



Mandible shape in marsupial and placental carnivorous mammals: a morphological comparative study using geometric morphometrics

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Received 16 August 2011; accepted for publication 9 September 2011

We analysed mandible shape of the orders Dasyuromorpha, Didelphimorphia, and Carnivora using two-dimensional geometric morphometrics, in order to explore the relationship between shape, size, and phylogeny. We studied 541 specimens, covering most of the genera of the terrestrial Carnivora (115 species) and a wide sample of marsupials (36 species). The observed shape variation had an ecological component. As an example, omnivorous carnivores have thick mandibles and large talonids in the carnassials, while hypercarnivores possess short mandibles and reduced talonids. There is also a discrimination between different taxonomic groups (i.e. marsupials and Carnivora), indicating some kind of constraint. Size explains a large percentage of total variance (large species had shorter and stronger mandibles, with anteriorly displaced carnassials), was significant when phylogeny was taken into account with a comparative method, but not when size and shape were optimized on the phylogeny. Carnivora presents a larger disparity and variation in body size, which could be related to the difference in teeth replacement. The optimization of mandible shape on the phylogenetic tree indicates that functional aspects, such as diet, are a key factor in the evolution of the carnivore mandible, but also that there is a phylogenetic pattern that cannot be explained by differences in diet alone.

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doi: 10.1111/j.1096-3642.2011.00785.x

ADDITIONAL KEYWORDS: allometry – Carnivora – Dasyuromorphia – disparity – phylogenetic morphometrics.

INTRODUCTION

Mandible shape in mammals is closely related to diet and feeding behaviour, as it has a key function in food catching and processing (e.g. Turnbull, 1971; Hildebrand, 1974; and references therein). The mandible works as a lever that transmits the forces generated by masseteric, temporal, and pterygoid muscles, to the dentition that, in turn, serves to capture, pierce,

cut, and smash food items (Turnbull, 1971; Hildebrand, 1974; Greaves, 1982, 1988, 2008). The relationship between mandible and diet in the order Carnivora (placental carnivores) was explored using a variety of approaches ranging from qualitative descriptions to geometric morphometrics. Members of this order present a high diversity and a wide range of dietary habits that includes hypercarnivores, insectivores, omnivores, piscivores, and some herbivore species as well as those exhibiting a combination of feeding strategies (e.g. Davis, 1964; Gaspard, 1971; Turnbull, 1971; Savage, 1977; Radinsky, 1981a, b,

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1982; Greaves, 1983, 1985; Van Valkenburgh, 1989, 1991; Biknevičius & Ruff, 1992; Biknevičius & Van Valkenburgh, 1996; Werdelin, 1996; Christiansen & Adolfsson, 2005; Christiansen and Wroe, 2007; Therrien, 2005a, b; Meloro *et al.*, 2008; Figueirido, Palmqvist & Pérez-Claros, 2009; and references therein; Figueirido *et al.*, 2010; Meloro, 2011; Meloro & O'Higgins, 2011). Most previous studies of this type have shown the presence of shape–function relationships and allometric and phylogenetic patterns (e.g. Werdelin, 1986, 1987, 1989; Wroe & Milne, 2007; Meloro *et al.*, 2008).

Recent studies using a selected sample of Carnivora (Figueirido *et al.*, 2010) showed a convergent pattern in the rise of herbivory in different clades, something that was previously noted for hypercarnivore taxa (e.g. Radinsky, 1981a, b, 1982; Van Valkenburgh, 1989, 1991, 2007; Werdelin, 1989, 1996; Holliday & Steppan, 2004), but also some morphological differences related to their phylogenetic position in the order Carnivora.

Early comparison of Carnivora to groups of marsupial carnivores (Dasyuromorphia), using cranial measurements and multivariate statistics, found that the marsupials have a more pronounced development of the masseteric muscle, a longer lower jaw, and a smaller temporal muscle, but with a larger moment arm (Werdelin, 1986, 1987). However, convergences were also found; for example, canids (especially *Vulpes vulpes*) and *Thylacinus* share a long dental series and other cranial similarities, while *Sarcophilus* and *Crocota* have a posteriorly displaced lower carnassial (Werdelin, 1986, 1987). More recently, Jones (2003) found convergence between Carnivora and Dasyuromorphia, specifically between hyenids and the Tasmanian devil (*Sarcophilus*), and using a similar approach. Jones also grouped the marsupial wolf (*Thylacinus*) in the morphometric space shared with felids and canids, but closer to canids. *Thylacinus* is apparently more similar to small canids than to the grey wolf (*Canis lupus*; Jones, 2003; see also Werdelin, 1986; Jones & Stoddart, 1998). Finally, *Dasyurus* spp. is closer to some mustelids in skull morphology (Jones, 2003). However, dasyurids have long rostrums and a narrow and flattened skull with a small braincase compared with Carnivora, indicating the presence of a phylogenetic pattern in the skull shape of these mammals. Recent work that included a larger sample (43 species) and three-dimensional landmarks (Wroe & Milne, 2007; Goswami, Milne & Wroe, 2011) also revealed clear phylogenetic differences and convergences between marsupials and Carnivora, but the mandible was not included in these analyses. Different marsupials and carnivorans share similar rostrum size and muscular attachment

areas, traits that are correlated with diet and bite forces, while marsupials have stronger and wider zygomatic arches, nasals with a longer and wider posterior half, flatter skulls, and a posteriorly displaced glenoid cavity in comparison with carnivorans, showing the presence of a phylogenetic pattern in the shape of the skull (Wroe & Milne, 2007).

Comparisons of the morphological characteristics between these groups indicate that marsupial carnivores possess less variation in dentition and skull than Carnivora. Butler (1946) and Werdelin (1986, 1987) explained this pattern by suggesting the presence of constraints generated by differences in dentition eruption and replacement. Body size distribution is also larger in carnivorans, with marsupial carnivores at the lower end of the range of body mass values (Wroe & Milne, 2007). Contrary to these early findings, recent geometric–morphometric analysis (Goswami *et al.*, 2011) found a similar level of disparity in the skull shape of these groups, but, again, the mandible was not included in these analyses.

Here, we explore the variation of mandibular shape in a large sample of placental and marsupial carnivores using a geometric–morphometric approach to test the following relationships: the shape–function relationships; the presence of convergence and/or phylogenetic pattern between marsupials and Carnivora; the presence of differences in morphological disparities between these groups; and the allometric pattern of mandible shape. Another aim of this work is to explore the evolution of the mandible through optimization of the shape (i.e. ancestral shape and size reconstructions) on phylogenetic trees.

MATERIALS AND METHODS

SAMPLES

A total of 541 mandibles belonging to 151 species of extant marsupials (Dasyuromorphia, Didelphimorphia, Peramelemorphia, Microbiotheria) and placental carnivores (Carnivora) were used in this study (Table 1). Clades of marsupials were selected based on the presence of carnivorous species or relatives. The material belongs to the mammal collections of the following Institutions: American Museum of Natural History (AMNH); Field Museum of Natural History; National Museum of Natural History, Smithsonian Institution (USNM); Museo de La Plata (MLP); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN); Naturhistoriska Riksmuseet (NHR); Museum national d'Histoire naturelle (NMNH); Rijksmuseum van Natuurlijke Historie

Table 1. Detail of the number of species and specimens per main taxonomic group

Taxa	Species	Specimens
Marsupialia	36	145
Dasyuromorphia	20	87
Didelphimorphia	12	45
Microbiotheria	1	4
Peramelemorphia	3	9
Carnivora	115	396
Caniformia	69	252
Ailuridae	1	3
Canidae	23	103
Mephitidae	6	18
Mustelidae	24	71
Procyonidae	7	21
Ursidae	8	36
Feliformia	46	144
Eupleridae	5	10
Felidae	18	71
Herpestidae	9	21
Hyaenidae	3	15
Nandiniidae	1	2
Viverridae	10	25
Total	151	541

(RMNH); and Yale Peabody Museum (YPM) (Supporting Information, Table S1). Only adult specimens with fully erupted dentition were included and, when possible, we tried to sample equal numbers of males and females, up to six in total per species. As we used lower carnassial morphology (i.e. trigonid/talonid development of m1 in Carnivora and m4 in marsupials) we did not include taxa with reduced dentition and no carnassials (e.g. living Pinnipedia, *Proteles*). The lower fourth molar (m4) was chosen as an analogue of carnivore m1 because m4 usually presents the more carnassial-like shape (i.e. with larger trigonid, and more reduced talonid), is closest to the condyle, and it is in the 'correct' biomechanical place for a carnassial in an adult marsupial (see Werdelin, 1986, 1987).

We classified the species according to their diet, using the available bibliography (e.g. Strahan, 1995; Vieira & Astúa de Moraes, 2003; Nowak, 2005; Wilson & Mittermeier, 2009), and following the modifications of the classification proposed by Van Valkenburgh (1989): Hypercarnivores, most of their diet is composed by other vertebrates; Mesocarnivores, feed mainly on other vertebrates (usually smaller species than themselves), but also plants and invertebrates; Omnivores, plants and invertebrates represent a large proportion of the diet; Herbivores, feed mostly on plant materials; Insectivores, feed mostly on

insects. We also collected body mass data from the same bibliographical sources (see supporting Table S1).

METHODS

Twenty-nine landmarks were used to describe the lateral view of the mandible. Mandibles were photographed aligning the sagittal plane of the mandibular corpus parallel to a horizontal plane (i.e. base of the camera stand or table) (Fig. 1).

We used landmarks of types 1, 2, and 3 (*sensu* Bookstein, 1991), which were digitized using the software tpsDig 2.09 (Rohlf, 2006). Prior to use of tpsDig we used the program MakeFan6 (Sheets, 2003) to correctly place the type 3 landmarks (see Bookstein, 1997). The software tpsUtil 1.40 (Rohlf, 2008) was used to compile image files and to perform other basic operations. Landmark configurations were superimposed through generalized procrustes analysis (GPA; Goodall, 1991; Rohlf, 1999) with the software tpsRelw 1.45 (Rohlf, 2007a). The latter was also used to obtain matrices of partial and relative warp scores (Bookstein, 1989; Rohlf, 1993; Zelditch *et al.*, 2004), setting the alpha parameter to 0 (by doing this, the relative warp analysis becomes a principal components analysis).

Hypotheses regarding the phylogenetic constraint of the mandible, and the influence of the dietary habits on the evolution of the mandible, were evaluated with multivariate analysis of variance (MANOVA), and discriminant analyses were used to test for shape differences between diet classes and different clades using the programs R 2.9.2 (R Development Core Team, 2008) and MorphoJ 1.01b (Klingenberg, 2008). As dependent variables, we included the relative warps (RWs) obtained in the geometric morphometric analysis, restricting the number of RWs used to keep it below the number of specimens of the category with the fewest individuals (i.e. number of species in the smaller category – 1). In the discriminant analysis, the same probability of classification was assigned to each group and the percentage of posterior correct reclassification was calculated using cross validation (CV; Reyment, Blackith & Campbell, 1984; Jackson, 1993; Mendoza, Janis & Palmqvist, 2002). We tested the separation between Carnivora and marsupials, and between groups inside these main clades. Didelphimorphia, Dasyuromorphia, and Peramelimorphia were considered for the marsupials. Microbiotheria was excluded due to the low number of samples. For the Carnivora, three nested discriminant analyses were performed: one between Feliformia and Caniformia; the second within Feliformia, considering Felidae, Viverridae, Herpestidae, Eupleridae, and Hyaenidae; and the last

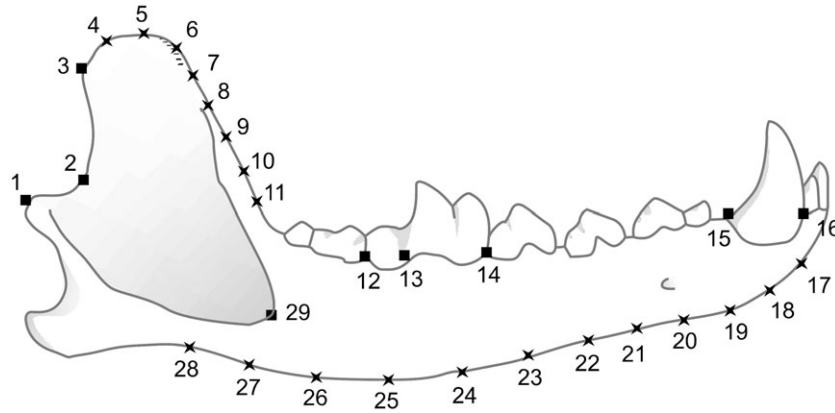


Figure 1. Lateral view of a *Canis lupus* mandible showing the landmarks and semilandmarks used. Squares, landmarks; X, semilandmarks; 1, caudal extreme of the condyle; 2, most concave point of the mandibular notch; 3, dorso-caudal angle of the coronoid process; 4–11, semilandmarks; 12, distal extreme of the lower carnassial; 13, distal border of the protoconid projected to the base of the crown; 14, mesial border of the lower carnassial; 15, distal extreme of the c1; 16, mesial extreme of the c1; 17–28, semilandmarks; 29, anterior border of the masseteric fossa.

within Caniformia, considering Canidae, Ursidae, Mephitidae, Mustelidae, and Procyonidae. Nandiniidae and Ailuridae were excluded because of low sample size.

To test the hypothesis that carnivores have more disparity in the mandible shape than marsupials, we used the trace of the variance–covariance matrix (MD) of the mean relative warp scores per species (see Zelditch *et al.*, 2004) and a permutation test (10 000 resamples). The permutation test was done pooling marsupials and carnivore species and then regrouping them randomly in groups with the original sample of marsupial species (two groups of 36). In each permutation the number of times that the random differences were greater than or equal to the observed one were counted to obtain the significance of the disparity difference. Because Carnivora has a larger sample in terms of specimens and taxa (396 and 115 versus 145 and 36, respectively), the carnivore disparity was calculated in each permutation sampling randomly 36 species of carnivores, and the difference with the marsupial disparity was obtained. The same approach was used with size variation, but using the variance of this variable.

Because centroid size presented a non-normal distribution, as determined by a Shapiro–Wilks test (Zar, 1984), differences between Carnivora and marsupials were evaluated through descriptive statistics (mean, median, standard deviation and variance, minimum, maximum), and application of the Levene and Mann–Whitney tests (Zar, 1984). Due to the lack of normality in this variable, centroid size was transformed to \log_{10} values previous to allometric analyses.

The potential influence of the size on the evolution of mandible shape was studied with an allometric

analysis, which was performed regressing shape (i.e. partial warps, and uniform components) on centroid size with the tpsRegr 1.34 software (Rohlf, 2007b). The significance of the regression was tested with the generalized Goodall F-test and a permutation test with 1000 resamples (see Rohlf, 2007b). To take into account the phylogenetic structure of datasets, we constructed a phylogenetic covariance matrix from the combined phylogenetic tree, and performed an allometric regression with the Phylogenetic Generalized Least Squares (PGLS) comparative method (Martins & Hansen, 1997). These analyses were carried out using APE libraries (Paradis, Claude & Strimmer, 2004) for R 2.9.2 (R Development Core Team, 2008). To construct the phylogenetic matrix, we assigned discrete values to nodes, starting from the value ‘1’ for the node placed furthest from the root, in the most diverse clade. We then proceeded to number the intermediate nodes between that node and the root, assigning them increasing values. The remaining node values were assigned in decreasing order from those already enumerated. To quantify the phylogenetic distances, the distance between two species was coded as the value assigned to the nearest common ancestral node. Thus, all the taxa belonging to a single clade are assigned shorter distances to other taxa of the same clade than with respect to taxa that do not belong to that clade. Similar procedures have been used in previous studies (e.g. Grafen, 1989; Gittleman & Kot, 1990; Miles & Dunham, 1992), and are numerically similar to constructing an ultrametric distance matrix considering a length of ‘1’ for all branches (Rohlf, 2001).

To explore the evolution of mandible shape, size, and diet, we used optimization methods that

reconstruct ancestral states and allowed us to explore the change of these characters along the phylogeny of the groups. We employed the methods proposed by Catalano, Goloboff & Giannini (2010) and Goloboff & Catalano (2011), to optimize the landmark configurations on phylogenetic trees using maximum parsimony algorithms, which use a modification of the Sankoff optimization (see Goloboff & Catalano, 2011). These methods allow the reconstruction of the displacement of each landmark in two dimensions in this case, as they are independent 'characters'. The summation of individual landmark optimization (i.e. the reconstruction of its ancestral position in each node) gives the ancestral landmark configuration of every node of the tree (for more details see Catalano *et al.*, 2010). The aligned landmark configurations (mean per species), obtained from the GPA superimposition, were used in the optimizations. Centroid size (mean per species) was also optimized as a continuous variable (see Goloboff, Mattoni & Quinteros, 2006), to explore size changes and their relationship with shape changes. Diet was optimized using a step matrix (Sankoff, 1975) which allows weighting the cost of the change (steps) between different diet states. We coded one step between most of the transformations among states; two steps to the changes between the states omnivore–hypercarnivore, mesocarnivore–herbivore, and insectivore–herbivore; three steps for the change between the states herbivore–hypercarnivore. This is because diet classes could be seen as a specialization in any kind of diet (i.e. meat, plants, insects) consumed by omnivores. For example, to go from hypercarnivores to herbivores it is required to pass through less carnivorous states such as mesocarnivores, and omnivores taking a cost of transformation of three steps. In this way the continuous variation that exists in diet is preserved.

The phylogenetic hypothesis used in this paper is a 'manual' combination of the most recent and extensive (in terms of taxa and character sampling) published phylogenies: Krajewski & Westerman 2003, and Beck, 2008 (for the main clades of marsupials and Australian marsupials in particular); Flynn *et al.* 2005 (for the the main clades of Carnivora); Gaubert *et al.* 2005 (for Viverridae); Johnson *et al.* 2006 (for felids); Koepfli *et al.* 2006, 2007, 2008 (for hyaenids, procyonids, and mustelids, respectively); Krause *et al.* 2008 (for bears); Flores, 2009 (for didelphimorphians); Patou *et al.* 2009 (for Herpestidae); Wolsan & Sato, 2009; Sato *et al.*, 2009 (for the position of *Lyncodon* within the mustelidae); Prevosti, 2010 (for canids) (supporting Fig. S1). The consistency index (CI) was used to measure the homoplasy present in these 'characters' (Kluge & Farris, 1969). All the optimization procedures and tests were performed using the software TNT 1.1 (Goloboff, Farris & Nixon, 2008)

freely available thanks to the Willi Hennig Association at <http://www.zmuk.dk/public/phylogeny>. These methods also allow us to test the hypothesis of the presence of a phylogenetic constraint in the evolution of mandible shape and size. To analyse the correlation between discrete variables (diet and shape optimization) and centroid size and body mass, we counted the number of times that these variables change in the same branch in all branches that show some change in any of them. The significance of this correlation was tested by permuting the changes of each character on the branches 10 000 times, and counting every time the number of cases where the two characters change in the same branch. This way of testing correlations has a drawback: it does not take into account a delayed response of one variable against the other (the change in one variable occurs in nodes below the change of the other), and thus it is a conservative way of comparing the correlation of the optimization of each variable. As there is no implemented method to correlate shape and size in a cladistic manner (i.e. correlating shape and size optimizations; see Giannini & Goloboff, 2010), we think that this is a first approximation to test the presence of allometry with this approach.

RESULTS

SHAPE ANALYSIS

The first relative warp (RW1) explained 44.06% of the total variance, and showed toward one extreme of the axis a short and extremely robust mandible, low-placed condyles (at the level of the alveolar margin), the anterior border of the masseteric fossa displaced forwardly (almost in line with the posterior end of the carnassial), longer carnassial trigonid, and large canines (Figs 2A, B, 3A, B). The shortening of the corpus occurred mostly in its anterior half, between the carnassial and the canine. On the other extreme of the axis were opposite morphologies (e.g. longer and slender corpus, higher condyles, anterior border of the masseteric fossa posteriorly displaced, shorter carnassial trigonid, and smaller canine; Figs 2, 3).

RW2 explained 15.47% of the variance, and specimens with positive scores had a posteriorly inclined coronoid process, a straight corpus, and a smaller anteriorly positioned carnassial with a shorter talonid (Figs 2, 3). Negative scores were correlated with a more vertical coronoid process, a bowed corpus, a posteriorly extended condyle, and larger carnassial, posteriorly displaced and with a longer talonid (Figs 2A, B, 3A, B).

RW3 (12.71% of the explained variance) is related to changes in the carnassials, with specimens in one extremity possessing a backward positioned

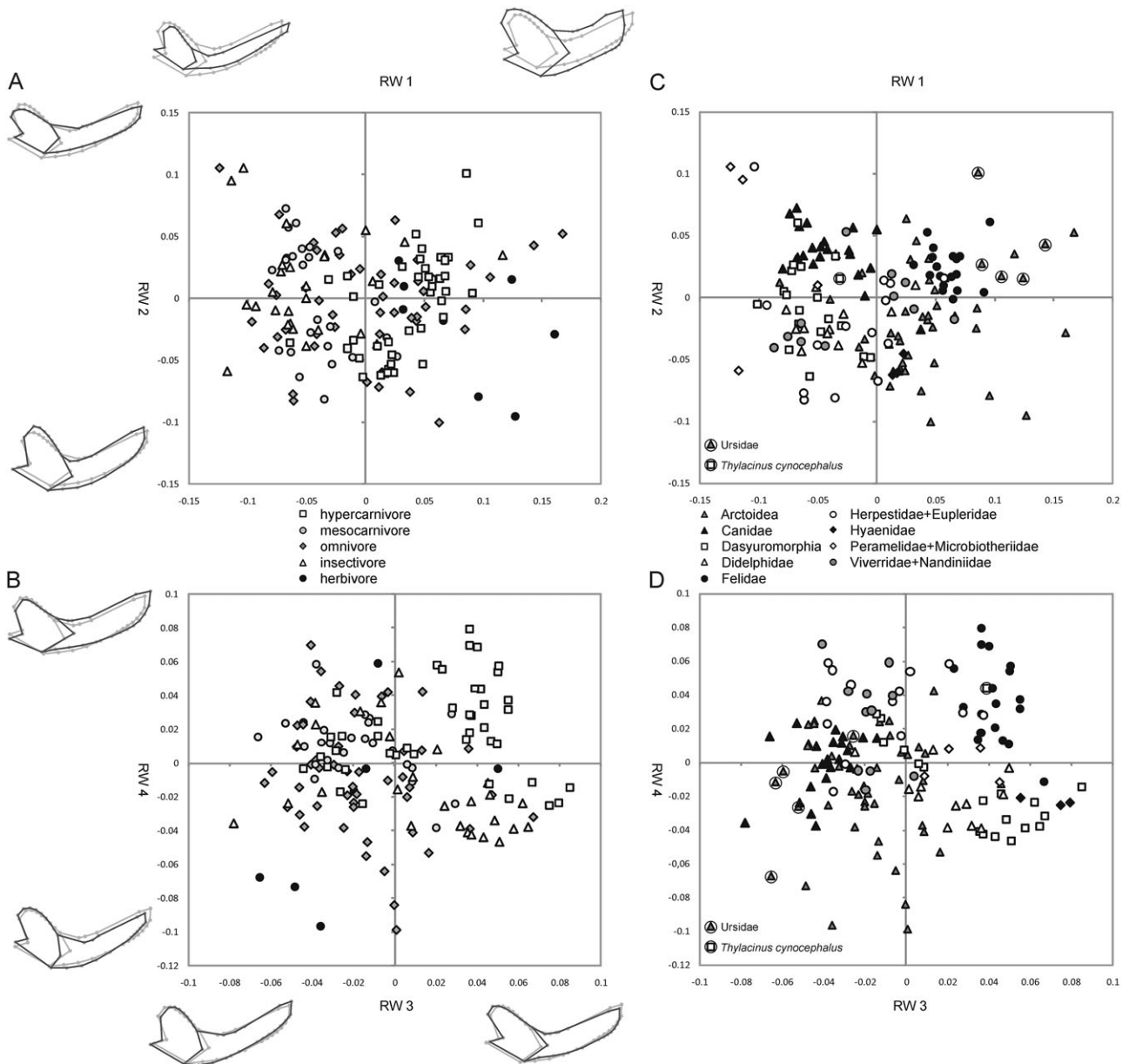


Figure 2. Mandible shape variation along the first four relative warps (RW). A, relative warp 1 versus 2, showing the distribution of diet classes; B, relative warp 3 versus 4, showing the distribution of diet classes; C, relative warp 1 versus 2, showing the distribution of taxonomic groups; D, relative warp 3 versus 4, showing the distribution of taxonomic groups. Shape reconstructions show the extreme shape of each RW in black lines against the consensus shape in grey lines.

carnassial with an extremely reduced talonid, low corpus below and posterior to the carnassial, and a straight and higher coronoid process that is posteriorly inclined (Figs 2, 3). Those in the other extremity of the axis bear mandibles with higher corpus, the carnassial anteriorly displaced with a long talonid, and lower and wider coronoid process.

RW4 explained 8.31% of the total variance, and separated in one extremity of the axis specimens with

small coronoid process, carnassial with a small talonid and a large trigonid that was caudally placed, the masseteric fossa anteriorly displaced, a large canine, a thick anterior half of the corpus, and a low positioned condyle (Fig. 2). In the other extremity of the RW4 axis were species with a very tall and narrow coronoid process, a very high condyle, carnassial with a small trigonid and a large talonid placed anteriorly, a small canine, the masseteric fossa

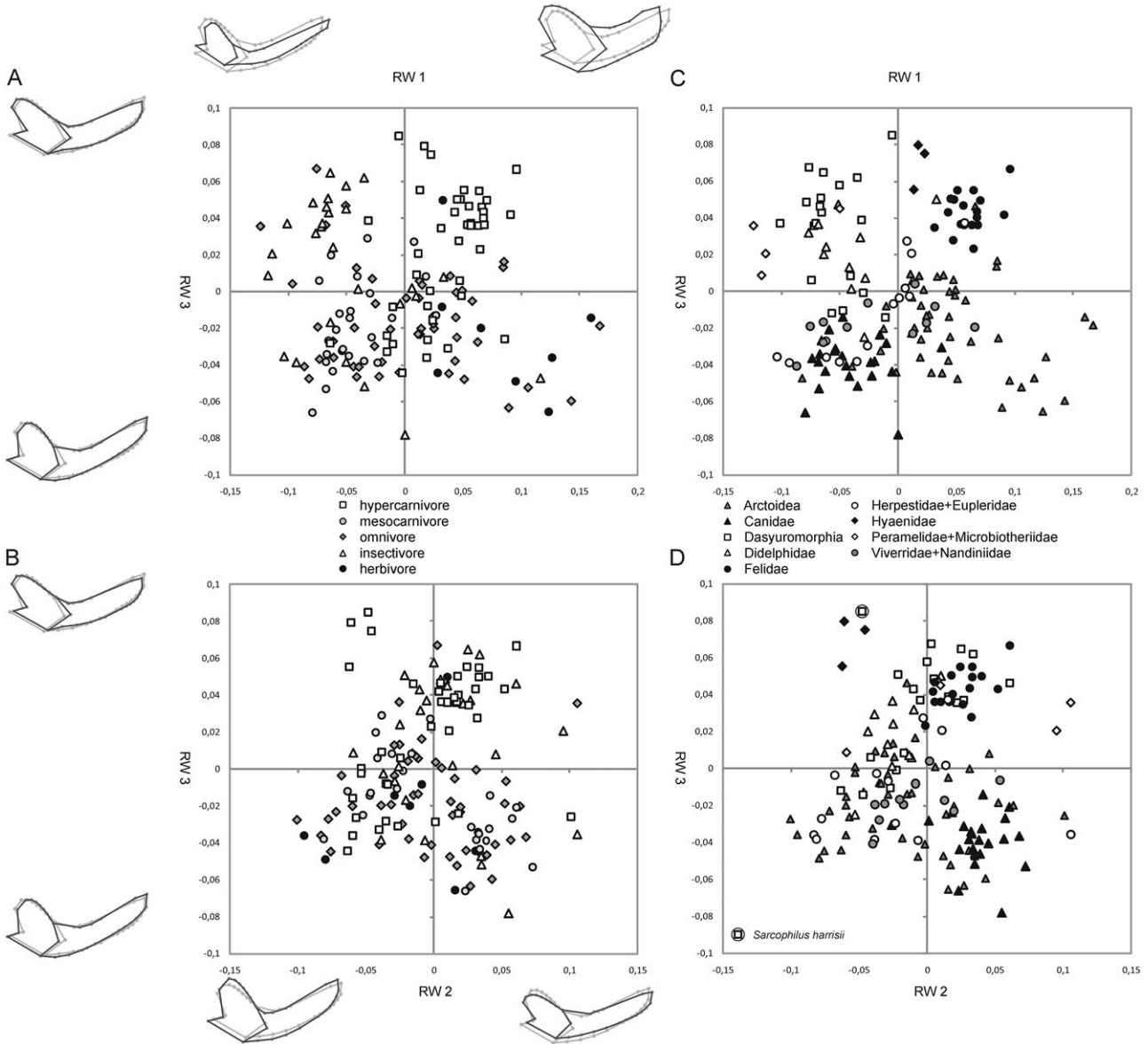


Figure 3. Mandible shape variation along the first three relative warps (RW). A, relative warp 1 versus 3 showing the distribution of diet classes; B, relative warp 2 versus 3 showing the distribution of diet classes; C, relative warp 1 versus 3, showing the distribution of taxonomic groups; D, relative warp 2 versus 3, showing the distribution of taxonomic groups. Shape reconstructions show the extreme shape of each RW in black lines against the consensus shape in grey lines.

displaced caudally, and a thick posterior half of the corpus, but with a relatively weaker and tapered anterior half (Fig. 2).

The graphs plotting RW1–2 and 3–4 (Figs 2A, B, 3A, B) did not show a clear separation of each diet category, but most hypercarnivores tended to be concentrated in the upper right quadrant of the RW3–4 graph (Fig. 2B), and some herbivores were separated in the extremity of the lower-left quadrant of the RW3–4 graph and on the lower right of the RW1–2

graph (Fig. 2A). The main clades of Carnivora and marsupials overlapped widely, but most of them were clustered in specific areas of the graphs: marsupials on the negative scores of RW1 (Fig. 2C); Felidae on the upper-right quadrant of the RW1–2 graph (Fig. 2C) and the upper-right border of RW3–4 (Fig. 2D); Ursidae on the upper-right quadrant of the RW1–2 graph and negative scores on RW3; Herpestidae with positive scores on RW4; Hyaenidae with negative scores on RW2 and positive scores of RW4;

Table 2. Percentage of posterior reclassification, with cross-validation, of the discriminant functions

Function	Total	Groups				
		He	Hy	In	Me	Om
Whole sample – Diet	58.28	62.5	73.81	55.56	72.00	38.75
Marsupialia – Diet	71.43	–	0.00	75.00	77.78	77.78
Carnivora – Diet	47.83	71.43	67.5	18.18	62.5	26.83
Marsupialia vs. Carnivora	99.34	M	C			
		100.00	99.13			
Marsupialia – Taxonomy	87.5	Da	Di	Pe		
		94.44	91.67	0		
Feliformia – Caniformia	92.17	Fe	Ca			
		92.17	94.20			
Caniformia – Taxonomy	63.23	Can	Mep	Mu	Pro	Urs
		95.65	33.33	37.5	42.86	63.24
Feliformia – Taxonomy	82.22	Eu	Fel	Herp	Hya	Viv
		40.00	100.00	66.67	100.00	80.00

He, herbivores; Hy, hypercarnivores; In, insectivores; Me, mesocarnivores; Om, omnivores; M, Marsupialia; C, Carnivora; Da, Dasyuromorphia; Di, Didelphimorphia; Pe, Peramelemorphia; Fe, Feliformia; Ca, Caniformia; Can, Canidae; Mep, Mephitidae; Mu, Mustelidae; Pro, Procyonidae; Urs, Ursidae; Eu, Eupleridae; Fel, Felidae; Herp, Herpestidae; Hya, Hyaenidae; Viv, Viverridae.

Canidae on the upper-left quadrant of the RW1–2 graph, and negative scores on RW3 (Fig. 2C, D). *Thylacinus* fell within the space occupied by canids in the RW1–2 graph, and *Dasyurus* with viverrids and herpestids, but other clades were also placed in these regions of the graph (Fig. 2C).

When combining RW1–3 and RW2–3, some interesting distributions could be observed. For example, the separation among marsupials and carnivorans is clear in the RW1–3 graph (Fig. 3C), in which marsupials fell mostly in the upper-left quadrant, with more slender and longer corpus, posteriorly placed carnassial, a higher and more rectangular, posteriorly inclined coronoid process, and a higher condyle (Fig. 3C). In this graph, bears occupied the opposite position (lower-right quadrant) with a short and thick corpus, a low condyle, the carnassial anteriorly displaced with a large talonid, and a more vertical and squared coronoid process (Fig. 3C). By contrast, *Sarcophilus* and hyaenids were at the upper-left extreme of the RW2–3 graph, sharing a posterior displacement of the carnassial with a small talonid, and an anterior position of the masseteric fossa (Fig. 3D).

DIETARY AND TAXONOMIC SEPARATION

A significant discrimination pattern was obtained between dietary groups (Wilks' lambda = 0.25, $F = 8.53$, $P < 0.00001$; Table 2), but the correct reclassification rate was relatively low (58.28%). The function gave a moderate separation of hypercarnivores and mesocarnivores, followed by herbivores (Table 2).

Most groups overlapped widely on the canonical axes, but hypercarnivores tended to be separated in the first axis, herbivores in the second axis, and mesocarnivores and insectivores in the third axis (Fig. 4). Hypercarnivores tend to have an anteriorly displaced masseteric fossa reaching the posterior border of the carnassial, a reduction of the talonid of the carnassials, and a thick mandible corpus. Herbivores presented a thick corpus with a strong subangular lobule, a high condyle, a very tall coronoid process, a large canine, an anteriorly displaced carnassial, and a very large talonid. Mesocarnivores, insectivores, and omnivores were very similar to the consensus shape, but the first group had a longer and slender mandible corpus and the second group showed an opposite tendency (Fig. 4).

When performing separate diet analyses for carnivores and marsupials, we obtained similar results for the first group (Wilks' lambda = 0.25, $F = 7.47$, $P < 0.00001$; RC = 47.83; Table 2). Marsupials were better discriminated through their diets (Wilks' lambda = 0.05, $F = 6.32$, $P < 0.001$; RC = 71.43; Table 2), and the three diets included had more than 70% of CV (Table 2). Herbivores were not included in the discriminate function because of its low sample size (one species). These functions mainly separated hypercarnivore marsupials with a low condyle, an anteriorly displaced masseteric fossa, a robust and short mandible corpus, and a posteriorly placed carnassial with a large trigonid and a small talonid (Fig. 5), but this was not reflected in the CV (Table 2) because of the low sample size of this group (two

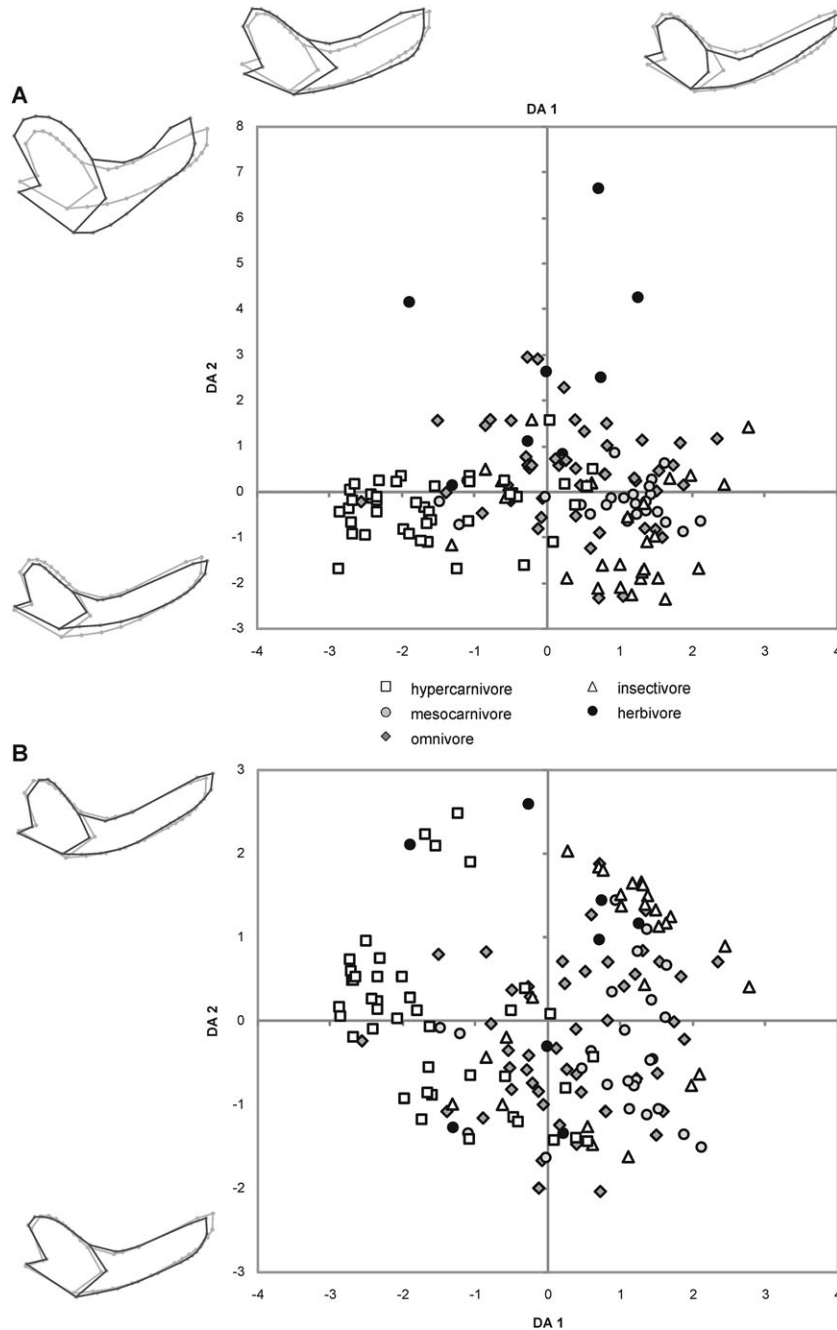


Figure 4. Canonical analysis of variance of diet classes. A, factor 1 versus 2; B: factor 1 versus 3. Shape reconstructions show the extreme shape of each RW in black lines against the consensus shape in grey lines.

species). Other categories also showed good separation (Fig. 5; Table 2).

Discriminant analysis and MANOVA detected significant differences between Carnivora and Marsupialia (Wilks' lambda = 0.06, $F = 47.84$, $P < 0.0001$). The classification matrix showed a perfect discrimination, resulting in 99.34% of the total specimens correctly reclassified. Marsupials had a straight corpus, the

carnassial molar and masseteric fossa posteriorly situated, a smaller carnassial, and a higher condyle than the consensus form. Mandibles of the placental carnivores presented the opposite trend (Fig. 6).

Among marsupials there was a good separation between the main three clades (Wilks' lambda = 0.04, $F = 6.73$, $P < 0.0001$, CV = 87.50). Didelphimorphia and Dasyuromorphia showed good separation, but not

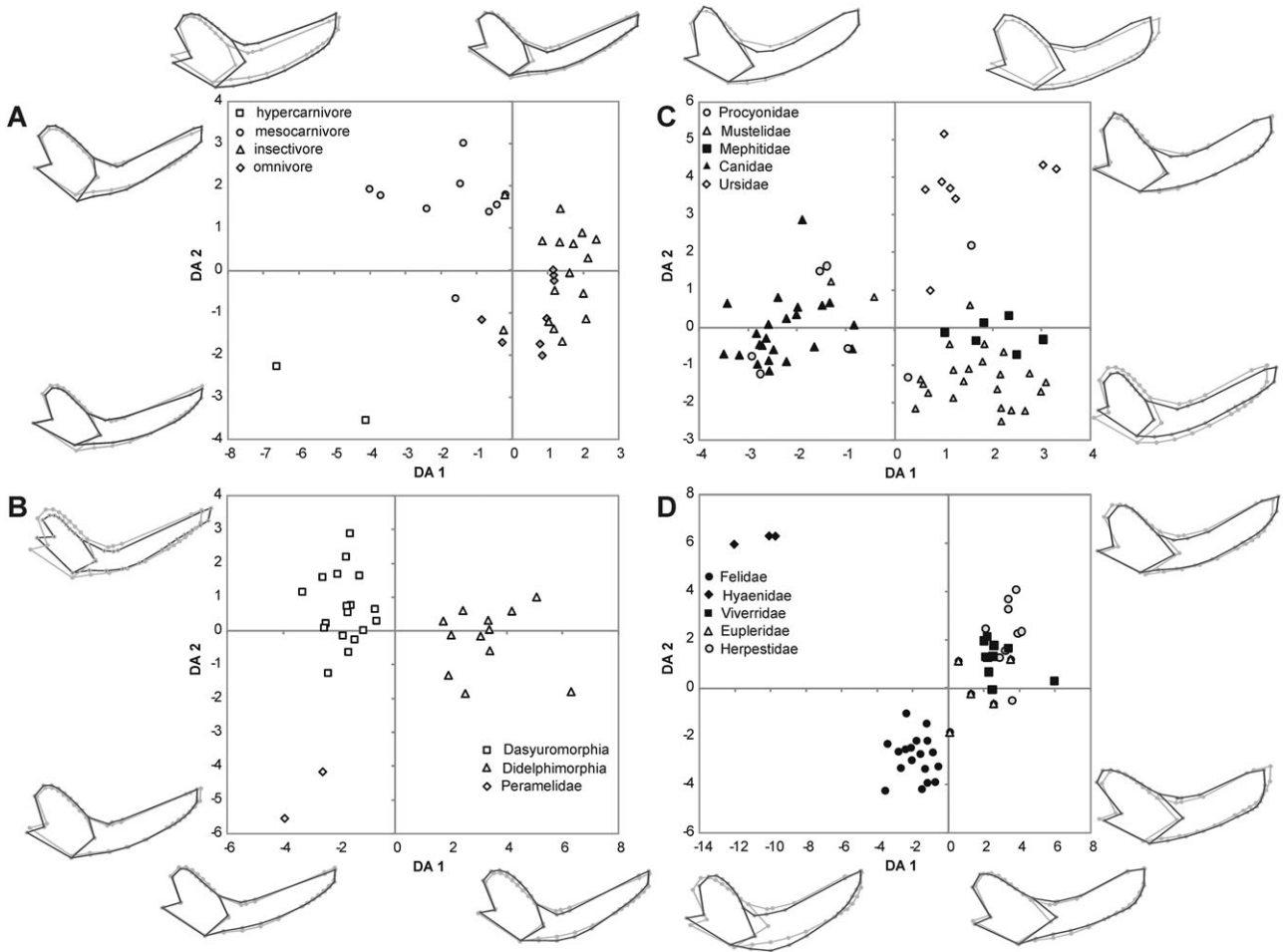


Figure 5. Canonical analysis of variance of taxonomic groups and diet classes. A, dietary discrimination in marsupials (factor 1 versus 2); B, discrimination of main Carnivora clades (factor 1 versus 2); C, discrimination of main Caniformia clades (factor 1 versus 2); D, discrimination of main Feliformia clades (factor 1 versus 2). Shape reconstructions show the extreme shape of each RW in black lines against the consensus shape in grey lines.

Peramelemorphia because of its low sample size (two species) (Table 2). Peramelemorphia had a long and slender corpus, a very high condyle, a very reduced coronoid process, and m1 with a reduced trigonid and an enlarged talonid (Fig. 5). Dasyurids had a more bowed corpus and a wider coronoid process with a more convex anterior border than Didelphimorphia.

Caniformia and Feliformia showed a good and significant separation (Wilks' lambda = 0.16, $F = 12.26$, $P < 0.0001$, CV = 94.20). Caniformia had a longer, slender mandible, a more posteriorly displaced masseteric fossa, a more vertical coronoid process, and a carnassial with a larger talonid and that is more anteriorly placed than in feliforms (Fig. 6; Table 2).

In Caniformia, the separation between families was also significant (Wilks' lambda = 0.03, $F = 18.35$, $P < 0.0001$, CV = 63.24). Canids and ursids showed good discrimination, but not the other families

(Table 2). Canids had a longer and slender corpus and a higher condyle, while ursids possessed a shorter and robust corpus, a lowered condyle, and a large and anteriorly placed carnassial (Fig. 5).

The families of Feliformia also showed a good, significant discrimination (Wilks' lambda = 0.003, $F = 15.7$, $P < 0.0001$, CV = 82.22). This function separated felids and hyaenids perfectly and gave a good discrimination of viverrids (Table 2). Felidae were separated because of their straight, short, and robust corpus, the long and posteriorly inclined coronoid process, the lowered condyle, the anteriorly displaced masseteric fossa, and the extreme reduction of the talonid in the carnassial. Hyaenids possessed a more curved corpus, with a very convex ventral border, a higher condyle, a more developed talonid in the m1, and a more vertical and shorter coronoid process (Fig. 5).

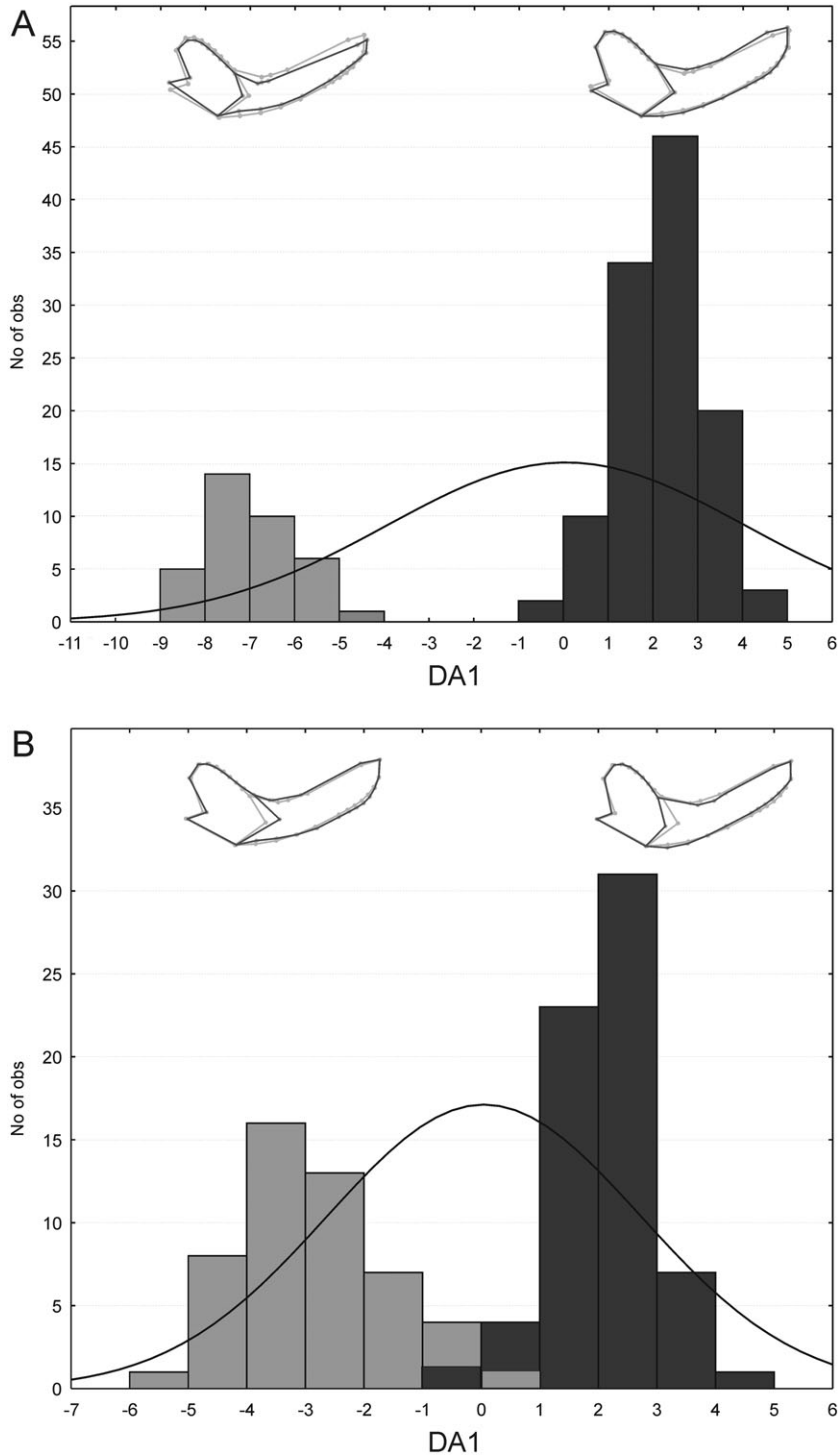


Figure 6. Canonical analysis of variance of taxonomic groups. A, Methateria (light grey) versus Carnivora (dark grey); B, Caniformia (dark grey) versus Feliformia (light grey).

SIZE VARIABILITY AND SHAPE DISPARITY

Members of the order Carnivora had more variability in centroid size than marsupials ($S^2 = 96\ 506.45$ versus $64\ 433.57$, respectively) with a higher median

($153\ 893.8$ versus $69\ 224.25$, respectively). These differences were highly significant ($P < 0.01$) under the Levene ($F = 7.32$) and Mann–Whitney ($U = 650$) tests, respectively. The permutation test also found a

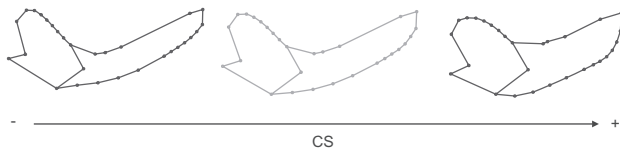


Figure 7. Allometric relationship between mandible shape and size. Consensus configuration is in the middle, shape of the largest species (*Ursus arctos*) to the left, and shape of the smallest species (*Planigale maculate*) to the right.

significant difference in variance ($P = 0.003$). There is a wide superposition of the range, but Carnivora reached higher values not occupied by any marsupial (maximum = 523.72 versus 397.75, respectively), while not reaching the lowest values seen in marsupials (minimum = 49.79 versus 22.59, respectively). Body mass showed the same pattern (data not shown), and was highly correlated with the centroid size (see below). Shape disparity was greater in Carnivora (MD = 0.0097) than in marsupials (MD = 0.0054), something that could be seen on the RW graphs (Figs 2, 3), and this difference was significant under the permutation test ($P < 0.0028$). Using the mean of each species and setting the permutation test to use the number of marsupial species, equalizing sample size between groups, gave the same results.

ALLOMETRY

The variation due to the allometric factor was significant under the Goodall ($F = 74.74$, $P < 0.0001$) and Resample ($P = 0.001$) tests, and explained a large proportion of the total variance (82%). Larger centroids were related to short and robust mandibles, a low and wide coronoid process, anteriorly displaced carnassials, and large canines (Fig. 7). Smaller centroids showed a tendency to correspond to long and slender mandibles, a high coronoid process, posteriorly displaced carnassials with a well-developed talonid, and small canines (Fig. 7). PGLS confirmed the existence of a significant allometric relationship and explained 71% of the total variance.

PHYLOGENY AND SHAPE OPTIMIZATION

The optimization of centroid size and body mass on the phylogeny takes 529.23 (CI = 0.09) and 118.06 steps (CI = 0.25), respectively, and were highly significant ($P = 0.00005$). In marsupials, the optimization of centroid size indicated a reduction of mandible size at the base of Didelphinae (node 222), Thylamyini (node 250), Dasyuridae (node 179), *Antechinus* (node 185), and Sminthopsini + Planigalini (node 178) and an

increase at the base of Didelphini (node 219), an inner node (243), *Dasyurus* + *Sarcophilus* + *Dasyuroides* (node 236), Peralimorphia (node 263), and *Dasyurus maculatus* + *D. viverrinus* + *D. geoffroyi* (node 240). In Carnivora, size decreases were detected in a clade of viverrids (*Hemigalus* + *Chrotogale*, node 223), South American foxes (*Lycalopex* spp., node 273), Mephitidae (node 229), *Melogale* plus other mustelids (node 172), an *Ictonyx* clade (nodes 258, 260) and the nodes of the *Lutra* + *Lutrogale* + *Amblyonyx* group (165, 166). An increase of centroid size occurred in Hyaenidae (node 231), pantherines (node 277), *Panthera* (node 289), Ursidae (node 160), *Ursus maritimus* + *U. arctos* (node 291), Canini (node 198), *Lycan* plus 'advanced' *Canis* (node 217), *Procyon* (node 289), and Lutrinae (node 169). Furthermore, there were many changes on the terminal branches (supporting Fig. S2). With few exceptions, the optimization of body size resulted in the same transformations, but it recorded increases at Caniformia (node 161) and the *Canis* clade (node 213) and decreases in Hesperetidae (node 202) and Procyonidae (node 207).

Diet optimization showed that there were several transformations (62 steps, CI = 0.06), while several internal nodes were ambiguous, especially the lower ones. However, the nodes of Hyaenidae and Felidae were recovered as hypercarnivores, Canidae as meso-carnivore, Arctoidea, Mephitidae, Procyonidae, and Mustelidae as omnivores, and most of the internal nodes of Dasyuromorphia as insectivores (except for the *Dasyuroides* + *Dasyurus* clade, which was meso-carnivore) (supporting Fig. S3).

The optimization of mandible shape on the phylogeny showed that most internal nodes had generalized shapes. The transformation of this character on the phylogeny required 15.06 steps to explain the shape observed in the terminal taxa. Due to the size of the tree, it is impossible to show the shape optimization in a figure, but the obtained optimization can be seen in supporting Fig. S4. We also present the main changes at internal nodes in Figure 8. Most of the extreme changes took place at terminal branches, which correspond to species or genera, especially the 'extreme' morphologies represented by some taxa (e.g. *Myrmecobius*, *Perameles*, *Caluromys*, *Ailuropoda*, *Ailurus*, *Potos*, *Arctictis*, *Eupleres*, *Speothos*, *Otocyon*, *Arctonyx*, and *Ehnydra*). The most common changes were the anterior or posterior displacement of the masseteric fossa and the carnassial, the shortening/lengthening of the mandible, the deepening of the corpus, the enlargement/reduction of the coronoid process, its change from a more posterior and curved process to a vertical and straighter one, and the change in the height of the condyle (supporting Fig. S4). The marsupial basal node (node 184) presented a long mandible with a posteriorly placed

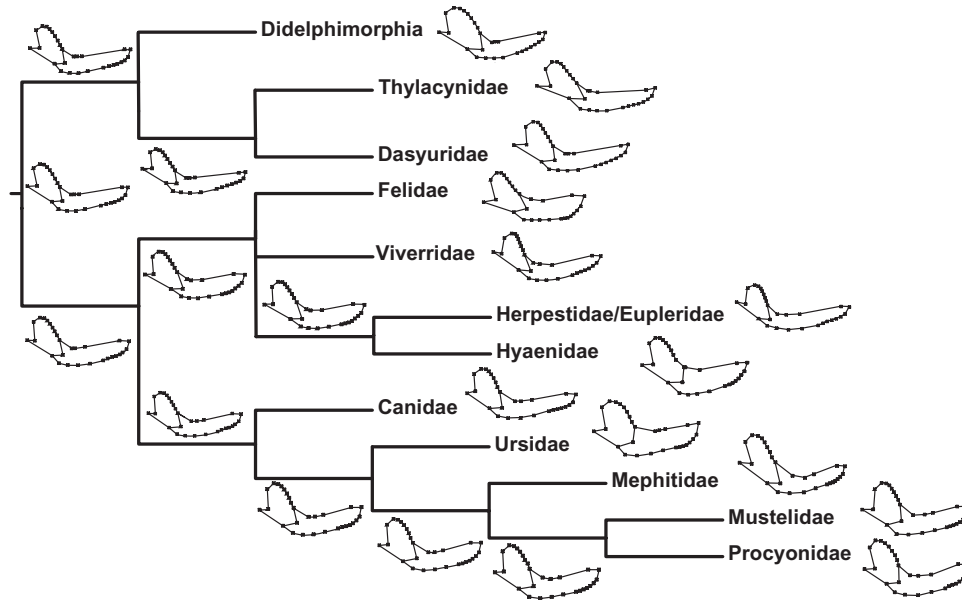


Figure 8. Simplified phylogeny showing the optimization of mandible shape on the main clades.

carnassial, a rectangular coronoid process that was posteriorly inclined, and a condyle that was above the alveolar margin of the corpus (Fig. 8; supporting Fig. S4). This pattern was the basic morphology reconstructed in the internal nodes of the marsupials, with few small changes in some of them. In the *Dasyurus* + *Sarcophilus* + *Dasyuroides* clade (node 236) there was a synapomorphic change that involves an anteroventral expansion of the masseteric fossa. *Sarcophilus* presented as autapomorphies a strengthening of the corpus and a distal displacement of the carnassial, while a lowering of the condyle (to the alveolar level), a change to a wider coronoid process, and a strong anterior expansion of the masseteric fossa occurred in *Thylacinus* (supporting Fig. S4).

The Carnivora node (159) had members with a large carnassial and a longer, more anteriorly placed trigonid, changes that were recorded as synapomorphies for the order (supporting Fig. S4). Feliformia (node 158) had an anterior displacement of the masseteric fossa as a derived change, Hyaenidae (node 230) showed a marked deepness of the mandible corpus (specially in its posterior half) and an enlargement of the canine, and Felidae (node 156) presented an enlargement of the canine, an extreme reduction of the carnassial talonid, a lowering of the condyle, and a deepness of the anterior part of the mandible corpus (supporting Fig. S4).

Caniformia (node 162) presented a derived anterior shifting of the carnassials, while Canidae (node 199) had a long and slender corpus, a posterior displacement of the anterior border of the masseteric fossa, and a reduction of the coronoid process (supporting

Fig. S4). The sister clade of Canidae, Arctoidea (node 161), presented a shortening of the mandible and a higher mandible corpus at its caudal half as synapomorphies. Ursidae (node 160) had a short and thick corpus, an anteriorly placed carnassial (especially on node 255, *Tremarctos* + Ursinae), a very convex anterior border of the coronoid process, and a large canine.

The RW analyses including the ancestral shape configurations gave similar results to those obtained only with living taxa, but also showed that most of the ancestral shapes were contained in the space delimited by living relatives (supporting Fig. S5). The Eupleridae node was the nearest to the consensus shape in the RW1–2 graph, followed by the Carnivora, Feliformia, Herpestidae, and Viverridae nodes, while Viverridae was the closest to the Carnivora ancestral shape. Marsupials and Didelphidae are placed near the basal root of the tree.

Body mass and centroid size optimization were significantly related ($r = 0.44–0.70$, $P = 0.010$), but no significant association was found between these variables and shape, between these variables and diet, and between shape and diet ($P = 0.9999$).

DISCUSSION

MANDIBLE SHAPE: DIET, SIZE, AND CONVERGENCES

Our study, based on the largest sample in terms of species and specimens currently available, confirms the observations of early authors (see below). There is a clear relationship between diet groups and shape, especially for hypercarnivores and herbivores, which

share a shortening and strengthening of the mandible corpus (see Sacco & Van Valkenburgh, 2004; Meloro *et al.*, 2008; Figueirido *et al.*, 2009, 2010). The relationship between the presence of a thick corpus and these diet groups has been observed previously by different authors using different methodologies (e.g. Biknevičius & Ruff, 1992; Biknevičius & Van Valkenburgh, 1996; Sacco & Van Valkenburgh, 2004; Meloro *et al.*, 2008), and was also related to the presence of thick jaw muscles and bite force (Wroe, McHenry & Thomason, 2005; Christiansen & Wroe, 2007). Hypercarnivores differ from other groups by the presence of an anteriorly displaced masseteric fossa, a robust anterior portion of the corpus, a lower condyle, and a large, posteriorly placed carnassial, which possesses a reduced talonid and a long trigonid. This configuration of the mandible and the carnassial increases the effectiveness of meat consumption and prey capture through an increase of the mechanical advantage and the size of masseteric and temporal muscles (e.g. condyle position, masseteric fossa extension) and a combined enlargement of the shearing crests and reduction of crushing areas in the carnassial (e.g. Butler, 1946; Turnbull, 1970; Greaves, 1980; Radinsky, 1981a, b; Biknevičius & Van Valkenburgh, 1996; Astúa de Moraes *et al.*, 2000; Sacco & Van Valkenburgh, 2004; Meloro *et al.*, 2008; Hogue & ZiaShakeri, 2010). The reduction of the coronoid process could be related to a maximization of the jaw gape, especially during hunting and biting (e.g. Emerson & Radinsky, 1980; Akersten, 1985; Martin, 1989; Antón & Galobart, 1999; Sunquist & Sunquist, 2002; Antón *et al.*, 2004; Salesa *et al.*, 2005; Slater & Van Valkenburgh, 2008).

The difference of the strength of the corpus between herbivores and hypercarnivores could be explained by differences in the load pattern imposed by biting (Figueirido *et al.*, 2009). In hypercarnivores a high canine bite force is important to capture their prey, and it is related to a thick anterior part of the corpus. This pattern is typical of felids, the most numerous group with this morphology, because other hypercarnivores such as hyaenids and some canids present a different pattern of horizontal corpus shape, because they also exert strong bites with last premolars or postcarnassial molars, respectively (see Biknevičius & Ruff, 1992; Biknevičius & Van Valkenburgh, 1996; Therrien, 2005a, b). In herbivores, the strongest bite force is applied in the molars, which consequently leads to a reinforcement of the posterior portion of the corpus (Figs 2, 3; Figueirido *et al.*, 2009). Herbivores represent the opposite tendency to hypercarnivores in some features, having a large coronoid process, a higher condyle, and an anteriorly placed carnassial with a large talonid (Figs 2–5). This is related to an expansion of the crushing area and reduction of the

shearing crests of the molars (e.g. Van Valkenburgh, 1989), while the expansion of the posterior part of the corpus and the higher condyle increase the area of insertion of the masseteric muscle and maximize its mechanical advantage. The change in the coronoid process could be interpreted as an enlargement and increase of efficiency of the temporal muscle, which could be related to the use of anterior teeth (incisors, canines) during food processing or in agonistic confrontations. But it could also be a way to increase the bite force, and/or stabilize the bite at the carnassial, in mammals that lack or have less lateral movements in comparison with other herbivores (i.e. artiodactyls; cf. Ewer, 1973; Sacco & Van Valkenburgh, 2004; Figueirido *et al.*, 2009).

We also confirmed the convergence of some marsupials and carnivores with regard to some diet-related mandible characters (see above), as is the case for the bone-eaters hyenids and *Sarcophilus*, canids and *Thylacinus* (e.g. Werdelin, 1986, 1987; Biknevičius & Ruff, 1992; Jones, 2003; cf. Wroe & Milne, 2007; see above and Figs 2, 3). *Dasyurus* tended to be placed in the morphospace limited by herpestids and viverrids (Figs 2, 3), as was previously claimed by some authors (cf. Jones, 2003), but this area was also occupied by other carnivorans, indicating that they are convergent with a wide range of carnivores. Other cases of morphological convergences occurred in Carnivora between felids and *Cryptoprocta* and between some herbivore procyonids and ursids (*Ailuropoda* and *Potos*). This was also observed in the optimization of the mandible shape, in which several characters traditionally related to diet (e.g. anterior displacement of carnassial and masseteric fossa, position of condyle) showed numerous changes towards the same direction in different branches of the tree (supporting Fig. S4). The high level of homoplasy presented by mandible shape is congruent with the ecological component, common to marsupials and carnivores, detected in the skull shape by Wroe & Milne (2007). This is something that seems to be related to the adaptive (or aptative at least; see Gould & Vrba, 1982; Gould, 2002) value of the mandible shape at different evolutionary scales (see also Figueirido *et al.*, 2010).

Although we have detected an ecological component in mandible shape, the discrimination of diet groups is not as high. There is wide overlap between dietary groups in the RW and canonical analyses (Figs 2A–B, 3A–B, 4, 5A) and a low correct reclassification rate for the discriminant functions (CV below 66% with the total sample).

Size could be a confounding factor in the diet–shape relationship through the arising of allometric patterns. The multivariate regression confirmed the existence of allometry, with larger species having shorter and thick corpus (Fig. 7), even when the

phylogeny is contemplated with the use of PGLS. Our results agree with those of Meloro *et al.* (2008), who found significant relationships with and without taking phylogeny into account, but not with those of Figueirido *et al.* (2010), who found a non-significant relationship after controlling for phylogenetic effects. This could be related to differences in sample size and the taxonomic scope (the first work included 104 species and 270 specimens of living and fossil carnivores; the second, 23 species and 184 specimens of living caniforms) or to differences in methodologies used. The lack of a significant relationship between shape and size using optimizations could be generated by several factors. First, the correlation of the changes of two variables on a phylogeny is not the same as a correlation of two variables controlling the phylogenetic pattern (i.e. PGLS; see Giannini & Goloboff, 2010). Second, one possible problem of the method used in the present work is that we were not able to account for a delay in the response of shape to size changes (Giannini & Goloboff, 2010), something that could be tested in the future.

An issue directly related to body size is that there are many very small marsupials beyond the lower size limit of Carnivora (< 0.1 kg, see above). These cannot be scored as hypercarnivores or even mesocarnivores, because there are no potential vertebrate prey of a size that these tiny marsupials could hunt. Because they eat a large proportion of insects, they are coded as omnivores or insectivores using the proposed classification. Additionally, the use of discrete diet groups introduces some artefacts. First, these categories are not really discrete, but at best transitional ends (Van Valkenburgh, 1989; Van Valkenburgh & Koepfli, 1993), something that makes the classification of some species difficult, because they have intraspecific and/or seasonal variation of diet. Second, there is little information for some species, and thus their assignment to different diet groups is tentative. These factors contributed to a loss of information quality and could have acted against the recovery of the proper shape–diet relationship. Nevertheless, this is the only way to explore diet–shape relationships with a wide taxonomic sample, and these findings may be tested again in the future with more ecological information.

One interesting point is that we found a better relationship between mandible shape and diet in marsupials than in Carnivora, as found by Wroe & Milne (2007) in the skull of these mammals. Carnivora showed wider shape changes, but it is clear that a large proportion of this variance is not related to diet, but rather, at least in part, to phylogenetic patterns. This could be seen in the MANOVA/discriminant analyses and also in the optimization of mandible shape. In probability, a relevant proportion of the

‘extra’ variation of Carnivora mandible shape is related to constraints, as was suggested by Wroe & Milne (2007) for skull morphology.

As is discussed below, phylogeny is another factor present in the shape variation of these groups; moreover, ethological differences, such as hunting strategies, could introduce another confounding factor in the shape–function relationship (e.g. Van Valkenburgh & Koepfli, 1993; Sacco & Van Valkenburgh, 2004).

DISPARITY

As was established earlier with other methodologies, taxon sampling, and anatomical elements (e.g. Werdelin, 1987; Wroe & Milne, 2007; Cooper & Steppan, 2010), shape disparity and size variation is greater in Carnivora than in marsupials (Figs 2, 3). One interesting point is that marsupials occupy a lower body size range compared with Carnivora, but it is not clear why Carnivora did not invade this lower range (below 0.10 kg), which is occupied by a considerable diversity of marsupials in South America and Australia. One possibility is that other groups of mammals (e.g. ‘Insectivora’) filled this range of sizes in the continents where Carnivora evolved (mainly Eurasia, and also North America), precluding the evolution of very small species. The lower disparity of marsupials was explained as the result of a constraint in the dental eruption pattern of Metatheria (Werdelin, 1987), but also by differences in jaw musculature conditioned by a distinct relative brain size (Wroe & Milne, 2007). In this context, the origin of a different tooth replacement pattern, which allows the restriction of some parts of the dentition to specific uses (e.g. shearing, grinding) in Carnivora, constitutes an evolutionary novelty (one of the classical synapomorphies of this group) that probably caused their large diversification in terms of species, ecological types, and shapes. Other clades of carnivorous mammals (e.g. Creodonta and the marsupials discussed here) that do not have this novelty failed to achieve a similar diversification (Werdelin, 1987; Van Valkenburgh, 1999; Wroe & Milne, 2007). The diversity and disparity differences are clearly not an artefact of the sample size bias against marsupials (see above) or of the longer time of evolution in Carnivora, pointing to faster evolutionary rates in the placental clade. Carnivora is a natural group that has its origin in the early Cenozoic (Flynn *et al.*, 2005; Wesley-Hunt & Flynn, 2005), while the marsupials included here belong to four different large clades, two of them that became separated in the Mesozoic (Didelphimorphia, Microbiotheria), and the other two in the Palaeocene (Dasyuromorphia and Peramelimorphia; Goin, 2003; Kemp, 2005; Beck, 2008). If we take in

consideration the fossil record, we would have expected a greater difference with a larger disparity in Carnivora, because this group has more extinct morphotypes than the clades of marsupials studied here (see the taxa described in Van Valkenburgh, 1999, 2007; Wesley-Hunt & Flynn, 2005 for an example). Our findings contradict the findings of Goswami *et al.* (2011) who found a similar level of disparity in the skull of Carnivora and marsupial carnivores. This could be explained by a different ‘variability’ in skull versus lower mandible, because mandible is less constrained and more associated with food consumption and processing (see above). A wider study of the mandible that includes fossils is ongoing and will help to test if the inclusion of extinct taxa modified our findings.

PHYLOGENY

One factor that appears to affect the diet–mandible shape relationship is the phylogenetic signal present in the mandible. We corroborated the separation of different clades at different levels of the phylogeny (see above) as established by several authors (Radinsky, 1981a, b; Wroe & Milne, 2007; Meloro *et al.*, 2008; Figueirido *et al.*, 2010). Examples of the ‘taxonomic’ pattern was the clustering of some clades in the morphospace delimited by the RW graphs (Figs 2C, D, 3C, D) or their good discrimination obtained in the discriminant analysis–MANOVA (i.e. the distinction between placentals and marsupials, feliforms and caniforms, and of other families; Figs 5, 6). The only taxonomic groups that did not show consistent separation were Herpestidae, Eupleridae and Viverridae in Feliformia, and Mustelidae, Mephitidae and Procyonidae in Caniformia, taxa that include a large number of ‘generalized’ shapes (cf. Radinsky, 1981b; Andersson, 2005; Wroe & Milne, 2007). This ‘taxonomic’ pattern could also be observed in the shape optimization (Fig. 8; supporting Fig. S4), in which the ancestral shape reconstructed for each of the main clades was similar to that inferred by discriminant analyses (Figs 5, 6, 8; supporting Fig. S4). This indicates that despite the high homoplasy shown by this character, there is a phylogenetic signal in the shape of the mandible. In conjunction with the observed relationship between mandible shape and diet, it is clear that a large portion of the variation of the mandible is a ‘combination’ of ecological and phylogenetic factors. But the high homoplasy observed notwithstanding, mandible shape and diet sometimes possess a joint phylogenetic signal, as can be seen in felids. Felids have a hypercarnivorous diet and possess a short robust mandible with a large carnassial at its basal node (Fig. 8; supporting Fig. S4; see below). Something similar was seen in Ursidae,

Canidae, and other clades, which could be interpreted as clades originating with specific diet habits. This does not mean other changes may not occur in other directions (i.e. different diet) in any branch of these clades (e.g. origin of hypercarnivory in canids; see below).

The optimization of shape on the phylogenetic tree of the studied mammals allowed an exploration of its evolution and its relationship to other variables. The ancestral reconstructions obtained agreed with the traditional descriptions of these mammalian carnivores and recovered the appearance of highly derived morphologies in different parts of the tree (cf. Radinsky, 1981a, b, 1982; Van Valkenburgh, 1989, 1991, 2007; Werdelin, 1989, 1996; Figueirido *et al.*, 2010). We consider that with these new comparative methods (see Giannini & Goloboff, 2010; Goloboff & Catalano, 2011) shape can be analysed in the same way as other characters in the context of a cladistic study. This might allow us to explore the covariation of different continuous features (e.g. shape, size, bite force) directly on a phylogeny, without the need of decomposing it into a phylogenetic distance matrix or using other approaches (i.e. modelling the error in GLS analysis, or calculating ‘evolutionary contrasts’) in which ‘traditional’ comparative methods deal with phylogenetic information (Felsenstein, 1985; Harvey & Pagel, 1991; Diniz Filho, Sant’ Ana & Bini, 1998; Diniz Filho, 2000).

The general view obtained from the optimization is that functional aspects related to diet are a key factor in the evolution of carnivore mandible shape, something reflected in the high level of homoplasy (parallelisms) present in mandible shape, but that there is a phylogenetic pattern that is not possible to explain based on diet alone. This approach also allowed us to explore how certain morphologies are obtained, and in some cases showed that a similar condition, like the increased height of the corpus, is alternatively obtained by a ventral displacement of the ventral margin, a dorsal displacement of the alveolar margin, or a combination of both. Therefore, shape optimization could be useful to identifying different patterns of evolution in the shape of a structure. The obtained reconstructions for several basal nodes (especially the most basal one) are in fact artefacts imposed by the taxa included. In future, taxon sampling must be expanded to include fossils and other clades between Carnivora and Marsupialia allowing the hypothetical shape obtained here to be tested.

ACKNOWLEDGEMENTS

We thank the curators that helped during the visits to Museum Collections: Itatí Olivares, Diego Verzi, Ross

MacPhee, Bruce Patterson, Min-Tho Schulenberg, William Stanley, Linda Gordon, Walter Joyce, Valentina Segura, and David 'El Turko' Flores. Santiago Catalano and Norberto Giannini helped with the optimization of shape and the implementation of the Delcor analysis. Diego de Moraes and Fabio de A. Machado provided comments on an early version of the manuscript. Pieter Booth and Thiago Macek helped us with the English text. The American Museum of Natural History, the Field Museum of Natural History, and the Florida Museum of Natural History provided collection study grants to F.J.P. CONICET and FAPESP provided financial support. This is a contribution to the PIP 112 200801 01054.

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SUPPORTING INFORMATION

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

Table S1. Table with sampled species, taxonomic information, relative warp scores (RW), centroid size, body mass, and diet classification.

Fig. S1. Phylogenetic tree used in the optimization analyses. Node numbers are indicated.

Fig. S2. Centroid size optimization.

Fig. S3. Diet optimization.

Fig. S4. Mandible shape optimization. Landmark configuration (red lines and points) at the nodes and terminal branches represent the ancestral and the living species mandible shape. The blue lines indicate the derived changes from the ancestral position of a landmark to the position that they have in the branch (the point of the red line mandible configuration).

Fig. S5. Mandible shape variation along the first three relative warps (RW) showing taxonomic groups and the ancestral shape for each node of the tree in Fig. S1. A, relative warp one versus two; B, relative warp three versus four.

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