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General palaeontology, systematics and evolution (Vertebrate palaeontology)

Body shape and life style of the extinct rodent *Canariomys bravoii* (Mammalia, Murinae) from Tenerife, Canary Islands (Spain)*Morphologie et style de vie du rongeur éteint Canariomys bravoii (Mammalia, Murinae) de Tenerife (Îles Canaries, Espagne)*Jacques Michaux^{a,*}, Lionel Hautier^b, Rainer Hutterer^c, Renaud Lebrun^a, Franck Guy^d, Franciso García-Talavera^e^a CNRS, UMR 5554, ISEM, Université Montpellier II, 34095 Montpellier, France^b Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK^c Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany^d CNRS, UMR 6046, INEE, IPHEP, Université de Poitiers, 86022 Poitiers, France^e Museo de Ciencias Naturales de Tenerife, 38080 Santa Cruz de Tenerife, Islas Canarias, Spain

ARTICLE INFO

Article history:

Received 30 November 2011

Accepted after revision 25 June 2012

Available online 22 August 2012

Presented by Philippe Taquet

Keywords:

Microtomography
Ecomorphology
Locomotion
Evolution
Insularity
Canary Islands

Mots clés :

Microtomographie
Écomorphologie
Locomotion
Évolution
Insularité
Îles Canaries

ABSTRACT

A three-dimensional reconstruction of the skeleton of the giant rat of Tenerife (Canary Islands, Spain) *Canariomys bravoii* was obtained by computerized microtomography. Body size, body mass, and body shape were estimated, and limb morphofunctional indices used to infer the style of life of this recently extinct rat. A sample of recent Murinae, including the Philippines endemic giant cloud rat *Phloeomys cumingi*, was used for comparison. It appears that *C. bravoii* differed from most continental rats by its relatively large size, body proportions, and tail length. Among its distinctive features, claws almost similarly developed on fore and hind limbs, and feet longer than hands evoke an intermediate body shape between rats and arboreal murines like *Phloeomys*. *C. bravoii* was a strong and powerfully muscled rat able to move on different substrates from floor to trees, and probably had digging skills.

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R É S U M É

Une reconstitution en trois dimensions du squelette du rat géant de Tenerife (Îles Canaries, Espagne) *Canariomys bravoii* a été obtenue à partir d'acquisitions en microtomographie. Taille corporelle, masse corporelle, et forme du corps ont été estimées, et le style de vie fut déduit d'indices morphofonctionnels des membres. Des Murinae récents parmi lesquels *Phloeomys cumingi*, rat géant endémique des Philippines ont servi aux comparaisons. *C. bravoii* différait de la plupart des rats continentaux par sa grande taille, les proportions du corps, et la longueur de la queue. Parmi ses caractéristiques distinctives, les griffes presque d'égale importance aux membres antérieurs et postérieurs, et les pieds plus longs que les mains, évoquent une forme intermédiaire entre les rats et les vrais Murinae arboricoles comme *Phloeomys*. *C. bravoii* était un rat musclé, capable de se déplacer sur des substrats divers depuis le sol jusqu'au sommet des arbres, et capable de creuser.

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1. Introduction

Mammals show high capacity for adaptation to environmental changes. They migrate or speciate, and their evolution may accelerate when colonizing islands. The Canary Islands, which are volcanic islands without any former or recent connection to the nearby continent, are of particular interest because they bear a good fossil record of recently extinct rodents. They form an archipelago close to the Tropic of Cancer, the easternmost islands of which are situated ca 100 km off the African coast at the level of the Sahara desert. This situation resulted in the settlement of an unbalanced fauna of terrestrial vertebrates, composed of a few genera of lizards and mammals, the latter being represented by three rodents and one shrew. All rodents were members of the Murinae (Old World rats and mice): *C. bravoii* on Tenerife (Crusafont-Pairo and Petter, 1964), *Canariomys tamarani* on Gran Canaria (López-Jurado and López-Martínez, 1991; López-Martínez and López-Jurado, 1987), and *Malpaisomys insularis* on Lanzarote, Fuerteventura and some nearby islets (Hutterer et al., 1988). *M. insularis* was the sole rodent to be associated with another native mammal, *Crociodura canariensis*, a shrew still living today (Hutterer et al., 1987). The two *Canariomys* species were the size of a large rat while *Malpaisomys* was the size of a large mouse. All known fossils of the extinct rodents are Holocene or Late Pleistocene in age. These rodents, together with the giant lizards, became extinct during Prehispanic times as the result of human settlement (Atoche et al., 1995; Navarro et al., 1990). The date of the native mammalian settlement on the Canary Islands is unknown due to the lack of fossils older than the Late Pleistocene (Michaux et al., 1996). Pliocene and Miocene sediments with terrestrial turtles (Hutterer et al., 1998) have yielded no mammals so far. The estimated molecular time of divergence of the endemic shrew provided scanty clues on the chronology of settlement of the endemic Canarian mammalian fauna. *C. canariensis* diverged from an African species around 1.61–4.30 Myr ago (Dubey et al., 2008). The present study still follows the interpretation of López-Martínez and López-Jurado (1987), who considered a Late Miocene divergence of the two species of *Canariomys* from the Arvicanthini (López-Martínez and López-Jurado, 1987; Musser and Carleton, 2005). The molecular calibration of the Murinae recently provided a date of ca. 8.4 My for the separation of the tribe Arvicanthini, while the oldest fossils referred to members of the tribe are 6 to 7 My old (Lecompte et al., 2008).

C. bravoii has been known since the middle of the last century but has never been described in detail, except in concert with the description of *C. tamarani* given by López-Martínez and López-Jurado (1987). While these authors considered *C. tamarani* an herbivorous rodent with a terrestrial mode of life, including some digging skills, *C. bravoii* was interpreted as a generalist rat characterized by an omnivorous diet, quadrupedal locomotion, and likely to show some abilities for climbing trees. Later, several studies aimed at going deeper into the understanding of the palaeobiology of these extinct rodents. The massive shape of the mandible, which is very similar in the two *Canariomys* species, is better explained by the

large size of these rodents rather than by a particular diet (Firmat et al., 2010). The stable isotope ratios indicated a diet dominated by vegetal matter in *C. bravoii* (Bocherens et al., 2003, 2006). Microwear patterns also confirmed that the two species of *Canariomys* had a diet dominated by plant materials excluding grasses (Firmat et al., 2010). Surprisingly, whereas skeletal and tooth remains show differences that clearly support a specific distinction, *C. bravoii* and *C. tamarani* were likely to have had a very similar diet.

A better paleobiological interpretation was only possible after the discovery of a fairly complete skeleton of *C. bravoii*, and by using an enlarged sample of Murinae for comparison, including some rat-like species and insular species such as the native Philippine Cloud rats *Phloeomys* and *Crateromys* (Oliver et al., 1993). *Phloeomys* and *Crateromys* are large arboreal, slow-moving rodents characterized by a diet based on vegetal matter (Oliver et al., 1993; Schauenberg, 1978). In this article, we seek answers to the following questions: Does the semi-complete skeleton of *C. bravoii* indicate a rat-like murine? Does this skeleton indicate a specialized mode of locomotion, or adaptation to a wide range of environmental conditions?

2. Material and methods

An almost complete but disarticulated skeleton of *C. bravoii* (TFMCFV872; Museo de la Naturaleza y el Hombre, Santa Cruz) was found in 1982 by J.-J. Hernández Pacheco in the Cueva del Viento, a lava tube in the North of Tenerife, which yielded Holocene remains (Michaux et al., 1996). It consists of all the postcranial bones except ribs, breast bone, collar bones, hyoid bone, and knee caps. Mandibles and skull of this specimen were not well preserved, so a complete cranium of *C. bravoii* (TFMCFV873; Museo de la Naturaleza y el Hombre, Santa Cruz) was added for the study together with a cranium of *C. tamarani* (ZFMK 2010.308; Zoologisches Forschungsmuseum Alexander Koenig, Bonn) in order to complement the data of López-Martínez and López-Jurado (1987). Skulls and skeletons of several Old World rats were used for comparison (Muséum national d'histoire naturelle, Paris): two species that evolved in isolation, *Phloeomys cumingi* (Waterhouse, 1839) and *Crateromys schadenbergi* (Meyer, 1895), and several continental species such as the rather large *Sundamys muelleri* (Jentink, 1879), *Rattus rattus* (Linnaeus, 1758), *Rattus norvegicus* (Berkenhout, 1769), *Mus musculus* (Linnaeus, 1758), and *Arvicanthis niloticus* (Geoffroy, 1803).

Two approaches have been followed. First, in addition to the semi-complete *C. bravoii* skeleton, skeletons of *P. cumingi*, *R. norvegicus*, and skulls of *C. bravoii*, *C. tamarani*, *P. cumingi*, *R. rattus* were scanned using a computerized microtomography (μ CT) scanner. Pixel size and slice thickness were adjusted according to specimen size. Voxel size ranged from 79.78 μ m for the sub-complete skeleton of *C. bravoii* to 37.6 μ m for the other specimens. Following volume data segmentation with Avizo 6.3 (VSG) via thresholding, 3D surfaces representing the cranium and the

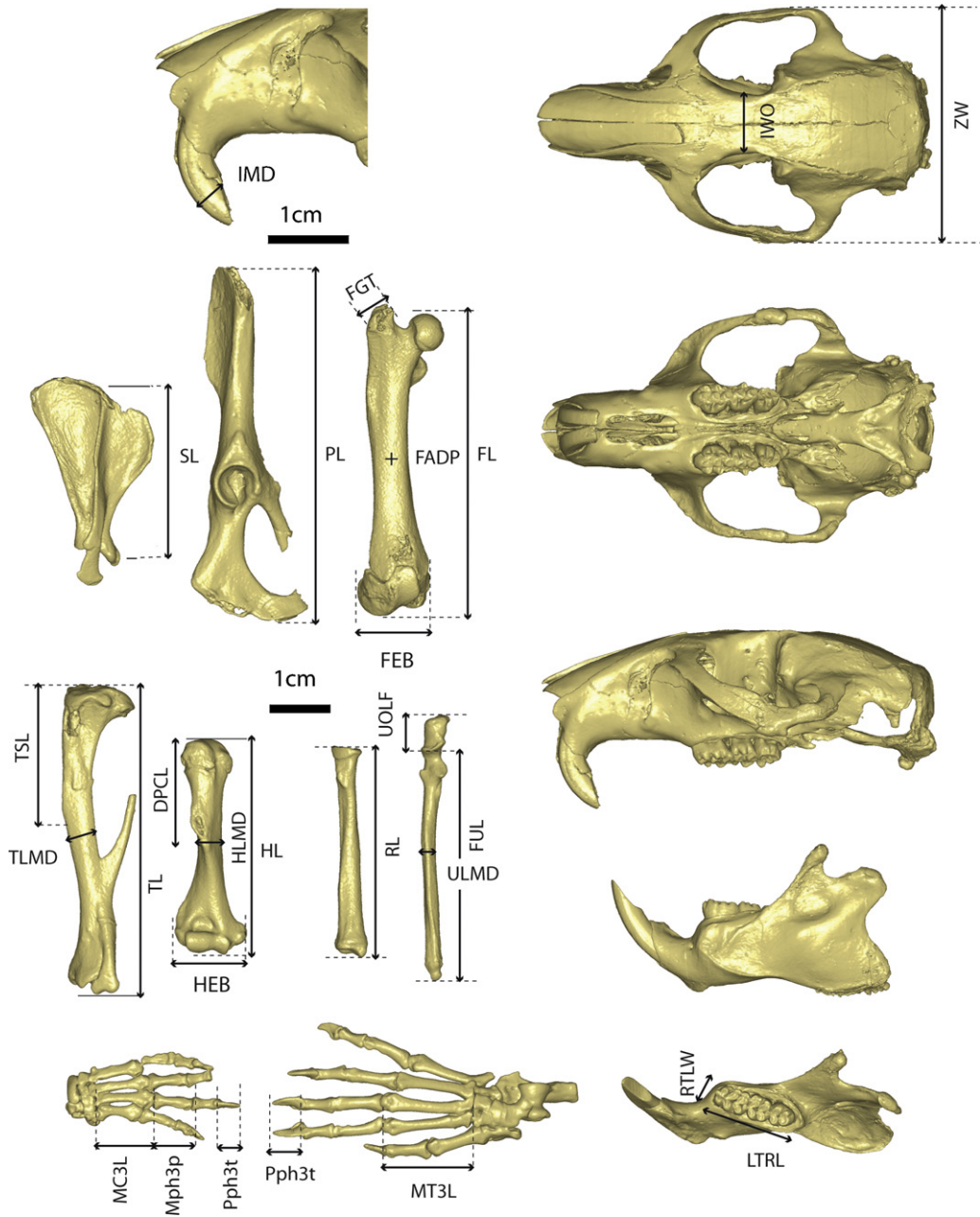


Fig. 1. Illustrations of *Canariomys bravoii* skull (dorsal, ventral and lateral views) and mandible (dorsal and lateral views) TFMC873, and measurements taken on skull and postcranial bones based on TFMC872 for bones and TFMC873 for the skull and mandible (see Section 2 for abbreviations).

Fig. 1. Illustrations du crâne (vues dorsale, ventrale et latérale) et de la mandibule (vues dorsale et latérale) de *Canariomys bravoii* (TFMC873) et mesures prises sur le crâne et les os post-cranéens d'après le spécimen TFMC872 pour les os et TFMC873 pour le crâne et la mandibule (voir Section 2 pour les abréviations).

bones of these specimens were reconstructed, on which measurements were taken. Second, measurements were taken from digital photos of skulls and skeletons of a sample of eight species (MNHN Paris collections): *P. cumingi*, *C. schadenbergi*, *S. muelleri*, *A. niloticus*, *M. insularis*, *R. rattus*, *M. musculus*. Measurements (Fig. 1), which allowed us to estimate the size and body mass of *C. bravoii*, as well as several morphofunctional indices in relation to its

locomotion mode, following Samuels and Van Valkenburgh (2008). For *C. tamarani* and *M. insularis* measurements were obtained from López-Martínez and López-Jurado (1987) and Hutterer et al. (1988), respectively.

The measurements are defined as follows for limbs and girdles: SL: Scapula Length; PL: Pelvis Length; HEB: Epicondylar Breadth of the Humerus; HL: Humerus length; HLMD: Midshaft mediolateral Diameter of the Humerus;

DPCL: Length of the Deltopectoral Crest; UMLD: Midshaft mediolateral Diameter of the Ulna; RL: Radius length; FUL: Functional Length of the Ulna; UOL: Length of Olecranon Process; FADP: Midshaft Anteroposterior Diameter of the Femur; FEB: Femur Distal Epicondylar Breadth; FGT: Height of the Greater Trochanter of the Femur; FL: Femur Length; TL: Tibia Length; TMLD: Midshaft Mediolateral Diameter of the Tibia; TSL: Tibial tuberosity Length; MC3L: Metacarpal 3 Maximum Length; Mph3p: Maximum Length of Proximal phalanx 3; Mph3t: Maximum Length of Phalanx 3 of the forelimb; MT3L: Maximum Length of Metatarsal 3; PPh3t: Maximum Length of Distal Phalanx 3. A few cranial measurements were also used to infer body mass (LTRL: Lower Tooth Row Length; LTRW: Lower Tooth Row Width, IMD: Mesiodistal Diameter of the Upper Incisor at wear level), and size of eye sockets that may indicate the orientation of the eyes (IOW, Interorbital Width; ZW, zygomatic Width).

Morphofunctional indices follow Samuels and Van Valkenburgh (2008): SMI: Shoulder moment index (DPCL/HL); BI: Brachial index (RL/HL); HRI: Humeral robustness index (HMD/HL); HEB: Humeral epicondylar index (HEB/HL); OLI: Olecranon length index (UOLF/FUL); URI: Ulnar robustness index (UMLD/FUL); CI: Crural index (TL/FL); FRI: Femoral robustness index (FADP/FL); GI: Gluteal index (FGT/FL); FEB: Femoral epicondylar index (FEB/FL); TRI: Tibial robustness index (TMLD/TL); TSI: Tibial spine index (TSL/TL); PES: Index of relative length of the foot (MT3L/FL); IM: Intermembral index $(HL + RL)/(FL + TL)$; MANUS: Manus digit 3 proximal phalanx length divided by metacarpal 3 length (Mph3p/MC3L). It indicates the relative proportions of proximal and distal elements of the manus and size of the palmar surface; CLAW: Manus digit 3 terminal phalanx length divided by pes digit 3 terminal phalanx length (Mph3t/Pph3t). It indicates the size of manual claws relative to the pedal claws.

Statistical procedures were performed with Statistica (version 6.0). The morphological variability of extant and extinct rodents was quantified using Samuels and Van Valkenburgh's (2008) procedure based on measurements of morphological (e.g. osteological and muscular) characteristics used to compute indices. For each analysis, a set of 13 robustness, morphofunctional and proportion indices were considered: SMI, BI, HRI, HEB, OLI, URI, CI, GI, FRI, FEB, TRI, TSI, and IM. Manova, in association with a test of significance (Wilk's Lambda test), was performed on these indices in order to assess the effects of life style. A factorial discriminant analyses (DA) was used to infer the mode of locomotion of *C. bravoii* (Fig. 2). Variables used for running these analyses were first the postcranial indices provided by limb measurements, groups being assemblages of taxa of known mode of locomotion. The database provided by Samuels and Van Valkenburgh (2008) was used following Bover et al. (2010). This database included 37 species of rodents distributed into seven categories of locomotion: terrestrial, semiaquatic, arboreal, fossorial, semifossorial, gliding, and ricochetal. The postcranial indices of the complete specimens of the extant *P. cumingi* and *M. musculus*, and the extinct *C. bravoii* were integrated into the dataset as ungrouped cases. The number of measured individuals per species is variable and occasionally very low. A specimen of *R. norvegicus* was also measured in order to estimate the

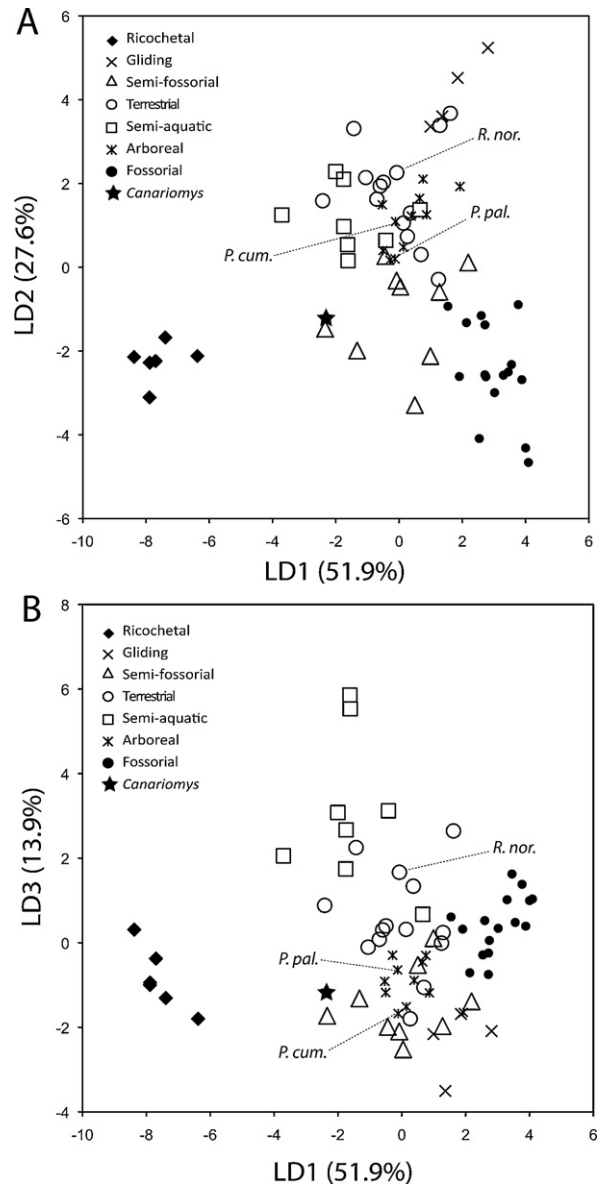


Fig. 2. Factorial discriminant analysis among groups of different locomotor habits. (A) Plot of axes one and two; (B) Plot of axes one and three.

Fig. 2. Analyse factorielle discriminante des différents groupes à partir des modes de locomotion. (A), Distribution selon les axes 1 et 2; (B), selon les axes 1 et 3.

reliability of the measurements compared to the results of Samuels and Van Valkenburgh (2008).

Allometric relationships known between the proportions of the skeleton and the body mass in rodents allowed for an estimation of the body mass of *C. bravoii* and *C. tamarani* following the formulas given by Parra and Jaeger (1998) and Hopkins (2008). Different measurements were considered: IMD (Mesiodistal Diameter of the Upper Incisor at wear level) (Parra and Jaeger, 1998), LTRL (Lower Tooth Row Length) and the RTRA or Rectangular Lower Tooth Row Area (LTRL \times LTRW) (Hopkins, 2008).



Fig. 3. 3D reconstruction of *Canariomys bravoii* skeleton according to specimens TFMC872 (semi-complete skeleton) and TFMC873 (skull).

Fig. 3. Reconstitution 3D du squelette de *Canariomys bravoii*, d'après les spécimens TFMC872 (squelette sauf crâne) et TFMC873 (crâne).

3. Results

Fig. 3 presents the 3D reconstruction of the skeleton of *C. bravoii* based on the semi-complete skeleton TFMCV1782, except the skull, which is from specimen TFMCV1783, and Figs. 1 and 4 illustrate several postcranial bones from the semi-complete skeleton.

3.1. Body size

Estimated head and body length of *C. bravoii* is 227 mm and tail length at least 157 mm. Values for *C. tamarani* were respectively 287 mm and 200 mm (López-Martínez and López-Jurado, 1987). For *P. cumingi* the head and body length is between 400–435 mm, and tail length between 270 and 315 mm (Nowak, 1999). Relative tail length can be estimated through the number and the length of caudal vertebrae depends on the completeness of the fossilized specimen. *C. bravoii* had at least 21 caudal vertebrae while *C. tamarani* had about 32 such vertebrae (López-Martínez and López-Jurado, 1987).

3.2. Body mass

Hopkins' approach (2008) provided several estimations of the body mass of *C. bravoii*. LTRL (Lower Tooth Row Length) gives an estimation ca 830 g for the specimen TFMCV1783, ten species of Murinae being used as reference. The area of the lower dental row (LTRL \times LTRW) provides a body mass of ca. 1020 g taking the same reference species. Taking 43 species of muroids with a body mass below 5 kg, the estimated body mass is ca 930 g, and with 70 species of rodents under 5 kg, 890 g. According to these same regressions, the body mass of the studied individual is estimated as between 758 and 871 g. The body mass of *C. tamarani* is ca 824 g based on LTRL (López-Martínez and López-Jurado, 1987). The Mesiodistal Diameter of the Upper Incisor at wear level (IMD, Parra and Jaeger, 1998) yields a body mass of 797 g for TFMCV1783, and 633 g for the studied nearly complete specimen TFMCV1782. These results are below the estimates previously given by Michaux et al. (1996).

3.3. Body shape

Forelimbs are shorter in *C. bravoii* than in *P. cumingi* and *R. norvegicus* (IM). Index EP indicates that *R. norvegicus* has longer feet than *P. cumingi* and *C. bravoii*, values in *C. bravoii* being intermediate. MANUS index shows that hands have

a larger plantar area in *P. cumingi* than in *C. bravoii* and *R. norvegicus*. CLAW index shows that foot claws are stronger than hand claws in *C. bravoii* and *R. norvegicus*. *C. bravoii* shows high values of robustness indices (HRI, URI, FRI, and TRI) compared to *P. cumingi*, *R. norvegicus* and *R. rattus*: values are greater, except FRI, and *R. norvegicus* and *R. rattus* are close to *C. bravoii*.

The zeugopodes and stylopodes of *C. bravoii* are robust. Indices characterizing forelimbs (SMI, HEB, and OLI) show that *C. bravoii* differs by a stronger deltoid crest (Fig. 4: Image 5a, b), a more powerful humerus epicondyle, and a shorter olecranon process relative to ulna length compared to the three species used as reference. For indices in relation to hind limbs (GI, FEB, and TSI), all the highest values but FEB (relative width of the femoral epicondyle) are displayed by *P. cumingi*. The FEB value in *C. bravoii* is slightly higher than in *P. cumingi*. The tibial tuberosity (TSI) is relatively less developed in *C. bravoii* than in *P. cumingi* and *R. norvegicus*.

The ratio SL/PL distinguishes *C. bravoii* from *P. cumingi* and *R. norvegicus*, the scapula being less developed in *C. bravoii*; only the acromion of the latter's scapula is stronger compared to *R. norvegicus* (Fig. 4: 2). However *P. cumingi* has more developed girdles in relation to the size of the skull (SL/CBL, PL/CBL). The stylopod of *P. cumingi* is longer than its zeugopod (BI and IC).

3.4. Morphofunctional indices

Compared to Samuels and Van Valkenburgh (2008), we found very similar results for the specimens of *R. norvegicus* that we measured, indicating the reliability of our measurements. Noteworthy observations are: High robustness indices (HRI, URI, FRI, TRI), the rather weak MANUS (palmar area), and the low IM calculated for *C. bravoii* exclude the fossorial, gliding, semiaquatic, and ricochetral locomotion categories (Samuels and Van Valkenburgh, 2008). It is very unlikely that *C. bravoii* belongs to the first two locomotion categories; high FRI, HRI, BI, CI, and PES indices exclude any attribution to the ricochetral mode of life. Several indices in *C. bravoii* (OLI, CLAW, FRI, FEB, and EP) are close to indices observed for tree-dwelling rodents according to Samuels and Van Valkenburgh (2008). However, BI and MANUS indices do not indicate a long humerus and hands as expected for such rodents. Robust limbs (HRI, URI, and FRI), with long and strong muscles (SMI, HEB, GI, FEB, TSI) could also indicate a semifossorial rodent but *C. bravoii* displays short forelimbs (high BI), rather weak claws, and its limbs are of a different length (IM=0.7). *C. bravoii* has a weak olecranon process, low value of OLI characterizing forelimbs not clearly modified for digging. BI and MANUS indices are close to the mean values for a terrestrial locomotion (Samuels and Van Valkenburgh, 2008). Nevertheless many rodents, ricochetral included, show some abilities in digging.

A discriminant analysis (Fig. 2) following Samuels and Van Valkenburgh (2008), with the addition of the *P. cumingi* (arboreal), *M. musculus* (terrestrial), the extinct taxon as an unclassified case, and *R. norvegicus* to test the reliability of our measurements, allowed their discrimination among groups of different locomotory habits.

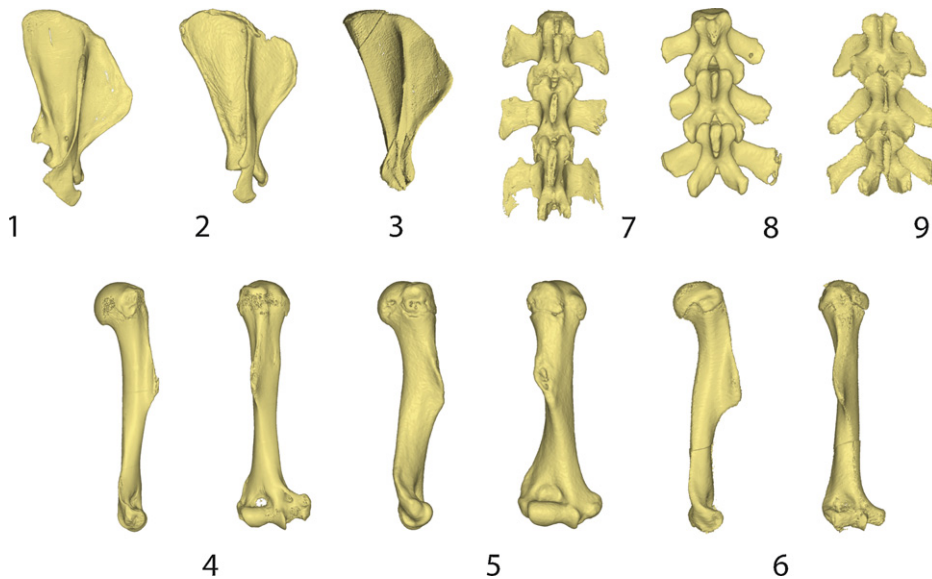


Fig. 4. Scapula, humerus and first caudal vertebrae of *Phloeomys cumingi* (1, 4, 7; MNHN CG 1882-144), *Canariomys bravoii* (2, 5, 8; TFCM872) and *Rattus norvegicus* (3, 6, 9). Each bone scaled to the same size. 1–3: right scapula; 4–6: right humerus (respectively a, medial and b, posterior views); 7–9: first caudal vertebrae (dorsal view).

Fig. 4. Omoplate, humérus et premières vertèbres caudales de *Phloeomys cumingi* (1, 4, 7; MNHN CG 1882-144), *Canariomys bravoii* (2, 5, 8; TFCM872) et *Rattus norvegicus* (3, 6, 9). Chaque os mis à une même taille. 1–3 : omoplate droite; 4–6 : humérus droit, (respectivement vue médiale et vue postérieure); 7–9 : premières vertèbres caudales, (vue dorsale).

Morphologies in relation with these locomotory habits could be separated on the first three discriminant axes that accounted for 51.9%, 27.6%, and 13.9%, respectively. MANOVAS on robustness, morphofunctional and proportion indices indicated a significant differentiation of the morphology within the dataset involving the different locomotory habits (Wilk's Lambda test: Value = 0.00259, $F = 6.891$, $P < 0.001$). LD1 mainly distinguished ricochetal rodents from all other lifestyles, LD2 tended to discriminate gliding and fossorial taxa, and LD3 mainly separated semiaquatic ones. *C. bravoii* was included as an ungrouped case in the classification phases. This analysis shows that *C. bravoii* is closer to *Phloeomys* (*P. cumingi* and *P. pallidus*) than to *Rattus* (*R. norvegicus* and *R. rattus*), and seems to show morphological similarities with arboreal, semifossorial, and terrestrial rodents (Fig. 2). On the one hand, *C. bravoii* appears to be closer to the semifossorial rodents than arboreal forms on the first three discriminant axes (Fig. 2). On the other hand, and according to statistical analyses performed on postcranial indices, a posteriori probabilities (Appendix A) classify *C. bravoii* as an arboreal rodent first (86.9%) and then as a semifossorial to (12.8%). This classification showed 91.2% correct classification of species. Fossorial, gliding and ricochetal groups showed 100% correct classification while all other groups had less than 90% correct classification but more than 75%: 88.9% for semifossorial, 87.5% for semiaquatic, 81.8% for arboreal and 85.7 terrestrial. As previously noticed by Bover et al. (2010), most misclassifications were about arboreal and terrestrial taxa, their skeletal proportions remaining more variable. Mahalanobis distances (Appendix B) also indicate that the morphological features of *Canariomys* are very close to that of arboreal and semifossorial groups (d

[*C. bravoii* s-arboreal] = 23.62, and d [*C. bravoii*-semifossorial] = 27.04).

4. Discussion

Skeletons provide insight into the size of a mammal and its mode of life. The appendicular skeleton informs about locomotion habits, whereas the skull provides some information on the diet and the relative development of sense organs. The following discussion mainly focuses on *C. bravoii* but also involves *C. tamarani* as it offers another example of insular evolution that may resemble that of *C. bravoii*.

Before discussing the results, it is worth mentioning briefly the role of allometry. Using the same dataset, Samuels and Van Valkenburgh (2008) analyzed the influence of allometry on the postcranial morphology by performing regressions of log-transformed measurements against the log of the Geometric Mean (GM corresponds to a measure of body size; see Samuels and Van Valkenburgh (2008) for a complete description of the method). They found that most of the characters showed no significant deviation from isometry. Only the Femoral epicondylar breadth (FEB) and the metatarsal three length (MTL3L) showed a significant positive and negative allometry respectively (Samuels and Van Valkenburgh, 2008, Table 4 p. 1390). This virtual absence of interspecific allometry seems to match the pattern of geometric similarity described for small mammals (Biewener, 1990). In small mammals such as rodents, changes in limb posture and muscle insertion areas rather than strong skeletal allometry should compensate for an increase in size (Samuels and Van Valkenburgh, 2008), a situation that likely

prevailed in our analysis. Fig. 4 shows that *C. bravoii* differs from *R. norvegicus* by stronger humerus and caudal vertebrae, while *Phloeomys* has a more slender humerus and a much longer acromion, this process being longer in *C. bravoii* than in *R. norvegicus*.

The rather similar head to body proportions in *C. bravoii*, *C. tamarani*, and *P. cumingi* suggest that the tails of both *Canariomys* species had probably the same balancing function as in *P. cumingi*, a result that is in agreement with the ability of climbing trees.

C. bravoii differed from continental rats by its relative large size, tail length, and body proportions. Its long hind limbs give it a squat posture as seen in other tree-dwelling mammals, as proposed by the reconstruction of its skeleton (Fig. 3). Feet longer than hands also suggest an intermediate body shape between rats and arboreal murine like *Phloeomys*. Postcranial robustness indices HRI, URI, and TRI show that *C. bravoii* was able to climb in trees. On the other hand, indices TSI, SMI, GI, and HEB support a semifossorial mode of life. Index FEB tends to locate *C. bravoii* close to tree-dwelling rodents, while its OLI index seems only compatible with a modest digging capacity. CLAW and IM indices indicate a rather weak development of claws on the forelimbs. Claws of similar length on the hands and feet, and rather long posterior limbs are compatible with climbing on trees and walking on branches. *C. bravoii* was a strong and powerfully muscled rat able to move on different substrates from the ground floor up to trees, also showing some skills for digging, at least for scratching the ground for food.

Evolution of mammals on islands results in the origination of species that may strongly differ from their continental relatives. *P. cumingi*, which is restricted to the island of Luzon (Philippines), shows many characteristics of an insular mammal (Musser and Heaney, 1992): large size with unusual body proportions. However, the comparison with the Canary Archipelago is not straightforward. The Philippines Archipelago is located in a zone of complex geological history, and *Phloeomys* had to compete repeatedly with newcomers. The *Phloeomys* lineage had individualized earlier than the *Canariomys* lineages. The molecular phylogeny provided by Lecompte et al. (2008) put different lineages of Murinae into a time sequence, the *Phloeomys* and *Crateromys* lineage being the oldest, followed by the *Rattus/Sundamys* group and the Arvicanthini. Compared with *Phloeomys*, the two species of *Canariomys* have experienced a different situation by evolving during a shorter time, without any mammalian competitor, along with an herbivorous giant lizard. No snake occurs in the Canary Islands today, and the only hint of a former existence is a single vertebra from Upper Miocene sediments of Lanzarote (Barahona et al., 1998). Each *Canariomys* simply had to exploit available resources, a situation that could explain the weak differentiation of their skeletal features compared to continental rats. In contrast, *Phloeomys* evolved in a competitive context and in the presence of an array of predators such as carnivores and wild pigs (Heaney et al., 2010), or large snakes (Taylor, 1922), and as a response might have had to develop a specialized arboreal life style.

Tenerife had until recently an important forest cover with the exception of xerophilous vegetation in the dry

lower part of the island, and poor vegetation above 1800 m (Del-Arco et al., 2006; Del-Arco, 2008). Such a situation has been roughly maintained since the Pliocene. Prior to the Pliocene, warm waters prevailed around the archipelago, and the flora was sub-tropical to tropical (Meco et al., 2010; Schmincke, 1968). Many members of this flora survive today where altitude and winds maintain a rather high humidity all year long. The laurel forests as well as the lowland plant communities of Tenerife and Gran Canaria harbour many local tree species with edible fruits, such as *Apollonias barbujana*, *Arbutus canariensis*, *Laurus azorica*, *Myrica faya*, *Ocotea foetida*, *Persea indica*, *Phoenix canariensis*, *Pinus canariensis*, *Pistacia lentiscus*, *Viburnum tinus*, or *Visnea mocanera* (Kunkel, 1982). Introduced Ship rats (*R. rattus*) have invaded the laurel forest of all islands and feed principally on these fleshy fruits, with a preference for smaller fruits (Delgado Garcia, 2000). According to size differences, this suggests that the extinct *Canariomys* was able to feed regularly on larger fruits, a conclusion in accordance with microwear analyses (Firmat et al., 2010).

The still unknown ancestor of *C. bravoii* found in Tenerife a wide range of environmental conditions, among which forests and shrubs offered protection against birds of prey. The somewhat reduced orbital cavity in the two *Canariomys* species may consequently mirror the modification observed in *Phloeomys*. However, causes for evolving such an association of morphological features were different: on the one hand, a protective cover and the lack of terrestrial predators, on the other hand, a shift toward forested refuge zones.

Once successfully settled, the ancestor of *C. bravoii* had to face strong intra-specific competition, and suffered from exceptional environmental contingencies such as volcanic eruptions or brief climatic events. The rat-sized murine of African origin evolved into a heavily built rat whose skeleton had little in common with that of a big rat. The changes observed in the proportions of its limbs indicate that *C. bravoii* could perform a rather wide spectrum of activities on the floor as well as in trees, including some skills for digging. This latter possibility can be a side effect of size increase and adaptation to a more vegetation-based diet. Search for fallback foods under harsh environmental conditions may have played a role in the evolution of *C. bravoii*, a result that mirrors the interpretation of its dental microwear patterns (Firmat et al., 2010). It is worth mentioning here that some semifossorial skills were also assumed for the extinct dormouse of the Balearic Islands: *Hypnomys* is considered to have had a wider niche than its continental ancestor *Eliomys* (Bover et al., 2010; Hautier et al., 2009). Similarly, the extinct Murinae *Mikrotia* of the Gargano Peninsula (Parra et al., 1999) is interpreted as semifossorial. The digging skills might be in relation to the widening of the niche under isolation.

Acknowledgments

This note was written as a tribute to Professor Nieves Lopéz-Martínez, our friend, companion in the field, and leading Spanish palaeontologist who died in 2010. She was part of our research team and, as such, contributed to the revival of studies of the island fauna of the Canary Islands.

Lionel Hautier gratefully acknowledges Sidney Sussex College (Cambridge, United Kingdom) and a research grant from the Leverhulme Trust (United Kingdom). Dr Christiane Denys gave access to the MNHN collections, Suzanne Jiquel and Anne-lise Charrault (ISEM, Montpellier) helped. Microtomographic images of the semi-complete skeleton were acquired at the Centre de

Microtomographie of University of Poitiers. The present work developed results of a preliminary study initiated by Mikael Antocio during the academic year 2010–2011, at the Paleontology Department, University of Montpellier-2. Supplementary data can be obtained from J. Michaux (jjmichau@univ-montp2.fr). Publication ISEM–UMR 5554 n° 2012-080.

Appendix A. Post-probabilities calculated from the discriminant analysis performed on postcranial indices.

	Classif.	Ricochetal	Gliding	Semifossorial	Terrestrial	Semiaquatic	Arboreal	Fossorial
<i>Allactaga hotsoni</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Dipodomys deserti</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Dipodomys merriami</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Dipus aegypticus</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Pedetes capensis</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Pygeretmus pumilio</i>	Ricochetal	1.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
<i>Petaurista petaurista</i>	Gliding	0.000000	0.999945	0.000001	0.000014	0.000000	0.000040	0.000000
<i>Anomalurus pelii</i>	Gliding	0.000000	0.999978	0.000000	0.000018	0.000000	0.000003	0.000000
<i>Hylomys nigripes</i>	Gliding	0.000000	0.998160	0.000007	0.001260	0.000000	0.000573	0.000000
<i>Glaucomys sabrinus</i>	Gliding	0.000000	0.999996	0.000000	0.000004	0.000000	0.000000	0.000000
<i>Ammospermophilus leucurus</i>	Semifossorial	0.000000	0.000003	0.722250	0.024286	0.000001	0.253451	0.000009
<i>Cynomys gunnisoni</i>	Semifossorial	0.000000	0.000001	0.864424	0.003585	0.000000	0.123308	0.008682
<i>Chelemys macronyx</i>	Semifossorial	0.000000	0.000000	0.140217	0.002308	0.000002	0.006429	0.851044
<i>Hystrix cristata</i>	Semifossorial	0.000000	0.000000	0.952598	0.000001	0.000000	0.000114	0.047286
<i>Marmota flaviventris</i>	Semifossorial	0.000000	0.000019	0.598963	0.015048	0.000000	0.351863	0.034107
<i>Xerus inauris</i>	Semifossorial	0.000002	0.000000	0.994910	0.000385	0.000002	0.004701	0.000001
<i>Tamias palmeri</i>	Semifossorial	0.000000	0.000002	0.913817	0.009693	0.000000	0.076344	0.000143
<i>Spermophilus beecheyi</i>	Semifossorial	0.000000	0.000000	0.939564	0.000726	0.000000	0.059683	0.000027
<i>Oxymycterus dasytrichus</i>	Semifossorial	0.000000	0.000000	0.996700	0.000092	0.000003	0.003094	0.000112
<i>Rattus rattus</i>	Terrestrial	0.000000	0.000003	0.000890	0.960153	0.003390	0.035564	0.000000
<i>Sigmodon hispidus</i>	Terrestrial	0.000000	0.000000	0.012774	0.818499	0.001079	0.167629	0.000019
<i>Zapus princeps</i>	Terrestrial	0.000000	0.000000	0.000086	0.966301	0.030243	0.003369	0.000000
<i>Perognathus parvus</i>	Terrestrial	0.000000	0.000681	0.007777	0.812351	0.041001	0.138190	0.000000
<i>Peromyscus maniculatus</i>	Terrestrial	0.000000	0.000188	0.000483	0.988373	0.001890	0.009066	0.000001
<i>Onychomys leucogaster</i>	Terrestrial	0.000000	0.000056	0.359626	0.260095	0.000016	0.377226	0.002981
<i>Neotoma cinerea</i>	Terrestrial	0.000000	0.000010	0.159139	0.788363	0.000000	0.052466	0.000023
<i>Napaeozapus insignis</i>	Terrestrial	0.000000	0.000000	0.000000	0.941849	0.058091	0.000060	0.000000
<i>Microtus californicus</i>	Terrestrial	0.000000	0.000021	0.000000	0.997030	0.002873	0.000076	0.000000
<i>Dinomys branickii</i>	Terrestrial	0.000000	0.000000	0.024431	0.053479	0.000017	0.896856	0.025217
<i>Clethrionomys californicus</i>	Terrestrial	0.000000	0.004430	0.000023	0.975941	0.000057	0.019549	0.000000
<i>Hyomys goliath</i>	Terrestrial	0.000000	0.000000	0.002401	0.515936	0.064895	0.416741	0.000027
<i>Rattus norvegicus</i>	Terrestrial	0.000000	0.000000	0.000022	0.963876	0.027973	0.008130	0.000000
<i>Mus musculus</i>	Terrestrial	0.000000	0.000001	0.000288	0.989450	0.000612	0.009649	0.000000
<i>Hydromys chrysogaster</i>	Semiaquatic	0.000000	0.000000	0.000007	0.014715	0.984956	0.000322	0.000000
<i>Castor canadensis</i>	Semiaquatic	0.000000	0.000000	0.000000	0.000001	0.999999	0.000000	0.000000
<i>Arvicola terrestris</i>	Semiaquatic	0.000000	0.000006	0.001985	0.931798	0.002146	0.063999	0.000066
<i>Colomys goslingi</i>	Semiaquatic	0.000000	0.000000	0.000001	0.005151	0.994844	0.000004	0.000000
<i>Nectomys squamipes</i>	Semiaquatic	0.000000	0.000000	0.000022	0.080252	0.916944	0.002782	0.000000
<i>Neofiber alleni</i>	Semiaquatic	0.000000	0.000000	0.000007	0.010652	0.989279	0.000061	0.000002
<i>Ondatra zibethicus</i>	Semiaquatic	0.000000	0.000000	0.000000	0.000069	0.999931	0.000000	0.000000
<i>Myocastor coypus</i>	Semiaquatic	0.000000	0.000000	0.000000	0.000218	0.999778	0.000004	0.000000
<i>Phloeomys pallidus</i>	Arboreal	0.000000	0.000000	0.184578	0.020198	0.000064	0.795138	0.000021
<i>Phloeomys cumingi</i>	Arboreal	0.000000	0.000000	0.000275	0.000209	0.000000	0.999516	0.000000
<i>Ratufa affinis</i>	Arboreal	0.000000	0.003631	0.024526	0.069082	0.000000	0.902736	0.000025
<i>Coendou prehensalis</i>	Arboreal	0.000000	0.000000	0.000177	0.021447	0.000007	0.978368	0.000000
<i>Erethizon dorsatum</i>	Arboreal	0.000000	0.000000	0.000396	0.017888	0.000009	0.981706	0.000001
<i>Nyctomys sumichrasti</i>	Arboreal	0.000000	0.000000	0.063127	0.026588	0.000488	0.909747	0.000050
<i>Sciurus niger</i>	Arboreal	0.000000	0.000010	0.619312	0.092102	0.000005	0.288511	0.000060
<i>Sphiggurus mexicanus</i>	Arboreal	0.000000	0.000000	0.004002	0.036314	0.000004	0.959677	0.000002
<i>Paraxerus cepapi</i>	Arboreal	0.000000	0.000001	0.470902	0.177756	0.000032	0.351294	0.000015
<i>Tamiasciurus hudsonicus</i>	Arboreal	0.000000	0.000839	0.105631	0.357835	0.000010	0.535576	0.000109
<i>Tylomys nudicaudus</i>	Arboreal	0.000000	0.000019	0.005069	0.145191	0.000103	0.849618	0.000000
<i>Cannomys badius</i>	Fossorial	0.000000	0.000000	0.000131	0.000027	0.000000	0.000055	0.999786
<i>Heliophobius argenteocinereus</i>	Fossorial	0.000000	0.000000	0.000030	0.000000	0.000000	0.000000	0.999970
<i>Heterocephalus glaber</i>	Fossorial	0.000000	0.000000	0.048279	0.000077	0.000000	0.001721	0.949924
<i>Orthogeomys grandis</i>	Fossorial	0.000000	0.000000	0.001713	0.000001	0.000000	0.000004	0.998283
<i>Pappogeomys tylosrhinus</i>	Fossorial	0.000000	0.000000	0.000004	0.000000	0.000000	0.000000	0.999996
<i>Nannospalax leucodon</i>	Fossorial	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	1.000000
<i>Cryptomys hottentotes</i>	Fossorial	0.000000	0.000000	0.007088	0.000011	0.000000	0.000055	0.992846

Appendix A (Continued)

	Classif.	Ricochetal	Gliding	Semifossorial	Terrestrial	Semiaquatic	Arboreal	Fossorial
<i>Geomys bursarius</i>	Fossorial	0.000000	0.000000	0.000026	0.000000	0.000000	0.000000	0.999973
<i>Georychus capensis</i>	Fossorial	0.000000	0.000000	0.001018	0.000652	0.000000	0.000332	0.997998
<i>Geoxus valdivianus</i>	Fossorial	0.000000	0.000000	0.000214	0.000000	0.000000	0.000000	0.999786
<i>Aplodontia rufa</i>	Fossorial	0.000000	0.000000	0.144593	0.003230	0.000000	0.023719	0.828457
<i>Rhizomys pruinosus</i>	Fossorial	0.000000	0.000000	0.007583	0.000002	0.000000	0.000348	0.992068
<i>Spalax giganteus</i>	Fossorial	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	1.000000
<i>Tachyoryctes splendens</i>	Fossorial	0.000000	0.000000	0.131122	0.016138	0.000240	0.037394	0.815106
<i>Thomomys bottae</i>	Fossorial	0.000000	0.000000	0.000095	0.000000	0.000000	0.000002	0.999902
<i>Zygoeomys trichopus</i>	Fossorial	0.000000	0.000000	0.000191	0.000000	0.000000	0.000000	0.999808
<i>Canariomys bravoii</i>	–	0.000001	0.000000	0.128766	0.001755	0.000005	0.869473	0.000000

Appendix B. Mahalanobis distances, calculated from the discriminant analysis performed on postcranial indices.

	Classification	Ricochetal	Gliding	Semifossorial	Terrestrial	Semiaquatic	Arboreal	Fossorial
<i>Allactaga hotsoni</i>	Ricochetal	4.8748	143.1386	70.28303	78.9031	69.42630	84.92175	119.9528
<i>Dipodomys deserti</i>	Ricochetal	8.7465	125.8093	64.78619	80.8469	68.05927	78.77656	119.6085
<i>Dipodomys merriami</i>	Ricochetal	10.9906	112.4812	57.82093	73.4211	69.27384	72.16354	102.3486
<i>Dipus aegypticus</i>	Ricochetal	4.9341	155.3464	83.41865	87.5152	72.58284	96.96768	133.0186
<i>Pedetes capensis</i>	Ricochetal	20.4752	177.0417	81.05199	103.4747	92.27757	99.19269	139.2537
<i>Pygeretmus pumilio</i>	Ricochetal	2.2852	141.6477	69.80256	82.4107	72.61061	84.57883	122.6323
<i>Petaurista petaurista</i>	Gliding	124.8740	2.6832	32.74669	27.4918	61.51294	24.96833	58.4672
<i>Anomalurus pelii</i>	Gliding	169.6639	7.2574	54.06588	31.5890	67.91587	34.44120	69.6548
<i>Hylopetes nigripes</i>	Gliding	110.3723	1.7572	27.15630	17.6117	42.79405	18.70602	48.4779
<i>Glaucomys sabrinus</i>	Gliding	147.2140	4.9876	50.24936	32.5104	57.99079	38.37032	66.7231
<i>Ammospermophilus leucurus</i>	Semifossorial	61.2707	26.5609	3.23746	10.9061	29.41516	5.73320	26.9739
<i>Cynomys gunnisoni</i>	Semifossorial	84.9314	29.9505	3.59460	15.4490	38.79349	7.89070	13.9468
<i>Chelemys macronyx</i>	Semifossorial	85.2986	63.3870	17.14306	26.2405	38.97276	23.70922	14.6872
<i>Hystrix cristata</i>	Semifossorial	84.8207	81.7562	17.58579	45.7241	50.21520	36.04094	24.7425
<i>Marmota flaviventris</i>	Semifossorial	107.7787	28.2612	9.17460	17.4262	39.31191	10.63985	16.0567
<i>Xerus inauris</i>	Semifossorial	35.3395	59.9681	9.61324	26.2136	35.86631	20.72423	39.7296
<i>Tamias palmeri</i>	Semifossorial	64.2291	28.6965	4.08756	14.0636	34.38263	9.45366	22.7608
<i>Spermophilus beecheyi</i>	Semifossorial	70.0540	34.9967	4.32112	19.5357	40.68490	10.23520	26.4204
<i>Oxymycterus dasytrichus</i>	Semifossorial	44.7532	54.5625	7.43319	26.9049	32.71136	19.38477	26.7675
<i>Rattus rattus</i>	Terrestrial	81.4823	33.1925	23.13272	10.0490	20.22236	16.15821	43.1166
<i>Sigmodon hispidus</i>	Terrestrial	79.6127	34.1789	13.30001	5.8635	18.00773	8.55265	27.4738
<i>Zapus princeps</i>	Terrestrial	51.1638	47.3556	27.82894	10.0680	15.87722	20.90343	52.5163
<i>Perognathus parvus</i>	Terrestrial	68.9507	22.3460	19.09568	10.6818	15.53527	13.74213	43.9796
<i>Peromyscus maniculatus</i>	Terrestrial	75.9929	30.2467	29.97478	15.6124	27.01247	24.51313	44.0480
<i>Onychomys leucogaster</i>	Terrestrial	79.4861	24.5400	8.64251	10.1742	28.46382	8.94829	19.3791
<i>Neotoma cinerea</i>	Terrestrial	92.3646	42.3494	24.53665	22.2200	52.75606	27.15723	43.3948
<i>Napaeozapus insignis</i>	Terrestrial	87.1078	46.1847	45.07938	12.7273	17.17971	31.55214	64.8563
<i>Microtus californicus</i>	Terrestrial	136.0678	32.4404	48.79477	13.4443	24.02417	31.92804	48.6195
<i>Dinomys branickii</i>	Terrestrial	100.4418	52.9243	24.09767	23.4144	38.34780	17.29290	25.1850
<i>Clethrionomys californicus</i>	Terrestrial	120.7567	20.3833	32.53064	12.0990	30.46174	19.43762	45.6880
<i>Hyomys goliath</i>	Terrestrial	89.1867	39.3635	19.24237	9.3859	12.41306	9.33058	29.4047
<i>Rattus norvegicus</i>	Terrestrial	89.9458	35.8961	27.15484	6.6436	12.60379	15.71210	39.5047
<i>Mus musculus</i>	Terrestrial	73.2806	28.2984	18.90215	3.5049	17.16305	12.28321	37.6209
<i>Hydromys chrysogaster</i>	Semiaquatic	65.0224	61.8263	30.17900	15.6942	6.16750	22.85339	46.5043
<i>Castor canadensis</i>	Semiaquatic	110.0045	125.1110	77.68797	59.0238	29.78432	66.09283	80.5595
<i>Arvicola terrestris</i>	Semiaquatic	88.1730	26.5886	16.71764	5.2985	16.32666	10.17267	24.6777
<i>Colomys goslingi</i>	Semiaquatic	43.1404	64.1204	42.24042	25.7201	14.07387	39.33216	69.0421
<i>Nectomys squamipes</i>	Semiaquatic	71.4837	47.9675	32.76736	17.2847	11.29366	23.52626	56.0957
<i>Neofiber alleni</i>	Semiaquatic	81.5374	53.8692	30.14515	16.2280	6.04623	26.05715	34.1739
<i>Ondatra zibethicus</i>	Semiaquatic	98.5008	103.8543	70.40780	41.2148	20.93594	69.02828	70.2321
<i>Myocastor coypus</i>	Semiaquatic	96.5833	75.5995	66.54662	45.2334	27.25212	52.73952	83.5770
<i>Phloeomys pallidus</i>	Arboreal	74.8466	43.4608	10.42216	15.7308	26.12336	7.90262	29.7115
<i>Phloeomyscumingi</i>	Arboreal	100.8033	58.7924	37.11208	38.5477	54.79209	21.11852	58.2840
<i>Ratufa affinis</i>	Arboreal	116.1052	18.5005	16.30166	15.1142	40.17353	9.49164	31.1920
<i>Coendou prehensalis</i>	Arboreal	105.8875	38.3240	25.14747	16.4396	31.35964	8.31669	41.7575
<i>Erethizon dorsatum</i>	Arboreal	100.1174	37.3813	25.17353	18.4360	32.46948	9.94333	38.9259
<i>Nyctomys sumichrasti</i>	Arboreal	76.7557	47.8079	19.14173	21.7548	28.62962	14.20703	34.5909
<i>Sciurus niger</i>	Arboreal	71.0652	24.1255	3.69639	8.3915	27.06662	5.62548	23.3377
<i>Sphiggurus mexicanus</i>	Arboreal	88.0369	34.2897	17.23216	13.7050	30.88668	6.67390	33.4466
<i>Paraxerus cepapi</i>	Arboreal	61.1155	30.0527	4.26727	7.0994	23.21563	5.25466	26.1036
<i>Tamiasciurus hudsonicus</i>	Arboreal	87.0919	16.8978	8.84838	7.2918	27.05743	6.00294	23.7542
<i>Tylomys nudicaudus</i>	Arboreal	79.5895	35.0268	25.51339	19.6871	33.07672	15.67130	45.3407
<i>Cannomys badius</i>	Fossorial	144.7281	54.8053	28.86720	32.9127	41.80806	30.99364	12.1390
<i>Heliophobius argenteocinereus</i>	Fossorial	134.4653	72.6795	32.27204	44.1723	54.53308	43.56647	12.6024
<i>Heterocephalus glaber</i>	Fossorial	127.7072	58.7917	26.06329	39.8334	53.12617	33.13297	21.2552

Appendix B (Continued)

	Classification	Ricochetal	Gliding	Semifossorial	Terrestrial	Semiaquatic	Arboreal	Fossorial
<i>Orthogeomys grandis</i>	Fossorial	113.4000	60.3202	17.07719	34.0328	46.99656	29.66913	5.4920
<i>Pappogeomys tylosrhinus</i>	Fossorial	141.0475	78.6626	38.38349	45.3171	55.46479	47.56144	14.5545
<i>Nannopalax leucodon</i>	Fossorial	153.2433	96.4103	45.23299	69.9818	75.25994	64.18793	15.9945
<i>Cryptomys hottentotus</i>	Fossorial	104.2064	69.7314	22.10130	35.9412	46.79585	32.28264	13.3677
<i>Geomys bursarius</i>	Fossorial	144.4069	76.0703	31.32835	44.7106	63.90432	41.87840	11.3938
<i>Georchus capensis</i>	Fossorial	123.9413	57.4134	31.72252	33.4959	49.16560	34.36488	19.0973
<i>Geoxus valdivianus</i>	Fossorial	123.3825	93.8533	36.20292	58.9714	75.25084	53.80822	20.4567
<i>Aplodontia rufa</i>	Fossorial	105.2802	50.7564	15.02945	23.5157	45.69069	19.04607	12.6889
<i>Rhizomys pruinosus</i>	Fossorial	117.8941	69.6015	20.81560	38.1510	58.57933	27.38225	12.2185
<i>Spalax giganteus</i>	Fossorial	164.0724	111.3873	57.03946	79.0442	91.06104	80.31833	25.1300
<i>Tachyoryctes splendens</i>	Fossorial	93.4689	43.4227	12.74743	17.8210	25.12230	15.65800	10.2438
<i>Thomomys bottae</i>	Fossorial	134.6851	88.4652	37.29133	50.8927	67.73205	45.15771	19.9222
<i>Zygozomys trichopus</i>	Fossorial	139.2660	64.0208	29.25710	46.9316	55.31423	42.68514	13.2842
<i>Canariomys bravoii</i>	–	51.1315	87.1255	27.04283	36.5174	47.26388	23.62439	53.8262

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