Research Article

Intra- and interspecific variation in tooth morphology of *Procyon cancrivorus* and *P. lotor* (Carnivora, Procyonidae), and its bearing on the taxonomy of fossil South American procyonids

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Abstract

The family Procyonidae (raccoons, coatis, olingos, ringtails, kinkajous, and their extinct relatives) consists of six extant genera and is restricted to North and South America. Currently recognized fossil species suggest that procyonid diversity was previously much greater, including six extinct genera throughout South America. However, it is unusual that so many confamilial taxa are represented in a relatively brief span of time and restricted geographic region, and, considering that six of ten are based on badly preserved specimens, often fragments of bone with worn teeth, the validity of many of these taxa is suspect. As a step towards reevaluating past procyonid diversity in South America, we sought to identify the degree of intra- and interspecific variation in six molariform teeth of extant *Procyon*, particularly to identify which teeth are potentially most useful for identifying fossil procyonids. The six molariform cheek teeth analyzed consistently yielded smaller intra- than interspecific variation, permitting high accuracy of taxonomic classification. However, this accuracy varied by tooth, and the upper and lower first molars proved to be the most reliable. Thus, these particular teeth should be preferred, if available, as bases for recognizing extinct species of procyonids or reevaluating currently recognized extinct species, as a means to prevent *nomina dubia*.

Introduction

The family Procyonidae comprises six living genera (*Procyon* Storr, 1780; *Nasua* Storr, 1780; *Potos* Geoffroy Saint-Hilaire and Cuvier, 1795; *Bassaricyon* Allen, 1876; *Bassariscus* Coues, 1887; and *Nasuella* Hollister, 1915), geographically restricted to the New World. The past diversity of this family was apparently much greater, containing 16 fossil genera described so far (North America: *Amphictis* Pomel, 1853; *Parahyaenodon* Ameghino, 1904; *Broiliana* Dehm, 1950; *Bassaricyonoides* Baskin and Morea in Baskin, 2003; *Parapotos* Baskin, 2003; *Probassariscus* Merriam, 1911; *Edaphocyon* Wilson, 1960; *Arctonasua* Baskin, 1982; *Protoprocyon* Linares, 1981; *Paranasua* Baskin, 1982; South America: *Cyonasua* Ameghino, 1885; *Pachynasua* Rovereto, 1914; *Brachynasua* Ameghino and Kraglievich, 1925; *Amphinasua* Moreno and Mercerat, 1891; *Oligobunis* Burmeister, 1891; and *Chapalmalania* Ameghino, 1908; see Baskin, 2004; Forasiepi et al., 2007; Soibelzon, 2011; Soibelzon and Prevosti, 2012; Forasiepi et al., 2014).

Procyon comprises three extant species: the genotypic *P. lotor* Linnaeus (1758), the common raccoon; *P. pygmaeus* Merriam (1901), the Cozumel raccoon, distributed throughout Cozumel Island, México; and *P. cancrivorus* Cuvier (1798), the crab-eating raccoon. The natural range of *Procyon lotor* extends from Colombia to southern Canada, and it has also been introduced to several Caribbean islands and parts of Europe and Asia. Body length for this species ranges from 46 to 71 centimeters and body mass from 3 to 9 kg, both parameters exhibit age, sex, and geographic variation (Kaufmann, 1982; Sanderson, 1987;

Marín et al., 2012). *Procyon lotor* has a generalized dentition with 40 teeth (dental formula: I 3/3, C 1/1, P 4/4, M 2/2). The first lower molars (carnassials) are not as sharp and pointed as those of a specialized carnivore, but the molars are not as wide as those of herbivores. As part of the dental variation of the species, the first premolars may be absent and extra teeth have been reported (Goldman, 1950). Common raccoons are omnivorous and opportunistic feeders, consuming fleshy fruits, nuts, acorns, corn, grains, insects, frogs, crayfish, eggs, and virtually any other animal and vegetable matter (Palmer and Fowler, 1975; Kaufmann, 1982).

Procyon cancrivorus occurs from Costa Rica southwards to most areas of South America east of the Andes, including eastern and western Paraguay, northern Argentina, Brazil, and Uruguay. In Panamá and Colombia, the geographical range of *P. cancrivorus* overlaps that of *P. lotor* (Eisenberg and Redford, 1999; De La Rosa and Nocke, 2000; Marín et al., 2012). Body length commonly ranges from 54 to 65 cm, and body mass is commonly between 3 and 7 kg. Similar to its sister taxon, *P. cancrivorus* displays unspecialized carnassials and flat-crowned molars with a dental formula of I 3/3, C 1/1, P 4/4, M 2/2 = 40. Its diet consists mainly of very hard food items such as mollusks, fish, insects, crabs, lobster, other crustaceans, small amphibians, and turtle eggs, as well as vegetables and nuts (Emmons, 1990; De La Rosa and Nocke, 2000; Feldhamer et al., 2003; Márquez and Fariña, 2003; Phillips, 2005).

The skulls of these two species can be distinguished by the position of Steno's foramen (see character 2 of Ahrens, 2012, 673) and by the degree of extension of the palate beyond the M2; this distance is greater than ¼ of the total palatal length in *P. lotor*, whereas it is less than this distance in *P. cancrivorus*. Additionally, the molariform teeth of *P. cancrivorus* are more massive than those of *P. lotor*, featuring cusps that

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are wider, more rounded, and blunt (Goldman, 1950; Lotze and Anderson, 1979). The M1 of *P. lotor* presents a small parastyle (see character 57 of Ahrens, 2012) that is absent in *P. cancrivorus*. Additionally, the talonid of the m1 is wider than the trigonid (see character 72 of Ahrens, 2012) in *P. lotor*, while *P. cancrivorus* displays the opposite condition.

Six extinct genera have been assigned to South American Procyonidae to date. Though all six were previously considered to be restricted to Argentina, Forasiepi et al. (2014) recently published two new records for Colombia and Venezuela. The apparent diversity of South American fossil procyonids may be illusory, however, and only two are considered valid: *Cyonasua* and *Chapalmalania* (Patterson and Pascual, 1972; Berman, 1994; Soibelzon, 2007, 2011; Soibelzon and Prevosti, 2012; Forasiepi et al., 2014). *Cyonasua* encompasses ten species, while *Chapalmalania* includes two (see Soibelzon, 2007, 2011). Both genera are recorded mainly during the Upper Tertiary (Late Miocene to Pliocene), with a few records of *Cyonasua* in the Quaternary of Argentina (*C. meranii*, Ensenadan Age, Early to Middle Pleistocene). The fossil record of the ten named species is very poor, and most are represented only by their holotype. In addition the holotypes, of six of the ten species, are bone fragments with worn teeth that prevent accurate identification and comparisons. That a large number of taxa have been described for a relatively short time span, collected from a restricted geographical area, and based on badly preserved specimens raises reasonable doubt about the validity of these taxa.

In this work, we applied 2D geometric morphometric techniques to analyze the teeth of *Procyon lotor* and *P. cancrivorus* with the following goals: (1) to assess intraspecific variance of each of six molariform teeth (upper and lower fourth premolar, first molar, and second molar) in both species; (2) to compare the magnitude of intra- and interspecific variance demonstrated by each tooth between the two species; (3) to evaluate the relationship between molariform tooth morphology and body size; (4) to weigh the usefulness of each tooth to distinguish between *Procyon lotor* and *P. cancrivorus*.

According to the main goals listed above, we tested the following hypotheses: (1) the molars and premolars of *Procyon* present quantifiable intra- and interspecific variation; (2) intraspecific variation is lower than interspecific variation; (3) observed shape changes are not correlated with tooth size; (4) molariform teeth have variable usefulness for reliable taxonomic identification. The present contribution represents an exploratory taxonomic study of the genus *Procyon* and, given that the extant genus *Procyon* is similar in morphology and body size to the extinct *Cyonasua*, a first step towards revising the South American procyonid fossil record.

Material and methods

For geometric morphometric analysis, digital photographs of the lower and upper right molariform dentition (i.e., lower: p4, m1, m2; upper: P4, M1, M2) were taken in occlusal view with mandibles placed perpendicular to the focal plane. Although molars are 3D structures, the occlusal surface and the cusps are in a similar plane, i.e. the structure is so flat that it is almost two-dimensional; thus its characteristics can be captured using a 2D approach, avoiding the problems generated by different depths of structures pointed out by Cardini (2014). The sample consisted of 33 individuals of *Procyon cancrivorus* from northeastern Argentina, Uruguay and Brazil and 33 individuals of *P. lotor* representing localities throughout Central and North America. Although sexual dimorphism has been reported for species of *Procyon* in some morphological characteristics (Goldman, 1950), no information is available regarding the occurrence of sex-related shape differences in the molariform teeth; in other Carnivora, sexual dimorphism affects tooth size, not shape (Turner, 1984; Hillson, 2005) and involves mainly the canine teeth (Gittleman and Van Valkenburgh, 1997)). Consequently, males and females, as well as some specimens that lacked sex data, were pooled for these analyses. For morphological terms we follow Ahrens (2012).
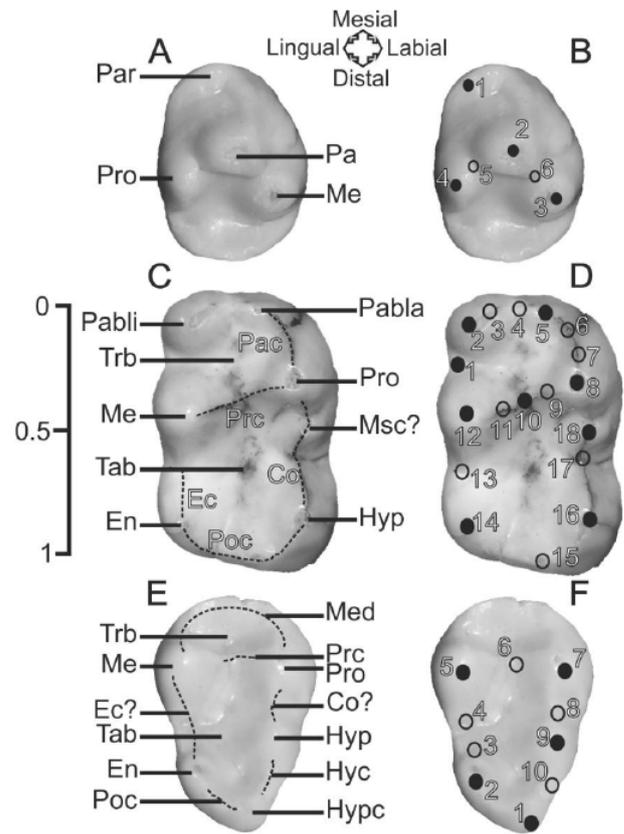
Figure 1 – A, C, and E. Occlusal view of the lower right dentition: (A) fourth premolar, p4; (C) first molar, m1; and (E) second molar, m2, showing nomenclature of cusps and cristids. Co: Cristida obliqua, Co?: Cristida obliqua?, Ec: Entocristid, Ec?: Entocristid?, En: Entoconid, Hyc: Hypocristid, Hyp: Hypoconid, Hypc: Hypoconulid, Me: Metaconid, Med: Mesial edge, Msc?: Mesoconid?, Pa: Paraconid, Pabla: Paraconid bifid labial, Pabli: Paraconid bifid lingual, Par: Parastylid, Pac: Paracristid, Poc: Postcristid, Prc: Protocristid, Pro: Protoconid, Prc: Protocristid, Tab: Talonid basin, Trb: Trigonid basin. Dashed lines indicate cristids. B, D, and F show the position of landmarks (black circles) and semilandmarks (white circles) used for geometric morphometric analysis (see Materials and Methods). All landmarks were placed on apices of corresponding cusps. Graphic scale in cm.

Location of landmarks and semilandmarks
Lower tooth series
Fourth lower premolar (p4). A total of six landmarks and semilandmarks were defined (Fig. 1 A, B): (1) parastylid (Par); (2) paraconid (Pa); (3) metaconid (Me); (4) protoconid (Pro); (5) semilandmark denoting the bottom of the basin developed between paraconid and protoconid; (6) semilandmark denoting bottom of the basin developed between paraconid and metaconid.

First lower molar (m1). A total of eighteen landmarks and semilandmarks were defined (Fig. 1 C, D): (1) lingual border of the basin developed between paraconid and metaconid; (2) lingual apex of the bifid paraconid (Pabli); (3) and (4) semilandmarks between both apices of the bifid paraconid; (5) labial apex of the bifid paraconid (Pabla); (6) and (7) semilandmarks along the paracristid (Pac) between labial apex of the bifid paraconid and protoconid; (8) protoconid (Pro); (9) semilandmark along the protocristid (Prc) on the protoconid lingual side; (10) contact between protoconid and metaconid bases along the protocristid (Prc); (11) semilandmark along the protocristid (Prc) on the metaconid labial side; (12) metaconid (Me); (13) semilandmark along the entocristid (Ec); (14) entoconid (En); (15) semilandmark along the postcristid (Poc); (16) hypoconid (Hyp); (17) semilandmark along the cristid obliqua (Co); (18) mesoconid? (Msc?).

Second lower molar (m2). Ten landmarks and semilandmarks were defined (Fig. 1 E, F): (1) hypoconulid (Hypc); (2) entoconid (En); (3) and (4) semilandmarks located along the entocristid? (Ec?) between entoconid and metaconid; (5) metaconid (Me); (6) semilandmark along the mesial edge of the crown (Med); (7) Protoconid (Prc); (8) semil-

189
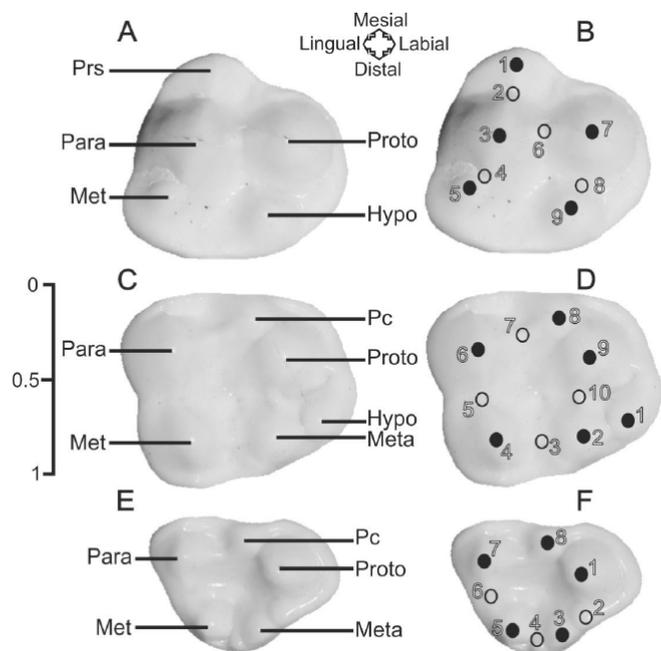
Figure 2 – A, C, and E. Occlusal view of the upper right dentition: (A) fourth premolar, P4; (C) first molar, Ml; and (E) second molar, M2, showing nomenclature of cusps. Hypo: Hypocone, Met: Metacone, Meta: Metaconule, Prs: Parastyle, Para: Paracone, Pc: Paraconule, Proto: Protocone. B, D, and F show the position of landmarks (black circles) and semilandmarks (white circles) used for geometric morphometric analysis (see Materials and Methods). All landmarks were placed on apices of corresponding cusps. Graphic scale in cm.

andmark along the cristid obliqua? (Co?); (9) hypoconid (Hyp); (10) semilandmark along the hypocristid (Hyc).

Upper tooth series

Fourth upper premolar (P4). Nine landmarks and semilandmarks were defined (Fig. 2 A, B): (1) parastyle (Prs); (2) semilandmark located between the parastyle and paracone (Para) bases; (3) paracone; (4) semilandmark placed between the paracone and metacone (Met) bases; (5) metacone; (6) semilandmark located between the paracone and protocone (Proto) bases; (7) protocone; (8) semilandmark placed between the protocone and hypocone bases; (9) hypocone (Hypo).

First upper molar (M1). Ten landmarks and semilandmarks were defined (Fig. 2 C, D): (1) hypocone (Hypo); (2) metaconule (Meta); (3) semilandmark located between the metaconule and metacone (Met) bases; (4) metacone; (5) semilandmark placed between metacone and paracone (Para) bases; (6) paracone; (7) semilandmark located between the paracone and paraconule (Pc) bases; (8) paraconule; (9) protocone (Proto); (10) semilandmark placed between the protocone and metaconule bases.

Second upper molar (M2). Eight landmarks and semilandmarks were defined (Fig. 2 E, F): (1) protocone (Proto); (2) semilandmark placed between the protocone and metaconule (Meta) bases; (3) metaconule; (4) semilandmark located between the metaconule and metacone (Met) bases; (5) metacone; (6) semilandmark placed between the metacone and paracone (Para) bases; (7) paracone; (8) paraconule (Pc).

All landmarks and semilandmarks were digitized by the same person (SGR), using the program `tpsDig` 2.14 (Rohlf, 2009). The configurations of points were Procrustes superimposed to remove differences in location, orientation and scaling (i.e., non-shape variation; Adams et al., 2013). Semilandmarks were slid using the square Procrustes distance criterion (Bookstein, 1997; Perez et al., 2006) in the program `tpsRelw` 1.49 (Rohlf, 2010). The distribution of individuals in shape space was explored by means of a Principal Components Analysis (Monteiro and dos Reis, 1999; Zelditch et al., 2004) of the Procrustes coordinates, and shape changes were visualized by means of deformation grids.

Possible influence of size on shape was evaluated by multivariate linear regression of the shape variables on log-transformed centroid size for each species (Monteiro, 1999; Zelditch et al., 2000, 2004). A discriminant analysis (Manly, 1994) was performed to assess the differentiation of *P. lotor* and *P. cancrivorus* for each tooth type, and accuracy of the classifications was evaluated using leave-one-out cross-validation (Lachenbruch, 1967); shape differences between the group means were calculated as Mahalanobis distance (Mahalanobis, 1936; Zelditch et al., 2004) and their significance assessed by means of a parametric T-square test. Measurement error was evaluated by comparing repeated digitization of landmarks using Procrustes ANOVA (Klingenberg and Monteiro, 2005; Viscosi and Cardini, 2011). Multivariate analyses were performed using the program MorphoJ (Klingenberg, 2011).

Institutional abbreviations

ETMNH: East Tennessee Museum of Natural History, USA. **MACN**: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina. **MFA**: Museo "Florentino Ameghino", Argentina. **MNRJ**: Museu Nacional do Rio de Janeiro, Brazil. **USNM**: National Museum of Natural History, Smithsonian Institute, USA.

Specimens analysed

Procyon cancrivorus: MACN 17–116, MACN 32–254, MACN 33–7, MACN 41–190, MACN 47–375, MACN 50–36, MACN 50–39, MACN 50–70, MACN 16190, MACN 60, MACN 13816, MACN 23121, MACN 23181, MNRJ 3094, MNRJ 4879, MNRJ 5503, MNRJ 5504, MNRJ 5643, MNRJ 7256, MNRJ 11203, MNRJ 25657, MNRJ 32377, MNRJ 32378, MNRJ 32380, MNRJ 32383, MNRJ 15707, MNRJ 28802, MNRJ 7577, MNRJ 23885, MNRJ 32384, MFA 555, MFA 607, MFA 907.

P. lotor: ETMNH CC 22, ETMNH CC 75, USNM 079029, USNM 081808, USNM 087566, USNM 126699, USNM 132216, USNM 135455, USNM 139755, USNM 148660, USNM 148923, USNM 156890, USNM 170892, USNM 204013, USNM 205778, USNM 210203, USNM 248503, USNM 249983, USNM 255045, USNM 255075, USNM 255076, USNM 255077, USNM 256057, USNM 265433, USNM 285161, USNM 287111, USNM 287611, USNM 316210, USNM 320752, USNM 336220, USNM 360725, USNM 507422, USNM 568726.

Results

### Morphometric analysis

Measurement error

Variation between individuals was highly significant and four times greater than variation due to error (1.27%) according to the Procrustes ANOVA.

Fourth lower premolar (p4)

Individuals of *P. lotor* and *P. cancrivorus* were separated in the morphospace of the first two PCs, although with moderate overlap (Fig. 3 A). PC1 explained 45.4% of the shape variation and is associated with differences in labiodistal placement of LM2 and LM4 relative to LM1 and LM3. Thus, with increasing PC1 scores, the protoconid (LM4) and paraconid (LM2) move are located further from the parastylid (LM1) and closer to the metaconid (LM3). *Procyon lotor* plots mainly with positive PC1 scores, while *P. cancrivorus* predominantly falls along the negative PC1 axis. PC2 explained 26.3% of the variation and the species are not separated along PC2, showing considerable overlap and similar ranges of variation. The regression showed non-significant influence of size on overall shape change ($p > 0.05$ for either species). Discriminant analysis revealed a significant difference between the means for *P. lotor* and *P. cancrivorus* (Mahalanobis distance: 2.47; $p < 0.0001$).

First lower molar (ml)

Each species occupied a distinct portion of the morphospace with negligible overlap (Fig. 3 B). PC1 explained 30.5% of shape variation and is associated with the relative dimensions of the overall crown. Spe-
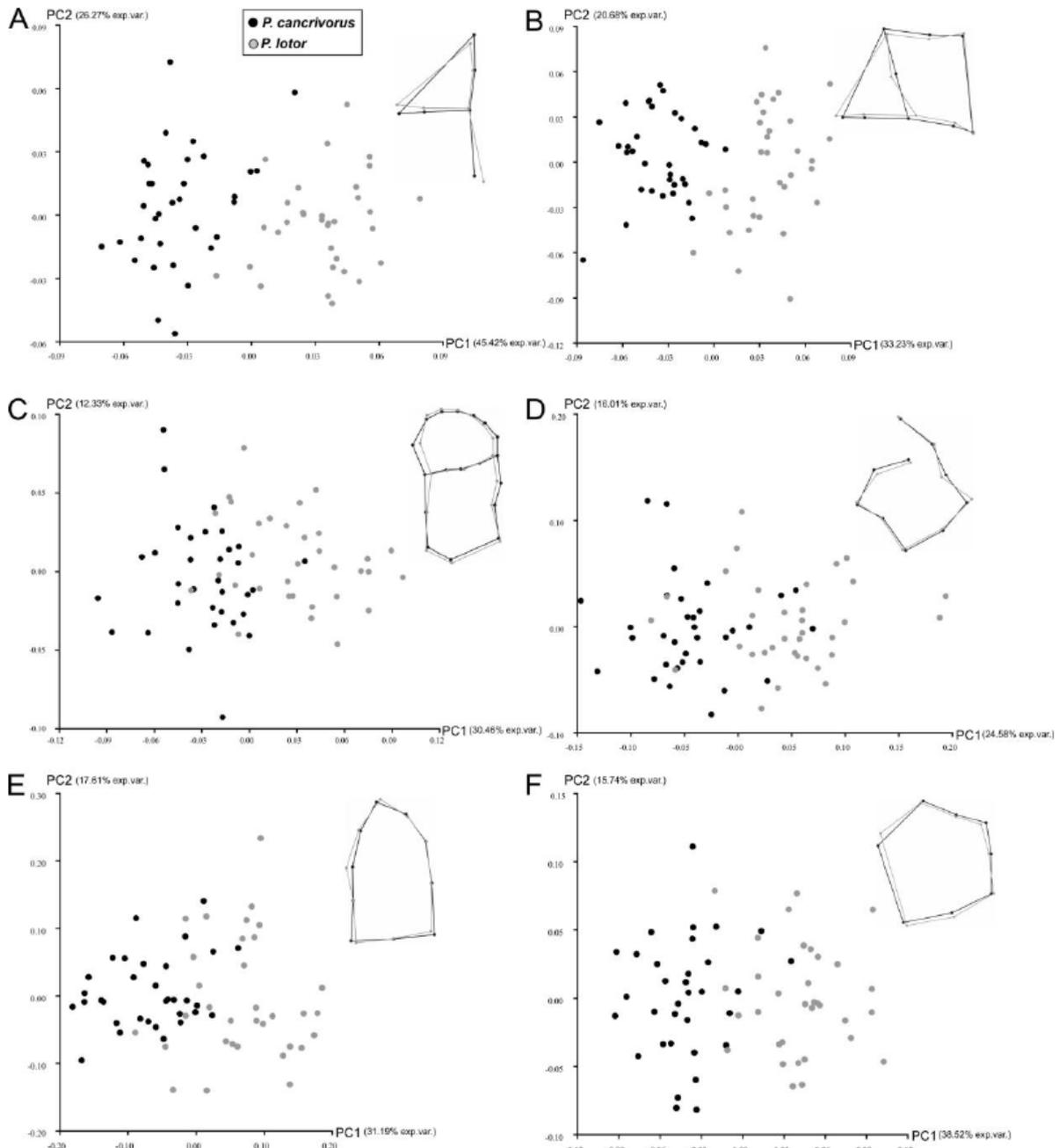
Figure 3 – Scatterplot of shape space defined by first and second principal components; superimposed diagrams illustrate shape differences between species. (A) p4; (C) m1; (E) m2; (B) P4; (D) M1; (F) M2. Percentage of explained variation indicated next to each PC. Black dots and lines: *Procyon cancrivorus*, gray dots and lines: *P. lotor*.

cifically, *P. lotor*, plotting with positive PC1 scores, presents an m1 that is labio-lingually narrower relative to its length, particularly at the level of trigonid, while *P. cancrivorus* plots with negative PC1 scores and presents a broader m1 crown. These species do not show any distinct grouping pattern along PC2 which accounts for 12.3% of the variation. There was no significant influence of size on overall shape change ($p>0.05$ for either species). Discriminant analysis indicated a statistically significant difference between the species means (Mahalanobis distance: 6.61; $p<0.0001$).

Second lower molar (m2)

The two species demonstrated considerable overlap in the morphospace of the first two PCs (Fig. 3 C). PC1, which explains 31.2% of the shape variation, summarizes changes in the width of the trigonid relative to the talonid, the former of which is wider in *P. lotor*, plotting with positive PC1 scores, than in *P. cancrivorus* along negative PC1. No grouping pattern was detected along PC2, which explains 17.61% of

the variation. Regression of shape onto size did not yield a statistically significant relationship for either species ($p>0.05$). Discriminant analysis indicated a statistically significant difference between the species means (Mahalanobis distance: 2.41; $p<0.0001$).

Fourth upper premolar (P4)

Both species occupy distinct regions of the PC1-PC2 morphospace with minimal overlap (Fig. 3 D). PC1 explains 33.2% of shape variation and is primarily related to the position of the paracone. *Procyon cancrivorus* plots at the negative end of PC1 and demonstrates a linear arrangement of labial (LM7-9) and lingual (LM1-5) cusps and a paracone (LM3) that is relatively closer to the parastyle (Prs) than to the metacone (LM5). With increasing PC1 scores, the paracone is located in a more disto-labial position, closer to the metacone as well as to the protocone (LM7) and hypocone (LM9). Consequently, the P4 of *P. lotor*, plotting with positive PC1 scores, presents a relatively narrower arrangement of cusps. PC2 explains 20.7% of shape variation

Tooth type	P. cancrivorus	P. lotor	% correctly allocated specimens	Mahalanobis distance
Upper M1	33	31	96.9	2.91*
Lower m1	31	30	92.4	6.61*
Upper P4	30	29	89.4	3.69*
Upper M2	27	29	84.8	4.32*
Lower p4	28	27	83.3	2.47*
Lower m2	25	24	74.2	2.41*

and shows complete overlap of the two species. Regressions did not show significant relationship between shape and centroid size for either species ($p>0.05$). Discriminant analysis showed a statistically significant difference between the species means (Mahalanobis distance: 3.69; $p<0.0001$).

First upper molar (M1)

The PCA demonstrated virtually no overlap between the two species of *Procyon*, with *P. lotor* occupying the positive PC1 axis and *P. cancrivorus* the negative PC1 axis (Fig. 3 E). PC1 explains 24.6% of the shape variation and is associated with several changes in landmark configuration with increasing PC1 scores: the paraconule (LM8) and protocone (LM9) occupy a more lingual position, resulting in a relatively narrower configuration of cusps on this tooth; counter to this, the hypocone (LM1) is located in a more labial position in relation to the metacone (LM2). No grouping pattern was observed along PC2, which explains 16% of the variation. Regression of shape onto size was not statistically significant for either species ($p>0.05$). Discriminant analysis yielded significant differences between the species means (Mahalanobis distance: 4.32; $p<0.0001$).

Second upper molar (M2)

The two species were not clearly distinguishable in PC1-PC2 morphospace, exhibiting extensive overlap along both axes (Fig. 3 F). PC1 explains 38.5% of the shape variation and follows a similar but weaker trend when compared to the other teeth, with *P. lotor* tending toward positive scores and *P. cancrivorus* toward negative scores. The predominant shape change associated with increasing PC1 scores is mesiodistal compression, particularly driven by decreasing the distance between the paraconule (LM8) and protocone (LM1) and between the paracone (LM7) and metacone (LM5). Thus, the M2 of *P. cancrivorus* is roughly equidimensional and pentagonal, whereas that of *P. lotor* is more rectangular. PC2 explains 15.7% of the shape variation, and no separation of the species was apparent. Regression of shape onto size was not statistically significant for either species ($p>0.05$). Discriminant analysis indicated a statistically significant difference between the species means (Mahalanobis distance: 2.91; $p<0.0001$).

Intraspecific variation and classification of specimens

In all the teeth analyzed, the magnitude, as indicated by the volume of morphospace occupied of intraspecific variation was similar for both species (see Fig. 3). The fourth premolars (P4 and p4) presented the greatest magnitude of variation, followed by the m2; the first molars (M1 and m1) displayed the lowest ranges of intraspecific variation. In agreement with these differences, cross-validation showed that the most accurate classifications were associated with the first molars (Tab. 1), while more classification errors were recorded for the fourth premolars and second molars, especially those of the lower dentition.

Discussion and conclusions

We found that intra- and interspecific shape variation in the molars and fourth premolars of *Procyon lotor* and *P. cancrivorus* are detectable via 2D geometric morphometrics and that intraspecific variation is sufficiently less than interspecific variation such that teeth were correctly classified with 73-100% accuracy. Tooth size did not have a significant influence on these shape differences. Furthermore, results indicate that the magnitude of intra- and interspecific variation between *P. lotor* and *P. cancrivorus* varies according to the tooth considered, as reflected in the PCAs and DAs, and the differential usefulness of each tooth type is evident. The most helpful molariform teeth to carry out taxonomic determinations are the first upper and lower molars, whereas the fourth premolars and second molars are less useful (see Tab. 1). It should be noted that some of the more reliable teeth are also those with greater number of recognizable structures (i.e., those with more landmarks), while the lower accuracy of species identification using premolars could be related to the fewer recognizable landmarks in these tooth types. Beyond this, our results are consistent with previous analyses on carnivores (e.g., Gingerich, 1974; Prevosti and Lamas, 2006) that identified the first lower molar (carnassial) as one of the least intraspecifically variable teeth and thus most potentially useful in searching for patterns of taxonomically informative morphological variation.

As mentioned earlier, one of our main goals, in the context of the diversity of extinct and extant procyonids, was to find out whether molariform teeth differ in their relative usefulness for reliable taxonomic identification. Thus, beyond the overall good accuracy of these teeth, we were interested on the small, but quantifiable, shape overlap that might lead to the misidentification and/or establishment of morphospecies based on dental features that represent the range of intraspecific variation of a given taxon. Previous assignations of fossil isolated molars to *Procyon cancrivorus*, such as those of Soibelzon et al. (2010) and Rodriguez et al. (2013), which apply geometric morphometrics, may thus be examined in light of these results. For example, the first of these analyses (Soibelzon et al., 2010), based on a first lower molar, is arguably more reliable than the second (Rodriguez et al., 2013), based on a lower second molar, and this is reflected in their relative warp plots (see Fig. 3 of both papers: Soibelzon et al., 2010; Rodriguez et al., 2013). Specifically, *P. lotor* and *P. cancrivorus* overlap along RW1 for m2, but no such overlap occurs for m1. Still, we agree with the assignation of that particular m2 (UNIRIO-PM 1007) to *P. cancrivorus* in the context of its associated analysis (posterior probability$\geqslant$0.99, overall percent correct m2 classification = 84.9%; Rodriguez et al., 2013).

Our results not only represent novel information about the extant variation in *P. cancrivorus* and *P. lotor*; but the detection of variable degrees of intraspecific variation presented by each of the six teeth analyzed also provides useful information regarding the reliability of each tooth type for taxonomic assignation within the genus *Procyon* that may be extended to extant and extinct procyonids in general. Particularly in the case of *Cyonasua*, its conspicuous dental morphological variation, combined with the poor preservation and fragmentary nature of its materials, may, in part, account for the multiplicity of described species. The present results highlight that the morphology of some tooth types shows considerable overlap between procyonid species, and thus this should be taken into account when making taxonomic decisions based on isolated fossil teeth. It is possible that some South American fossil procyonids represent *nomina dubia* and that the apparent interspecific variation used to justify the assignation of those species actually falls within the range of intraspecific variation of a fewer number of species.

Although our analysis included a relatively small sample and thus its implications are restricted, we consider that these results, and the application of geometric morphometrics, may be useful for researchers who work with fossil procyonids and taxa with similar challenges in terms of small sample sizes (Cardini and Elton, 2007). Geometric morphometric analyses may help to minimize the degree of subjectivity in the taxonomic assignations of isolated molars. Future similar analyses using morphometric approaches may also contribute to understanding the influence of different factors on tooth morphology, particularly the differences recorded in ranges of intraspecific variation, as seen recently for some New World primates (Nova Delgado et al., 2015). ✍

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