)
	Vegetarian	Omnivorous	
Vegetarian	24–23	2–3	92.31–88.46
Omnivorous	3–2	24–25	88.89–92.60
			Mean success: 90.60–90.52

metric data describing mandible shape show a highly significant difference between both species (Wilks' lambda = 0.106; $F = 28.830$; d.f. = 5, 17; $P < 0.00001$ over five PCs). Figure 2A illustrates the shape variation on the first PCA plane. PC1 (43.1% of the total variance), for which both species are distinct, is mainly related to shape changes on the posterior part of the mandible (Fig. 2B). It must also be acknowledged that the *C. bravoii* specimens are more widely distributed on the first plane of the PCA than the specimens from the single *C. tamarani* sample, and that they are grouped more or less according to their locality of origin.

For both approaches (correcting or not for evolutionary allometry), the proportion of correctly classified murine species was similar, and reached 90% (Table 2). These results are illustrated by projecting the scores of each species on the discriminant axis. These scores are

plotted against mandible size (Fig. 3), which is significantly influenced by diet ($F = 9.987$; d.f. = 1, 51; $P < 0.003$). Based on raw data, including the size-related component of shape variation, vegetarian and omnivorous murines can be clearly discriminated according to mandible shape, except for the vegetarian species *Millardia meltada* Gray, 1837 (Fig. 3A). Based on shape variables corrected for evolutionary allometry (Fig. 3B), *Phloeomys cumingi* Waterhouse, 1839, *Crateromys heaneyi* Gonzales & Kennedy, 1996, and *Pithecheir melanurus* Cuvier, 1838, among the largest species in the database according to mandible size, represented the only vegetarian taxa misclassified as omnivorous ($P > 99\%$ in each case), whereas they were correctly reclassified as vegetarian by the discriminant model including allometric variation ($P > 99\%$). Compared with omnivorous species, vegetarian species have mandibles that tend to exhibit a deeper horizon-

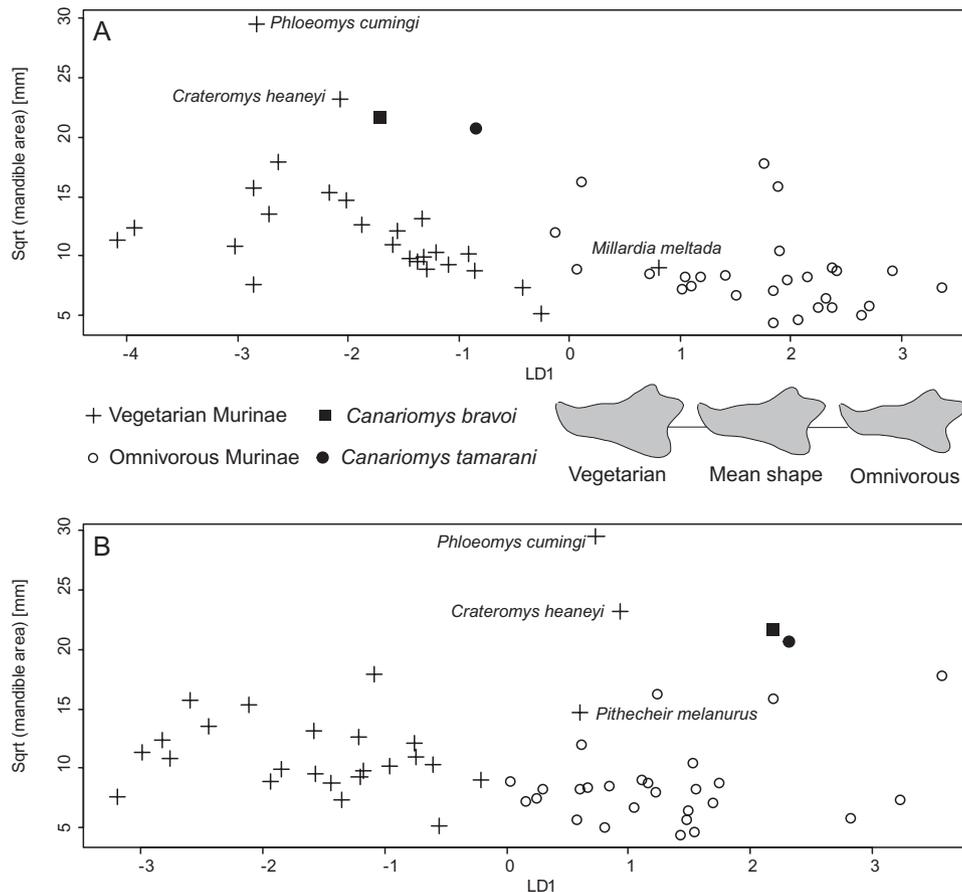


Figure 3. Linear discriminant analysis axis from an analysis of diet using elliptic Fourier coefficients D_1 – D_7 from mandible outlines. Discriminant scores based on Fourier coefficients, including the component related to evolutionary allometry (A) and on the residuals of the evolutionary allometry (B), are plotted against mandible size. The leave-one-out cross-validation procedure used to test the confidence in the paleodietary inferences from the shape-based discriminant analysis indicates the robustness of both models. *Canariomys bravoii* and *Canariomys tamarani* have been projected on each discriminant axis. Mandible reconstructions in the middle correspond to the mean shapes of each trophic group compared with the overall mean shape.

tal ramus in lateral view, a less anteriorly projected incisor sheath, a more pronounced coronoid process, a less extended condylar one, and a broader angular process (Fig. 3).

When *Canariomys* species are compared with extant species on the discriminant axis, evolutionary allometry being retained (Fig. 3A), they both fall within the range of the vegetarian species, and the model classifies *C. bravoii* and *C. tamarani* as vegetarian with high probabilities ($P > 99\%$ and $P > 94\%$, respectively). Such classifications are not unexpected when considering the reconstructions of *Canariomys* mandible mean shapes in Figure 2A. When evolutionary allometry is corrected (Fig. 3B), as for *Ph. cumingi*, *Cr. Heaneyi*, and *Pi. melanurus*, both species of *Canariomys* are not classified as vegetarian but as omnivorous, with high probabilities ($P > 99\%$ for each species). In any case both *Canariomys* remain

close to each other, and it may be first inferred that they are likely to have shared similar diets. In addition, removing the evolutionary allometry effect did not affect the reclassification of most of the species, but led to a misclassification of the largest ones.

MICROWEAR PATTERNS

Observation of dental facets under light stereomicroscopy furnished reliable pictures for both species (Fig. 4). The point here is that the microwear analysis does not statistically distinguish the two *Canariomys* species. Neither the multivariate (Wilks' lambda = 0.900; $F = 0.924$; d.f. = 3, 25; $P = 0.444$) nor the univariate analysis of variance (Table 3) succeeds to detect between significant differences of species in microwear patterns.

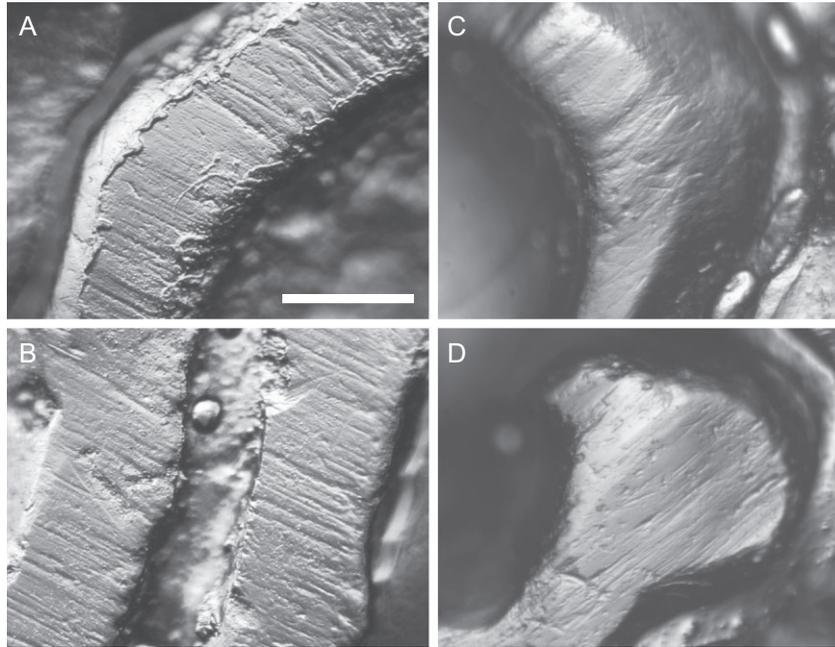


Figure 4. Microwear patterns observed on lingual facets of the hypocone of upper M1 teeth under light stereomicroscopy. A, *Canariomys bravoii*. B, *Canariomys tamarani* (lingual facet, right side). C, *Golunda ellioti*, a grass-eating murine. D, *Grammomyss poensis*, a fruit–plant–insect-eating murine (according to Gomes Rodrigues *et al.*, 2009). Scale bar: 200 μ m.

Table 3. Results of the univariate analysis of variance for N_{fs} , N_{ls} and N_{lp} microwear variables

	d.f.	Mean squares	<i>F</i>	<i>P</i>
Fine scratches				
Effect	1	0.150	0.0109	0.9175
Residuals (intraspecific)	27	13.630		
Large scratches				
Effect	1	0.227	0.0475	0.8291
Residuals (intraspecific)	27	4.778		
Large pits				
Effect	1	16.450	2.0481	0.1639
Residuals (intraspecific)	27	8.032		

Extant murid species are plotted on the discriminant axes, considering the microwear variables N_{fs} , N_{ls} , and N_{lp} (Fig. 5). The first axis bears 96% of the intergroup variance and is positively associated with the number of fine scratches, and is negatively associated with the numbers of wide scratches and large pits. Insect–plant and fruit–plant–insects trophic groups are poorly discriminated from each other, whereas grass-eater murine species are clearly distinct, partly because of their higher number of fine scratches and their lower number of wide ones. The insect–plant eater *Uranomys ruddi* Dollman, 1909 is, however, associated with this last group on the first discriminant axis. According to Gomes Rodrigues *et al.* (2009), the microwear

pattern of this deomyine species is characterized by a large number of fine scratches, probably caused by the abundance of dust in its open environment, which explains its position within grass-eater species. At the opposite end, the microwear patterns of more generalist feeders tend to exhibit a lower number of fine scratches and a higher number of large ones. The second discriminant axis appears to be as poorly reliable in distinguishing between trophic groups; however, this analysis supports the conclusion of Gomes Rodrigues *et al.* (2009), who separated generalist taxa (fruit–plant–insect eaters) with a large number of large scratches from taxa specialized in grass eating, exhibiting a large number of fine

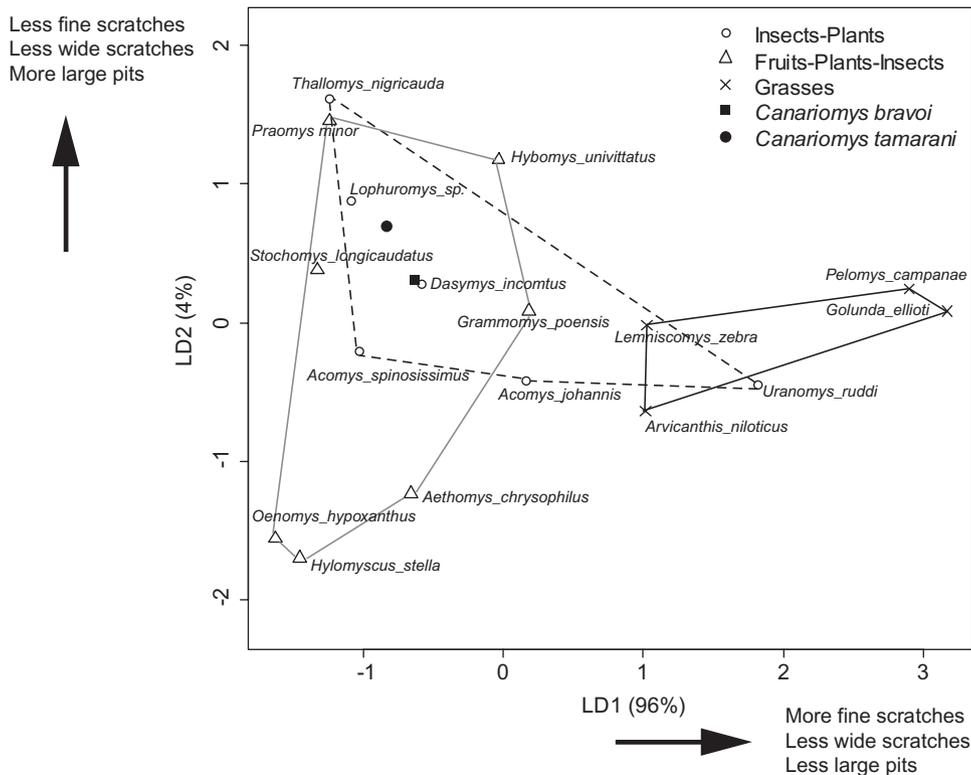


Figure 5. Plot of the linear discriminant analysis axes of microwear variables (N_{fs} , N_{ws} , and N_{lp}) versus diet. LD1 and LD2 are the first and second discriminant axes (proportions of the between-group variation explained by each function in brackets), respectively. The dietary classification follows Gomes Rodrigues *et al.* (2009).

scratches. Projected on this discriminant plane, both *Canariomys* species are close to each other, and both fall within the generalist group, suggesting a relatively opportunistic diet. The coarse features easily visible on the dental facets of both *Canariomys* species (Fig. 4) agree with such a conclusion. However, a more accurate determination of their diets from these microwear data is probably impossible.

DISCUSSION

Despite their overall similarities, *C. bravoii* and *C. tamarani* appear to differ in their mandible shape; however, these differences are weak compared with the total murine diversity. The shape difference between the *C. bravoii* samples is not considered here, as its interpretation needs supplementary data about chronology, past climate, and environment.

SIMILARITY IN DIET DESPITE ANATOMICAL DIFFERENCES

Whatever the method, the two *Canariomys* species appear to have shared a rather similar diet, despite

some differences in their tooth and, to a lesser degree, mandible morphology. Microwear patterns failed to detect any significant differences in the diet of these species, and point to rats feeding on a diverse diet, including plants, fruits, insects, but not grasses. The coarse scratches present on dental facets in both *Canariomys* species can be interpreted as the result of hard material intake: fruits, hard seeds, or insects (Townsend & Croft, 2008; Gomes Rodrigues *et al.*, 2009). Such similarity might point to an adaptation to the rather similar environment and vegetation on their native islands: Tenerife and Gran Canaria. Both islands possess an elevated relief (significant surface above 1000 m elevation). This shared topographic pattern combined with the local climatic conditions lead to similar diversities and repartitions of vegetal communities, similarities that probably already existed thousands of years ago. The massive shape of the mandible points to a vegetarian diet, a result that may be tempered by considering the possible allometry-related contribution of shape variation in these giant rodents. Hence, mandible morphology does not contradict the vegetarian diet for *C. bravoii* suggested from stable isotopes (Bocherens *et al.*, 2003,

2006). Such a conclusion is compatible with the comparison of the *Canariomys* microwear patterns with those of living murids eating plant material, except grasses.

Thus, the two *Canariomys* species share a range of similarities: similar microwear patterns, similar mandible outlines when compared with the diversity of the murine family, and similar sizes. Yet, they also diverge on several points, including minor differences in mandible shape and marked differences in molar morphology, and confronting these different aspects point to an apparent incongruence. Mosaic evolution between tooth and mandible has been evidenced on islands (Renaud & Michaux, 2007). Both features may be differentially sensitive to ecophenotypic variation (Caumul & Polly, 2005), to divergence resulting from drift in an isolated insular population, or to selective pressures related to insular ecological conditions (e.g. Renaud & Michaux, 2007). An alternative, although not mutually exclusive, hypothesis would be that the two *Canariomys* species display a mosaic of 'grass-eating' teeth associated with slightly more 'omnivorous-like' mandibles, the somewhat stouter mandible of *C. bravoii* being associated with more low-crowned molars, and the reverse being the case for *C. tamarani*. This situation could illustrate a case of compensation between different structures evolving as part of an integrated organism, as it has been noted that dietary adaptation may be achieved in uncorrelated changes in organs implicated in food processing and digestion (Vorontsov, 1999). However, it remains difficult to link the observed differences in mandible shape with functional adaptations to the consumption of a more or less resistant food. This mosaic combination of traits (marked differences in teeth despite vegetarian-like mandibles for both species) may result from past dietary adaptations, suggesting complex ecological histories for the *Canariomys* lineages. This combination of traits may also result from differences already present between the ancestors of the two *Canariomys* species, thereby hypothesizing that teeth are more conservative than mandibles, a pattern likely exemplified in other island endemic rodents (e.g. Thaler, 1972; Hautier *et al.*, 2009).

An alternative interpretation of the morphological specialization in molar and mandible shape would be to relate this phenotypic evolution not to the most commonly eaten food, but to foods only occasionally consumed, for instance during periods of food scarcity, as fallback foods can have an important impact on evolutionary output (see review in Marshall & Wrangham, 2007). However, the congruence between mandible shape and dental microwear results tends to undermine this hypothesis.

MANDIBLE AND MICROWEAR SIGNALS FOR DIET RECONSTRUCTION

It should be noted that the different methods used here for inferring palaeodiets do not actually trace the same aspects of feeding behaviour. Microwear patterns reflect how abrasive the most recent food items consumed were. In particular, grass eaters can be traced by the fine scratches caused by the abundance of silica phytoliths in this food item (Gomes Rodrigues *et al.*, 2009). Hence, microwear patterns are indicators of the diet for the particular animal considered, and they can vary within a species or even within a population, or along a rodent's life, as a result of geographic and/or seasonal variations in diet (Butet, 1994; Leirs, Verhagen & Verheyen, 1994; Schradin & Pillay, 2006). In contrast, the mean mandible shapes considered as the modern reference for the present ecomorphological study represent interspecific differences on the scale of the murine subfamily. They do not trace the diet of a given animal, but instead result from up to several million years of evolution caused by drift or long-term adaptation to dietary changes, buffering short-term and local variations in feeding strategies. Selective pressures acting on mandible shape are probably related to the strength required in the various muscles inserted on the mandible. An increased angular process on a massive mandible, as observed on *Canariomys*, should correspond to wider insertions for the masticatory muscles, which can be indirectly interpreted as a long-term response to an overall more resistant food (Michaux *et al.*, 2007). However, subtle anatomical differences were observed on *Canariomys* mandibles: a masseteric ridge more conspicuous on *C. bravoii* and the bulge for the incisor capsule more visible on *C. tamarani*. Such characters that are probably related to functional differences cannot be interpreted without considering the teeth.

The various methods therefore trace different aspects and time scales of variations in diet, a fact that may explain the potential discrepancies when combining their results, together with the actual huge diversity of diets beyond the categories considered (vegetarian versus omnivorous).

MANDIBLE SHAPE: DIET, ALLOMETRY, OR BOTH?

The interpretation of the mandible shape in an ecomorphological approach is further complicated by the interference with size-related variations, as evidenced by our results. In a size-in approach, both *Canariomys* species were classified as vegetarian, whereas the size-out approach attributed them to the omnivorous murines, together with other large living insular species of the modern referential (*Ph. cumingi*, *Cr. heaneyi*, and *Pi. melanurus*). This suggests that a vegetarian-like mandible can be at least partly

shaped by size increase in the case of these murines. Indeed, an allometric shape variation has been evidenced within murines (Michaux *et al.*, 2007), corresponding to more massive mandibles, with stouter condylar and angular processes for a larger size. An increase in the body size of the animal leads to an increasing weight of the mandible, with consequences on the functioning of masticatory muscles: the heavier the mandible, the more strength is required for its forward and upward movements (Sato, 1997). Hence, both the consumption of more resistant matter and an increase in size may select for larger zones of insertion of the masticatory muscles, possibly leading to a convergent evolution towards massive mandibles. As both species are giants among the living Murinae, the similar mandible shapes of the two *Canariomys* probably result in part from this allometric effect.

This is an issue of particular concern when applying the referential, mostly based on mainland species, to insular rodents. Evolution towards larger body size is a well-documented aspect of the insular syndrome for small mammals (Foster, 1964; Lomolino, 1985). Hence, the allometric effect on mandible shape should be particularly prone to interfere with the signature of dietary adaptation. Furthermore, niche widening frequently occurs on islands because of decreased interspecific competition, with insular rodents adapting with time to a diet based on a wider spectrum of items than their continental ancestor (e.g. *Hypnomys* in Mallorca; Hautier *et al.*, 2009). Accordingly, both *Ph. cumingi* and *Cr. heaneyi* display uncommon diets based on bark, but also eat young vegetation and fruits (Schauenberg, 1978; Nowak, 1999). It is noteworthy that they fall within the range of overlap between vegetarian and omnivorous species in the original analysis of mandible shape diversity (Michaux *et al.*, 2007). The size-free analysis report them as omnivorous species, a classification pattern similar to the one obtained for the two *Canariomys* species. A parsimonious interpretation of these ecomorphological results could suggest dietary ecologies comparable with the ones of the living *Ph. cumingi* and *Cr. heaneyi* for both *Canariomys* species. Given their geographic localization and phylogenetic position, these two taxa from Southeast Asia certainly experienced evolutionary histories radically different from those of the *Canariomys* lineages. Nevertheless, a large body size is often reported to correlate with the consumption of food that is both abundant and of lower calorific value (i.e. plant materials; Case, 1979). Our results for living murine rodents agree with this observation, with vegetarian species being significantly larger than omnivorous ones. Consequently, a size increase and an adaptation to a more vegetarian diet, potentially correlated with each other, could both have promoted the massive mandibles of *Canariomys*.

Thus, our results support the hypothesis that both *Canariomys* species adapted to similar diets mainly based on plant materials, except grass.

CONCLUSION

Mandible outline and microwear analyses both suggest that extinct *Canariomys* possessed rather similar diets. Microwear likely supports the absence of grass consumption. Our results agree with the sole isotope analysis of *C. bravoii* suggesting a vegetarian diet (Bocherens *et al.*, 2003, 2006). These conclusions together with the previous study of López-Martínez & López-Jurado (1987) once more illustrate the mosaic character of evolution: molar crown and mandible shape did not show concerted trends, despite the large size increase of both *Canariomys* species and their probable similar diets. The incongruence between dietary signals expressed by molars and mandibles suggests that the evolutionary histories of both *Canariomys* species could have been more complex than formerly assumed. The lack of a fossil record until late in the Pleistocene remains difficult to overcome in shedding light on evolutionary processes and historical events that intervened in the evolution of these insular lineages, certainly dating back over several million years.

Our study nevertheless provides additional data concerning the ecology and the evolution of the endemic Canarian rats. However, further approaches are strongly advised to compare both species, as *C. bravoii* and *C. tamarani* furnish an exceptional situation where two large murine rodents evolved separately on two islands of the same archipelago. These extinct species remind us of the propensity of island mammal fauna to yield intriguing cases of phenotypic evolution, as well as reminding us of the frailty of island endemics, with a large number of them already belonging to the fossil record.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Database and dietary classes used in the ecomorphological analysis of mandible outline.

Appendix S2. Database and dietary classes used in the dental microwear analysis.

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