ORIGINAL PAPER

CrossMark

Evolution of the Carnassial in Living Mammalian Carnivores (Carnivora, Didelphimorphia, Dasyuromorphia): Diet, Phylogeny, and Allometry

Sergio D. Tarquini [1] · M. Amelia Chemisquy [1,2] · Francisco J. Prevosti [1,2]

Abstract
Different living mammals have developed a carnivorous habit (e.g., Carnivora, Dasyuridae, Thylacinidae, some Didelphidae). They exhibit different specializations for carnivory; however, they share some characters such as a carnassial molar. Previous studies have correlated the shape of molars with diet using morphometric indices or surface scans. In this work, we used 3D geometric morphometrics to explore the shape of the lower carnassials of 235 specimens corresponding to 71 extant species of Carnivora and six extant species of Marsupialia, both Didelphimorphia and Dasyuromorphia. We statistically estimated the effect of size, diet, and phylogeny on molar shape. All the analyses indicated a higher correlation between diet and molar shape, and a better correlation between molar shape and the position of each species on the phylogeny. Therefore, if we take into account the phylogenetic pattern, we can use molar morphology to infer diet of fossil species. Finally, this work evaluates for the first time, in a quantitative way, which of the lower molars of the Metatheria (m3 or m4) is the best analogue to the m1 of Carnivora; our results indicated the m4 is the best analogue.

Keywords Canonical phylogenetic ordination · Diet classification · Dietary proxies · Evolutionary constraints · Geometric morphometrics

Introduction

Carnivorous animals are considered an important component of ecosystems; in fact some authors have proposed that predators are regulators of herbivore biomass (Hairston et al. 1960). Within living mammals, different taxa have developed a carnivorous diet: within both Placentalia (e.g., some members of Carnivora and Cetacea; Flynn and Wesley-Hunt 2005) and Marsupialia (e.g., Dasyuridae, Thylacinidae, and some members of Didelphidae; Jones 2003; Goin et al. 2016).

✉ Sergio D. Tarquini
starquini92@gmail.com

1 Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR – Provincia de La Rioja, UNLAR, SEGEMAR, UNCa, CONICET), Entre Ríos y Mendoza s/n (5301), Anillaco, La Rioja, Argentina

2 Departamento de Ciencias Exactas, Fisicas y Naturales, Universidad Nacional de la Rioja (UNLaR), Av Luis M. de la Fuente s/n (5300), La Rioja, La Rioja, Argentina

Associated with this dietary habit, we can find different morphological specializations in the dentition, jaw morphology, senses, and musculature, among others (e.g., Savage 1977; Werdelin 1987; Biknevicius and Van Valkenburgh 1996; Van Valkenburgh 2007). In terrestrial carnivorous mammals, the molars are used to process meat, functioning as cutting and grinding tools (Van Valkenburgh 1989). The anterior half of the lower molar, the trigonid, equipped with a cutting blade (the paracristid connecting the paraconid to the protoconid), cuts when contacting the metacrista of the upper molar; whereas the posterior half, the talonid, acts as grinding platform when contacting the protocone of the upper molar (Biknevicius and Van Valkenburgh 1996; Evans and Sanson 2006). However, there is great variation in tooth morphology between species, which is at least partly related to dietary habits (e.g., Goin et al. 1992; Hogue and Ziashakeri 2010; Ungar 2010).

Most carnivorous placental mammals are grouped into the Order Carnivora. Carnivorans are equipped with a distinctive P4/m1 carnassial pair, named the carnassial shear, restricted to this tooth locus only, which distinguishes this clade from other groups of Mammalia (Van Valkenburgh 1989; Ungar 2010). Nevertheless, this is a plesiomorphic character for Carnivora, which is present in all carnivoramorphans (i.e., Carnivora, "Miacidae," and Viverravidae; Flynn and Wesley-Hunt 2005).

The present success of Carnivora is owing, to a large extent, to the evolutionary versatility related to this dental specialization (Butler 1946; Werdelin 1987; Van Valkenburgh 1989, 2007); that is, we can find a gradient from the more carnivorous species with bladelike carnassials (e.g., felids) to the least carnivorous species with generalized molars (e.g., bears; Ewer 1973; Biknevicius and Van Valkenburgh 1996; Ungar 2010).

On the other hand, within marsupials there are some clades with mostly carnivorous species (i.e., Dasyuromorphia). Some species feed exclusively on vertebrate prey, such as the thylacine (*Thylacinus cynocephalus*), the Tasmanian devil (*Sarcophilus harrisii*), and the spotted-tailed quoll (*Dasyurus maculatus*), while others feed on arthropods, such as the little agile antechinus (*Antechinus agilis*) (Lee and Cockburn 1985; Jones 2003; Baker 2015). Their Neotropical counterparts are mostly generalist species; however, we can discern a continuum from basically frugivorous species (e.g., *Caluromys philander*) to mainly carnivorous ones (e.g., *Lutreolina crassicaudata*) (Lee and Cockburn 1985; Vieira and Astúa de Moraes 2003; Astúa 2015). Unlike placental carnivores, marsupials have molars with a similar morphological pattern (with the exception of the last upper molar), with differences in size and no specialization to an exclusive function such as slicing or grinding. Consequently, each marsupial molar retains a cutting blade and a grinding area in the lower molars, forming three pairs of carnassials (M1-M3/m2-m4; Savage 1977; Muizon and Lange-Badré 1997; Jones 2003). However, while three pairs of carnassials are present in adults, each pair has a preponderant function in different ontogenetic stages (i.e., M2/m3 in subadults and M3/m4 in adults; Werdelin 1987; van Nievelt and Smith 2005; Macedo et al. 2006; Ceotto et al. 2009; Forasiepi and Sánchez-Villagra 2014). This is related to this exceptional pattern of molar growth, given that every time a molar erupts, it is in an advantageous position of the jaw, optimizing bite force (i.e., average distance between the condyle and the canine; Werdelin 1987). Thus, the jaw grows at the posterior end of the ramus and a new molar erupts in this position, with the posteriormost molars the ones that occupy the most advantageous biomechanical position in adults, and usually are the largest molars (Butler 1946; Werdelin 1986, 1987). In view of the above, some authors (Werdelin 1986; Prevosti et al. 2012a) considered the m4 of marsupials as analogous to the carnassial of Carnivora (m1), while others (Jones 2003) considered both m3 and m4 to be important for shearing meat.

Traditional studies of tooth function have associated various quantitative measures of tooth shape (i.e., morphometric ratios or angles) with the degree of vertebrate flesh consumed by the animal (e.g., Crusafont-Pairó and Truyols-Santonja 1956; Kay 1975; Van Valkenburgh 1989; Goin et al. 1992; Popowics 2003; Evans et al. 2005; Meloro and Raia 2010; Asahara et al. 2016). In recent works, there are two major morphological approaches: one uses three-dimensional modeling to relate complexity of the molar surface with diet, taking into account the effects of occlusion and wear on molars (Evans et al. 2007; Smits and Evans 2012; Pineda-Munoz et al. 2017), while the other uses 2D geometric morphometric methods to analyze molar shape, digitalizing the entire mandible or just the molar (Meloro et al. 2008, 2015; Chemisquy et al. 2015; Magnus and Cáceres 2017; Echarri et al. 2017).

In spite of their morphological differences and the phylogenetic distance between them, Carnivora and Marsupialia are good examples for analyzing similarities in tooth shape due to ecological similarities (i.e., convergences and parallelisms; de Muizon and Lange-Badré 1997; Jones 2003; Prevosti et al. 2012a; Smits and Evans 2012; Asahara et al. 2016). In this study, we used 3D geometric morphometric methods and multivariate analyses to elucidate the relationship of the lower carnassial shape with diet and size in a phylogenetic framework, and to evaluate the existence of convergences and evolutionary constraints. Additionally, this study discusses the likelihood of the carnassial shape to represent a good proxy for inferring dietary habits in extinct predatory mammals.

Materials and Methods

Samples

We digitized the first lower molar (m1) of 217 specimens corresponding to 71 extant species of Carnivora and the third and fourth lower molars (m3 and m4) of 18 specimens corresponding to six extant species of Marsupialia, including both Didelphimorphia and Dasyuromorphia (Online Resource 1). Only adult specimens with fully erupted dentition were included, and we selected molars with little wear. To cover the range of morphological variation, we included six specimens per species, trying to sample an equal number of males and females, as well as from different provenances (see Online Resource 2: Sexual dimorphism for more detail). Because we analyzed in detail lower carnassial morphology, we did not include taxa with reduced dentition, homodont dentition, or those which have highly modified carnassials (e.g., *Myrmecobius fasciatus*, Pinnipedia, *Potos flavus*, *Proteles cristata*). Although we tried to cover most of the shape variation and taxonomic diversity of Carnivora and Marsupialia, some families were underrepresented (e.g., Dasyuridae, Herpestidae, and Viverridae) due to their limited representation in the collections that we could visit. In the case of Didelphimorphia, we only included the species with the largest molars (i.e., *Lutreolina*, *Didelphis*) because of the size limit in the precision of the available digitalizing arm (see Online Resource 2: Molar size limit for more detail).

Based on previous papers (Taylor 1986; Padial et al. 2002; Torre et al. 2003; Vieira and Astúa de Moraes 2003; Kruuk 2006; Dragoo 2009; Rosalino and Santos-Reis 2009; Sillero-Zubiri

2009; Sunquist and Sunquist 2009; Garshelis 2009; Goillot et al. 2009; Holekamp and Kolowski 2009; Kays 2009; Larivière and Jennings 2009; Baker 2015; Helgen and Veatch 2015), we classified the species according to their diet, following the classification proposed by Van Valkenburgh (1989) with minor modifications: Hypercarnivores —feed primarily on other vertebrates; Mesocarnivores —feed mainly on other vertebrates, but also plants and invertebrates; Omnivores —meat, plants, and invertebrates represent a similar proportion of the diet; Herbivores —feed mostly on plant material; Insectivores —feed mostly on insects; Piscivores —feed mostly on fish.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MLP, Museo de La Plata, La Plata; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciudad Autónoma de Buenos Aires; MNHN, Muséum National d'Histoire Naturelle, Paris.

Landmarks

Using a MicroScribe G2X digitizer (Immersion Corporation) together with the MicroScribe Utility Software V.6.0.2, we recorded nine landmarks (ldk) in three dimensions on different anatomical structures of the molar: paraconid (ldk 1), carnassial notch in the paracristid (ldk 2), protoconid (ldk 3), metaconid (ldk 4), hypoconid (ldk 6), entoconid (ldk 7), and the mesial and distal edges of trigonid and talonid (ldk 5, 8 and 9; Fig. 1). We also recorded a significant number of semi-landmarks to delimit the base of the crown (Fig. 1). The application Resample (Reddy et al. 2006) was used to resample and slide the semi–landmark coordinates, and to reduce the sample to ten semi–landmarks in total (Fig. 1; Perez et al. 2006). We tested all landmarks for repeatability (see Online Resource 2: Quantification of landmark error for more detail). In the case of species with molars with missing cusps, we proceeded as indicated by Klingenberg (2008) and Oxnard and O'Higgins (2009): if the metaconid was missing (ldk 4), we placed this landmark in the protoconid position; if the cusps of the talonid were missing (ldk 6 or 7), we placed these landmarks on the distal edge of the tooth (Fig. 1).

Shape Analyses of Molars of Marsupials

In the case of marsupials, we evaluated first if the morphology of m3 and m4 had significant differences. We aligned landmark configurations by performing a generalized Procrustes analysis (GPA; Goodall 1991; Rohlf 1999), and then performed a Procrustes ANOVA with re-sampling to take into account the small sample size; where the Procrustes coordinates were the dependent variables, and species and the number of molars were the independent variables (Goodall 1991; Anderson 2001; Adams and Collyer 2016). In order to incorporate the phylogenetic relationships, we performed a
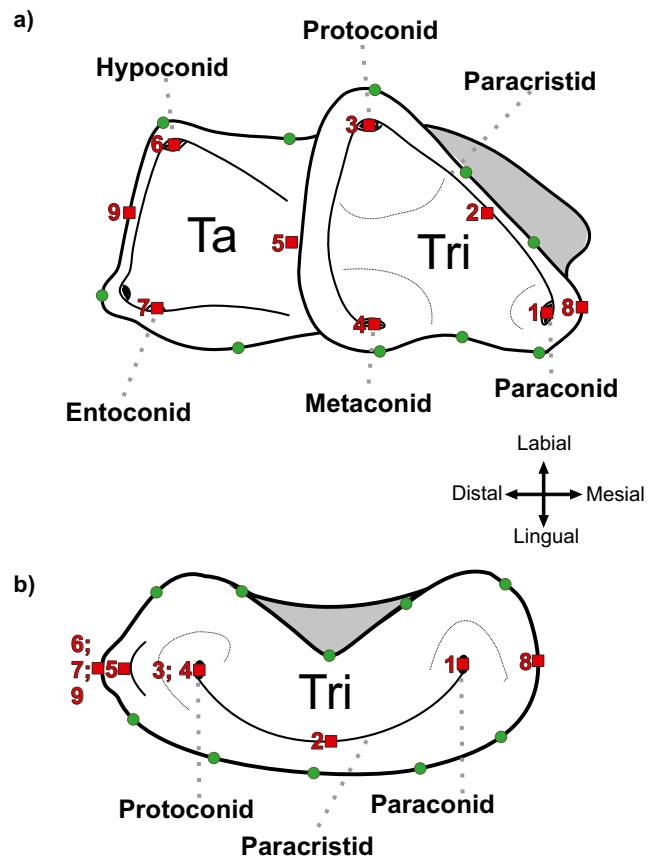
Fig. 1 Diagram of landmarks used in this study. Red squares, landmarks; green circles, semi-landmarks. Landmarks: 1) paraconid; 2) carnassial notch in the paracristid; 3) protoconid; 4) metaconid; 5) distal edge of trigonid; 6) hypoconid; 7) entoconid; 8) mesial edge of trigonid; 9) distal edge of talonid. **a**) Occlusal view of generalized molar (e.g., *Didelphis albiventris*), **b**) Occlusal view of reduced molar (e.g., *Panthera onca*)

phylogenetic ANOVA (Adams 2014a) with the same parameters as the previous analysis. The generalized Procrustes analysis, the Procrustes ANOVA, and the phylogenetic ANOVA were calculated using geomorph library (Adams et al. 2017) for the software R 3.1.3 (R Core Team 2015).

Finally, in order to determine which molar correlated best with the diet in marsupials and to quantify which molar was the best analogue to the m1 of Carnivora, we performed two last tests. In the first one, we put all the data (m1 of placentals and m3 and m4 of marsupials) in one morphospace and then estimated the average shape of the molars of the placentals in each dietary category. After that, we measured the Procrustes distances between the calculated averages and the molars of each marsupial of the same dietary category. In addition, we compared the measured Procrustes distances. For example, we took a specimen of *Didelphis albiventris*, which is recognized as an omnivorous species, and compared the Procrustes distance between its m4 and the average shape of omnivorous placentals and the Procrustes distance between its m3 and the average shape of omnivorous placentals. We tested if the differences between distances (m1-m3 vs. m1-m4) are

significant by using a permutations test (1000 runs). Procrustes distances and permutations test were calculated using geomorph library (Adams et al. 2017) for the software R 3.1.3 (R Core Team 2015).

In the second test, we evaluated the morphology of m3 and m4 separately, creating two datasets: all m1 of Carnivora plus m3 of Marsupialia (dataset m1 + m3); and all m1 of Carnivora plus m4 of Marsupialia (dataset m1 + m4). Then we performed a between–group PCA (bg-PCA) and a discriminant analysis (DA) with the scores of the bg-PCA. Although the problems of performing a DA with geometric morphometry data are known (Kemsley 1996; Sheets et al. 2006), most of these problems are reduced by first performing a bg-PCA (Mitteroecker and Bookstein 2011). Bg-PCA leads to a better group separation than the ordinary PCA by preserving the original Procrustes distances in the shape space, but avoids the overfitting achieved by the canonical variate analysis (Klingenberg and Monteiro 2005; Mitteroecker and Gunz 2009; Strauss 2010; Kovarovic et al. 2011; Mitteroecker and Bookstein 2011; Seetah et al. 2012). To consider the probability of correct random reclassification, we performed a cross-validated DA (Kovarovic et al. 2011). The discriminant power of the DA was estimated with the percentage of correct posterior reclassification (PCPR). Bg-PCA was performed using the software MorphoJ 1.06b (Klingenberg 2011) and discriminant analyses were performed using the MASS library (Venables and Ripley 2002) for the software R 3.1.3 (R Core Team 2015).

Shape and Statistical Analyses of Carnivorans and Marsupials

Using the dataset m1 + m3 and the dataset m1 + m4, we performed the following analyses. First, landmark configurations were aligned by performing a generalized Procrustes analysis (GPA; Goodall 1991; Rohlf 1999) and the distribution of the specimens in the shape space was analyzed by carrying out a Principal Component Analysis (PCA) of the Procrustes coordinates. Then, we ran a multivariate regression between log centroid size and Procrustes coordinates to test allometric relationships between size and shape. All analyses were done using the software MorphoJ 1.06b (Klingenberg 2011).

The relationship between tooth morphology and diet was explored using a bg-PCA, which projects the data onto the principal components of the group means (Mitteroecker and Bookstein 2011; Seetah et al. 2012). As we mentioned above, bg-PCA leads to a better group separation than the ordinary PCA given that it includes two steps: first, a PCA with the centroid of groups distributions (i.e., averaging the observations according to the dietary categories) and then, all data are projected on the principal components obtained (Mitteroecker and Bookstein 2011; Seetah et al.

2012). Bg-PCA was performed using the software MorphoJ 1.06b (Klingenberg 2011).

To complement the observations on the relationship between tooth morphology and phylogeny, we constructed a chronophylomorphospace by mapping a calibrated phylogeny onto the morphospace. The phylogenetic matrix was constructed from a combined phylogenetic tree, following the same procedures as in Prevosti et al. (2012a). The combined phylogenetic tree was built based on recently published phylogenies (Flores 2009; Eizirik et al. 2010; Eizirik 2012; Sato et al. 2012; Austin et al. 2013; Kutschera et al. 2014; Li et al. 2016; Westerman et al. 2016). First appearances (FAs) of species and minimum dates of internal nodes were taken either from the literature or the Paleobiology Database (http://paleodb.org) (Online Resource 3). With these data, we calibrated the phylogeny using the paleotree library (Bapst 2012) for the software R 3.1.3 (R Core Team 2015). Additionally, we calculated the K_{mult}, a multivariate generalization of the K statistic of Blomberg et al. (2003), to evaluate the phylogenetic signal in a dataset relative to what is expected under a Brownian motion model of evolution (Adams 2014b). The significance was tested by 1000 random permutations of the shape data among the tips of the phylogeny. Chronophylomorphospace and K_{mult} were estimated using geomorph and rgl libraries (Adams et al. 2017; Adler et al. 2017) for the software R 3.1.3 (R Core Team 2015).

To evaluate statistically the effect of phylogeny, size, and diet on the shape we used the Canonical Phylogenetic Ordination (CPO) method following Chemisquy et al. (2015). This method consists of the application of a redundancy or canonical correspondence analysis including phylogenetic information, as was proposed by Giannini (2003). This method allows us to analyze how much of the shape (a multidimensional variable) is explained by the factors mentioned above in a variance partitioning approach. With this method, it is also possible to measure how much of each factor explains shape, constraining the effect of other factors (i.e., how much of the carnassial shape variance is explained by diet without the contribution of phylogeny and/or size). For this method, we performed a Redundancy Analysis (RDA; Legendre and Legendre 1998) using shape (i.e., the landmark configurations of the aligned and averaged species) as the community matrix, and centroid size, diet, and phylogeny as constraints. Phylogenetic information was taken from the Matrix Representation using Parsimony of the tree (MRP), which consists of a binary matrix where the columns represent the membership of each taxon to a clade (see Giannini 2003). In order to discard collinear variables from the phylogeny, we used both Forward and Backward Stepwise Regression Analysis for reducing the number of nodes of the phylogeny and finding the model with lowest Akaike Information Criterion (AIC) value (Legendre and Legendre 1998; Godínez Domínguez and Freire 2003). The resampling of the data, the RDA analyses with their

significance, and the AIC estimations were performed using the software R 3.1.3 (R Core Team 2015) and its package vegan (Oksanen et al. 2015).

Bearing in mind that there are a lot of phylogenetic comparative methods, some authors proposed to analyze the same dataset using more than one method to avoid their limitations (Martins et al. 2002). Consequently, to complement the CPO, we ran a Phylogenetic ANOVA (or D-PGLS; Adams 2014a; Adams and Collyer 2016). This method performs a Procrustes ANOVA in a phylogenetic framework, describing patterns of shape variation and covariation for a set of Procrustes-aligned coordinates (Grafen 1989; Martins and Hansen 1997; Adams 2014a). Given that this method assumes a Brownian motion model of evolution, we included the calibrated phylogeny (Adams 2014a). For comparison, we also performed a non-phylogenetic evaluation using a Procrustes ANOVA (or GLS; Goodall 1991) following Adams (2014a). We found it interesting to compare methodologies that incorporate phylogenetic information in two different ways: Phylogenetic ANOVA as part of the error I and CPO as part of the model (Martins and Hansen 1997; Raia et al. 2010). Procrustes ANOVA and Phylogenetic ANOVA were performed using the geomorph library (Adams et al. 2017) for the software R 3.1.3 (R Core Team 2015).

The datasets generated during the current study are available from the corresponding author upon reasonable request.

Results

Shape Analyses of Molars of Marsupials

Procrustes ANOVA reveals a significant relationship between shape and number of molar (m3 or m4), i.e., the shape of the third molar differs from that of the fourth molar (Online Resource 4). In fact, when we include the phylogeny in the analysis, the correlation increases (from 11.50 to 42.63%; Online Resource 4). This means that the morphologies of m3 and m4 are different.

When we include all the molars in a sole dataset and measure the Procrustes distances between marsupial and carnivoran molars, we observe that the m4 of marsupials is the closest molar to the m1 of carnivorans in 93% of the cases (Online Resource 4). Procrustes distances between m1-m3 (0.25 in average) and between m1-m4 (0.22 in average) are significantly different (p-value = 0.0152; Online Resource 4). This high percentage would indicate that, in this context, the m4 of marsupials is a better analogue to the carnivoran m1, than the m3. Moreover, when we separate marsupial molars in two datasets (m1 + m3 and m1 + m4), we find similar results in both of them, with some differences in the PCA, the bg-PCA, and the RDA. However, when performing DA to quantify which of the two marsupial lower molars is the best analogue to the carnivoran m1, we observe that dataset m1 + m4

better reclassifies the diet of marsupials (dataset m1 + m3 erroneously reclassifies the diet of 12 of the 18 marsupials included, whereas in dataset m1 + m4 only two specimens were incorrectly reclassified; Online Resource 4). This is in concordance with the pattern of distribution in the PCA based on dataset m1 + m3, where marsupials are more displaced towards negative values of PC1 than the same marsupials in dataset m1 + m4 (Fig. 2 and Online Resources 4 and 5). Therefore, m4 is more modified than m3 (i.e., m4 has a higher protoconid, a smaller talonid, sometimes without entoconid). All this suggests that, for this sample of marsupials, the m4 morphology is a better proxy for their diet, and it is a better analogue to the carnivoran m1, than the m3. For this reason we show the results of the analysis with the dataset m1 + m4.

General Approach of the Relationship between Tooth Morphology and Diet

The first principal component (PC1) explains 55.78% of the total variance. Specimens at the positive end of PC1 have a molar with longer trigonid, without metaconid, with the paracristid parallel to the mesiodistal axis, and the talonid is reduced or absent (Fig. 2). On the negative end of PC1, specimens have molars with a shorter trigonid and a longer and wider talonid. The cusps of the trigonid and talonid of these specimens have a similar height, and the paracristid is oblique or even transversal to the mesiodistal axis (Fig. 2). PC2 explains 8.68% of the total variance. Specimens at the positive end of PC2 have wider molars, without an entoconid and with a short protoconid (Fig. 2). Specimens at the negative end of PC2 exhibit the opposite tendency (Fig. 2).

A clear pattern is found along PC1, from negative to positive values showing a continuum between herbivores, omnivores, mesocarnivores, and hypercarnivores (Fig. 3). Along PC2, these categories widely overlap and only piscivores are partially separated towards the positive values (Fig. 3). Hypercarnivores have mostly positive values for PC1, the most positive being the Felidae. Some other hypercarnivorous species (certain herpestids, mustelids, and canids) overlap along PC1 with mesocarnivores, and insectivores, and marginally with omnivores (Figs. 2 and 3). On the other hand, the hypercarnivorous ursid, *Ursus maritimus*, is placed in the morphospace near the rest of the bears, which is shared by herbivores, omnivores, mesocarnivores and insectivores. Most of the mesocarnivores possess negative values of PC1 (although close to zero), and only the mesocarnivorous hyaenas and dasyurids have positive values (Figs. 2 and 3). The remaining mesocarnivores (i.e., mesocarnivorous didelphids, viverrids, mustelids, and canids) share the morphospace with hypercarnivores, omnivores, and insectivores (Figs. 2 and 3). Omnivores have solely negative values in PC1 (Fig. 3). Omnivorous canids and didelphids overlap with mesocarnivores and insectivores; omnivorous mustelids overlap with hypercarnivores, mesocarnivores, and
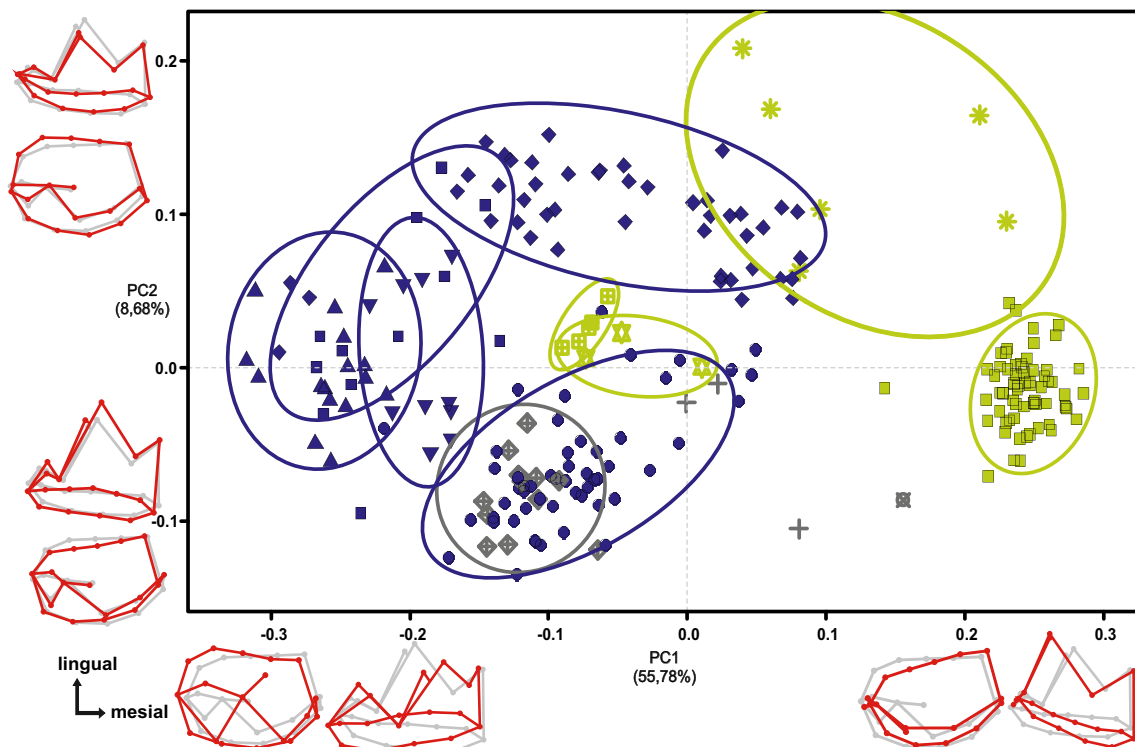
Fig. 2 Morphospace defined by the first two principal components (PC1 and PC2) from the PCA of dataset m1 + m4, showing the distribution of taxonomic groups. Change in molar morphology in occlusal and labial view, consensus shape (grey) and extreme shape of each PC (dark red). In dark blue are represented the Caniformia: ● Canidae, ■ Mephitidae, ◆ Mustelidae, ▲ Procyonidae, ▼ Ursidae; in dark grey, the Marsupialia: + Dasyuridae, ⊗ Thylacinidae, ◈ Didelphidae; and in light green, the Feliformia: ■ Felidae, ✩ Herpestidae, ✳ Hyaenidae, ⊞ Viverridae

piscivores; while omnivorous mephitids, procyonids, and ursids overlap with herbivores and piscivores (Figs. 2 and 3). Herbivores also have negative values along PC1. In particular, the herbivorous procyonids show the most extreme negative values, while herbivorous ursids are close to other bears, sharing the morphospace with herbivores, omnivores, mesocarnivores, and insectivores (Figs. 2 and 3). Insectivores are widely dispersed along PC1, thus overlapping with herbivorous, omnivorous, mesocarnivorous, and hypercarnivorous species (Fig. 3). Finally, piscivores (only represented by Lutrinae) are well grouped in the negative quadrant for the PC1 and positive for the PC2, marginally sharing the morphospace with mesocarnivores and omnivores (Fig. 3).

The bg-PCA does not provide any clear improvement of the results obtained by the PCA. It shows a similar distribution pattern among diet categories along the bg-PC1 (explaining 64.89% of the total variance; Fig. 4). Bg-PC2 explains 17.14% of the total variance, and piscivores are located on the positive end of PC2, separated from the remaining categories (Fig. 4). Bg-PC3 explains 10.69% of the total variance and separates insectivores towards the positive values, which are limited to a well-defined portion of the morphospace, although they have similar values to some omnivores and mesocarnivores (Fig. 5). Finally, bg-PC4 explains 6.59% of the total variance and discriminates the hypercarnivores, with negative values (except for the hypercarnivorous canids and

ursids), from the mesocarnivores with positive values (except for the mesocarnivorous hyaenids) (Fig. 5).

General Approach of the Relationship between Tooth Morphology and Phylogeny

When the taxonomy of the studied specimens is taken into account into the PCA (Figs. 2 and 6), the plot shows how the different taxa occupy different areas of the morphospace. Some of them are superimposed, and others do not overlap with other groups. For example, the Caniformia tend to be separated on PC1 from the Feliformia (Fig. 2). Within the taxonomic groups, it is possible to observe certain order according to diet. For example, in hyaenas, *Crocuta crocuta* (with hypercarnivorous habits) has higher positive values than *Hyaena hyaena* (with mesocarnivorous habits, Fig. 6). Moreover, at a higher taxonomic level it is noteworthy that bone-crushing hyaenas (higher positive values of PC2) are well discriminated from meat-slicing felids (lesser and negative values of PC2) among Feliformia (Figs. 2 and 6). Among Caniformia, in turn, canids exhibit negative values of PC2, with higher and sharper carnassials than mustelids (higher positive values of PC2). Also, marsupials occupy a middle position along PC1, but Dasyuromorphia has higher values than Didelphidae (Fig. 2). Even if we incorporate time and include phylogenetic relationships, we can observe better the
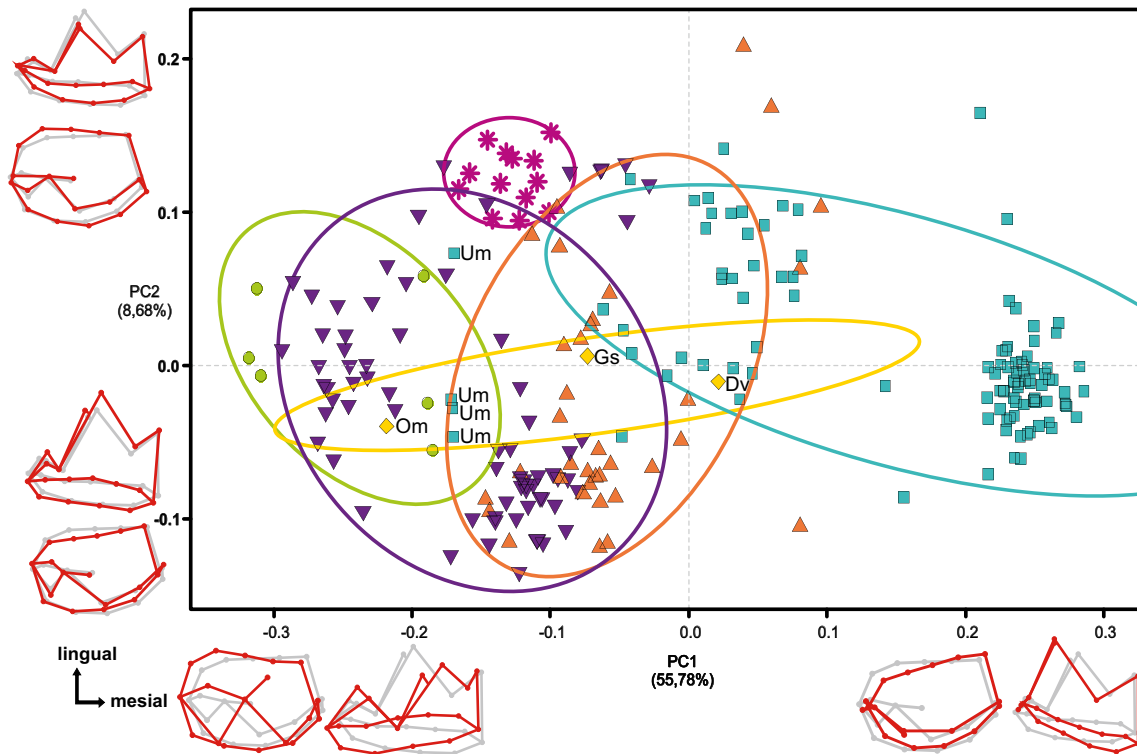
Fig. 3 Morphospace defined by the first two principal components (PC1 and PC2) from the PCA of dataset m1 + m4, showing the distribution of dietary groups. Change in molar morphology in occlusal and labial view, consensus shape (grey) and extreme shape of each PC (dark red). 🟢 Herbivore; 🟦 Hypercarnivore; 🔶 Insectivore; 🔺 Mesocarnivore; 🔻 Omnivore; ✳️ Piscivore. Abbreviations: Dv, *Dasyurus viverrinus*; Gs, *Galerella sanguinea*; Om, *Otocyon megalotis*; Um, *Ursus maritimus*
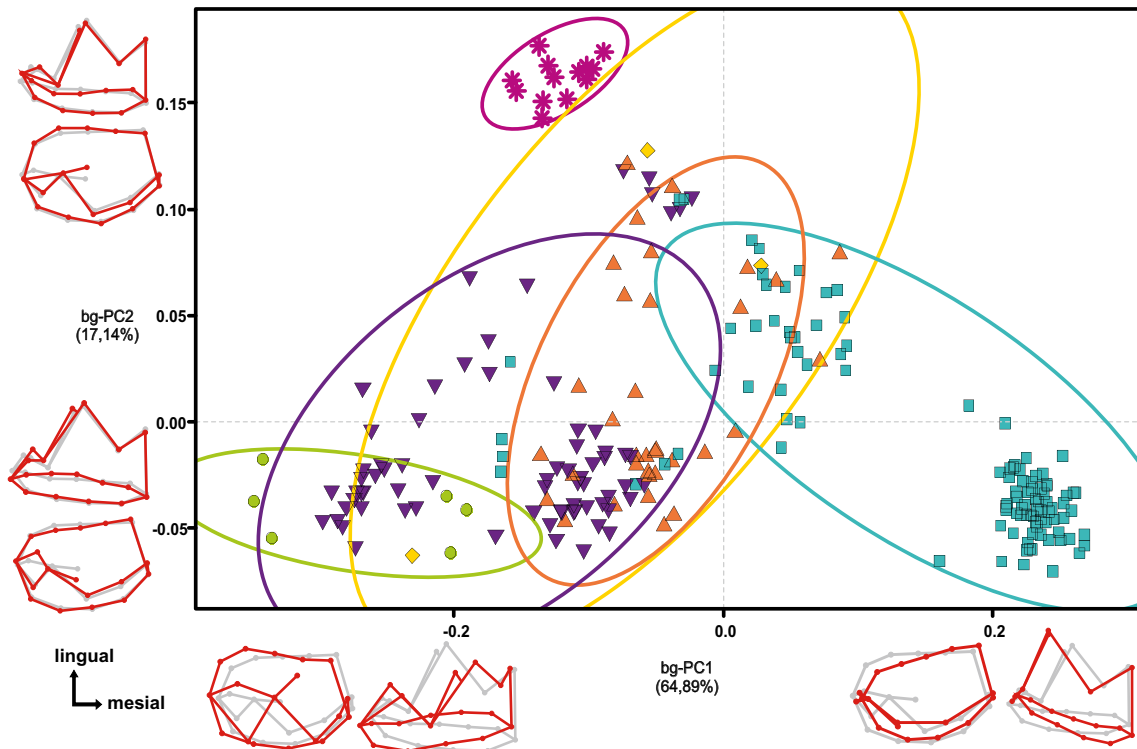

Fig. 4 Morphospace defined by the first two principal components (bg-PC1 and bg-PC2) from the bg-PCA of dataset m1 + m4, showing the distribution of dietary groups. Change in molar morphology in occlusal and labial view, consensus shape (grey) and extreme shape of each PC (dark red). 🟢 Herbivore; 🟦 Hypercarnivore; 🔶 Insectivore; 🔺 Mesocarnivore; 🔻 Omnivore; ✳️ Piscivore
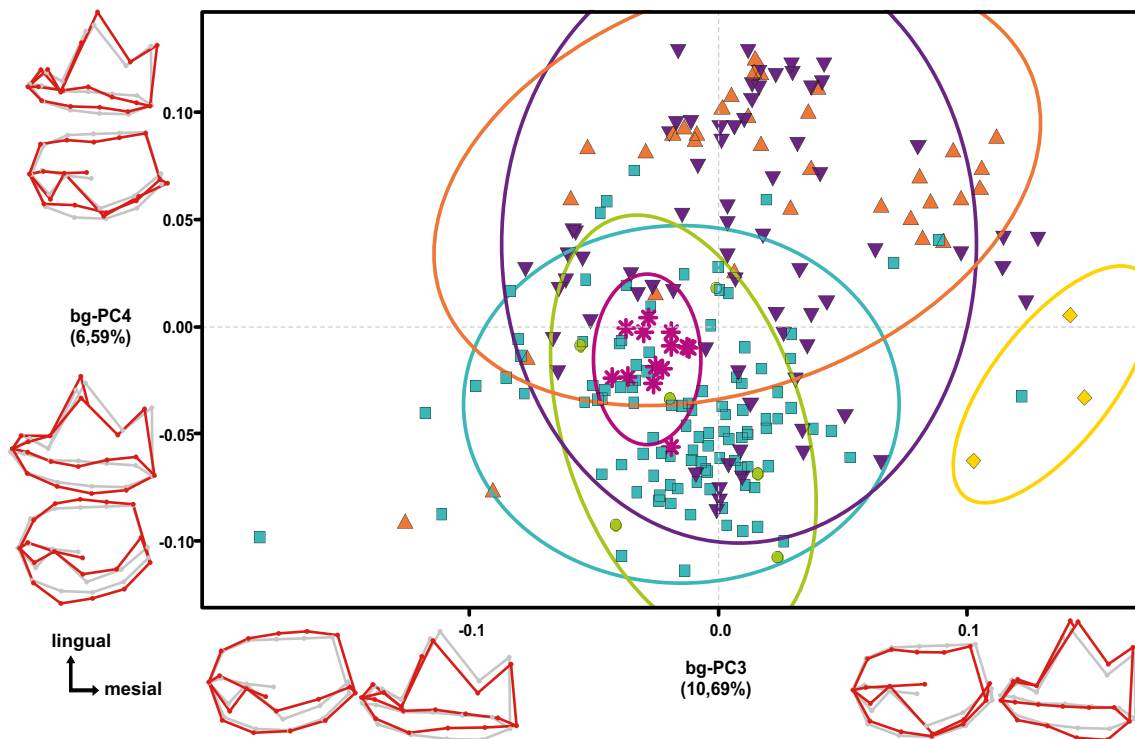
Fig. 5 Morphospace defined by the third and fourth principal components (bg-PC3 and bg-PC4) from the bg-PCA of dataset m1 + m4, showing the distribution of dietary groups. Change in molar morphology in occlusal and labial view, consensus shape (grey) and extreme shape of each PC (dark red). ● Herbivore; ◼ Hypercarnivore; ◆ Insectivore; ▲ Mesocarnivore; ▼ Omnivore; ✳ Piscivore

distribution of taxa (Online Resource 6). The optimized shape of the ancestor of marsupials tends to be separated on the PC2 from the optimized shape of the ancestor of carnivorans. Then the PC1 separates at the suborder level: Caniformia from Feliformia and Didelphimorphia from Dasyuromorphia (Online Resource 6). At the family level, such ancestor occupies a different position of the morphospace and then some descendants maintain the same morphology (such as Felidae) and others explore diverse morphology (such as Canidae or Mustelidae) (Online Resource 6). Finally, we observe how within each family, the separation of the species does not always agree with the phylogenetic relationships and responds to another factor (such as diet), meaning that there are several branches phylogenetically distant that cross or approximate. A clear example is *Speothos venaticus*, a hypercarnivorous canid, which is closer in the morphospace to *Cuon alpinus* (other hypercarnivorous canid) than to his sister species, *Chrysocyon brachyurus* (an omnivorous canid) (their Procrustes distances are 0.35 and 0.52, respectively; Online Resource 6).

These results are consistent with the significant phylogenetic signal found when estimating Blomberg's K ($K_{mult} = 0.26$; $P = 0.001$) and highlight the importance of taking into account the phylogeny. However, the value of $K_{mult} < 1$ indicates that sister species are more different than what would be expected under Brownian model, and so, besides the phylogeny there are other variables that need to be considered.

Allometry

Although the regression between shape and size is significant (p-value <0.0001), the variance explained by the correlation is very low (3.91%) and there is no clear pattern in the distribution of the taxa (Online Resource 7). Regarding taxonomy, the smallest taxa are specimens of Didelphidae, which do not have any size equivalent among the Carnivora of our study, in spite of their similar morphology (Online Resource 7). Concerning the distribution of diets, the largest sized taxa are hypercanivores (except for one herbivore, the panda bear) but there is no clear pattern for the medium and small taxa (Online Resource 7).

Relationship between Carnassial Morphology, Phylogeny, Size, and Ecology

The final model chosen by the AIC value by the forward stepwise regression analysis contains 35 phylogenetic variables for a total of 72 nodes (AIC = −325.08), whereas the model selected by the backward analysis possesses only 34 nodes (AIC = −325.74); for that reason we displayed the resulting model of the backward stepwise regression analysis (Online Resource 8). The CPO method reveals that the model using three factors as constraints (diet, size, and phylogeny) explains 93.83% of the total shape variation (Table 1).
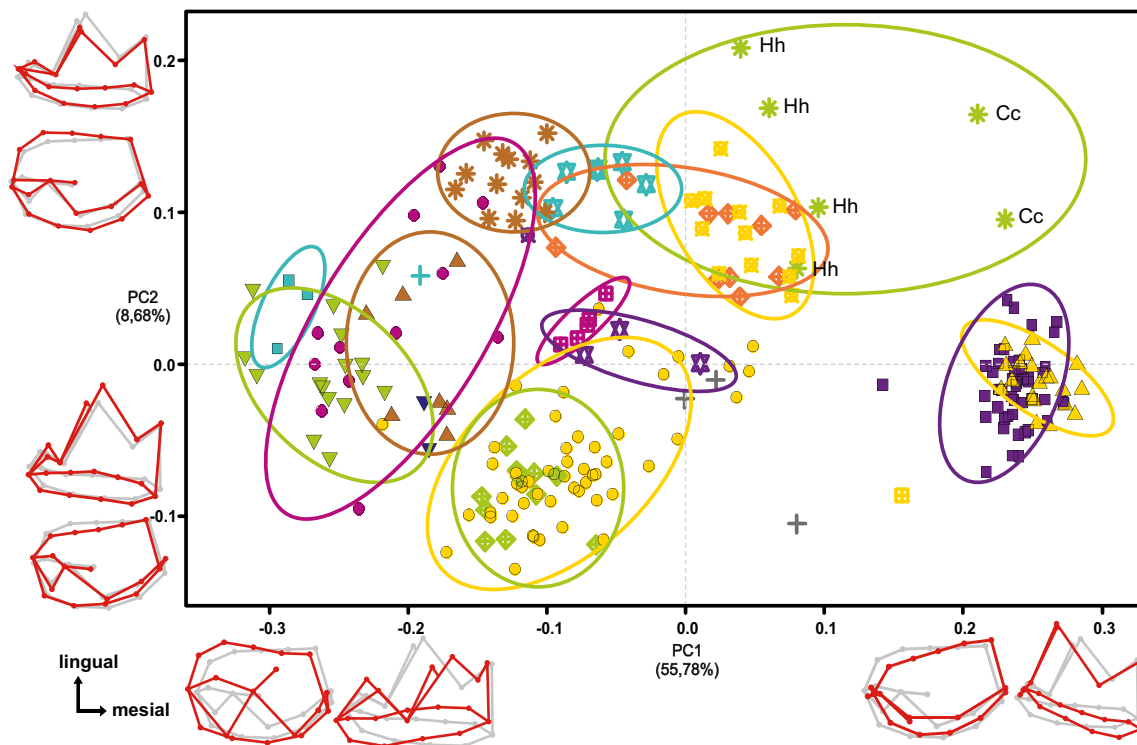
Fig. 6 Morphospace defined by the first two principal components (PC1 and PC2) from the PCA of dataset m1 + m4, showing the distribution of taxonomic groups. Change in molar morphology in occlusal and labial view, consensus shape (grey) and extreme shape of each PC (dark red). ✚ Ailuropodinae; ⬤ Canidae; ✚ Dasyurinae; ⬦ Didelphinae; ⬛ Felinae; ⊞ Genettinae; ✪ Guloninae; ✪ Herpestinae; ✳ Hyaeninae; ⬥ Ictonychinae; ✳ Lutrinae; ⬛ Melinae; ⬤ Mephitinae; ⊗ Mustelinae; ▲ Pantherinae; ▼ Procyonidae; ⊗ Taxidiinae; ⊞ Thylacinidae; ▼ Tremarctinae; ▲ Ursinae. Abbreviations: Cc, *Crocuta crocuta*; Hh, *Hyaena hyaena*

Centroid size represents 3.44% of the total variation, against 0.42% when using the remaining factors as conditioning matrix (Table 1). Diet explains 46.71% of the variance, but when the remaining factors are considered as conditioning matrix, the percentage falls down to 1.90% (Table 1). Finally, phylogeny explains 91.49% of the variation, against 46.71% with the remaining factors used as conditioning matrix (Table 1). All the models are significant (*p*-value <0.05).

Table 1 Results of the redundancy analyses of molar morphology, diet size and phylogeny

	%	P
Total	93.83	0.001
Diet	46.71	0.001
Diet ("partial var.")	1.90	0.003
Size	3.44	0.037
Size ("partial var.")	0.42	0.013
Phylogeny	91.49	0.001
Phylogeny ("partial var.")	44.00	0.001

%, percentage of variance explained by each analysis; P, probability for each analysis (all are significant at $P < 0.05$); partial var., partial variance explained by one factor (e.g., diet) but not by the others (i.e., size and phylogeny)

The Phylogenetic ANOVA and Procrustes ANOVA reveal similar results to CPO method. The former shows a significant relationship between diet and size and molar shape (46.38 and 3.46%, respectively; Table 2). However, when this relationship is examined in a phylogenetic context, the association is still significant, but diet and size explain little of the variation in molar shape (16.52 and 5.01%, respectively; Table 2).

Discussion

Carnassial Molars in Marsupials

Previous works have searched for differences and convergences between the dentition of carnivorous marsupials and placentals (e.g., de Muizon and Lange-Badré 1997; Jones 2003; van Nievelt and Smith 2005). Adult placentals are characterized by only one lower carnassial (m1), which erupts in its final position at the midpoint of the jaw, and remains there during growth (Werdelin 1987; Van Valkenburgh 1989; Biknevicius and Van Valkenburgh 1996). Conversely, in adult marsupials the three posterior molars can slice meat, but really each molar has a preponderant function in different ontogenetic stages (Werdelin 1987; Ceotto et al. 2009; Forasiepi and Sánchez-Villagra 2014). Our results show that m4 is more

Table 2 Results of the procrustes ANOVA and phylogenetic ANOVA

	PROCRUSTES ANOVA			PHYLOGENETIC ANOVA		
	R^2	F	P	R^2	F	P
Diet	0.4638	12.2036	0.001	0.1652	2.7798	0.001
Size	0.0346	4.5528	0.008	0.0501	4.2126	0.007

R^2, coefficient of determination for each model term; P, probability for each analysis (all are significant at $P < 0.05$)

specialized to carnivory than m3, and the m4 morphology correlates better with the observed diet of adults than m3 morphology (Online Resource 4). It is noteworthy that when marsupials are subadults, their m3 is located in the position of the jaw that optimizes bite force (the m4 has not erupted yet; Werdelin 1987; Macedo et al. 2006; Ceotto et al. 2009), and some carnivorous marsupials present differences in their diets between adults and subadults (Jones 1995; Jones and Barmuta 2000; Thompson et al. 2003; Ceotto et al. 2009). The difference in molar morphology (m3 vs. m4) observed in our analyses could be a possible explanation to this change in diets through ontogeny.

Relationship between Tooth Morphology and Diet

Previous studies have shown that there is a correlation between the morphology of the lower molars and the diet of animals, which is expected as carnassials are directly used to process food. Those studies were based either on morphometric indices that consider, e.g., the cutting blade length of trigonid with respect to the grinding area of talonid (RGA; Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993; Prevosti et al. 2013) or the shear crest length (Strait 1993; Hogue and Ziashakeri 2010), or morphometric angles, e.g., between the paracristid and the mesiodistal axis (Lower angle, AI; Goin et al. 1992) or the relationship between the height of the protoconid and the length of the talonid (Angle α; Crusafont-Pairó and Truyols-Santonja 1953, 1956; Meloro and Raia 2010). In the present study, such correlation is corroborated, first visually in the PCA and bg-PCA graphs (where a continuum is observed between diet categories along the first axis; Figs. 3 and 4), and secondly quantitatively in the RDA and Procrustes ANOVA results (47% of the molar shape variation can be explained by the diet; Tables 1 and 2). We observed that hypercarnivorous species have molars with long and high cutting blades, reduced talonids, paracristids arranged parallel to the dental axis (observable at the positive end of the first axis), whereas the morphology inverts as the percentage of meat in the diet of these animals decreases (observable at the negative end of the first axis).

It is noteworthy that we did not obtain a good separation between diet categories, and there were different degrees of

overlap among them. This might be in part related to the intrinsic definition of diets. The choice among the categories used is not trivial, given that this will determine how species are expected to cluster. Some authors classify mammals based on classic trophic relationships (herbivores, carnivores, and omnivores), while others use feeding categories (Kay et al. 1978; Langer and Chivers 1994; Ungar 2010; Pineda-Munoz and Alroy 2014). A disadvantage common to all categories is the discretization of a continuous variable such as diet into classes, whose chosen limits are questionable (Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993; Prevosti et al. 2012b; Echarri et al. 2017). In addition, several species show significant geographic and seasonal variation in their diet (e.g., Steinmetz et al. 2013; Lanszki et al. 2015; Graw and Manser 2016; Krawczyk et al. 2016), and would therefore be classified into different categories if their populations were analyzed separately (Kay et al. 1978; Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993; Prevosti et al. 2012a; Echarri et al. 2017). Finally, it is necessary to take into account that the different methodologies for the study of diet of species are a proxy, and the different tools are actually registering different evidence of the items consumed, and perhaps ignoring other items, thus adding to the problem of the complexity of working with different sources of diet inferences (Kay and Hylander 1978; Evans 2013; Christensen 2014; Calandra and Merceron 2016; Davis and Pineda Munoz 2016; Krawczyk et al. 2016; Pineda-Munoz et al. 2017).

Some of these problems could be exemplified with the omnivore category. First, omnivores include some species whose diet is little known. So although they are considered omnivores, they might have some unknown main food resources in their diet, which has not yet been described. Second, there are animals without main items in their diets, also called generalists in others works (Pineda-Munoz and Alroy 2014), but in some cases, they must face the same biomechanical constraints as specialist animals (Kay et al. 1978; Ungar 2010; Figueirido et al. 2013). For example, the consumption of arthropods might create a structural constraint because of the exoskeletal chitin, shaping the molars more in accordance with an insect-based diet, even when the insects are not the main item in the diet of the animal (Kay et al. 1978). Therefore, within omnivores, we may include species without main items, but with different proportions of items. As a consequence, species classified as omnivorous have a wide variety of molar morphologies, and therefore a great dispersion in the morphospace (both in the present and in previous works; Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993; Prevosti et al. 2012a; Pineda-Munoz and Alroy 2014; Echarri et al. 2017).

Another problematic category is the insectivores, because they have a large dispersion in the morphospace (0.03; Figs. 3 and 4). Additionally, this category has a low number of representatives (only three species) due to several reasons: (i)

insectivorous didelphids (e.g., some species of *Monodelphis* and *Thylamys*; Vieira and Astúa de Moraes 2003; Astúa 2015) could not be included because of their molar size, i.e., smaller than the size limit of the digitizing arm that we used; (ii) for other clades with insectivorous habits, such as *Suricata suricatta*, *Fossa fossana*, or *Melursus ursinus* (Garshelis 2009; Gilchrist et al. 2009; Goodman 2009), there were no materials available in the studied collections; (iii) finally, there are other insectivorous taxa that have highly modified or reduced molars, as the hyena *Proteles cristata* or the dasyuromorph *Myrmecobius fasciatus*, which could be not included in our analyses due to the lack of anatomical landmarks in common with our sample (Cooper 2005; Holekamp and Kolowski 2009; Ungar 2010; Friend 2015). Additionally, although the three included species have an insectivorous diet (i.e., insects are their main food resource), they have different overall dietary habits. *Galerella sanguinea* and *Dasyurus viverrinus* supplement their diet with meat of vertebrates (micromammals, small birds, and carrion) while the consumption of vertebrate meat in *Otocyon megalotis* is incidental (Petter 1969; Blackhall 1980; Gilchrist et al. 2009; Sillero-Zubiri 2009; Baker 2015; Graw and Manser 2016). This could explain why *G. sanguinea* and *D. viverrinus* are closer to the mesocarnivores and hypercarnivores, whereas *O. megalotis* is closer to species whose diets include a lower percentage of meat of vertebrates (Fig. 3).

Relationship between Tooth Morphology and Phylogeny

In addition to the relationship with diet, a strong correlation between molar morphology and phylogenetic relationships was also found. In the PCA graphs (Figs. 2 and 6 and Online Resource 6) we can observe how the different clades occupy a well-delimited morphospace, consistent with the K_{mult} statistic, which shows significant phylogenetic signal. Also in the RDA, the phylogeny explains a high percentage of the total variance (91.49% of the variation with the remaining factors as conditioning matrix, and 46.71% of the shape variation by itself; Table 1) and is the main factor that explains carnassial variation. In the case of diet, the percentage of variance explained was reduced when we excluded what is explained by phylogeny, both in the RDA and Phylogenetic ANOVA (size always explained a low percentage of molar variance in the multivariate regression, RDA, and Phylogenetic ANOVA, so its contribution can be left out; Tables 1 and 2 and Online Resource 7). This means that diet and phylogeny are correlated, but that phylogeny has a greater impact on the shape of these molars, and that the dietary variation in our sample is phylogenetically structured.

The correlation between the morphology of the lower molars and phylogeny has been previously described by many authors (Crusafont-Pairó and Truyols-Santonja 1953, 1956; Van

Valkenburgh 1989; Van Valkenburgh and Koepfli 1993; Meloro et al. 2008; Meloro and Raia 2010; Chemisquy et al. 2015), and is highlighted in our results in the separation of the two clades of Carnivora: Feliformia and Caniformia (Fig. 2 and Online Resource 6). It is noteworthy that Viverridae and Herpestidae share the morphospace with the Caniformia, instead of the other Feliformia (Fig. 2 and Online Resource 6). The same pattern was observed using morphometric angles of the molars (Crusafont-Pairó and Truyols-Santonja 1956; Meloro and Raia 2010) and some authors described this as the convergence in carnassial morphology between the feliform Viverridae and Hespestidae from Africa and southern Eurasia and the small Caniformia from North America (Meloro and Raia 2010). However, it is necessary to reconstruct shape in an explicit phylogenetic context, based on the optimization of shape on a phylogeny, to analyze the evolution of the characters and to be able to determine which state is plesiomorphic and which one is derived. Other authors stated that the hypercarnivore morphotype is the derived state, so that the Viverridae and Hespestidae from Africa and southern Eurasia and the small Caniformia from North America would have a plesiomorphic state (Holliday 2010; Solé and Ladevèze 2017).

Regarding Caniformia, it is interesting to note that Mustelidae, the family with most of the species within Carnivora, is the one with the most morphological disparity in the carnassial molar (Crusafont-Pairó and Truyols-Santonja 1953, 1956; Wilson 2009). Figure 2 showed how Mustelidae are clustered in the morphospace because of their similar values in the second axis, but still, they occupy a large range of values within the first axis. This morphological disparity made some authors of the last century propose to separate Mustelidae into different families (Crusafont-Pairó and Truyols-Santonja 1956), and more recently into several subfamilies, with Mustelidae maintained at a family rank (Koepfli et al. 2008; Sato et al. 2012). Each subfamily has a peculiar molar morphology, and for this reason occupies a well-defined portion of the morphospace in our analyses (Fig. 6).

The case of Ursidae is worth mentioning, given that this group has only eight living species, which occupy very different ecological niches, including for example *Ursus maritimus* (polar bear) that feeds almost exclusively on seals, *Ailuropoda melanoleuca* (giant panda) whose diet is based on bamboo, and *Melursus ursinus* (sloth bear) that basically consumes termites (Garshelis 2009; Wilson 2009). However and in spite of the ecological diversity, the variation in the morphology of the carnassial molar is insignificant with respect to the variation that was seen in the other clades (Crusafont-Pairó and Truyols-Santonja 1953; Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993), and for this same reason ursids occupy a limited range of values of PC1 (Fig. 2). Sacco and Van Valkenburgh (2004), using morphometric indexes of the mandible and m1 of ursids, showed a separation between the dietary categories. However, they used a different

classification of diets from the one used in the present study (e.g., they considered the brown bear and polar bear, both as carnivorous bears), so they reached completely different conclusions. Given our classification of diets, we did not find a clear pattern of distribution of the shape of the molars on the morphospace according to the diet of bears.

Regarding the potential use of carnassial shape to infer diet of fossil and extinct mammals, it is necessary to consider that molar morphology is not only influenced by the diet of the animals, but is also affected by the evolutionary trajectories that bias the inferences (Kay and Hylander 1978; Chemisquy et al. 2015; Davis and Pineda Munoz 2016). Continuing with the example of the bears, all the species have similar carnassial molars, but different feeding habits. At first sight we could invoke a phylogenetic constraint, but phylogeny is the study of evolutionary changes over time; in itself, phylogeny cannot act as a constraint (Blomberg and Garland 2002; Losos 2011; Shanahan 2011). Actually, in response to various evolutionary processes (e.g., developmental or genetic constraints; Asahara et al. 2016; Solé and Ladevèze 2017), the resulting molar morphology of a living species may possess traits that are retained from the ancestral morphotype, the diets of which were slightly different. As a result, the morphology of the molar does not correlate perfectly with the diet of the current animal, but may be influenced by the diet of the shared ancestors (this is supported by the results of the RDA and Phylogenetic ANOVA), somehow evidencing not only the main food resource of the current diets, but also the items that they are capable of processing. In any case, taking into account the phylogenetic pattern, the molar morphology represents an efficient proxy to infer diet of fossil species.

Conclusions

This work evaluates for the first time, in a quantitative way, which of the lower molars of the Marsupialia (m3 or m4) is the best analogue to the m1 of Carnivora. Although marsupials have three pairs of carnassial molars (M1-M3/m2-m4; Savage 1977; de Muizon and Lange-Badré 1997; Jones 2003), the m4 is more similar to a placental carnassial (i.e., a Carnivora m1), and due to its position relative to the condyle in adults, some authors (Werdelin 1986; Prevosti et al. 2012a) have already suggested m4 as the best analogue to the Carnivora carnassial. This hypothesis is supported by the analyses performed in this contribution.

As teeth are the principal structure involved in the breakdown of food in mammals, the morphology of cusps and crests is expected to show different levels of correlation with diet (Van Valkenburgh 1989; Van Valkenburgh and Koepfli 1993). On the other hand, our analyses showed that other factors are more important, and that the correlation between shape and diet departs from optimality in several ways. Phylogeny is the main factor that explains carnassial shape

variation. Therefore, in a robust phylogenetic framework the correlation between molar morphology and diet is best fitted, and so inferences can be made on fossil species.

Carnivory has a long evolutionary history across a broad range of mammals, with multiple cases of convergence between eutherians (Carnivora and Creodonta) and metatherians (Dasyuromorphia, Didelphidae, Thylacoleonidae, Sparassodonta). A better understanding of the evolution of their diets in a phylogenetic and ecological framework would allow to a better comprehension of the decline and extinction of some carnivore guilds.

References

Adams DC (2014a) A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. Evolution 68:2675–2688. https://doi.org/10.1111/evo.12463

Adams DC (2014b) A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Syst Biol 63:685–697. https://doi.org/10.1093/sysbio/syu030

Adams DC, Collyer ML (2016) On the comparison of the strength of morphological integration across morphometric datasets. Evolution 70:2623–2631. https://doi.org/10.1111/evo.13045

Adams DC, Collyer ML, Kaliontzopoulou A, Sherratt E (2017) Geomorph: software for geometric morphometric analyses. R package version 3.0.5. https://cran.r-project.org/package=geomorph

Adler D, Murdoch D, Nenadic O, Urbanek S, Chen M, Gebhardt A, Bolker B, Csardi G, Strzelecki A, Senger A, Eddelbuettel D (2017) rgl: 3D Visualization Using OpenGL. R package version 0.98.22. https://CRAN.R-project.org/package=rgl

Anderson MJ (2001) A new method for non parametric multivariate analysis of variance. Aust Ecol 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Asahara M, Saito K, Kishida T, Takahashi K, Bessho K (2016) Unique pattern of dietary adaptation in the dentition of Carnivora: its advantage and developmental origin. Proc R Soc B 283:20160375 . https://doi.org/10.1098/rspb.2016.0375

Astúa D (2015) Family Didelphidae (opossums). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 5. Monotremes and Marsupials. Lynx Edicions, Barcelona, pp 70–186

Austin JJ, Soubrier J, Prevosti FJ, Prates L, Trejo V, Mena F, Cooper A (2013) The origins of the enigmatic Falkland Islands wolf. Nat Commun 4:1552 . https://doi.org/10.1038/ncomms2570

Baker AM (2015) Family Dasyuridae (carnivorous marsupials). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 5. Monotremes and Marsupials. Lynx Edicions, Barcelona, pp 232–348

Bapst DW (2012) paleotree : an R package for paleontological and phylogenetic analyses of evolution. Methods Ecol Evol 3:803–807. https://doi.org/10.1111/j.2041-210X.2012.00223.x

Biknevicius AR, Van Valkenburgh B (1996) Design for killing: craniodental adaptations of predators. In: Gittleman JL (ed) Carnivore Behavior, Ecology, and Evolution. Vol. 2. Cornell Univerty Press, New York, pp 393–428

Blackhall S (1980) Diet of the eastern native-cat, *Dasyurus viverrinus* (Shaw), in southern Tasmania. Wildl Res 7:191–197. https://doi.org/10.1071/WR9800191

Blomberg SP, Garland TJ (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J Evol Biol 15:899–910 . https://doi.org/10.1046/j.1420-9101.2002.00472.x

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Butler PM (1946) The evolution of carnassial dentitions in the Mammalia. Proc Zool Soc Lond 116:198–220. https://doi.org/10.1111/j.1096-3642.1946.tb00117.x

Calandra I, Merceron G (2016) Dental microwear texture analysis in mammalian ecology. Mammal Rev 46:215–228. https://doi.org/10.1111/mam.12063

Ceotto P, Finotti R, Santori R, Cerqueira R (2009) Diet variation of the marsupials *Didelphis aurita* and *Philander frenatus* (Didelphimorphia, Didelphidae) in a rural area of Rio de Janeiro state, Brazil. Mastozool Neotrop 16:49–58

Chemisquy MA, Prevosti FJ, Martin G, Flores DA (2015) Evolution of molar shape in didelphid marsupials (Marsupialia: Didelphidae): analysis of the influence of ecological factors and phylogenetic legacy. Zool J Linn Soc 173:217–235. https://doi.org/10.1111/zoj.12205

Christensen HB (2014) Similar associations of tooth microwear and morphology indicate similar diet across marsupial and placental mammals. PLoS One 9:e102789. https://doi.org/10.1371/journal.pone.0102789

Cooper CE (2005) *Myrmecobius fasciatus* (Dasyuromorphia: Myrmecobiidae). Mammal Species 43:129–140. https://doi.org/10.1644/881.1

Crusafont-Pairó M, Truyols-Santonja J (1953) Un ensayo goniométrico sobre la carnicera inferior de los Fisípedos. Estud Geológicos 18:225–256

Crusafont-Pairó M, Truyols-Santonja J (1956) A biometric study of the evolution of fissiped carnivores. Evolution 10:314–332

Davis M, Pineda Munoz S (2016) The temporal scale of diet and dietary proxies. Ecol Evol 6:1883–1897. https://doi.org/10.1002/ece3.2054

de Muizon C, Lange-Badré B (1997) Carnivorous dental adaptations in tribosphenic mammals and phylogenetic reconstruction. Lethaia 30:353–366. https://doi.org/10.1111/j.1502-3931.1997.tb00481.x

Dragoo JW (2009) Family Mephitidae (skunks). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 532–563

Echarri S, Ercoli MD, Chemisquy MA, Turazzini G, Prevosti FJ (2017) Mandible morphology and diet of the South American extinct metatherian predators (Mammalia, Metatheria, Sparassodonta). Earth Environ Sci Trans R Soc Edinburgh 106:277–288. https://doi.org/10.1017/S1755691016000190

Eizirik E (2012) A molecular view on the evolutionary history and biogeography of neotropical carnivores (Mammalia, Carnivora). In: Patterson BD, Costa LP (eds) Bones, Clones, and Biomes: The History and Geography of Recent Neotropical Mammals. University of Chicago Press, Chicago, pp 123–142

Eizirik E, Murphy WJ, Koepfli KP, Johnson WE, Dragoo JW, Wayne RK, O'Brien SJ (2010) Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. Mol Phylogenet Evol 56:49–63 . https://doi.org/10.1016/j.ympev.2010.01.033

Evans AR (2013) Shape descriptors as ecometrics in dental ecology. Hystrix 24:133–140. https://doi.org/10.4404/hystrix-24.1-6363

Evans AR, Sanson GD (2006) Spatial and functional modeling of carnivore and insectivore molariform teeth. J Morphol 267:649–662. https://doi.org/10.1002/jmor.10285

Evans AR, Fortelius M, Jernvall J, Eronen JT (2005) Dental ecomorphology of extant European carnivorans. In: Żądzińska E (ed) Current Trends in Dental Morphology Research: 13th International Symposium on Dental Morphology. University of Lódz Press, Lódz, pp 223–232

Evans AR, Wilson GP, Fortelius M, Jernvall J (2007) High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81. https://doi.org/10.1038/nature05433

Ewer RF (1973) The Carnivores. Cornell Univerty Press, New York

Figueirido B, Tseng ZJ, Martín-Serra A (2013) Skull shape evolution in durophagous carnivorans. Evolution 67:1975–1993. https://doi.org/10.1111/evo.12059

Flores DA (2009) Phylogenetic analyses of postcranial skeletal morphology in didelphid marsupials. Bull Am Mus Nat Hist 320:1–81

Flynn JJ, Wesley-Hunt GD (2005) Carnivora. In: Rose KD, Archibald JD (eds) The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades. The Johns Hopkins University Press, Baltimore and London, pp 175–198

Forasiepi AM, Sánchez-Villagra MR (2014) Heterochrony, dental ontogenetic diversity, and the circumvention of constraints in marsupial mammals and extinct relatives. Paleobiology 40:222–237. https://doi.org/10.1666/13034

Friend JA (2015) Family Myrmecobiidae (numbat). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 5. Monotremes and Marsupials. Lynx Edicions, Barcelona, pp 222–231

Garshelis DL (2009) Family Ursidae (bears). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 448–497

Giannini NP (2003) Canonical phylogenetic ordination. Syst Biol 52:684–695. https://doi.org/10.1080/10635150390238888

Gilchrist JS, Jennings AP, Veron G, Cavallini P (2009) Family Herpestidae (Mongooses). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 262–329

Godínez Domínguez E, Freire J (2003) Information theoretic approach for selection of spatial and temporal models of community organization. Mar Ecol Prog Ser 253:17–24

Goillot C, Blondel C, Peigné S (2009) Relationships between dental microwear and diet in Carnivora (Mammalia) - Implications for the reconstruction of the diet of extinct taxa. Palaeogeogr Palaeoclimatol Palaeoecol 271:13–23. https://doi.org/10.1016/j.palaeo.2008.09.004

Goin FJ, Velázquez C, Scaglia O (1992) Orientación de las crestas cortantes en el molar tribosfénico. Sus implicancias funcionales en didelfoideos (Marsupialia) fósiles y vivientes. Rev del Mus La Plata (Nueva Ser 9:183–198)

Goin FJ, Woodburne MO, Zimicz AN, Martin GM, Chornogubsky L (2016) A Brief History of South American Metatherians: Evolutionary Contexts and Intercontinental Dispersals. Springer, Cham

Goodall C (1991) Procrustes methods in the statistical analysis of shape. J R Stat Soc Ser B 53:285–339

Goodman SM (2009) Family Eupleridae (Madagascar carnivores). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 330–351

Grafen A (1989) The phylogenetic regression. Philos Trans R Soc B Biol Sci 326:119–157. https://doi.org/10.1098/rstb.1989.0106

Graw B, Manser M (2016) Life history patterns and biology of the slender mongoose (*Galerella sanguinea*) in the Kalahari Desert. J Mammal 98(2):332–338. https://doi.org/10.1093/jmammal/gyw178

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425. https://doi.org/10.1086/282146

Helgen KM, Veatch EG (2015) Recent extinct Australian marsupials and monotremes. In: Wilson DE, Mittermeier RA (eds) Handbook of the

Mammals of the World. Vol. 5. Monotremes and Marsupials. Lynx Edicions, Barcelona, pp 17–31

Hogue AS, Ziashakeri S (2010) Molar crests and body mass as dietary indicators in marsupials. Aust J Zool 58:56–68. https://doi.org/10.1071/ZO09084

Holekamp KE, Kolowski JM (2009) Family Hyaenidae (hyenas). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 234–261

Holliday JA (2010) Evolution in Carnivora: identifying a morphological bias. In: Goswami A, Friscia A (eds) Carnivoran Evolution: New Views on Phylogeny, Form, and Function. Cambridge University Press, New York, pp 189–224

Jones ME (1995) Guild structure of the large marsupial carnivores in Tasmania. Ph.D. dissertation, University of Tasmania, Hobart.

Jones ME (2003) Covergence in ecomorphology and guild structure among marsupial and placental carnivores. In: Jones ME, Dickman CR, Archer M (eds) Predators with Pouches. CSIRO Publishing, Collingwood, pp 285–296

Jones ME, Barmuta LA (2000) Niche differentiation among sympatric Australian dasyurid carnivores. J Mammal 81:434–447. https://doi.org/10.1644/1545-1542(2000)081<0434

Kay RF (1975) The functional adaptions of primate molar teeth. Am J Phys Anthropol 43:195–216

Kay RF, Hylander WL (1978) The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In: Montgomery GG (ed) The Ecology of Arboreal Folivores. Smithsonian Institution Press, Washington, D.C., pp 173–191

Kay RF, Sussman RW, Tattersall I (1978) Dietary and dental variations in the genus *Lemur*, with comments concerning dietary-dental correlations among Malagasy primates. Am J Phys Anthropol 49:119–127. https://doi.org/10.1002/ajpa.1330490118

Kays R (2009) Family Procyonidae (raccoons). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 504–531

Kemsley EK (1996) Discriminant analysis of high-dimensional data: a comparison of principal components analysis and partial least squares data reduction methods. Chemom Intell Lab Syst 33:47–61. https://doi.org/10.1016/0169-7439(95)00090-9

Klingenberg CP (2008) Novelty and "homology-free" morphometrics: what's in a name? Evol Biol 35:186–190. https://doi.org/10.1007/s11692-008-9029-4

Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Resour 11:353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Klingenberg CP, Monteiro LR (2005) Distances and directions in multidimensional shape spaces: Implications for morphometric applications. Syst Biol 54:678–688. https://doi.org/10.1080/10635150590947258

Koepfli K-P, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK (2008) Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol 6:10. https://doi.org/10.1186/1741-7007-6-10

Kovarovic K, Aiello LC, Cardini A, Lockwood CA (2011) Discriminant function analyses in archaeology: are classification rates too good to be true? J Archaeol Sci 38:3006–3018. https://doi.org/10.1016/j.jas.2011.06.028

Krawczyk AJ, Bogdziewicz M, Majkowska K, Glazaczow A (2016) Diet composition of the Eurasian otter *Lutra lutra* in different freshwater habitats of temperate Europe: a review and meta-analysis. Mammal Rev 46:106–113. https://doi.org/10.1111/mam.12054

Kruuk H (2006) Otters: Ecology, Behaviour and Conservation. Oxford University Press, New York

Kutschera VE, Bidon T, Hailer F, Rodi JL, Fain SR, Janke A (2014) Bears in a forest of gene trees: phylogenetic inference is complicated by incomplete lineage sorting and gene flow. Mol Biol Evol 31:2004–2017. https://doi.org/10.1093/molbev/msu186

Langer P, Chivers DJ (1994) Classification of foods for comparative analysis of gastro-intestinal tract. In: Chivers DJ, Langer P (eds) The Digestive System in Mammals: Food Form and Function. Cambridge University Press, Cambridge, pp 74–86

Lanszki J, Kurys A, Heltai M, Csányi S, Ács K (2015) Diet composition of the golden jackal in an area of intensive big game management. Ann Zool Fennici 52:243–255. https://doi.org/10.5735/086.052.0403

Larivière S, Jennings AP (2009) Family Mustelidae (weasels and relatives). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 564–656

Legendre P, Legendre L (1998) Numerical Ecology, 2nd edition. Elsevier, Amsterdam

Li G, Davis BW, Eizirik E, Murphy WJ (2016) Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). Genome Res 26:1–11. https://doi.org/10.1101/gr.186668.114

Losos JB (2011) Seeing the forest for the trees: the limitations of phylogenies in comparative biology. Am Nat 177:709–727. https://doi.org/10.1086/660020

Macedo J, Loretto D, Vieira MV, Cerqueira R (2006) Classes de desenvolvimento em marsupiais: um método para animais vivos. Mastozool Neotrop 13:133–136

Magnus LZ, Cáceres N (2017) Phylogeny explains better than ecology or body size the variation of the first lower molar in didelphid marsupials. Mammalia 81: 119–133. https://doi.org/10.1515/mammalia-2015-0070

Martins EP, Hansen TF (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646–667

Martins EP, Diniz-Filho JAF, Housworth EA (2002) Adaptive constraints and the phylogenetic comparative method: a computer simulation test. Evolution 56:1–13. https://doi.org/10.1111/j.0014-3820.2002.tb00844.x

Meloro C, Raia P (2010) Cats and dogs down the tree: the tempo and mode of evolution in the lower carnassial of fossil and living Carnivora. Evol Biol 37:177–186. https://doi.org/10.1007/s11692-010-9094-3

Meloro C, Clauss M, Raia P (2015) Ecomorphology of Carnivora challenges convergent evolution. Org Divers Evol 15:711–720. https://doi.org/10.1007/s13127-015-0227-5

Meloro C, Raia P, Piras P, Barbera C, O'Higgins P (2008) The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. Zool J Linn Soc 154:832–845. https://doi.org/10.1111/j.1096-3642.2008.00429.x

Mitteroecker P, Bookstein F (2011) Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. Evol Biol 38:100–114. https://doi.org/10.1007/s11692-011-9109-8

Mitteroecker P, Gunz P (2009) Advances in geometric morphometrics. Evol Biol 36:235–247. https://doi.org/10.1007/s11692-009-9055-x

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2015) vegan: Comunity Ecology Package. R package version 2.3–5. http://CRAN.R-project.org/package=vegan

Oxnard C, O'Higgins P (2009) Biology clearly needs morphometrics. Does morphometrics need biology? Biol Theory 4:84–97. https://doi.org/10.1162/biot.2009.4.1.84

Padial JM, Avila E, Sanchez JM (2002) Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. Mammal Biol 67:137–146

Perez IS, Bernal V, Gonzalez PN (2006) Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. J Anat 208:769–784

Petter G (1969) Interpretation évolutive des caractères de la denture des viverridés africains. Mammalia 33:607–625

Pineda-Munoz S, Alroy J (2014) Dietary characterization of terrestrial mammals. Proc R Soc Lond B 281:20141173

Pineda-Munoz S, Lazagabaster IA, Alroy J, Evans AR (2017) Inferring diet from dental morphology in terrestrial mammals. Methods Ecol Evol 8:481–491. https://doi.org/10.1111/2041-210X.12691

Popowics TE (2003) Postcanine dental form in the Mustelidae and Viverridae (Carnivora: Mammalia). J Morphol 256:322–341. https://doi.org/10.1002/jmor.10091

Prevosti FJ, Turazzini GF, Ercoli MD, Hingst-Zaher E (2012a) Mandible shape in marsupial and placental carnivorous mammals: a morphological comparative study using geometric morphometrics. Zool J Linn Soc 164:836–855. https://doi.org/10.1111/j.1096-3642.2011.00785.x

Prevosti FJ, Forasiepi AM, Ercoli MD, Turazzini GF (2012b) Paleoecology of the mammalian carnivores (Metatheria, Sparassodonta) of the Santa Cruz Formation (late early Miocene). In: Vizcaíno SF, Kay RF, Bargo MS (eds) Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge, pp 173–193

Prevosti FJ, Forasiepi A, Zimicz N (2013) The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? J Mammal Evol 20:3–21. https://doi.org/10.1007/s10914-011-9175-9

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Raia P, Carotenuto F, Meloro C, Piras P, Pushkina D (2010) The shape of contention: adaptation, history, and contingency in ungulate mandibles. Evolution 64:1489–1503. https://doi.org/10.1111/j.1558-5646.2009.00921.x

Reddy D, Kim J, Raaum R (2006) Resample.exe. http://life.bio.sunysb.edu/morph/soft-utility.html

Rohlf FJ (1999) Shape statistics: Procrustes superimpositions and tangent spaces. J Classif 16:197–223. https://doi.org/10.1007/s003579900054

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. Mammal Rev 39:67–78. https://doi.org/10.1111/j.1365-2907.2008.00134.x

Sacco T, Van Valkenburgh B (2004) Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). J Zool 263:41–54. https://doi.org/10.1017/S0952836904004856

Sato JJ, Wolsan M, Prevosti FJ, D'Elía G, Begg C, Begg K, Hosoda T, Campbell KL, Suzuki H (2012) Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Mol Phylogenet Evol 63:745–757. https://doi.org/10.1016/j.ympev.2012.02.025

Savage RJG (1977) Evolution in carnivorous mammals. Palaeontology 20:237–271

Seetah TK, Cardini A, Miracle PT (2012) Can morphospace shed light on cave bear spatial-temporal variation? Population dynamics of *Ursus spelaeus* from Romualdova pećina and Vindija, (Croatia). J Archaeol Sci 39:500–510. https://doi.org/10.1016/j.jas.2011.10.005

Shanahan T (2011) Phylogenetic inertia and Darwin's higher law. Stud Hist Philos Biol Biomed Sci 42:60–68. https://doi.org/10.1016/j.shpsc.2010.11.013

Sheets HD, Covino KM, Panasiewicz JM, Morris SR (2006) Comparison of geometric morphometric outline methods in the discrimination of age-related differences in feather shape. Front Zool 3:15. https://doi.org/10.1186/1742-9994-3-15

Sillero-Zubiri C (2009) Family Canidae (dogs). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 352–447

Smits PD, Evans AR (2012) Functional constraints on tooth morphology in carnivorous mammals. BMC Evol Biol 12:146. https://doi.org/10.1186/1471-2148-12-146

Solé F, Ladevèze S (2017) Evolution of the hypercarnivorous dentition in mammals (Metatheria, Eutheria) and its bearing on the development of tribosphenic molars. Evol Dev 19:56–68. https://doi.org/10.1111/ede.12219

Steinmetz R, Garshelis DL, Chutipong W, Seuaturien N (2013) Foraging ecology and coexistence of Asiatic black bears and sun bears in a seasonal tropical forest in Southeast Asia. J Mammal 94:1–18. https://doi.org/10.1371/journal.pone.0014509

Strait SG (1993) Differences in occlusal morphology and molar size in frugivores and faunivores. J Hum Evol 25:471–484

Strauss RE (2010) Discriminating groups of organisms. In: Elewa AMT (ed) Morphometric for Nonmorphometricians. Springer, Heidelberg, pp 73–91

Sunquist ME, Sunquist FC (2009) Family Felidae (cats). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 54–169

Taylor RJ (1986) Notes on the diet of the carnivorous mammals of the Upper Henty River region, western Tasmania. Pap Proc R Soc Tasmania 120:7–10

Thompson EN, Biknevicius AR, German RZ (2003) Ontogeny of feeding function in the gray short-tailed opossum *Monodelphis domestica*: empirical support for the constrained model of jaw biomechanics. J Exp Biol 206:923–932. https://doi.org/10.1242/jeb.00181

Torre I, Ballesteros T, Degollada A (2003) Changes in the diet of the genet (*Genetta genetta* Linnaeus, 1758) in relation to small mammal-prey availability: possible choice of the bank vole? Galemys 15:25–36

Ungar PS (2010) Mammal Teeth: Origin, Evolution, and Diversity. The Johns Hopkins University Press, Baltimore

van Nievelt AFH, Smith KK (2005) To replace or not to replace: the significance of reduced functional tooth replacement in marsupial and placental mammals. Paleobiology 31:324–346. https://doi.org/10.1666/0094-8373(2005)031[0324:TRONTR]2.0.CO;2

Van Valkenburgh B (1989) Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In: Gittleman JL (ed) Carnivore Behavior, Ecology, and Evolution. Vol. 1. Springer US, New York, pp 410–436

Van Valkenburgh B (2007) Déjà vu: the evolution of feeding morphologies in the Carnivora. Integr Comp Biol 47:147–163. https://doi.org/10.1093/icb/icm016

Van Valkenburgh B, Koepfli K-P (1993) Cranial and dental adaptations to predation in canids. Symp Zool Soc Lond 65:15–37

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edition. Springer, New York

Vieira EM, Astúa de Moraes D (2003) Carnivory and insectivory in Neotropical marsupials. In: Jones ME, Dickman CR, Archer M (eds) Predators with Pouches. CSIRO Publishing, Collingwood, pp 271–284

Werdelin L (1986) Comparison of skull shape in marsupial and placental carnivores. Aust J Zool 34:109–117 . https://doi.org/10.1071/ZO9860109

Werdelin L (1987) Jaw geometry and molar morphology in marsupial carnivores: analysis of a constraint and its macroevolutionary consequences. Paleobiology 13:342–350

Westerman M, Krajewski C, Kear BP, Meehan L, Meredith RW, Emerling CA, Springer MS (2016) Phylogenetic relationships of dasyuromorphian marsupials revisited. Zool J Linn Soc 176:686–701. https://doi.org/10.1111/zoj.12323

Wilson DE (2009) Class Mammalia (mammals). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World. Vol. 1. Carnivores. Lynx Edicions, Barcelona, pp 17–47