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THE SCOPE OF TRADITIONAL AND GEOMETRIC MORPHOMETRICS FOR INFERENCES OF DIET IN CARNIVOROUS FOSSIL MAMMALS

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ABSTRACT. Molar morphology is one of the most used proxies for paleoecological inferences in mammals. Since the 19th century, several authors associated dental morphological traits with the diet of an animal by means of qualitative and descriptive analyses. More recently, different studies of tooth function have associated various quantitative traits of tooth shape (*i.e.*, morphometric ratios or angles) with the different items consumed by the animal. However, because different inferences of diet for the same species can be found in the literature, it is crucial to study the power of different proxies. In this work, we compared the utility of classic morphometric indices (RGA, AI and angle α) and three-dimensional landmarks configuration to infer diet. Based on a previously published dataset from our working group, we calculated the classic morphometric indices and performed three classification methods: linear discriminant analysis, quadratic discriminant analysis, and weighted random forest. Our results demonstrate that when using the geometric morphometrics approach, the diet of species is better reclassified than when using morphometric indices. Furthermore, intraspecific variation appears fundamental when making paleoecological inferences. In inferring ecological characteristics of extinct animals, studying morphological variation in extant organisms is a safeguard to prevent misinterpretations when reconstructing past ecologies.

KEYWORDS. Diet classification. Carnivora. Morphometric indices. Weighted random forest.

RESUMEN. ALCANCE DE LA MORFOMETRÍA TRADICIONAL Y GEOMÉTRICA A LA HORA DE INFERIR LA DIETA EN LOS MAMÍFEROS FÓSILES CARNÍVOROS. La morfología del molar es uno de los *proxies* más utilizados para las inferencias paleoecológicas en los mamíferos. Desde el siglo XIX,

varios autores asociaron algunos rasgos morfológicos dentales con la dieta del animal mediante análisis cualitativos y descriptivos. Más tarde, a partir del siglo pasado, diferentes estudios sobre la función dental han asociado varios rasgos cuantitativos de la forma del diente (es decir, proporciones o ángulos morfométricos) con el porcentaje de carne de vertebrados que consume el animal. Sin embargo, debido a que en la literatura se pueden encontrar diferentes inferencias de la dieta para la misma especie, es crucial llevar a cabo estudios que comparen la precisión de diferentes *proxies*. En este trabajo, comparamos la utilidad de los índices morfométricos clásicos (RGA, AI y ángulo α) y la configuración de *landmarks* tridimensionales con respecto a las inferencias de la dieta. Sobre la base de un conjunto de datos previamente publicado por nuestro grupo de trabajo, calculamos los índices morfométricos clásicos y realizamos tres métodos de clasificación: análisis discriminante lineal, análisis discriminante cuadrático y análisis de bosques aleatorios ponderados. Nuestros resultados demuestran que al usar la configuración de *landmarks*, la dieta de las especies se reclasifica mejor que cuando se usan índices morfométricos. Además, considerar la variación intraespecífica al hacer inferencias paleoecológicas parece fundamental. Teniendo el propósito de inferir características ecológicas en animales extintos, la consideración de la variación morfológica en los organismos actuales es una garantía para evitar cualquier interpretación errónea en las reconstrucciones de ecologías pasadas.

PALABRAS CLAVES. Clasificación de la dieta. Carnivora. Índices morfométricos. Bosques aleatorios ponderados.

THE analysis of diets is an important component of ecological and paleoecological studies (Price *et al.*, 2012; Kissling *et al.*, 2014; Davis and Pineda Munoz, 2016; Croft *et al.*, 2018a). Many proxies have been used to determine the diet of mammalian species, including direct observations of feeding behavior, stomach and fecal contents, dental microwear and mesowear, isotope analysis of nitrogen and carbon, and craniodental morphology, among others (see review in Davis and Pineda Munoz, 2016). Although often considered to represent the same parameter, these different proxies offer different evidences of the items consumed, have different scopes (*i.e.*, extant and/or fossil species), and are constrained by different methodological aspects (*i.e.*, cost, difficulty and time of study, availability of data) (Evans, 2013; Davis and Pineda Munoz, 2016). In particular, the study of molar morphology combines low cost and low methodological difficulty, thus making it one of the most widely used proxies in paleoecological studies of mammals (*e.g.*, Marshall, 1978; Goin *et al.*, 1992; Van Valkenburgh *et al.*, 2004; Vizcaíno *et al.*, 2006; Prevosti *et al.*, 2013; Croft *et al.*, 2018b; Harper *et al.*, 2018).

The versatility of tribosphenic molars has been shown to be a key innovation in the evolution of mammals, increasing the taxonomic diversity and ecological disparity of this group throughout their evolutionary history (Woodburne *et al.*, 2003; Luo, 2007). Molars are also usually the sole identifiable remains of an extinct mammal, and therefore have been intensively used for taxonomic classifications in addition to dietary reconstructions (*e.g.*, Marshall, 1978; Ungar, 2010; Goin and de los Reyes, 2011). Since the 19th century, several authors have associated certain dental morphological traits with dietary habits by means of qualitative and descriptive analyses (*e.g.*, Lund, 1839; Ryder, 1878; Cope, 1879; Butler, 1946; Marshall, 1978; Reig *et al.*, 1987; Berta, 1989). More recently, different studies of tooth function have correlated several quantitative

traits of tooth shape (*i.e.*, morphometric ratios or angles) with the different items consumed by the animal. These quantitative tools continue to be used today, and while some have used isolated indices (*e.g.*, Crusafont-Pairó and Truyols-Santonja, 1956; Goin *et al.*, 1992; Strait, 1993a, b; Evans *et al.*, 2005; Vizcaíno *et al.*, 2006; Prevosti *et al*., 2013), others have used several indices to define a morphospace (*e.g.*, Kay, 1975; Van Valkenburgh, 1989; Popowics, 2003; Wesley-Hunt, 2005; Friscia *et al.*, 2007; Asahara *et al.*, 2016; Croft *et al.*, 2018b). Moreover, with the development of new technologies, new dental shape descriptors have been developed to study molar morphology (Evans, 2013). On the one hand, some authors have defined metrics to reflect occlusal surface topography, such as the Dirichlet normal energy, relief index, and orientation patch count (Zuccotti *et al.*, 1998; Ungar and M'Kirera, 2003; Evans *et al.*, 2007; Boyer, 2008; Bunn *et al.*, 2011; Smits and Evans, 2012). On the other hand, other approaches to study tooth morphology have arisen with the development of geometric morphometric techniques, where shape is captured through the use of landmark coordinates (either two- or three-dimensional) and analyzed as a whole, taking into account several shape changes instead of a few measurements (Vizcaíno *et al.*, 2016). For example, some authors have digitized the molars with the aim of assessing the relationships between molar shape and diet: elliptic Fourier analysis has been applied in rodents (Gómez Cano *et al.*, 2013); 2D geometric morphometrics has been used in rodents (Caumul and Polly, 2005), primates (White, 2009), rhinos (Piras *et al.*, 2010), and in didelphid marsupials (Chemisquy *et al.*, 2015; Magnus and Cáceres, 2017); and 3D geometric morphometrics has been used in primates (Cooke, 2011; Singleton et al., 2011) and in carnivorous species (Tarquini *et al.*, 2018).

The strong form-function relationship of the dentition of living mammals has allowed paleontologists to make inferences of diet in fossil species (*e.g.*, Van

Valkenburgh, 1989; Goin *et al.*, 1992; Prevosti *et al.*, 2013; Zimicz, 2014a; Croft *et al.*, 2018b). Within a historical framework, diet reconstructions are crucial for constructing trophic webs, examining evolutionary changes in lineages, and inferring ancient climates and habitats (Pascual and Jaureguizar, 1990; Van Valkenburgh *et al.*, 2004; Dalerum and Angerbjörn, 2005; Prevosti *et al.*, 2013; Echarri *et al.*, 2017). However, in a recent study, we demonstrated the need to take certain precautions before making inferences, because the morphology of the molar not only correlates with diet but also is influenced by the phylogenetic position of each taxa (Tarquini *et al.*, 2018). In any case, the use of different techniques to analyze molar morphology generates the following question: are all methodologies utilized to quantify dental morphology equally reliable?

Usually, inferences of diet in South American predatory mammals are tackled with traditional morphometric analyses, using measurements from the lower molars such as the relative grinding area index or the angle of the paracristid to the tooth row (see Materials and Methods for further details; *e.g.*, Van Valkenburgh, 1991; Goin *et al.*, 1992; Zimicz, 2014b; Prevosti and Forasiepi, 2018). However, morphometric ratios or angles only represent some aspects of the shape, and the geometric and spatial relationships among the measurements are not considered (Bookstein, 1991; Rohlf and Marcus, 1993; Adams *et al.*, 2004; Zelditch *et al.*, 2004; Slice, 2007; Mitteroecker and Gunz, 2009). In other words, shape can be better approximated by landmark coordinates than by linear measurements, as has been demonstrated in numerous different test cases (*e.g.*, Fabre *et al.*, 2014; Schmieder *et al.*, 2015; Lallensack *et al.*, 2016). Subsequently, new approaches using 2D geometric morphometrics have been used to study the mandibles of South American predators (Meloro *et al.*, 2008; Prevosti *et al.*, 2012a; Echarri *et al.*, 2017). However, it is important to note that some problems have arisen with the use of 2D techniques for studying three-dimensional structures, such as the

photographic distortion and the difficulty to capture shape variation as a whole (Álvarez and Perez, 2013; Collins and Gazley, 2017). This led us to hypothesize that 3D geometric morphometrics may turn out to be a more powerful predictive tool than other previously used techniques based on linear measurements, as it represents different aspects of the molar at the same time.

MATERIALS AND METHODS

Samples and landmarks

The results of this study are based on the dataset of Tarquini *et al.* (2018), which includes digitalizations of the first lower molar (m1) of 213 specimens corresponding to 67 extant species of Carnivora, and the fourth lower molars (m4) of 14 specimens corresponding to 4 extant species of Marsupialia, including both Didelphimorphia and Dasyuromorphia (Supplementary Online Information 1). The carnivoran m1 and carnivorous marsupial m4 are considered to be functionally analogous teeth following Tarquini *et al.* (2018). The specimens belonging to the insectivore category from the parent dataset were excluded due to small sample size (only three species: *Dasyurus viverrinus*, *Galerella sanguínea*, and *Otocyon megalotis*). The classification of dietary categories in this study follows Tarquini *et al.* (2018): 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; Piscivores —feed mostly on fish.

The digitalization comprises nine three-dimensional landmarks (ldk): 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 ten semi-landmarks to delimit the base of the crown (Fig. 1). For information regarding landmark and semilandmark treatment, see Tarquini *et al.* (2018).

Morphometric indices

In the literature, several indices have been used to analyze the molar morphology of carnivorous mammals. The indices are relationships between measurements, such as the shear ratio (Strait, 1993a, 1993b; Hogue and Ziashakeri, 2010) and the relative lower grinding area (RGA; Van Valkenburgh, 1989; Prevosti *et al.*, 2013). RGA is measured as the square root of the area of the m1 talonid divided by the relative blade length (BL). The area was estimated as the product of maximum width (WT) and length (LT) of the talonid of m1, and the BL was estimated as the length of the m1 trigonid. We use the index as defined by Prevosti *et al.* (2013), modified from Valkenburgh (1989), which has two advantages: first, it can be applied in fossils that only have the carnassial preserved; and second, the RGA value can be compared in both Carnivora and Metatheria. Other indices include morphometric angles, such as those that describe the relationship 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; Wesley-Hunt, 2005; Meloro and Raia, 2010).

Using the configuration of landmarks mentioned above, we calculated the following morphometric indices with Rhinoceros 3D V5.0 software: angle α, AI, and RGA. The angle α was calculated using ldks 3, 8 and 9. For AI, ldk 1, 3, 8 and 9 were used. RGA was calculated using ldks 5, 8 and 9 and the two semilandmarks that define the maximum width of the talonid (Fig. 1).

We also calculated alternative RGAs taking into account a more accurate measurement of the blade length (BL', *i.e.*, distance between the paraconid, ldk 1, and the protoconid, ldk 3) and a more accurate measurement of the area of the m1 talonid (*i.e.*, polygon area (PA) formed by all semilandmarks of talonid) (Fig. 2). However, neither using the BL' nor using the PA led to better discriminating functions; consequently, the detailed results are not reported here.

Statistical analyses

We used the scores of between-group PCA (bg-PCA) conducted in Tarquini *et al.* (2018) for the new analyses (see below). The bg-PCA can be understood as a PCA in two steps: first, we made a PCA with the average shape of each dietary category, and then we plotted the entire dataset on these axes (Mitteroecker and Bookstein, 2011; Seetah *et al.*, 2012). We used the axes of bg-PCA as representatives of shape, which brings about two advantages. First, when the axes of the PCA are constructed, the variance of the whole sample is maximized, while in the bg-PCA, the variance of the dietary categories is maximized but without distorting the geometry of the multivariate space (Klingenberg and Monteiro, 2005; Mitteroecker and Bookstein, 2011). Second, fewer axes are obtained in bg-PCA (the number of categories minus one, in this case four) than in PCA, which avoids problems with the quantity of variables when using PC axes in discriminant analyses (Kovarovic *et al.*, 2011) but without discarding any morphological information.

In order to study the behavior of morphometric indices, we performed three analyses. First, we evaluated the covariation between indices to test independence in the case of using them as variables of the same analysis. We performed a Spearman correlation since the Shapiro-Wilk test demonstrated that the indices are not normally

distributed. The Shapiro-Wilk test, the Spearman correlation and regression analyses were performed using the *stats* package for the software R 3.5.1 (R Core Team, 2018). Second, we conducted a multivariate regression to quantify how much of the change in the shape (Procrustes coordinates) could be explained by the different indices. Finally, we performed a simple linear regression between the various indices and the axes of the bg-PCA. Following the regressions, a permutation test was performed to evaluate the complete independence between the dependent and independent variables. Regression analysis and the permutation test were performed using the software MorphoJ 1.06b (Klingenberg, 2011).

Although a PCA or bg-PCA would allow us to see the graphical distribution of the diet taking into account the values of the different predictor variables (angle α, AI, RGA, or landmark configuration), it is important to quantify the relative performance of each predictor variable to infer diets. That is the reason why we conducted several linear discriminant analyses (LDA): some with the scores of the bg-PCA (to analyze the scope of geometric morphometrics) and others with the morphometric indices, together and separately (to analyze the scope of traditional morphometrics). Given the known problems of performing a LDA with geometric morphometrics data (Kemsley, 1996; Sheets *et al.*, 2006), and to avoid a bias due to the analysis used, we also carried out two learning methods for classification: quadratic discriminant analyses (QDA) and random forest analyses (RF). The QDA is very similar to the LDA but does not assume identical covariance for each class and produces a quadratic boundary between the classes (Venables and Ripley, 2002; Dixon and Brereton, 2009). The RF is a nonmetric method based on bootstrap resampling techniques of decision trees, which have made it a powerful tool with greater precision than neural networks, classification trees, linear and quadratic DAs, and k-nearest neighbors (Breiman, 2001; Maroco *et al.*, 2011).

However, the regular RF is constructed to minimize the overall error rate, so it tends to be biased toward the majority class (Chen *et al.*, 2004; Zhu and Pierskalla, 2016). Given that our dataset is unbalanced (*i.e.*, there are six herbivores, 105 hypercarnivores, 34 mesocarnivores, 71 omnivores, and 13 piscivores), we proceeded to perform a weighted random forest (WRF), as proposed by Chen *et al.* (2004), which avoids the bias towards the most numerous classes. To evaluate the performance of classification methods based on different predictors, we compared the percentage of correct posterior reclassification (PCPR) and the error rate (% Error) calculated from the confusion matrix. This is obtained in an innate way by the bootstrap resampling in the WRF and from the cross-validation procedure in both LDA and QDA (Breiman, 2001; Venables and Ripley, 2002; Kovarovic *et al.*, 2011). PCPR was calculated globally and for each category; it is understood as the number of animals correctly reclassified in a dietary category divided by the total of animals belonging to that category. % Error was calculated for each category as the number of animals wrongly reclassified in a dietary category divided by the total of animals reclassified in that category. Additionally, as mentioned above, molar morphology has a significant phylogenetic signal, so that within each family, the degree of morphological variation is variable (Tarquini *et al*., 2018). For that reason, we repeated the classification methods only with the species of the Canidae subgroup, which is also a group where morphometric indices are widely used. LDA, QDA and WRF were performed using the *MASS* and *randomForest* packages (Liaw and Wiener, 2002; Venables and Ripley, 2002) in R 3.5.1 (R Core Team, 2018).

Intraspecific variation

When reviewing previous works, we noted that a few authors have considered intraspecific variation, whereas the majority have not. To compare criteria, we analyzed RGA values calculated from unpublished measurements taken by calipers (Prevosti,

2006) and compared using the average RGA value per species to using RGA values for each specimen separately.

RESULTS

The morphometric indices showed high and significant correlations: RGA vs. angle α (ρ = -0.87, p-value < 0.0001), RGA vs. AI (ρ = 0.88, p-value < 0.0001) and AI vs. angle α (ρ = -0.77, p-value < 0.0001). The regressions against the Procrustes coordinates showed that the indices have a low correlation with shape variation: RGA explained 53.30% of the change in the shape (p-value < 0.0001), AI explained 37.37% (p-value < 0.0001) and angle α explained 49.42% (p-value < 0.0001). By contrast, bg-PC1 (the axis that has the highest proportion of shape change in the bg-PCA) explained the shape variation better than any of the morphometric indices (76.59% percent of variance). Finally, when we analyzed the covariation between the bg-PCs and the morphometric indices, we observed that a large portion of variation explained by bg-PC1 could also be explained by the morphometric indices (percentage of covariance greater than 60%; Tab. 1), whereas there was a low covariation between the morphometric indices and the other axes of bg-PCA (percentage of covariance less than 20%; Tab. 1).

The three classification methods (LDA, QDA and WRF) returned a similar pattern of global PCPR (Tab. 2). The only differences observed were in the performance of the indices when comparing them to each other. However, in all cases when using the scores of the bg-PCA, the diet of a species was better reclassified than when using morphometric indices. Hereafter, we describe the results of WRF to transmit the idea more clearly, which are shown in Table 2 together with the results of the other two analyses. Using all the axes of the bg-PCA, the WRF correctly reclassified 89.96% of

the specimens; using only the first axis, the PCPR was 74.67% (Tab. 2). On the other hand, none of the analyses using individual morphometric indices exceeded 66 PCPR (Tab. 2). Even using all of the indices together, the PCPR was only 75.98% (Tab. 2).

It is interesting to note that the model with the scores of the bg-PCA had an excellent reclassification (higher PCPR and lower % Error) in the hypercarnivorous and piscivorous categories, and a good reclassification (higher PCRP and average % Error) in the mesocarnivorous and omnivorous categories, while it had a bad reclassification (low PCPR and average % Error) in the herbivorous category (Supplementary Online Information 2). Otherwise, the models with the morphometric indices tended to reclassify the different dietary categories with higher % Error (regardless of the value of PCPR) than the model with bg-PCs (Supplementary Online Information 2). Additionally, the indices tend to have a bias to hypercarnivores since it is usually the category with the highest PCPR and the lowest % Error (Supplementary Online Information 2).

When we subdivided the dataset and scrutinized only the Canidae, the results did not change substantially. The scores of the bg-PCA still better reclassified the diet of species than the morphometric indices (Tab. 3 and Supplementary Online Information 3). The discriminant function obtained with the scores of the bg-PCA had a 92.31 PCPR, while that obtained with the indices the PCRP did not exceed 68% (Tab. 3).

Finally, in the intraspecific variation test, we observed that when using the average value of RGA, the separation between dietary categories was clearer than when using all the values of each specimen (Supplementary Online Information 4). Using the average values, under this example, the diets could be classified with a series of logical rules: a taxon can be considered hypercarnivorous when the RGA index is lower than

0.45; mesocarnivorous when the RGA index range from 0.46 to at least 0.47; omnivorous when the RGA index ranges from 0.60 (perhaps lower) to 0.68; and insectivorous when the RGA index is larger than 1. However, when the index is between 0.48 and 0.59, the classification is ambiguous, and the taxon may be omnivorous or mesocarnivorous. On the other hand, if intraspecific variation is considered, the superposition zone is much larger. If the value of RGA is lower than 0.40, the taxon is hypercarnivorous; between 0.40 and 0.42, it may be hypercarnivorous or mesocarnivorous; between 0.43 and 0.48, it may be hypercarnivorous, mesocarnivorous or omnivorous; between 0.48 and 0.69, it may be mesocarnivorous or omnivorous; and larger than 1, it is insectivorous (Supplementary Online Information 4).

DISCUSSION

Because of the hardness of dental tissues, teeth are the mammalian body parts most likely to be preserved in the fossil record and, consequently, the elements most frequently found and studied (Carlson, 1989; Benton and Harper, 2009; Ungar, 2010). Combined with the importance of the teeth in the acquisition and processing of food, this makes tooth morphology an important source of information for understanding and inferring the ecological habits of fossil species (*e.g.*, Van Valen, 1969; Kay, 1975; Marshall, 1978; Van Valkenburgh, 1989; Prevosti *et al.*, 2013; Solé and Ladevèze, 2017; Tarquini *et al.*, 2018). Bearing that in mind, there have been different inferences of diet for the same species in the literature, making it necessary to carry out studies that include diverse proxies (*e.g.*, Soibelzon *et al.*, 2014; Pineda-Munoz *et al.*, 2017) or to compare the power of different proxies. Our results indicate that 3D geometric morphometrics is a very powerful tool to study molar morphology and is better than traditional morphometrics when it comes to predicting feeding habits. The discriminant

function obtained (regardless of the chosen classification method) displays a greater predictive power than that obtained from the indices (Tabs. 2 and 3). Since the PCPR tends to increase when adding explanatory variables, we performed the classification methods with the first bg-PC to compare against isolated indices, and with the first three bg-PCs against the combined indices. All comparisons showed that geometric morphometric data are better for classifying diets than classical morphometric indices (Tabs. 2 and 3). Although the bg-PC1 explained more shape variation than any of the indices, the variation within this first axis could be explained partially using the indices (*e.g.*, specimens at the positive end of bg-PC1 have a molar with the paracristid parallel to the mesiodistal axis and the talonid is reduced or absent; Tarquini *et al.*, 2018).

It is noteworthy that the bg-PCA, based on geometric data, provided a diffused low degree of separation between diet categories, with different degrees of overlap among them. Nevertheless, as we discussed in a previous work (Tarquini *et al.*, 2018), this might be in part related to the intrinsic definition of diets and the disadvantage of 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). This is why this problem is not intrinsically related to geometric morphometric, and in studies that include a broad taxonomic sampling (several species across all Carnivora), it appears difficult to choose a unique value of RGA (or equivalent index) to separate each dietary categories (Van Valkenburgh, 1989; Friscia *et al.*, 2007; Zimicz, 2012; Prevosti *et al.*, 2013). Some authors have chosen to use several indices to define morphospaces that better separate the categories (Van Valkenburgh, 1989; Friscia *et al.*, 2007), although these ratios have high correlation values between them (as also calculated here). This is due to the fact that the indices are calculated with anatomical points or landmarks in common. This

issue is easily circumvented with geometric morphometrics because it avoids any overrepresentation of data by working directly with the landmarks coordinates.

As we mentioned in the introduction, to improve the accuracy of dietary inferences from dental morphology it is necessary to take into account the phylogenetic framework (Tarquini *et al.*, 2018). This is the reason why we restricted our dataset to a less inclusive clade, the Canidae (Tab. 3 and Supplementary Online Information 3). Although there are differences in the performance of the indices when comparing them to each other (*e.g.*, RF and LDA indicated that the AI is the best diet estimator, while QDA indicated that the RGA is the best one), they all agreed that the scores of the bg-PCA better reclassified the diet of species. When examining where the differences in the reclassification were, the confusion matrix showed that, whatever the classification method, the morphometric indices principally struggled to discern correctly hypercarnivores form mesocarnivores. Van Valkenburgh (1991) pointed out that although the molars of hypercarnivorous canids (*Canis lupus*, *Cuon alpinus*, *Lycaon pictus*, and *Speothos venaticus*) are specialized, they do not reach the cat-like extreme condition seen in felids and, to a lesser degree, in hyaenids. For this reason, when we calculated the indices, hypercarnivores and mesocarnivores overlapped and were reclassified erroneously (Tab. 4). This problem was not mentioned by previous authors, since they worked with the average of the indices (see below).

When reviewing previous works, we also noted that another criterion that differs in the methodologies is the use of the average value of the index per species versus the use of the observed variation (*i.e.*, including the value of each specimen separately). In this work, we considered all specimens individually in order to properly account for intraspecific morphological variation. Goin *et al.* (1992) calculated a series of basic

statistics (such as mean, variance, standard deviation, etc.) to evaluate intraspecific morphological variation in the molars of didelphids, whereas in the majority of the other works (Van Valkenburgh, 1989; Prevosti *et al.*, 2013), the authors only used the average value, without specifying exactly how many specimens were measured for each species. To compare criteria, we analyzed the indices calculated from the landmarks and others from unpublished measurements taken by calipers (Prevosti, 2006) and discovered that if the maximum and minimum values of each species are considered, the ranges of overlap between the dietary categories used increases (Supplementary Online Information 4). In fact, it is possible that the use of a central tendency statistic minimizes the real overlap that exists between categories. However, this problem persists when there are few specimens per species (which is commonly the case in fossil taxa), since the average value of the specimens examined is not likely to be representative of the actual average value for the species, which in turn is likely to lead to misinterpretations in the ecology of the fossil species analyzed.

CONCLUSION

This work quantitatively evaluated the power of different proxies to describe the molar morphology of extant carnivore mammals and how it relates to diet. Our results demonstrated that 3D geometric morphometrics is better than traditional morphometrics to predict feeding habits, as using landmarks provides more information than working with isolated measurements or angles of teeth. Moreover, we discussed the importance of considering the intraspecific variation. As the ultimate purpose of these analyses is to infer ecological characteristics in fossils, misinterpretations in the ecology of the fossil specimens can be avoided when the variation of extant organisms is considered.

A better understanding of the methodology used to infer diets in fossils would allow a better comprehension of the ecology of these animals. Having more precise classifications about different ecological traits of the South American carnivorous mammals would allow us to test extinction hypothesis of some carnivore guilds with greater assurance.

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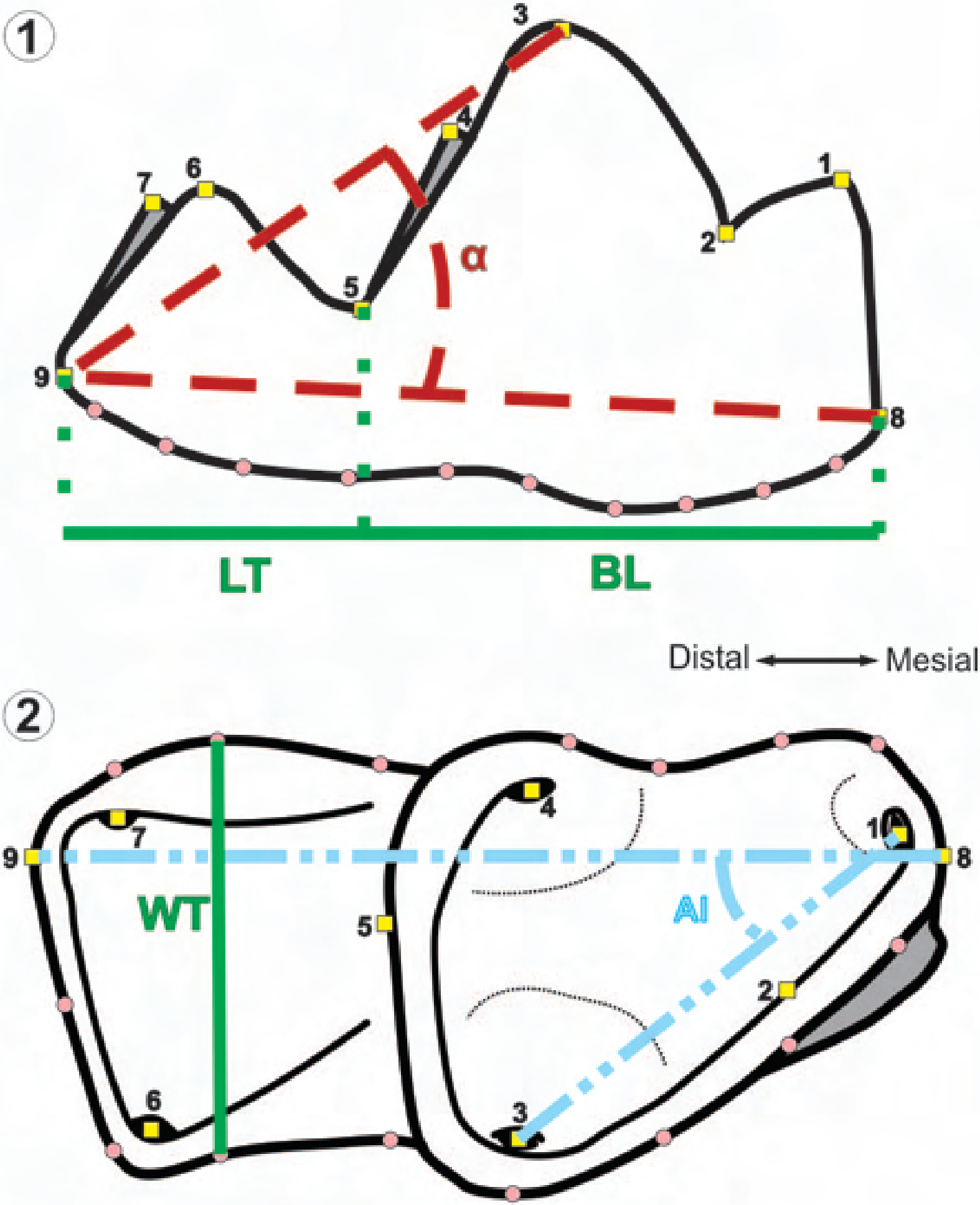
FIGURE CAPTIONS

Figure 1. Diagram of landmarks and measurements taken on specimens, in labial view **(1)** and occlusal view **(2)**. Yellow squares, landmarks; pink 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. Angle α (**α**) is shown in dark red dashed lines. Lower angle (**AI**) is shown in light blue dash-dotted lines. Measurements used for RGA are green solid lines: **BL**, relative blade length; **WT**, maximum width of the talonid; **LT** length of the talonid;

Figure 2. Alternative measurements taken on specimens to calculate alternative RGAs. Symbols of landmarks as in Figure 1. Measurements: **BL'**, alternative blade length; **PA**, polygon area of the talonid.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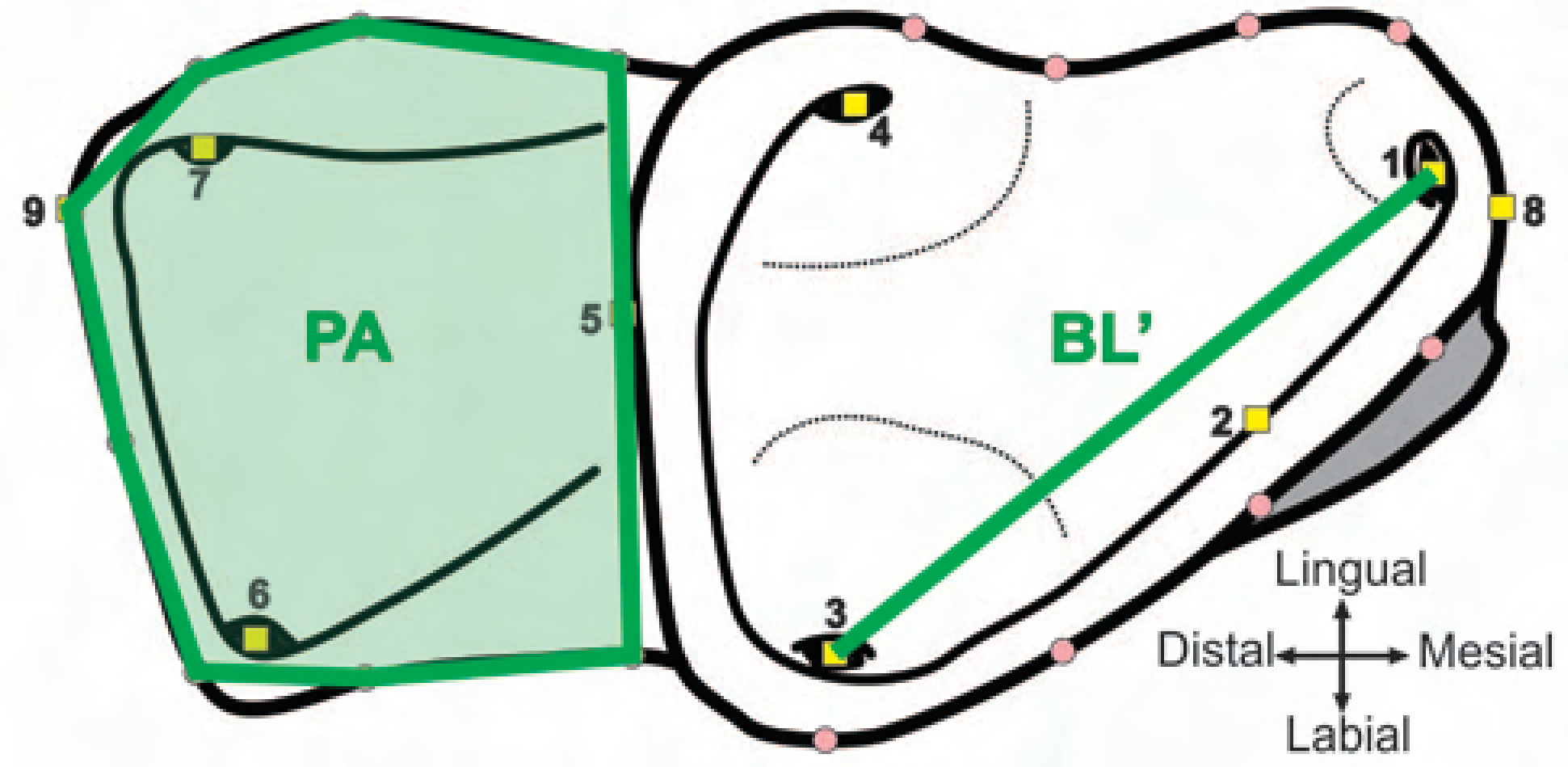
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Lingual
Distal
Mesial
Labial

TABLE 1 - Results of the regression analyses between morphometric indices and bgPCs

	RGA		*AI*		*Angle α*	
	%	*P*	*%*	*P*	*%*	*P*
bgPC1	*94.34*	*< 0.0001*	*64.97*	*< 0.0001*	*84.34*	*< 0.0001*
bgPC2	*06.92*	*< 0.0001*	*02.85*	*0.0104*	*18.29*	*< 0.0001*
bgPC3	*12.01*	*< 0.0001*	*04.31*	*0.0017*	*11.70*	*< 0.0001*
bgPC4	*09.21*	*< 0.0001*	*00.26*	*0.4565*	*10.84*	*< 0.0001*

%, percentage of variance explained; P, probability for each analysis

TABLE 2 - Summary of Confusion matrices of the different Discriminant Analyses displaying the global PCPR (Percentage of Correct Posterior Reclassification)

	Lineal Discriminant Analysis	*Quadratic Discriminant Analysis*	*Weighted Random Forests*
All (4) bg-PCs	*78.17%*	*79.91%*	*89.96%*
3 bg-PCs	*69.43%*	*72.49%*	*85.59%*
All (3) indices	*50.22%*	*60.26%*	*75.98%*
bg-PC1	*56.33%*	*57.64%*	*74.67%*
RGA	*50.66%*	*50.66%*	*62.01%*
AI	*46.72%*	*53.28%*	*65.07%*
Angle α	*51.09%*	*47.16%*	*50.66%*

TABLE 3 - Summary of Confusion matrices of the different Discriminant Analyses within Canidae displaying the global PCPR (Percentage of Correct Posterior Reclassification)

	Lineal Discriminant Analysis	*Quadratic Discriminant Analysis*	*Weighted Random Forests*
All (2) bg-PCs	*90.38%*	*90.38%*	*92.31%*
All (3) indices	*71.15%*	*65.38%*	*69.23%*
bg-PC1	*86.54%*	*84.62%*	*75.00%*
RGA	*50.00%*	*65.38%*	*61.54%*
AI	*57.69%*	*57.69%*	*67.31%*
Angle α	*36.54%*	*32.69%*	*42.31%*

TABLE 4 - Summary of dietary classification obtained from Weighted Random Forests within hypercarnivorous and mesocarnivorous Canidae

Collection number	*Species*	*Diet*	*All (3) indices*	*All (2) bg-PCs*
MLP-MA 1035	**Canis aureus**	*Mesocarnivore*	*Omnivore*	*Mesocarnivore*
MACN-MA 25123	**Canis latrans**	*Mesocarnivore*	*Hypercarnivore*	*Mesocarnivore*
MLP-PV S/N	**Canis latrans**	*Mesocarnivore*	*Omnivore*	*Mesocarnivore*
MLP-MA 1027	**Canis latrans**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 23.15	**Canis lupus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
MACN-MA 4256	**Canis lupus**	*Hypercarnivore*	*Mesocarnivore*	*Mesocarnivore*
MLP-MA 30	**Canis lupus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
AMNH(M) S/N	**Cuon alpinus**	*Hypercarnivore*	*Hypercarnivore*	*Hypercarnivore*
MACN-MA 15109	**Lycalopex culpeus**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 20813	**Lycalopex culpeus**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 23719	**Lycalopex culpeus**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 23915	**Lycalopex culpeus**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 31.59	**Lycalopex culpeus**	*Mesocarnivore*	*Mesocarnivore*	*Mesocarnivore*
MACN-MA 38.39	**Lycalopex culpeus**	*Mesocarnivore*	*Hypercarnivore*	*Mesocarnivore*
AMNH(M) S/N	**Lycaon pictus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
MACN-MA 38249	**Lycaon pictus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
AMNH(M) S/N	**Speothos venaticus**	*Hypercarnivore*	*Hypercarnivore*	*Hypercarnivore*
MACN-MA 16510	**Speothos venaticus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
MACN-MA 50.67	**Speothos venaticus**	*Hypercarnivore*	*Mesocarnivore*	*Hypercarnivore*
MACN-MA 35203	**Vulpes lagopus**	*Mesocarnivore*	*Mesocarnivore*	*Hypercarnivore*
MACN-MA 4.1	**Vulpes lagopus**	*Mesocarnivore*	*Hypercarnivore*	*Mesocarnivore*
MACN-MA 25149	**Vulpes vulpes**	*Mesocarnivore*	*Mesocarnivore*	*Omnivore*
MLP-MA 744	**Vulpes vulpes**	*Mesocarnivore*	*Omnivore*	*Mesocarnivore*
MLP-PV S/N	**Vulpes vulpes**	*Mesocarnivore*	*Hypercarnivore*	*Mesocarnivore*

The scope of traditional and geometric morphometrics for inferences of diet in carnivorous fossil mammals

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SUPPLEMENTARY ONLINE INFORMATION 1. Studied species and specimens and their dietary classification.

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Eutheria					
Carnivora					
Feliformia					
Felidae					
Felinae					
Acinonyx jubatus	MACN-MA 49.36	m1	-	Africa	Hypercarnivore (Sunquist & Sunquist, 2009)
Felis catus	MACN-MA 23688	m1	-	-	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 23700	m1	-	-	
	MACN-MA 23701	m1	-	-	
	MACN-MA 23702	m1	-	-	
Herpailurus yagouaroundi	MACN-MA 17254	m1	♀	Bolivia	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 23692	m1	♀	Misiones, Argentina	
	MACN-MA 25772	m1	♂	Salta, Argentina	
	MACN-MA 33.4	m1	♂	Mendoza, Argentina	
	MACN-MA 50104	m1	♂	-	
	MACN-MA 50555	m1	♂	Misiones, Argentina	
Leopardus colocolo	MACN-MA 16489	m1	-	Neuquén, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 22928	m1	♀	Salta, Argentina	
	MACN-MA 22934	m1	-	Santa Cruz, Argentina	
	MACN-MA 23176	m1	-	La Pampa, Argentina	
	MACN-MA 30103	m1	♂	Neuquén, Argentina	
Leopardus geoffroyi	MACN-MA 15425	m1	♂	Córdoba, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 22022	m1	-	Bs. As., Argentina	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Leopardus geoffroyi	MACN-MA 24214	m1	♂	La Rioja, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 23329	m1	♀	Neuquén, Argentina	
	MACN-MA 34337	m1	♀	La Pampa, Argentina	
	MACN-MA 39209	m1	♀	La Pampa, Argentina	
Leopardus guigna	MLP-MA 1297	m1	-	Chubut, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
Leopardus pardalis	MACN-MA 13464	m1	♀	Bolivia	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 13465	m1	♀	Misiones, Argentina	
	MACN-MA 50.98	m1	♂	Misiones, Argentina	
	MACN-MA 50101	m1	♀	Tucumán, Argentina	
	MACN-MA 50540	m1	♂	Santa Fé, Argentina	
	MACN-MA 51132	m1	♂	Bolivia	
Leopardus tigrinus	MACN-MA 23709	m1	♂	Misiones, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 51121	m1	-	Misiones, Argentina	
	MACN-MA 52.57	m1	♂	Misiones, Argentina	
Leopardus wiedii	MACN-MA 23694	m1	-	Misiones, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 24899	m1	♀	Misiones, Argentina	
	MACN-MA 50.94	m1	♂	Bolivia	
	MACN-MA 50.95	m1	-	Misiones, Argentina	
	MACN-MA 50.97	m1	♂	Bolivia	
	MACN-MA 51137	m1	♂	Bolivia	
Lynx rufus	MACN-MA 25.118	m1	♂	Mexico	Hypercarnivore (Sunquist & Sunquist, 2009)
	MLP-PV S/N	m1	♂	Millbridge, Maine, USA	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Puma concolor	MACN-MA 13339	m1	-	San Luis, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 20629	m1	-	La Pampa, Argentina	
	MACN-MA 30250	m1	♂	Neuquén, Argentina	
	MACN-MA 32.80	m1	♀	San Luis, Argentina	
	MACN-MA 36614	m1	♂	Santa Cruz, Argentina	
	MACN-MA 49295	m1	-	Salta, Argentina	
Pantherinae					
Panthera leo	MACN-MA 23.1	m1	-	Africa	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 25158	m1	-	Africa	
	MACN-MA 29904	m1	♀	Africa	
	MACN-MA 4254	m1	-	Africa	
	MACN-MA 4330	m1	-	Africa	
	MACN-MA 4337	m1	-	Africa	
Panthera onca	MACN-MA 21622	m1	-	Misiones, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 25.66	m1	-	Misiones, Argentina	
	MACN-MA 25769	m1	♀	Tucumán, Argentina	
	MACN-MA 4301	m1	-	South America	
	MACN-MA 7.8	m1	-	Bolivia	
	MACN-MA 8.43	m1	-	Bolivia	
Panthera pardus	MLP-MA 1040	m1	-	Africa	Hypercarnivore (Sunquist & Sunquist, 2009)
Panthera tigris	MACN-MA 25.54	m1	-	Sumatra	Hypercarnivore (Sunquist & Sunquist, 2009)
	MACN-MA 26.83	m1	-	India	
	MLP-MA 1048	m1	-	-	
	MLP-MA 1051	m1	-	-	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Panthera tigris	MLP-MA 112	m1	-	India	Hypercarnivore (Sunquist & Sunquist, 2009)
	MLP-MA 11-IV-48-1	m1	-	-	
Panthera uncia	MACN-MA 8.23	m1	-	Asia	Hypercarnivore (Sunquist & Sunquist, 2009)
Herpestidae					
Herpestinae					
Herpestes ichneumon	MLP-MA 1029	m1	-	Africa	Hypercarnivore (Rosalino *et al.*, 2009)
	MLP-MA 1323	m1	-	Africa	
Hyaenidae					
Hyaeninae					
Crocuta crocuta	MACN-MA 24525	m1	-	Africa	Hypercarnivore (Holekamp & Kolowski, 2009)
	MACN-MA 33277	m1	-	Africa	
Hyaena hyaena	MACN-MA 15.28	m1	-	Africa	Mesocarnivore (Holekamp & Kolowski, 2009)
	MACN-MA 25103	m1	-	Africa	
	MACN-MA 4.6	m1	-	Africa	
	MLP-MA 1039	m1	-	-	
Viverridae					
Genettinae					
Genetta genetta	MACN-MA 21104	m1	-	Spain	Mesocarnivore (Torre *et al.*, 2003)
	MACN-MA 21105	m1	-	Spain	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Genetta genetta	MACN-MA 21106	m1	-	Spain	Mesocarnivore (Torre *et al.*, 2003)
	MACN-MA 21107	m1	-	Spain	
	MACN-MA 23.43	m1	-	Africa	
Caniformia					
Canidae					
Canis aureus	MLP-MA 1035	m1	-	-	Mesocarnivore (Sillero-Zubiri, 2009)
Canis latrans	MACN-MA 25123	m1	-	North America	Mesocarnivore (Sillero-Zubiri, 2009)
	MLP-MA 1027	m1	-	Africa	
	MLP-PV S/N	m1	-	South Dakota, USA	
Canis lupus	MACN-MA 23.15	m1	-	Russia	Hypercarnivore (Sillero-Zubiri, 2009)
	MACN-MA 4256	m1	-	Europe	
	MLP-MA 30	m1	-	-	
Cerdocyon thous	MACN-MA 14322	m1	♂	Santa Fe, Argentina	Omnivore (Sillero-Zubiri, 2009)
	MACN-MA 14681	m1	♂	Salta, Argentina	
	MACN-MA 16189	m1	♂	Misiones, Argentina	
	MACN-MA 20456	m1	♀	Salta, Argentina	
	MACN-MA 48.10	m1	♀	Salta, Argentina	
	MACN-MA 50.61	m1	♀	Bolivia	
Chrysocyon brachyurus	MACN-MA 19146	m1	-	-	Omnivore (Sillero-Zubiri, 2009)
	MACN-MA 23984	m1	-	Corrientes, Argentina	
	MACN-MA 24043	m1	-	Corrientes, Argentina	
	MACN-MA 24750	m1	-	Paraguay	
	MACN-MA 3.73	m1	-	-	
	MACN-MA 53.49	m1	-	-	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Cuon alpinus	AMNH(M) S/N	m1	-		Hypercarnivore (Sillero-Zubiri, 2009)
Lycalopex culpaeus	MACN-MA 15109	m1	♂	Neuquén, Argentina	Mesocarnivore (Sillero-Zubiri, 2009)
	MACN-MA 20813	m1	♂	Neuquén, Argentina	
	MACN-MA 23719	m1	♂	Jujuy, Argentina	
	MACN-MA 23915	m1	♀	Ecuador	
	MACN-MA 31.59	m1	-	-	
	MACN-MA 38.39	m1	-	-	
Lycalopex griseus	MACN-MA 15186	m1	♂	Neuquén, Argentina	Omnivore (Sillero-Zubiri, 2009)
	MACN-MA 20205	m1	♂	Río Negro, Argentina	
	MACN-MA 20207	m1	♂	Río Negro, Argentina	
	MACN-MA 20278	m1	♀	Río Negro, Argentina	
	MACN-MA 20814	m1	♀	Río Negro, Argentina	
	MACN-MA 36480	m1	♀	Salta, Argentina	
Lycalopex gymnocercus	MACN-MA 14319	m1	♂	La Pampa, Argentina	Omnivore (Sillero-Zubiri, 2009)
	MACN-MA 16041	m1	♂	Córdoba, Argentina	
	MACN-MA 16049	m1	♂	La Pampa, Argentina	
	MACN-MA 29.35	m1	♀	La Pampa, Argentina	
	MACN-MA 49134	m1	♀	Salta, Argentina	
	MACN-MA 49148	m1	♀	La Pampa, Argentina	
Lycalopex vetulus	MLP-PV S/N	m1	-	Brazil	Omnivore (Sillero-Zubiri, 2009)
Lycaon pictus	AMNH(M) S/N	m1	-	Africa	Hypercarnivore (Sillero-Zubiri, 2009)
	MACN-MA 38249	m1	-	Africa	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Speothos venaticus	AMNH(M) S/N	m1	-	-	Hypercarnivore (Sillero-Zubiri, 2009)
	MACN-MA 16510	m1	♂	Misiones, Argentina	
	MACN-MA 50.67	m1	♂	Bolivia	
Urocyon cinereoargenteus	MACN-MA 6.33	m1	-	USA	Omnivore (Sillero-Zubiri, 2009)
	MLP-PV S/N	m1	-	Massachusetts, USA	
Vulpes lagopus	MACN-MA 35203	m1	-	Russia	Mesocarnivore (Sillero-Zubiri, 2009)
	MACN-MA 4.1	m1	-	Russia	
Vulpes vulpes	MACN-MA 25149	m1	-	Germany	Mesocarnivore (Padial *et al.*, 2002)
	MLP-MA 744	m1	-	Rome, Italy	
	MLP-PV S/N	m1	♂	Massachusetts, USA	
Vulpes zerda	MACN-MA 9.14	m1	-	Africa	Omnivore (Sillero-Zubiri, 2009)
Ursidae					
Ailuropodinae					
Ailuropoda melanoleuca	MNHN-ZM-AC 1874-273	m1	-	Tibet, China	Herbivore (Garshelis, 2009)
Tremarctinae					
Tremarctos ornatus	MACN-MA 17830	m1	♂	Bolivia	Herbivore (Garshelis, 2009)
	MACN-MA 50.87	m1	-	Bolivia	
Ursinae					
Helarctos malayanus	MACN-MA 25.49	m1	-	Indonesia	Omnivore (Garshelis, 2009)
Ursus americanus	MLP-MA 1011	m1	-	-	Omnivore (Garshelis, 2009)
Ursus arctos	MACN-MA 35208	m1	♂	Russia	Omnivore (Garshelis, 2009)
Ursus maritimus	MACN-MA 26124	m1	-	Norway	Hypercarnivore (Garshelis, 2009)
	MACN-MA 33.94	m1	-	Norway	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Ursus maritimus	MACN-MA 35204	m1	-	Russia	Hypercarnivore (Garshelis, 2009)
	MLP-MA 1004	m1	-	-	
Mephitidae					
Mephitinae					
Conepatus chinga	MACN-MA 13499	m1	♀	Corrientes, Argentina	Omnivore (Dragoo, 2009)
	MACN-MA 13714	m1	♂	Salta, Argentina	
	MACN-MA 23992	m1	-	Uruguay	
	MACN-MA 24002	m1	-	Río Negro, Argentina	
	MACN-MA 24006	m1	-	Río Negro, Argentina	
	MACN-MA 24719	m1	-	Río Negro, Argentina	
	MACN-MA 30393	m1	♂	Catán-Lil, Neuquén, Argentina	
Mephitis mephitis	MACN-MA 23520	m1	♀	USA	Omnivore (Dragoo, 2009)
	MACN-MA 23521	m1	♂	USA	
	MLP-PV S/N	m1	♀	Massachusetts, USA	
Spilogale gracilis	MACN-MA 34551	m1	♂	USA	Omnivore (Dragoo, 2009)
	MACN-MA 34552	m1	♀	USA	
Mustelidae					
Ictonychinae					
Galictis cuja	MACN-MA 13498	m1	♂	El Bolson, Río Negro, Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 13965	m1	♀	Catán-Lil, Neuquén, Argentina	
	MACN-MA 16254	m1	♀	Bs. As., Argentina	
	MACN-MA 16520	m1	♂	Cushamen, Chubut, Argentina	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Galictis cuja	MACN-MA 23291	m1	♂	Bs. As., Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 23793	m1	-	Bs. As., Argentina	
Galictis vittata	MACN-MA 50.91	m1	♀	Bolivia	Hypercarnivore (Larivière & Jennings, 2009)
Ictionyx libyca	MACN-MA 24.12	m1	-	Africa	Mesocarnivore (Larivière & Jennings, 2009)
Lyncodon patagonicus	MACN-MA 31214	m1	♂	Patquía, La Rioja, Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MLP-MA 29-XII-00-17	m1	-	Río Negro, Argentina	
Lutrinae					
Lontra felina	MACN-MA 34602	m1	-	Isla de los Estados, Argentina	Piscivore (Kruuk, 2006)
Lontra longicaudi	MACN-MA 13073	m1	♂	Misiones, Argentina	Piscivore (Kruuk, 2006)
	MACN-MA 24.13	m1	♀	Paraguay	
	MACN-MA 24662	m1	-	-	
	MACN-MA 24665	m1	-	America	
	MACN-MA 24666	m1	♀	Delta del Paraná, Argentina	
	MACN-MA 25357	m1	♀	Bs. As., Argentina	
	MACN-MA 30234	m1	-	Chaco, Argentina	
	MACN-MA 30246	m1	-	Chaco, Argentina	
	MACN-MA 5.11	m1	-	Santa Fé, Argentina	
Lontra provocax	MLP-MA 1282	m1	-	Tierra del Fuego, Argentina	Piscivore (Kruuk, 2006)
Pteronura braziliensis	MACN-MA 25783	m1	-	-	Piscivore (Kruuk, 2006)
	MACN-MA 33155	m1	-	Bolivia	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Guloninae					
Eira barbara	MACN-MA 20457	m1	♂	Iguazú, Misiones, Argentina	Omnivore (Larivière & Jennings, 2009)
	MACN-MA 31.61	m1	♀	Bolivia	
	MACN-MA 47202	m1	♀	Bolivia	
	MACN-MA 50.90	m1	♀	Misiones, Argentina	
	MACN-MA 50.92	m1	♂	Salta, Argentina	
	MACN-MA 52.38	m1	♂	Ecuador	
Martes martes	MACN-MA 4.50	m1	-	-	Mesocarnivore (Larivière & Jennings, 2009)
Melinae					
Meles meles	MACN-MA 41227	m1	-	Europe	Omnivore (Larivière & Jennings, 2009)
	MACN-MA 4250	m1	-	Southern Europe	
	MACN-MA 5.36	m1	-	Europe	
Mustelinae					
Mustela eversmanni	MACN-MA 35206	m1	-	Russia	Hypercarnivore (Larivière & Jennings, 2009)
Mustela nivalis	MLP-MA 1018	m1	-	Europe	Hypercarnivore (Larivière & Jennings, 2009)
Mustela putorius	MACN-MA 20645	m1	-	Spain	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 25148	m1	-	Europe	
	MLP-MA 6-111-36-35	m1	-	Spain	
Mustela sibirica	MACN-MA 35207	m1	♂	Russia	Hypercarnivore (Larivière & Jennings, 2009)
Neovison vison	MACN-MA 16327	m1	♂	Chubut, Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 17825	m1	♂	Bs. As., Argentina	
	MACN-MA 17826	m1	♂	Chubut, Argentina	
	MACN-MA 19186	m1	♀	Bs. As., Argentina	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Neovison vison	MACN-MA 19187	m1	♀	Bs. As., Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 19188	m1	♀	Chubut, Argentina	
Taxidiinae					
Taxidea taxus	MLP-PV S/N	m1	-	-	Mesocarnivore (Larivière & Jennings, 2009)
Procyonidae					
Bassaricyon alleni	MACN-MA 31.68	m1	-	Ecuador	Herbivore (Kays, 2009)
	MACN-MA 50.81	m1	♂	Bolivia	
	MACN-MA 50.82	m1	♂	Bolivia	
Nasua nasua	MACN-MA 49402	m1	♀	Bolivia	Omnivore (Kays, 2009)
	MACN-MA 49415	m1	♂	Misiones, Argentina	
	MACN-MA 49457	m1	♂	Misiones, Argentina	
	MACN-MA 50.77	m1	♀	Misiones, Argentina	
	MACN-MA 50535	m1	♂	Misiones, Argentina	
Procyon cancrivorus	MACN-MA 13816	m1	-	Jujuy, Argentina	Omnivore (Kays, 2009)
	MACN-MA 16190	m1	-	Tucumán, Argentina	
	MACN-MA 17116	m1	-	Santa Fe, Argentina	
	MACN-MA 32254	m1	♀	Corrientes, Argentina	
	MACN-MA 33.7	m1	♀	Jujuy, Argentina	
	MACN-MA 41109	m1	♀	San Javier, Santa Fe, Argentina	
Procyon lotor	MLP-MA 1005	m1	-	-	Omnivore (Kays, 2009)
	MLP-PV S/N	m1	♀	Massachusetts, USA	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
Metatheria					
Dasyuromorphia					
Dasyuridae					
Dasyurinae					
Dasyurus geoffroii	FMNH 35329	m4	♀	Australia	Mesocarnivore (Baker, 2015)
Thylacinidae					
Thylacinus cynocephalus	FMNH 81522	m4	-	Tasmania	Hypercarnivore (Helgen & Veatch, 2015)
Didelphimorphia					
Didelphidae					
Didelphinae					
Didelphis albiventris	MACN-MA 13139	m4	♀	Concordia, Entre Ríos, Argentina	Omnivore (Vieira & Astúa de Moraes, 2003)
	MACN-MA 24149	m4	♂	Bs. As., Argentina	
	MACN-MA 24150	m4	-	Corrientes, Argentina	
	MACN-MA 24169	m4	♂	Concordia, Entre Ríos, Argentina	
	MACN-MA 49.49	m4	-	Corrientes, Argentina	
	MACN-MA 49.51	m4	♂	Corrientes, Argentina	
Lutreolina crassicaudata	MACN-MA 13265	m4	♂	Bs. As., Argentina	Mesocarnivore (Vieira & Astúa de Moraes, 2003)
	MACN-MA 24110	m4	♂	Formosa, Argentina	
	MACN-MA 24111	m4	-	Corrientes, Argentina	
	MACN-MA 24112	m4	♂	Corrientes, Argentina	
	MACN-MA 24780	m4	-	Corrientes, Argentina	
	MACN-MA 50477	m4	♂	Bs. As., Argentina	

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.

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The scope of traditional and geometric morphometrics for inferences of diet in carnivorous fossil mammals

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SUPPLEMENTARY ONLINE INFORMATION 2. Confusion matrices of the different Discriminant Analyses using the scores of the classic indices and the bg-PCs. PCPR = Percentage of Correct Posterior Reclassification (global percentage shown in bold).

Linear Discriminant Analysis						
All (3) indices						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	3	0	0	2	1	50.00
Hypercarnivore	0	70	33	1	1	66.67
Mesocarnivore	0	1	23	6	4	67.65
Omnivore	17	0	26	13	15	18.31
Piscivore	1	0	1	5	6	46.15
%Error	85.71	1.41	72.29	51.85	77.78	**50.22**
RGA						
Herbivore	3	0	0	1	2	50.00
Hypercarnivore	0	72	31	2	0	68.57
Mesocarnivore	0	1	26	6	1	76.47
Omnivore	21	0	31	12	7	16.90
Piscivore	1	0	1	8	3	23.08
%Error	88.00	1.37	70.79	58.62	76.92	**50.66**
AI						
Herbivore	3	2	0	1	0	50.00
Hypercarnivore	1	90	12	2	0	85.71
Mesocarnivore	7	14	8	0	5	23.53
Omnivore	22	9	28	3	9	4.23
Piscivore	4	0	4	2	3	23.08
%Error	91.89	21.74	84.62	62.50	82.35	**46.72**
Angle α						
Herbivore	4	0	0	0	2	66.67
Hypercarnivore	4	70	20	9	2	66.67
Mesocarnivore	1	3	24	5	1	70.59
Omnivore	21	0	30	15	5	21.13
Piscivore	4	0	0	5	4	30.77
%Error	88.24	4.11	67.57	55.88	71.43	**51.09**

Linear Discriminant Analysis						
All (4) bg-PCs						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	5	0	0	1	0	83.33
Hypercarnivore	0	93	6	5	1	88.57
Mesocarnivore	0	0	28	3	3	82.35
Omnivore	17	0	8	40	6	56.34
Piscivore	0	0	0	0	13	100.00
%Error	77.27	0.00	33.33	18.37	43.48	**78.17**
3 bg-PCs						
Herbivore	5	0	0	1	0	83.33
Hypercarnivore	0	91	7	5	2	86.67
Mesocarnivore	0	4	23	6	1	67.65
Omnivore	20	0	17	27	7	38.03
Piscivore	0	0	0	0	13	100.00
%Error	80.00	4.21	51.06	30.77	43.48	**69.43**
bg-PC1						
Herbivore	3	0	0	3	0	50.00
Hypercarnivore	0	80	21	4	0	76.19
Mesocarnivore	0	2	27	0	5	79.41
Omnivore	24	0	13	8	26	11.27
Piscivore	0	0	0	2	11	84.62
%Error	88.89	2.44	55.74	52.94	73.81	**56.33**

Quadratic Discriminant Analysis						
All (3) indices						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	3	0	0	3	0	50.00
Hypercarnivore	1	77	25	0	2	73.33
Mesocarnivore	0	3	28	2	1	82.36
Omnivore	10	0	34	20	7	28.17
Piscivore	1	0	0	2	10	76.92
%Error	80.00	3.75	67.82	25.93	50.00	**60.26**
RGA						
Herbivore	3	0	0	1	2	50.00
Hypercarnivore	0	73	30	0	2	69.52
Mesocarnivore	0	2	26	0	6	76.47
Omnivore	19	0	33	3	16	4.23
Piscivore	0	0	1	1	11	84.62
%Error	86.36	2.67	71.11	40.00	70.27	**50.66**
AI						
Herbivore	3	2	0	0	1	50.00
Hypercarnivore	0	92	10	0	3	87.62
Mesocarnivore	0	16	6	1	11	17.65
Omnivore	9	10	23	10	19	14.08
Piscivore	0	0	2	0	11	84.62
%Error	75.00	23.33	85.37	9.09	75.56	**53.28**
Angle α						
Herbivore	3	0	0	1	2	50.00
Hypercarnivore	4	70	25	1	5	66.67
Mesocarnivore	1	3	26	2	2	76.47
Omnivore	21	0	32	4	14	5.63
Piscivore	5	0	1	2	5	38.46
%Error	91.18	4.11	69.05	60.00	82.14	**47.16**

Quadratic Discriminant Analysis						
All (4) bg-PCs						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	2	0	0	4	0	33.33
Hypercarnivore	0	93	8	4	0	88.57
Mesocarnivore	0	0	28	6	0	82.35
Omnivore	9	1	14	47	0	66.20
Piscivore	0	0	0	0	13	100.00
%Error	81.81	1.06	44.00	22.95	0.00	**79.91**
3 bg-PCs						
Herbivore	4	0	0	2	0	66.67
Hypercarnivore	0	88	13	4	0	83.81
Mesocarnivore	0	4	25	5	0	73.53
Omnivore	13	0	22	36	0	50.70
Piscivore	0	0	0	0	13	100.00
%Error	76.47	4.35	58.33	23.40	0.00	**72.49**
bg-PC1						
Herbivore	3	0	0	3	0	50.00
Hypercarnivore	0	88	13	4	0	83.81
Mesocarnivore	0	3	26	0	5	76.47
Omnivore	25	0	16	5	25	7.04
Piscivore	0	0	1	2	10	76.92
%Error	89.29	3.30	53.57	64.29	75.00	**57.64**

Weighted Random Forests						
All (3) indices						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	1	1	1	3	0	16.67
Hypercarnivore	0	93	9	3	0	88.57
Mesocarnivore	0	12	14	8	0	41.18
Omnivore	0	2	3	62	4	87.32
Piscivore	0	0	0	9	4	30.77
%Error	0.00	13.89	48.15	27.06	50.00	**75.98**
RGA						
Herbivore	2	0	0	3	1	33.33
Hypercarnivore	0	85	11	8	1	80.95
Mesocarnivore	1	12	8	12	1	23.53
Omnivore	1	9	9	44	8	61.97
Piscivore	1	2	1	6	3	23.08
%Error	60.00	21.30	62.07	39.73	78.57	**62.01**
AI						
Herbivore	0	2	1	3	0	0.00
Hypercarnivore	2	87	10	4	2	82.86
Mesocarnivore	0	12	10	11	1	29.41
Omnivore	2	3	11	49	6	69.01
Piscivore	0	1	1	8	3	23.08
%Error	100.00	17.14	69.70	34.67	75.00	**65.07**
Angle α						
Herbivore	0	1	0	2	3	0.00
Hypercarnivore	2	75	14	13	1	71.43
Mesocarnivore	0	12	9	12	1	26.47
Omnivore	3	16	11	32	9	45.07
Piscivore	2	3	1	7	0	0.00
%Error	100.00	29.91	74.29	51.52	100.00	**50.66**

Weighted Random Forests						
All (4) bg-PCs						
	Herbivore	*Hypercarnivore*	*Mesocarnivore*	*Omnivore*	*Piscivore*	*PCPR*
Herbivore	3	0	0	3	0	50.00
Hypercarnivore	0	97	2	6	0	92.38
Mesocarnivore	0	1	29	4	0	85.29
Omnivore	1	1	5	64	0	90.14
Piscivore	0	0	0	0	13	100.00
%Error	25.00	2.02	19.44	27.66	0.00	**89.96**
3 bg-PCs						
Herbivore	1	0	0	5	0	16.67
Hypercarnivore	0	99	3	3	0	94.29
Mesocarnivore	0	4	21	9	0	61.76
Omnivore	1	2	6	62	0	87.32
Piscivore	0	0	0	0	13	100.00
%Error	50.00	5.71	30.00	21.52	0.00	**85.59**
bg-PC1						
Herbivore	5	0	0	1	0	83.33
Hypercarnivore	0	92	10	2	1	87.62
Mesocarnivore	0	9	17	5	3	50.00
Omnivore	2	3	7	52	7	73.24
Piscivore	0	1	2	5	5	38.46
%Error	28.57	12.38	52.78	20.00	68.75	**74.67**

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SUPPLEMENTARY ONLINE INFORMATION 3. Confusion matrices of the Discriminant Analyses using the scores of the classic indices and the bg-PCs within Canidae. PCPR = Percentage of Correct Posterior Reclassification (global percentage shown in bold).

Linear Discriminant Analysis				
All (2) bg-PCs				
	Hypercarnivore	*Mesocarnivore*	*Omnivore*	*PCPR*
Hypercarnivore	8	1	0	88.89
Mesocarnivore	0	15	0	100.00
Omnivore	0	4	24	85.71
%Error	0.00	25.00	0.00	**90.38**
All (3) índices				
Hypercarnivore	5	4	0	55.56
Mesocarnivore	6	9	0	55.56
Omnivore	3	2	23	82.14
%Error	64.29	40.00	0.00	**71.15**
Bg-PC1				
Hypercarnivore	8	1	0	88.89
Mesocarnivore	0	14	1	93.33
Omnivore	0	5	23	82.14
%Error	0.00	30.00	4.17	**86.54**
RGA				
Hypercarnivore	0	9	0	0.00
Mesocarnivore	11	2	2	13.33
Omnivore	4	0	24	85.71
%Error	100.00	81.82	7.69	**50.00**
AI				
Hypercarnivore	5	4	0	55.56
Mesocarnivore	6	5	4	33.33
Omnivore	1	7	20	71.43
%Error	58.33	68.75	16.67	**57.69**
Angle α				
Hypercarnivore	0	4	5	0.00
Mesocarnivore	3	8	4	53.33
Omnivore	3	14	11	39.29
%Error	100.00	77.78	45.00	**36.54**

Quadratic Discriminant Analysis				
All (2) bg-PCs				
	Hypercarnivore	*Mesocarnivore*	*Omnivore*	*PCPR*
Hypercarnivore	8	1	0	88.89
Mesocarnivore	1	14	0	93.33
Omnivore	0	3	25	89.29
%Error	11.11	22.22	0.00	**90.38**
All (3) indices				
Hypercarnivore	4	5	0	44.44
Mesocarnivore	4	9	2	60.00
Omnivore	1	6	21	75.00
%Error	55.56	55.00	8.70	**65.38**
Bg-PC1				
Hypercarnivore	8	1	0	88.89
Mesocarnivore	1	13	1	86.67
Omnivore	0	5	23	82.14
%Error	11.11	33.33	4.17	**84.62**
RGA				
Hypercarnivore	7	2	0	77.78
Mesocarnivore	10	3	2	20.00
Omnivore	2	2	24	85.71
%Error	63.16	57.14	7.69	**65.38**
AI				
Hypercarnivore	5	4	0	55.56
Mesocarnivore	6	5	4	33.33
Omnivore	1	7	20	71.43
%Error	58.33	68.75	83.33	**57.69**
Angle α				
Hypercarnivore	2	3	4	22.22
Mesocarnivore	2	7	6	46.67
Omnivore	3	17	8	28.57
%Error	71.43	74.07	55.56	**32.69**

Weighted Random Forests				
All (2) bg-PCs				
	Hypercarnivore	*Mesocarnivore*	*Omnivore*	*PCPR*
Hypercarnivore	8	1	0	88.89
Mesocarnivore	0	14	1	93.33
Omnivore	0	2	26	92.86
%Error	0.00	17.65	3.70	**92.31**
All (3) indices				
Hypercarnivore	2	7	0	22.22
Mesocarnivore	4	8	3	53.33
Omnivore	0	2	26	92.86
%Error	66.67	52.94	10.34	**69.23**
Bg-PC1				
Hypercarnivore	8	1	0	88.89
Mesocarnivore	1	9	5	60.00
Omnivore	0	6	22	78.57
%Error	11.11	43.75	18.52	**75.00**
RGA				
Hypercarnivore	1	7	1	11.11
Mesocarnivore	6	6	3	40.00
Omnivore	0	3	25	89.29
%Error	85.71	62.50	13.79	**61.54**
AI				
Hypercarnivore	6	2	1	66.67
Mesocarnivore	4	6	5	40.00
Omnivore	1	4	23	82.14
%Error	45.45	50.00	20.69	**67.31**
Angle α				
Hypercarnivore	1	2	6	11.11
Mesocarnivore	2	4	9	26.67
Omnivore	6	5	17	60.71
%Error	88.89	63.64	46.88	**42.31**

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SUPPLEMENTARY ONLINE INFORMATION 4. Differences in classifications if the RGA is averaged by species or not.

The RGA values used in this study correspond to measurements taken by calliper (Prevosti, 2006). We compared the use of the average value of the RGA per species, versus the use of the observed variation (*i.e.*, including the value of each specimen separately). In the first case, we averaged the RGA per species, obtaining a single value per species. Under this example, the diets could be classified with a series of logical rules: *e.g.*, a taxon can be considered hypercarnivorous when the RGA index is lower than 0.45; insectivore when the RGA index is larger than 1. Although the limit between omnivores and mesocarnivores is ambiguous and it is usually determined arbitrarily.

RGA AVERAGED

Species	RGA	Diet	Classification based on the limits established by the RGA
Cuos alpinus	0.396	Hypercarnivore	Hypercarnivore
Lycaon pictus	0.427	Hypercarnivore	
Canis lupus	0.440	Hypercarnivore	
Speothos venaticus	0.447	Hypercarnivore	
Canis latrans	0.468	Mesocarnivore	Mesocarnivore
Vulpes lagopus	0.472	Mesocarnivore	
Cerdocyon thous	0.483	Omnivore	Omnivore / Mesocarnivore
Lycalopex culpeus	0.501	Mesocarnivore	
Chrysocyon brachyurus	0.510	Omnivore	
Vulpes vulpes	0.537	Mesocarnivore	
Lycalopex gymnocercus	0.540	Omnivore	
Canis aureus	0.570	Mesocarnivore	
Lycalopex griseus	0.573	Omnivore	
Vulpes zerda	0.596	Omnivore	Omnivore
Urocyon cinereoargenteus	0.630	Omnivore	
Lycalopex vetus	0.676	Omnivore	
Otocyon megalotis	1.092	Insectivore	Insectivore

In the second case, we used the intraspecific variation including the maximum and minimum values for each species. Considering these values, the overlap between the diet categories is much greater. The limits between hypercarnivores and mesocarnivores, hypercarnivores and omnivores, and omnivores and mesocarnivores, are ambiguous.

MAXIMUM AND MINIMUM RGA FOR EACH SPECIES

Species	RGA	Diet	Classification based on the limits established by the RGA
Cuon alpinus (max)	0.38315075	Hypercarnivore	Hypercarnivore
Speothos venaticus (max)	0.38899377	Hypercarnivore	
Canis lupus (max)	0.39954606	Hypercarnivore	
Vulpes lagopus (max)	0.40203548	Mesocarnivore	Hypercarnivore / Mesocarnivore
Lycaon pictus (max)	0.41193274	Hypercarnivore	
Lycalopex culpeus (max)	0.41656346	Mesocarnivore	
Cuon alpinus (min)	0.42707933	Hypercarnivore	
Lycalopex gymnocercus (max)	0.43352668	Omnivore	Hypercarnivore / Mesocarnivore / Omnivore
Canis latrans (max)	0.43876609	Mesocarnivore	
Lycaon pictus (min)	0.4401231	Hypercarnivore	
Chrysocyon brachyurus (max)	0.47260203	Omnivore	
Canis lupus (min)	0.47866607	Hypercarnivore	
Canis aureus (max)	0.48129375	Mesocarnivore	
Vulpes vulpes (max)	0.48323788	Mesocarnivore	
Speothos venaticus (min)	0.48422978	Hypercarnivore	
Canis latrans (min)	0.48460054	Mesocarnivore	Omnivore / Mesocarnivore
Lycalopex griseus (max)	0.50013523	Omnivore	
Cerdocyon thous (max)	0.50764504	Omnivore	
Vulpes lagopus (min)	0.53516599	Mesocarnivore	
Urocyon cinereoargenteus (max)	0.53516937	Omnivore	
Lycalopex culpeus (min)	0.55065397	Mesocarnivore	
Chrysocyon brachyurus (min)	0.55356594	Omnivore	
Vulpes vulpes (min)	0.56869599	Mesocarnivore	
Vulpes zerda (max)	0.59363335	Omnivore	
Vulpes zerda (min)	0.5982215	Omnivore	
Lycalopex griseus (min)	0.62284374	Omnivore	
Lycalopex gymnocercus (min)	0.62465886	Omnivore	
Cerdocyon thous (min)	0.65690314	Omnivore	
Lycalopex vetus (max)	0.66255223	Omnivore	
Lycalopex vetus (min)	0.69023133	Omnivore	
Urocyon cinereoargenteus (min)	0.69226584	Omnivore	
Canis aureus (min)	0.69539824	Mesocarnivore	
Otocyon megalotis (max)	1.05831893	Insectivore	Insectivore
Otocyon megalotis (min)	1.12532476	Insectivore	

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