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

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

39 **KEYWORDS.** Diet classification. Carnivora. Morphometric indices. Weighted random  
40 forest.

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

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

64 **PALABRAS CLAVES.** Clasificación de la dieta. Carnívora. Índices morfométricos.  
65 Bosques aleatorios ponderados.

66 THE analysis of diets is an important component of ecological and paleoecological  
67 studies (Price *et al.*, 2012; Kissling *et al.*, 2014; Davis and Pineda Munoz, 2016; Croft  
68 *et al.*, 2018a). Many proxies have been used to determine the diet of mammalian  
69 species, including direct observations of feeding behavior, stomach and fecal contents,  
70 dental microwear and mesowear, isotope analysis of nitrogen and carbon, and  
71 craniodental morphology, among others (see review in Davis and Pineda Munoz, 2016).  
72 Although often considered to represent the same parameter, these different proxies offer  
73 different evidences of the items consumed, have different scopes (*i.e.*, extant and/or  
74 fossil species), and are constrained by different methodological aspects (*i.e.*, cost,  
75 difficulty and time of study, availability of data) (Evans, 2013; Davis and Pineda  
76 Munoz, 2016). In particular, the study of molar morphology combines low cost and low  
77 methodological difficulty, thus making it one of the most widely used proxies in  
78 paleoecological studies of mammals (*e.g.*, Marshall, 1978; Goin *et al.*, 1992; Van  
79 Valkenburgh *et al.*, 2004; Vizcaíno *et al.*, 2006; Prevosti *et al.*, 2013; Croft *et al.*,  
80 2018b; Harper *et al.*, 2018).

81 The versatility of tribosphenic molars has been shown to be a key innovation in  
82 the evolution of mammals, increasing the taxonomic diversity and ecological disparity  
83 of this group throughout their evolutionary history (Woodburne *et al.*, 2003; Luo,  
84 2007). Molars are also usually the sole identifiable remains of an extinct mammal, and  
85 therefore have been intensively used for taxonomic classifications in addition to dietary  
86 reconstructions (*e.g.*, Marshall, 1978; Ungar, 2010; Goin and de los Reyes, 2011). Since  
87 the 19th century, several authors have associated certain dental morphological traits  
88 with dietary habits by means of qualitative and descriptive analyses (*e.g.*, Lund, 1839;  
89 Ryder, 1878; Cope, 1879; Butler, 1946; Marshall, 1978; Reig *et al.*, 1987; Berta, 1989).  
90 More recently, different studies of tooth function have correlated several quantitative

91 traits of tooth shape (*i.e.*, morphometric ratios or angles) with the different items  
92 consumed by the animal. These quantitative tools continue to be used today, and while  
93 some have used isolated indices (*e.g.*, Crusafont-Pairó and Truyols-Santonja, 1956;  
94 Goin *et al.*, 1992; Strait, 1993a, b; Evans *et al.*, 2005; Vizcaíno *et al.*, 2006; Prevosti *et*  
95 *al.*, 2013), others have used several indices to define a morphospace (*e.g.*, Kay, 1975;  
96 Van Valkenburgh, 1989; Popowics, 2003; Wesley-Hunt, 2005; Friscia *et al.*, 2007;  
97 Asahara *et al.*, 2016; Croft *et al.*, 2018b). Moreover, with the development of new  
98 technologies, new dental shape descriptors have been developed to study molar  
99 morphology (Evans, 2013). On the one hand, some authors have defined metrics to  
100 reflect occlusal surface topography, such as the Dirichlet normal energy, relief index,  
101 and orientation patch count (Zuccotti *et al.*, 1998; Ungar and M'Kirera, 2003; Evans *et*  
102 *al.*, 2007; Boyer, 2008; Bunn *et al.*, 2011; Smits and Evans, 2012). On the other hand,  
103 other approaches to study tooth morphology have arisen with the development of  
104 geometric morphometric techniques, where shape is captured through the use of  
105 landmark coordinates (either two- or three-dimensional) and analyzed as a whole, taking  
106 into account several shape changes instead of a few measurements (Vizcaíno *et al.*,  
107 2016). For example, some authors have digitized the molars with the aim of assessing  
108 the relationships between molar shape and diet: elliptic Fourier analysis has been  
109 applied in rodents (Gómez Cano *et al.*, 2013); 2D geometric morphometrics has been  
110 used in rodents (Caumul and Polly, 2005), primates (White, 2009), rhinos (Piras *et al.*,  
111 2010), and in didelphid marsupials (Chemisquy *et al.*, 2015; Magnus and Cáceres,  
112 2017); and 3D geometric morphometrics has been used in primates (Cooke, 2011;  
113 Singleton *et al.*, 2011) and in carnivorous species (Tarquini *et al.*, 2018).

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

116 Valkenburgh, 1989; Goin *et al.*, 1992; Prevosti *et al.*, 2013; Zimicz, 2014a; Croft *et al.*,  
117 2018b). Within a historical framework, diet reconstructions are crucial for constructing  
118 trophic webs, examining evolutionary changes in lineages, and inferring ancient  
119 climates and habitats (Pascual and Jaureguizar, 1990; Van Valkenburgh *et al.*, 2004;  
120 Dalerum and Angerbjörn, 2005; Prevosti *et al.*, 2013; Echarri *et al.*, 2017). However, in  
121 a recent study, we demonstrated the need to take certain precautions before making  
122 inferences, because the morphology of the molar not only correlates with diet but also is  
123 influenced by the phylogenetic position of each taxa (Tarquini *et al.*, 2018). In any case,  
124 the use of different techniques to analyze molar morphology generates the following  
125 question: are all methodologies utilized to quantify dental morphology equally reliable?

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



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

## 146 **MATERIALS AND METHODS**

### 147 *Samples and landmarks*

148         The results of this study are based on the dataset of Tarquini *et al.* (2018), which  
149 includes digitalizations of the first lower molar (m1) of 213 specimens corresponding to  
150 67 extant species of Carnivora, and the fourth lower molars (m4) of 14 specimens  
151 corresponding to 4 extant species of Marsupialia, including both Didelphimorphia and  
152 Dasyuromorphia (Supplementary Online Information 1). The carnivoran m1 and  
153 carnivorous marsupial m4 are considered to be functionally analogous teeth following  
154 Tarquini *et al.* (2018). The specimens belonging to the insectivore category from the  
155 parent dataset were excluded due to small sample size (only three species: *Dasyurus*  
156 *viverrinus*, *Galerella sanguínea*, and *Otocyon megalotis*). The classification of dietary  
157 categories in this study follows Tarquini *et al.* (2018): Hypercarnivores —feed primarily  
158 on other vertebrates; Mesocarnivores —feed mainly on other vertebrates, but also plants  
159 and invertebrates; Omnivores —meat, plants, and invertebrates represent a similar  
160 proportion of the diet; Herbivores —feed mostly on plant material; Piscivores —feed  
161 mostly on fish.

162         The digitalization comprises nine three-dimensional landmarks (ldk): paraconid  
163 (ldk 1), carnassial notch in the paracristid (ldk 2), protoconid (ldk 3), metaconid (ldk 4),  
164 hypoconid (ldk 6), entoconid (ldk 7), and the mesial and distal edges of trigonid and

165 talonid (ldk 5, 8 and 9) (Fig. 1). We also recorded ten semi-landmarks to delimit the  
166 base of the crown (Fig. 1). For information regarding landmark and semilandmark  
167 treatment, see Tarquini *et al.* (2018).

### 168 ***Morphometric indices***

169 In the literature, several indices have been used to analyze the molar morphology  
170 of carnivorous mammals. The indices are relationships between measurements, such as  
171 the shear ratio (Strait, 1993a, 1993b; Hogue and Ziashakeri, 2010) and the relative  
172 lower grinding area (RGA; Van Valkenburgh, 1989; Prevosti *et al.*, 2013). RGA is  
173 measured as the square root of the area of the m1 talonid divided by the relative blade  
174 length (BL). The area was estimated as the product of maximum width (WT) and length  
175 (LT) of the talonid of m1, and the BL was estimated as the length of the m1 trigonid.  
176 We use the index as defined by Prevosti *et al.* (2013), modified from Valkenburgh  
177 (1989), which has two advantages: first, it can be applied in fossils that only have the  
178 carnassial preserved; and second, the RGA value can be compared in both Carnivora  
179 and Metatheria. Other indices include morphometric angles, such as those that describe  
180 the relationship between the paracristid and the mesiodistal axis (lower angle, AI; Goin  
181 *et al.*, 1992) or the relationship between the height of the protoconid and the length of  
182 the talonid (angle  $\alpha$ ; Crusafont-Pairó and Truyols-Santonja, 1953, 1956; Wesley-Hunt,  
183 2005; Meloro and Raia, 2010).

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

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

### 195 *Statistical analyses*

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

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

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

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

238 However, the regular RF is constructed to minimize the overall error rate, so it tends to  
239 be biased toward the majority class (Chen *et al.*, 2004; Zhu and Pierskalla, 2016). Given  
240 that our dataset is unbalanced (*i.e.*, there are six herbivores, 105 hypercarnivores, 34  
241 mesocarnivores, 71 omnivores, and 13 piscivores), we proceeded to perform a weighted  
242 random forest (WRF), as proposed by Chen *et al.* (2004), which avoids the bias towards  
243 the most numerous classes. To evaluate the performance of classification methods based  
244 on different predictors, we compared the percentage of correct posterior reclassification  
245 (PCPR) and the error rate (% Error) calculated from the confusion matrix. This is  
246 obtained in an innate way by the bootstrap resampling in the WRF and from the cross-  
247 validation procedure in both LDA and QDA (Breiman, 2001; Venables and Ripley,  
248 2002; Kovarovic *et al.*, 2011). PCPR was calculated globally and for each category; it is  
249 understood as the number of animals correctly reclassified in a dietary category divided  
250 by the total of animals belonging to that category. % Error was calculated for each  
251 category as the number of animals wrongly reclassified in a dietary category divided by  
252 the total of animals reclassified in that category. Additionally, as mentioned above,  
253 molar morphology has a significant phylogenetic signal, so that within each family, the  
254 degree of morphological variation is variable (Tarquini *et al.*, 2018). For that reason, we  
255 repeated the classification methods only with the species of the Canidae subgroup,  
256 which is also a group where morphometric indices are widely used. LDA, QDA and  
257 WRF were performed using the *MASS* and *randomForest* packages (Liaw and Wiener,  
258 2002; Venables and Ripley, 2002) in R 3.5.1 (R Core Team, 2018).

### 259 ***Intraspecific variation***

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

263 2006) and compared using the average RGA value per species to using RGA values for  
264 each specimen separately.

## 265 **RESULTS**

266 The morphometric indices showed high and significant correlations: RGA vs.  
267 angle  $\alpha$  ( $\rho = -0.87$ , p-value  $< 0.0001$ ), RGA vs. AI ( $\rho = 0.88$ , p-value  $< 0.0001$ ) and AI  
268 vs. angle  $\alpha$  ( $\rho = -0.77$ , p-value  $< 0.0001$ ). The regressions against the Procrustes  
269 coordinates showed that the indices have a low correlation with shape variation: RGA  
270 explained 53.30% of the change in the shape (p-value  $< 0.0001$ ), AI explained 37.37%  
271 (p-value  $< 0.0001$ ) and angle  $\alpha$  explained 49.42% (p-value  $< 0.0001$ ). By contrast, bg-  
272 PC1 (the axis that has the highest proportion of shape change in the bg-PCA) explained  
273 the shape variation better than any of the morphometric indices (76.59% percent of  
274 variance). Finally, when we analyzed the covariation between the bg-PCs and the  
275 morphometric indices, we observed that a large portion of variation explained by bg-  
276 PC1 could also be explained by the morphometric indices (percentage of covariance  
277 greater than 60%; Tab. 1), whereas there was a low covariation between the  
278 morphometric indices and the other axes of bg-PCA (percentage of covariance less than  
279 20%; Tab. 1).

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

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

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

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

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

311 0.45; mesocarnivorous when the RGA index range from 0.46 to at least 0.47;  
312 omnivorous when the RGA index ranges from 0.60 (perhaps lower) to 0.68; and  
313 insectivorous when the RGA index is larger than 1. However, when the index is  
314 between 0.48 and 0.59, the classification is ambiguous, and the taxon may be  
315 omnivorous or mesocarnivorous. On the other hand, if intraspecific variation is  
316 considered, the superposition zone is much larger. If the value of RGA is lower than  
317 0.40, the taxon is hypercarnivorous; between 0.40 and 0.42, it may be hypercarnivorous  
318 or mesocarnivorous; between 0.43 and 0.48, it may be hypercarnivorous,  
319 mesocarnivorous or omnivorous; between 0.48 and 0.69, it may be mesocarnivorous or  
320 omnivorous; and larger than 1, it is insectivorous (Supplementary Online Information  
321 4).

## 322 **DISCUSSION**

323       Because of the hardness of dental tissues, teeth are the mammalian body parts  
324 most likely to be preserved in the fossil record and, consequently, the elements most  
325 frequently found and studied (Carlson, 1989; Benton and Harper, 2009; Ungar, 2010).  
326 Combined with the importance of the teeth in the acquisition and processing of food,  
327 this makes tooth morphology an important source of information for understanding and  
328 inferring the ecological habits of fossil species (*e.g.*, Van Valen, 1969; Kay, 1975;  
329 Marshall, 1978; Van Valkenburgh, 1989; Prevosti *et al.*, 2013; Solé and Ladevèze,  
330 2017; Tarquini *et al.*, 2018). Bearing that in mind, there have been different inferences  
331 of diet for the same species in the literature, making it necessary to carry out studies that  
332 include diverse proxies (*e.g.*, Soibelzon *et al.*, 2014; Pineda-Munoz *et al.*, 2017) or to  
333 compare the power of different proxies. Our results indicate that 3D geometric  
334 morphometrics is a very powerful tool to study molar morphology and is better than  
335 traditional morphometrics when it comes to predicting feeding habits. The discriminant



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

346         It is noteworthy that the bg-PCA, based on geometric data, provided a diffused  
347 low degree of separation between diet categories, with different degrees of overlap  
348 among them. Nevertheless, as we discussed in a previous work (Tarquini *et al.*, 2018),  
349 this might be in part related to the intrinsic definition of diets and the disadvantage of  
350 the discretization of a continuous variable such as diet into classes, whose chosen limits  
351 are questionable (Van Valkenburgh, 1989; Van Valkenburgh and Koepfli, 1993;  
352 Prevosti *et al.*, 2012b; Echarri *et al.*, 2017). This is why this problem is not intrinsically  
353 related to geometric morphometric, and in studies that include a broad taxonomic  
354 sampling (several species across all Carnivora), it appears difficult to choose a unique  
355 value of RGA (or equivalent index) to separate each dietary categories (Van  
356 Valkenburgh, 1989; Friscia *et al.*, 2007; Zimicz, 2012; Prevosti *et al.*, 2013). Some  
357 authors have chosen to use several indices to define morphospaces that better separate  
358 the categories (Van Valkenburgh, 1989; Friscia *et al.*, 2007), although these ratios have  
359 high correlation values between them (as also calculated here). This is due to the fact  
360 that the indices are calculated with anatomical points or landmarks in common. This

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

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

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

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

## 399 **CONCLUSION**

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

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

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696 **FIGURE CAPTIONS**

697 **Figure 1.** Diagram of landmarks and measurements taken on specimens, in labial view

698 **(1)** and occlusal view **(2)**. Yellow squares, landmarks; pink circles, semi-landmarks.

699 Landmarks: **1)** paraconid; **2)** carnassial notch in the paracristid; **3)** protoconid; **4)**

700 metaconid; **5)** distal edge of trigonid; **6)** hypoconid; **7)** entoconid; **8)** mesial edge of

701 trigonid; **9)** distal edge of talonid. Angle  $\alpha$  ( $\alpha$ ) is shown in dark red dashed lines. Lower

702 angle (**AI**) is shown in light blue dash-dotted lines. Measurements used for RGA are

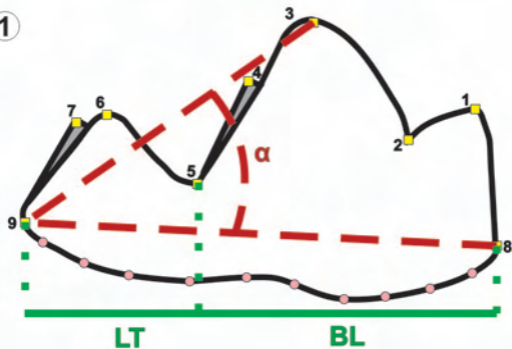
703 green solid lines: **BL**, relative blade length; **WT**, maximum width of the talonid; **LT**

704 length of the talonid;

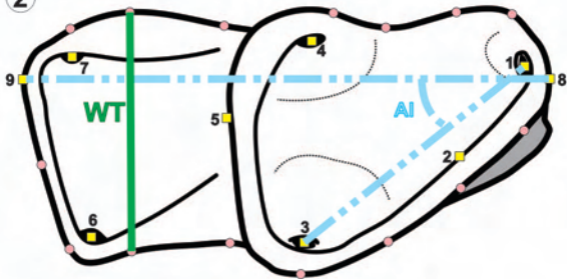
705 **Figure 2.** Alternative measurements taken on specimens to calculate alternative RGAs.

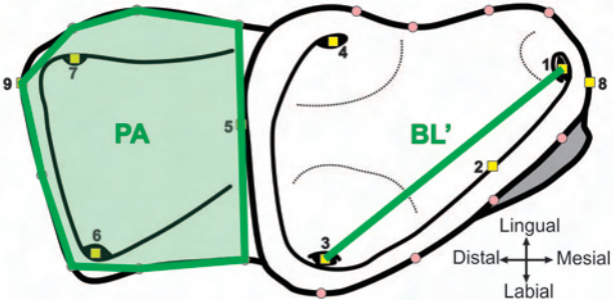
706 Symbols of landmarks as in Figure 1. Measurements: **BL'**, alternative blade length; **PA**,

707 polygon area of the talonid.

**1**

Distal ← Mesial

**2**



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

	RGA		AI		Angle $\alpha$	
	%	P	%	P	%	P
<i>bgPC1</i>	94.34	< 0.0001	64.97	< 0.0001	84.34	< 0.0001
<i>bgPC2</i>	06.92	< 0.0001	02.85	0.0104	18.29	< 0.0001
<i>bgPC3</i>	12.01	< 0.0001	04.31	0.0017	11.70	< 0.0001
<i>bgPC4</i>	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)*

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

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

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

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

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

## **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.

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

	<b>Species</b>	<b>Collection number</b>	<b>Digitized molar</b>	<b>Sex</b>	<b>Provenance</b>	<b>Diet (reference)</b>
	<i>Leopardus geoffroyi</i>	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	
	<i>Leopardus guigna</i>	MLP-MA 1297	m1	-	Chubut, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
	<i>Leopardus pardalis</i>	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	
	<i>Leopardus tigrinus</i>	MACN-MA 23709	m1	♂	Misiones, Argentina	Hypercarnivore (Sunquist & Sunquist, 2009)
		MACN-MA 51121	m1	-	Misiones, Argentina	
		MACN-MA 52.57	m1	♂	Misiones, Argentina	
	<i>Leopardus wiedii</i>	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	
		<i>Lynx rufus</i>	MACN-MA 25.118	m1	♂	
	MLP-PV S/N		m1	♂	Millbridge, Maine, USA	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
<i>Puma concolor</i>	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	
<b>Pantherinae</b>					
<i>Panthera leo</i>	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	
<i>Panthera onca</i>	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	
<i>Panthera pardus</i>	MLP-MA 1040	m1	-	Africa	Hypercarnivore (Sunquist & Sunquist, 2009)
<i>Panthera tigris</i>	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)
<i>Panthera tigris</i>	MLP-MA 112	m1	-	India	Hypercarnivore (Sunquist & Sunquist, 2009)
	MLP-MA 11-IV-48-1	m1	-	-	
<i>Panthera uncia</i>	MACN-MA 8.23	m1	-	Asia	Hypercarnivore (Sunquist & Sunquist, 2009)
<b>Herpestidae</b>					
<b>Herpestinae</b>					
<i>Herpestes ichneumon</i>	MLP-MA 1029	m1	-	Africa	Hypercarnivore (Rosalino <i>et al.</i> , 2009)
	MLP-MA 1323	m1	-	Africa	
<b>Hyaenidae</b>					
<b>Hyaeninae</b>					
<i>Crocuta crocuta</i>	MACN-MA 24525	m1	-	Africa	Hypercarnivore (Holekamp & Kolowski, 2009)
	MACN-MA 33277	m1	-	Africa	
<i>Hyaena hyaena</i>	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	-	-	
<b>Viverridae</b>					
<b>Genettinae</b>					
<i>Genetta genetta</i>	MACN-MA 21104	m1	-	Spain	Mesocarnivore (Torre <i>et al.</i> , 2003)
	MACN-MA 21105	m1	-	Spain	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
<i>Genetta genetta</i>	MACN-MA 21106	m1	-	Spain	Mesocarnivore (Torre <i>et al.</i> , 2003)
	MACN-MA 21107	m1	-	Spain	
	MACN-MA 23.43	m1	-	Africa	
<b>Caniformia</b>					
<b>Canidae</b>					
<i>Canis aureus</i>	MLP-MA 1035	m1	-	-	Mesocarnivore (Sillero-Zubiri, 2009)
<i>Canis latrans</i>	MACN-MA 25123	m1	-	North America	Mesocarnivore (Sillero-Zubiri, 2009)
	MLP-MA 1027	m1	-	Africa	
	MLP-PV S/N	m1	-	South Dakota, USA	
<i>Canis lupus</i>	MACN-MA 23.15	m1	-	Russia	Hypercarnivore (Sillero-Zubiri, 2009)
	MACN-MA 4256	m1	-	Europe	
	MLP-MA 30	m1	-	-	
<i>Cerdocyon thous</i>	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	
<i>Chrysocyon brachyurus</i>	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	-	-	

	<b>Species</b>	<b>Collection number</b>	<b>Digitized molar</b>	<b>Sex</b>	<b>Provenance</b>	<b>Diet (reference)</b>
	<i>Cuon alpinus</i>	AMNH(M) S/N	m1	-		Hypercarnivore (Sillero-Zubiri, 2009)
	<i>Lycalopex culpaeus</i>	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	-	-	
	<i>Lycalopex griseus</i>	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	
	<i>Lycalopex gymnocercus</i>	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	
	<i>Lycalopex vetulus</i>	MLP-PV S/N	m1	-	Brazil	Omnivore (Sillero-Zubiri, 2009)
	<i>Lycaon pictus</i>	AMNH(M) S/N	m1	-	Africa	Hypercarnivore (Sillero-Zubiri, 2009)
		MACN-MA 38249	m1	-	Africa	

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

	<b>Species</b>	<b>Collection number</b>	<b>Digitized molar</b>	<b>Sex</b>	<b>Provenance</b>	<b>Diet (reference)</b>
	<i>Ursus maritimus</i>	MACN-MA 35204	m1	-	Russia	Hypercarnivore (Garshelis, 2009)
		MLP-MA 1004	m1	-	-	
	<b>Mephitidae</b>					
	<b>Mephitinae</b>					
	<i>Conepatus chinga</i>	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	
	<i>Mephitis mephitis</i>	MACN-MA 23520	m1	♀	USA	Omnivore (Dragoo, 2009)
		MACN-MA 23521	m1	♂	USA	
		MLP-PV S/N	m1	♀	Massachusetts, USA	
	<i>Spilogale gracilis</i>	MACN-MA 34551	m1	♂	USA	Omnivore (Dragoo, 2009)
		MACN-MA 34552	m1	♀	USA	
	<b>Mustelidae</b>					
	<b>Ictonychinae</b>					
	<i>Galictis cuja</i>	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	



	<b>Species</b>	<b>Collection number</b>	<b>Digitized molar</b>	<b>Sex</b>	<b>Provenance</b>	<b>Diet (reference)</b>
	<i>Galictis cuja</i>	MACN-MA 23291	m1	♂	Bs. As., Argentina	Hypercarnivore (Larivière & Jennings, 2009)
		MACN-MA 23793	m1	-	Bs. As., Argentina	
	<i>Galictis vittata</i>	MACN-MA 50.91	m1	♀	Bolivia	Hypercarnivore (Larivière & Jennings, 2009)
	<i>Ictonyx libyca</i>	MACN-MA 24.12	m1	-	Africa	Mesocarnivore (Larivière & Jennings, 2009)
	<i>Lyncodon patagonicus</i>	MACN-MA 31214	m1	♂	Patquía, La Rioja, Argentina	Hypercarnivore (Larivière & Jennings, 2009)
		MLP-MA 29-XII-00-17	m1	-	Río Negro, Argentina	
	<b>Lutrinae</b>					
	<i>Lontra felina</i>	MACN-MA 34602	m1	-	Isla de los Estados, Argentina	Piscivore (Kruuk, 2006)
	<i>Lontra longicaudi</i>	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	
	<i>Lontra provocax</i>	MLP-MA 1282	m1	-	Tierra del Fuego, Argentina	Piscivore (Kruuk, 2006)
	<i>Pteronura braziliensis</i>	MACN-MA 25783	m1	-	-	Piscivore (Kruuk, 2006)
		MACN-MA 33155	m1	-	Bolivia	

Species	Collection number	Digitized molar	Sex	Provenance	Diet (reference)
<b>Guloninae</b>					
<i>Eira barbara</i>	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	
<i>Martes martes</i>	MACN-MA 4.50	m1	-	-	Mesocarnivore (Larivière & Jennings, 2009)
<b>Melinae</b>					
<i>Meles meles</i>	MACN-MA 41227	m1	-	Europe	Omnivore (Larivière & Jennings, 2009)
	MACN-MA 4250	m1	-	Southern Europe	
	MACN-MA 5.36	m1	-	Europe	
<b>Mustelinae</b>					
<i>Mustela eversmanni</i>	MACN-MA 35206	m1	-	Russia	Hypercarnivore (Larivière & Jennings, 2009)
<i>Mustela nivalis</i>	MLP-MA 1018	m1	-	Europe	Hypercarnivore (Larivière & Jennings, 2009)
<i>Mustela putorius</i>	MACN-MA 20645	m1	-	Spain	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 25148	m1	-	Europe	
	MLP-MA 6-111-36-35	m1	-	Spain	
<i>Mustela sibirica</i>	MACN-MA 35207	m1	♂	Russia	Hypercarnivore (Larivière & Jennings, 2009)
<i>Neovison vison</i>	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)
<i>Neovison vison</i>	MACN-MA 19187	m1	♀	Bs. As., Argentina	Hypercarnivore (Larivière & Jennings, 2009)
	MACN-MA 19188	m1	♀	Chubut, Argentina	
<b>Taxidiinae</b>					
<i>Taxidea taxus</i>	MLP-PV S/N	m1	-	-	Mesocarnivore (Larivière & Jennings, 2009)
<b>Procyonidae</b>					
<i>Bassaricyon alleni</i>	MACN-MA 31.68	m1	-	Ecuador	Herbivore (Kays, 2009)
	MACN-MA 50.81	m1	♂	Bolivia	
	MACN-MA 50.82	m1	♂	Bolivia	
<i>Nasua nasua</i>	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	
<i>Procyon cancrivorus</i>	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	
<i>Procyon lotor</i>	MLP-MA 1005	m1	-	-	Omnivore (Kays, 2009)
	MLP-PV S/N	m1	♀	Massachusetts, USA	

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

## 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).

<b>Linear Discriminant Analysis</b>						
<b>All (3) indices</b>						
	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	3	0	0	2	1	50.00
<i>Hypercarnivore</i>	0	70	33	1	1	66.67
<i>Mesocarnivore</i>	0	1	23	6	4	67.65
<i>Omnivore</i>	17	0	26	13	15	18.31
<i>Piscivore</i>	1	0	1	5	6	46.15
<i>%Error</i>	85.71	1.41	72.29	51.85	77.78	<b>50.22</b>

<b>RGA</b>						
	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	3	0	0	1	2	50.00
<i>Hypercarnivore</i>	0	72	31	2	0	68.57
<i>Mesocarnivore</i>	0	1	26	6	1	76.47
<i>Omnivore</i>	21	0	31	12	7	16.90
<i>Piscivore</i>	1	0	1	8	3	23.08
<i>%Error</i>	88.00	1.37	70.79	58.62	76.92	<b>50.66</b>

<b>AI</b>						
	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	3	2	0	1	0	50.00
<i>Hypercarnivore</i>	1	90	12	2	0	85.71
<i>Mesocarnivore</i>	7	14	8	0	5	23.53
<i>Omnivore</i>	22	9	28	3	9	4.23
<i>Piscivore</i>	4	0	4	2	3	23.08
<i>%Error</i>	91.89	21.74	84.62	62.50	82.35	<b>46.72</b>

<b>Angle <math>\alpha</math></b>						
	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	4	0	0	0	2	66.67
<i>Hypercarnivore</i>	4	70	20	9	2	66.67
<i>Mesocarnivore</i>	1	3	24	5	1	70.59
<i>Omnivore</i>	21	0	30	15	5	21.13
<i>Piscivore</i>	4	0	0	5	4	30.77
<i>%Error</i>	88.24	4.11	67.57	55.88	71.43	<b>51.09</b>



**Linear Discriminant Analysis**

**All (4) bg-PCs**

	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	5	0	0	1	0	83.33
<i>Hypercarnivore</i>	0	93	6	5	1	88.57
<i>Mesocarnivore</i>	0	0	28	3	3	82.35
<i>Omnivore</i>	17	0	8	40	6	56.34
<i>Piscivore</i>	0	0	0	0	13	100.00
<i>%Error</i>	77.27	0.00	33.33	18.37	43.48	<b>78.17</b>

**3 bg-PCs**

<i>Herbivore</i>	5	0	0	1	0	83.33
<i>Hypercarnivore</i>	0	91	7	5	2	86.67
<i>Mesocarnivore</i>	0	4	23	6	1	67.65
<i>Omnivore</i>	20	0	17	27	7	38.03
<i>Piscivore</i>	0	0	0	0	13	100.00
<i>%Error</i>	80.00	4.21	51.06	30.77	43.48	<b>69.43</b>

**bg-PCI**

<i>Herbivore</i>	3	0	0	3	0	50.00
<i>Hypercarnivore</i>	0	80	21	4	0	76.19
<i>Mesocarnivore</i>	0	2	27	0	5	79.41
<i>Omnivore</i>	24	0	13	8	26	11.27
<i>Piscivore</i>	0	0	0	2	11	84.62
<i>%Error</i>	88.89	2.44	55.74	52.94	73.81	<b>56.33</b>

**Quadratic Discriminant Analysis**

**All (3) indices**

	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	3	0	0	3	0	50.00
<i>Hypercarnivore</i>	1	77	25	0	2	73.33
<i>Mesocarnivore</i>	0	3	28	2	1	82.36
<i>Omnivore</i>	10	0	34	20	7	28.17
<i>Piscivore</i>	1	0	0	2	10	76.92
<b>%Error</b>	<b>80.00</b>	<b>3.75</b>	<b>67.82</b>	<b>25.93</b>	<b>50.00</b>	<b>60.26</b>

**RGA**

<i>Herbivore</i>	3	0	0	1	2	50.00
<i>Hypercarnivore</i>	0	73	30	0	2	69.52
<i>Mesocarnivore</i>	0	2	26	0	6	76.47
<i>Omnivore</i>	19	0	33	3	16	4.23
<i>Piscivore</i>	0	0	1	1	11	84.62
<b>%Error</b>	<b>86.36</b>	<b>2.67</b>	<b>71.11</b>	<b>40.00</b>	<b>70.27</b>	<b>50.66</b>

**AI**

<i>Herbivore</i>	3	2	0	0	1	50.00
<i>Hypercarnivore</i>	0	92	10	0	3	87.62
<i>Mesocarnivore</i>	0	16	6	1	11	17.65
<i>Omnivore</i>	9	10	23	10	19	14.08
<i>Piscivore</i>	0	0	2	0	11	84.62
<b>%Error</b>	<b>75.00</b>	<b>23.33</b>	<b>85.37</b>	<b>9.09</b>	<b>75.56</b>	<b>53.28</b>

**Angle  $\alpha$**

<i>Herbivore</i>	3	0	0	1	2	50.00
<i>Hypercarnivore</i>	4	70	25	1	5	66.67
<i>Mesocarnivore</i>	1	3	26	2	2	76.47
<i>Omnivore</i>	21	0	32	4	14	5.63
<i>Piscivore</i>	5	0	1	2	5	38.46
<b>%Error</b>	<b>91.18</b>	<b>4.11</b>	<b>69.05</b>	<b>60.00</b>	<b>82.14</b>	<b>47.16</b>

**Quadratic Discriminant Analysis**

<b>All (4) bg-PCs</b>						
	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	2	0	0	4	0	33.33
<i>Hypercarnivore</i>	0	93	8	4	0	88.57
<i>Mesocarnivore</i>	0	0	28	6	0	82.35
<i>Omnivore</i>	9	1	14	47	0	66.20
<i>Piscivore</i>	0	0	0	0	13	100.00
<b>%Error</b>	<b>81.81</b>	<b>1.06</b>	<b>44.00</b>	<b>22.95</b>	<b>0.00</b>	<b>79.91</b>

<b>3 bg-PCs</b>						
<i>Herbivore</i>	4	0	0	2	0	66.67
<i>Hypercarnivore</i>	0	88	13	4	0	83.81
<i>Mesocarnivore</i>	0	4	25	5	0	73.53
<i>Omnivore</i>	13	0	22	36	0	50.70
<i>Piscivore</i>	0	0	0	0	13	100.00
<b>%Error</b>	<b>76.47</b>	<b>4.35</b>	<b>58.33</b>	<b>23.40</b>	<b>0.00</b>	<b>72.49</b>

<b>bg-PCI</b>						
<i>Herbivore</i>	3	0	0	3	0	50.00
<i>Hypercarnivore</i>	0	88	13	4	0	83.81
<i>Mesocarnivore</i>	0	3	26	0	5	76.47
<i>Omnivore</i>	25	0	16	5	25	7.04
<i>Piscivore</i>	0	0	1	2	10	76.92
<b>%Error</b>	<b>89.29</b>	<b>3.30</b>	<b>53.57</b>	<b>64.29</b>	<b>75.00</b>	<b>57.64</b>

### **Weighted Random Forests**

#### **All (3) indices**

	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	1	1	1	3	0	16.67
<i>Hypercarnivore</i>	0	93	9	3	0	88.57
<i>Mesocarnivore</i>	0	12	14	8	0	41.18
<i>Omnivore</i>	0	2	3	62	4	87.32
<i>Piscivore</i>	0	0	0	9	4	30.77
<b>%Error</b>	0.00	13.89	48.15	27.06	50.00	<b>75.98</b>

#### **RGA**

<i>Herbivore</i>	2	0	0	3	1	33.33
<i>Hypercarnivore</i>	0	85	11	8	1	80.95
<i>Mesocarnivore</i>	1	12	8	12	1	23.53
<i>Omnivore</i>	1	9	9	44	8	61.97
<i>Piscivore</i>	1	2	1	6	3	23.08
<b>%Error</b>	60.00	21.30	62.07	39.73	78.57	<b>62.01</b>

#### **AI**

<i>Herbivore</i>	0	2	1	3	0	0.00
<i>Hypercarnivore</i>	2	87	10	4	2	82.86
<i>Mesocarnivore</i>	0	12	10	11	1	29.41
<i>Omnivore</i>	2	3	11	49	6	69.01
<i>Piscivore</i>	0	1	1	8	3	23.08
<b>%Error</b>	100.00	17.14	69.70	34.67	75.00	<b>65.07</b>

#### **Angle $\alpha$**

<i>Herbivore</i>	0	1	0	2	3	0.00
<i>Hypercarnivore</i>	2	75	14	13	1	71.43
<i>Mesocarnivore</i>	0	12	9	12	1	26.47
<i>Omnivore</i>	3	16	11	32	9	45.07
<i>Piscivore</i>	2	3	1	7	0	0.00
<b>%Error</b>	100.00	29.91	74.29	51.52	100.00	<b>50.66</b>

**Weighted Random Forests**

**All (4) bg-PCs**

	<i>Herbivore</i>	<i>Hypercarnivore</i>	<i>Mesocarnivore</i>	<i>Omnivore</i>	<i>Piscivore</i>	<i>PCPR</i>
<i>Herbivore</i>	3	0	0	3	0	50.00
<i>Hypercarnivore</i>	0	97	2	6	0	92.38
<i>Mesocarnivore</i>	0	1	29	4	0	85.29
<i>Omnivore</i>	1	1	5	64	0	90.14
<i>Piscivore</i>	0	0	0	0	13	100.00
<i>%Error</i>	25.00	2.02	19.44	27.66	0.00	<b>89.96</b>

**3 bg-PCs**

<i>Herbivore</i>	1	0	0	5	0	16.67
<i>Hypercarnivore</i>	0	99	3	3	0	94.29
<i>Mesocarnivore</i>	0	4	21	9	0	61.76
<i>Omnivore</i>	1	2	6	62	0	87.32
<i>Piscivore</i>	0	0	0	0	13	100.00
<i>%Error</i>	50.00	5.71	30.00	21.52	0.00	<b>85.59</b>

**bg-PCI**

<i>Herbivore</i>	5	0	0	1	0	83.33
<i>Hypercarnivore</i>	0	92	10	2	1	87.62
<i>Mesocarnivore</i>	0	9	17	5	3	50.00
<i>Omnivore</i>	2	3	7	52	7	73.24
<i>Piscivore</i>	0	1	2	5	5	38.46
<i>%Error</i>	28.57	12.38	52.78	20.00	68.75	<b>74.67</b>

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

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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).

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

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



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

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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.

<b>RGA AVERAGED</b>			
Species	RGA	Diet	Classification based on the limits established by the RGA
<i>Cuos alpinus</i>	0.396	Hypercarnivore	Hypercarnivore
<i>Lycaon pictus</i>	0.427	Hypercarnivore	
<i>Canis lupus</i>	0.440	Hypercarnivore	
<i>Speothos venaticus</i>	0.447	Hypercarnivore	Mesocarnivore
<i>Canis latrans</i>	0.468	Mesocarnivore	
<i>Vulpes lagopus</i>	0.472	Mesocarnivore	Omnivore / Mesocarnivore
<i>Cerdocyon thous</i>	0.483	Omnivore	
<i>Lycalopex culpeus</i>	0.501	Mesocarnivore	
<i>Chrysocyon brachyurus</i>	0.510	Omnivore	
<i>Vulpes vulpes</i>	0.537	Mesocarnivore	
<i>Lycalopex gymnocercus</i>	0.540	Omnivore	
<i>Canis aureus</i>	0.570	Mesocarnivore	
<i>Lycalopex griseus</i>	0.573	Omnivore	Omnivore
<i>Vulpes zerda</i>	0.596	Omnivore	
<i>Urocyon cinereoargenteus</i>	0.630	Omnivore	Insectivore
<i>Lycalopex vetus</i>	0.676	Omnivore	
<i>Otocyon megalotis</i>	1.092	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	
<i>Cuon alpinus</i> (max)	0.38315075	Hypercarnivore	Hypercarnivore	
<i>Speothos venaticus</i> (max)	0.38899377	Hypercarnivore		
<i>Canis lupus</i> (max)	0.39954606	Hypercarnivore		
<i>Vulpes lagopus</i> (max)	0.40203548	Mesocarnivore	Hypercarnivore / Mesocarnivore	
<i>Lycaon pictus</i> (max)	0.41193274	Hypercarnivore		
<i>Lycalopex culpeus</i> (max)	0.41656346	Mesocarnivore	Hypercarnivore / Mesocarnivore / Omnivore	
<i>Cuon alpinus</i> (min)	0.42707933	Hypercarnivore		
<i>Lycalopex gymnocercus</i> (max)	0.43352668	Omnivore		
<i>Canis latrans</i> (max)	0.43876609	Mesocarnivore		
<i>Lycaon pictus</i> (min)	0.4401231	Hypercarnivore		
<i>Chrysocyon brachyurus</i> (max)	0.47260203	Omnivore		
<i>Canis lupus</i> (min)	0.47866607	Hypercarnivore		
<i>Canis aureus</i> (max)	0.48129375	Mesocarnivore		
<i>Vulpes vulpes</i> (max)	0.48323788	Mesocarnivore		
<i>Speothos venaticus</i> (min)	0.48422978	Hypercarnivore		
<i>Canis latrans</i> (min)	0.48460054	Mesocarnivore		
<i>Lycalopex griseus</i> (max)	0.50013523	Omnivore		Omnivore / Mesocarnivore
<i>Cerdocyon thous</i> (max)	0.50764504	Omnivore		
<i>Vulpes lagopus</i> (min)	0.53516599	Mesocarnivore		
<i>Urocyon cinereoargenteus</i> (max)	0.53516937	Omnivore		
<i>Lycalopex culpeus</i> (min)	0.55065397	Mesocarnivore		
<i>Chrysocyon brachyurus</i> (min)	0.55356594	Omnivore		
<i>Vulpes vulpes</i> (min)	0.56869599	Mesocarnivore		
<i>Vulpes zerda</i> (max)	0.59363335	Omnivore		
<i>Vulpes zerda</i> (min)	0.5982215	Omnivore		
<i>Lycalopex griseus</i> (min)	0.62284374	Omnivore		
<i>Lycalopex gymnocercus</i> (min)	0.62465886	Omnivore		
<i>Cerdocyon thous</i> (min)	0.65690314	Omnivore		
<i>Lycalopex vetus</i> (max)	0.66255223	Omnivore		
<i>Lycalopex vetus</i> (min)	0.69023133	Omnivore		
<i>Urocyon cinereoargenteus</i> (min)	0.69226584	Omnivore		
<i>Canis aureus</i> (min)	0.69539824	Mesocarnivore		
<i>Otocyon megalotis</i> (max)	1.05831893	Insectivore	Insectivore	
<i>Otocyon megalotis</i> (min)	1.12532476	Insectivore		

### References

Prevosti, F.J. 2006. [*Grandes cánidos (Carnivora, Canidae) del Cuaternario de la República Argentina: sistemática, filogenia, bioestratigrafía y paleoecología*. PhD. Thesis, Universidad Nacional de La Plata, La Plata, 501 p. Unpublished.].