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THE SCOPE OF TRADITIONAL AND GEOMETRIC MORPHOMETRICS 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 α) 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 α) 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. Carnivora. 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

6

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 α; 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 α, AI, and

186   RGA. The angle α 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

9

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).

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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 α (ρ = -0.87, p-value < 0.0001), RGA vs. AI (ρ = 0.88, p-value < 0.0001) and AI

268   vs. angle α (ρ = -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 α 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

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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 PCRP 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 PCRP 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

14

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

15

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 form 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 α (**α**) 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

α

7 6 3 4 1 2 5 9 8

LT BL

②

Distal ←——→ Mesial

9 7 4 1 8 5 2 6 3

WT AI

PA

BL'

Lingual

Distal ↔ Mesial

Labial

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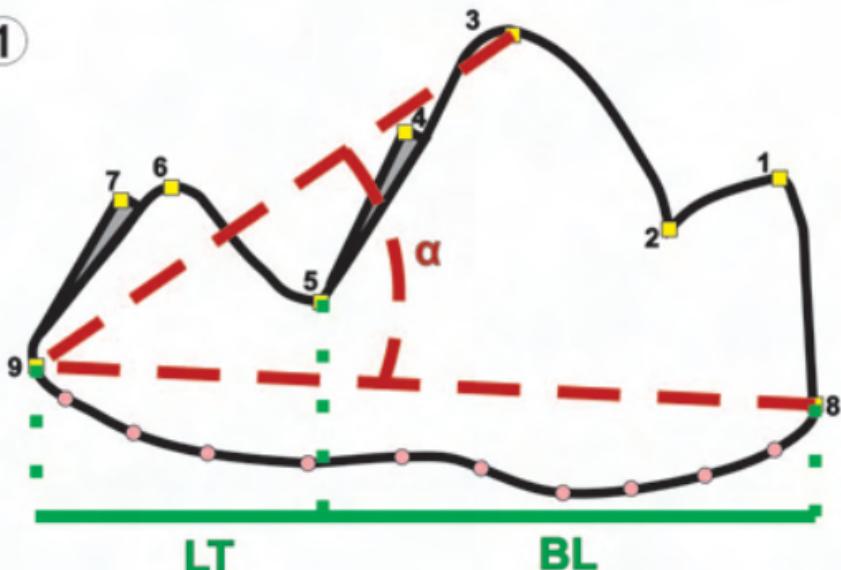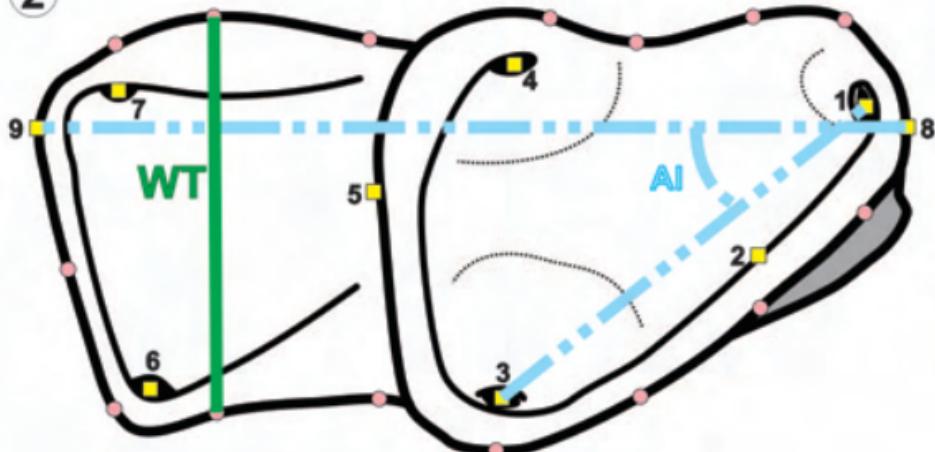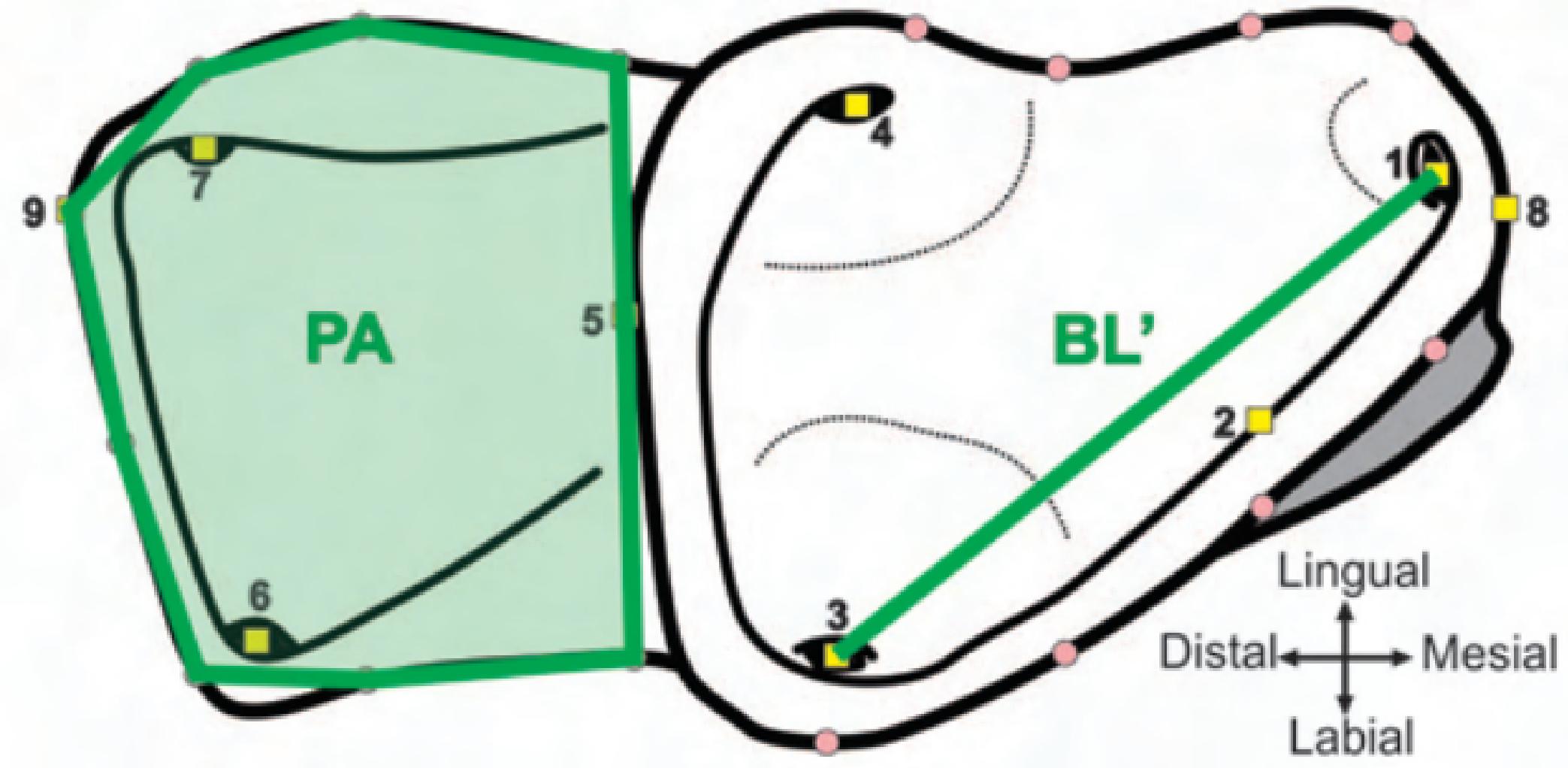
TABLE 1 - Results of the regression analyses between morphometric indices and bgPCs

%, 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 braz]iliensis	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	

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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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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	Hypercarnivore	Mesocarnivore	Omnivore	Piscivore	PCPR
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).

	Hypercarnivore	Mesocarnivore	Omnivore	PCPR
Linear Discriminant Analysis				
All (2) bg-PCs				
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	Mesocarnivore	Omnivore	PCPR
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	Mesocarnivore	Omnivore	PCPR
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	Mesocarnivore	Omnivore	PCPR
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	Mesocarnivore	Omnivore	PCPR
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	Mesocarnivore	Omnivore	PCPR
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*
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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	Hypercarnivore
Canis lupus	0.440	Hypercarnivore	Hypercarnivore
Speothos venaticus	0.447	Hypercarnivore	Hypercarnivore
Canis latrans	0.468	Mesocarnivore	Mesocarnivore
Vulpes lagopus	0.472	Mesocarnivore	Mesocarnivore
Cerdocyon thous	0.483	Omnivore	Omnivore / Mesocarnivore
Lycalopex culpeus	0.501	Mesocarnivore	Omnivore / Mesocarnivore
Chrysocyon brachyurus	0.510	Omnivore	Omnivore / Mesocarnivore
Vulpes vulpes	0.537	Mesocarnivore	Omnivore / Mesocarnivore
Lycalopex gymnocercus	0.540	Omnivore	Omnivore / Mesocarnivore
Canis aureus	0.570	Mesocarnivore	Omnivore / Mesocarnivore
Lycalopex griseus	0.573	Omnivore	Omnivore / Mesocarnivore
Vulpes zerda	0.596	Omnivore	Omnivore
Urocyon cinereoargenteus	0.630	Omnivore	Omnivore
Lycalopex vetus	0.676	Omnivore	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	

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.].