



First record of *Procyon cancrivorus* (G. Cuvier, 1798) (Carnivora, Procyonidae) in stratigraphic context in the Late Pleistocene of Brazil

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ARTICLE INFO

Article history:

Received 3 October 2012

Accepted 28 January 2013

Keywords:

Late Pleistocene

South America

Procyonidae

Procyon cancrivorus

Brazil

Tocantins

ABSTRACT

Although five genera of procyonids are currently present in South America, only two of the extant genera, *Procyon* and *Nasua* are represented in the South American fossil record. A recent discovery of a procyonid lower second molar in Late Pleistocene deposits of Aurora do Tocantins, northern Brazil, offers potential to further our understanding of the stratigraphic and temporal range of South American fossil procyonids. We use geometric morphometric analysis of two-dimensional landmarks and semilandmarks to explore morphological variation in the lower second molars of extant *Procyon lotor* and *Procyon cancrivorus* and multivariate methods to support the identification of the Pleistocene specimen as *P. cancrivorus*. This material represents the second fossil record of *P. cancrivorus* in South America. Procyonids entered South America in two phases: the first comprising by *Cyonasua* and *Chapadmalania* during the Late Miocene, and the other recent genera, beginning in the Late Pleistocene. These Late Miocene procyonids were more carnivorous than Late Pleistocene–Recent omnivorous taxa and possible went extinct due to competition with other placental carnivores that entered South America and diversified during the latest Pliocene–Early Pleistocene.

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1. Introduction

Procyonids are represented in South America by five living genera (*Bassaricyon* Allen, 1876, *Nasuella* Hollister, 1915, *Potos Geoffroy Saint-Hilaire and Cuvier, 1795*, *Procyon Storr, 1780* and *Nasua Storr, 1780*). From them, only *Procyon* and *Nasua* have fossil records (Late Pleistocene–Holocene) in Argentina, Brazil, Uruguay and Bolivia (Paula-Couto, 1970; Soibelzon et al., 2010). Of these, the only record with accurate stratigraphic information is that of *Procyon cancrivorus* of Argentina (see Soibelzon et al., 2010). *Procyon* comprises three species, *Procyon lotor* Linnaeus (1758) (raccoon), the only extant species of the genus in continental North America,

Procyon pygmaeus Merriam (1901) (Cozumel racoon) distributed throughout the Isla de Cozumel, México, and *P. cancrivorus* (Cuvier, 1798) (crab-eating racoon), found throughout South America (see Kays, 2009).

The aims of this work are to report a new material, assigned to the family Procyonidae on the basis of a comparative qualitative analysis, and use multivariate analyzes of geometric morphometric data to evaluate its assignation to a *Procyon* species. In addition, we describe the geologic and biostratigraphic context of the cave and discuss the implications of this finding in the context of the paleobiogeography and paleoecology of the Pleistocene of South America.

2. Material and methods

During field work carried out in February 2011 at Aurora do Tocantins (Tocantins State, northern Brazil, Fig. 1A), a lower second molar (UNIRIO-PM 1007, Fig. 1B) was unearthed at “Gruta do Urso” cave. This specimen was compared with the species *P. cancrivorus* and *P. lotor*. For the geometric morphometric analysis, digital photographs were taken in occlusal view of the lower right second molar

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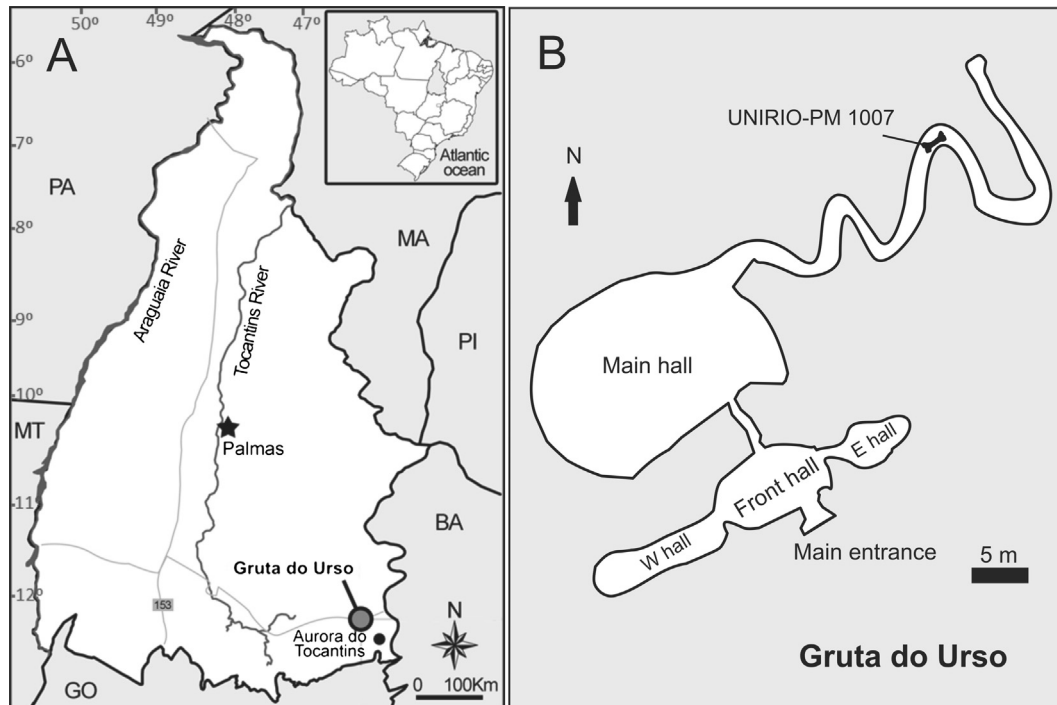


Fig. 1. A. Map depicting the location of “Gruta do Urso” cave (Tocantins State, Brazil) where UNIRIO-PM 1007 was found. B. Schematic representation of the “Gruta do Urso” cave, and the original position of the molar here described.

(m²) of the individual UNIRIO-PM 1007, 33 individuals of *P. cancrivorus* from a wide geographic range, and 33 individuals of *P. lotor* representing localities throughout North and Central America.

2.1. 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. UNIRIO-PM: Coleção de Paleontologia de Mamíferos da Universidade Federal do Estado do Rio de Janeiro, Brazil. USNM: National Museum of Natural History, National Museum of Natural History, Smithsonian Institute, USA.

2.2. Comparative materials

P. 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.

2.3. Geometric morphometrics

Ten landmarks and semilandmarks were defined (Fig. 2 (3)): (1) hypoconulid; (2) entoconid; (3) and (4) semilandmarks located

along the entocristid?; (5) metaconid; (6) semilandmark along the mesial edge; (7) protoconid; (8) semilandmark on the cristida obliqua; (9) hypocone; (10) semilandmark on the hypoconule. The landmarks and semilandmarks were digitized using the program tpsDig 2.14 (Rohlf, 2009). The configurations of points were transformed by Procrustes superimposition and semilandmarks were slid using the minimum bending energy criterion (Bookstein, 1997) in the program tpsRelw 1.49 (Rohlf, 2009). The distribution of individual configurations in the shape space was explored by means of a Principal Components Analysis (Relative Warps Analysis, RWA, Monteiro and Dos-Reis, 1999; Zelditch et al., 2004) of the Procrustes coordinates, and shape changes were visualized by means of deformation grids. A full description of geometric morphometric methods, which is beyond the scope of this work, can be found in Monteiro and Dos-Reis (1999), Zelditch et al. (2004) and Slice (2005).

The possible influence of size on shape variation was evaluated by multivariate linear regression of the shape variables on log-transformed centroid size (Monteiro, 1999; Zelditch et al., 2000, 2004). A discriminant analysis (Manly, 1994) was performed to assess the differentiation between the two living species and verify the assignation of the individual; accuracy of the classifications was evaluated using leave-one-out cross-validation (Lachenbruch, 1967). All multivariate analyzes were performed using the program MorphoJ (Klingenberg, 2010).

3. Results

3.1. Morphometric analysis

Individuals of *P. lotor* and *P. cancrivorus* were separated in the shape space, although with some overlap (Fig. 3). The first relative warp (RW1) explained 29.66% of the variation; main shape variation along this axis was associated to overall shape of the tooth (more oval in *P. lotor*, narrower and more quadrangular in *P. cancrivorus* which showed a more expanded talonid (see

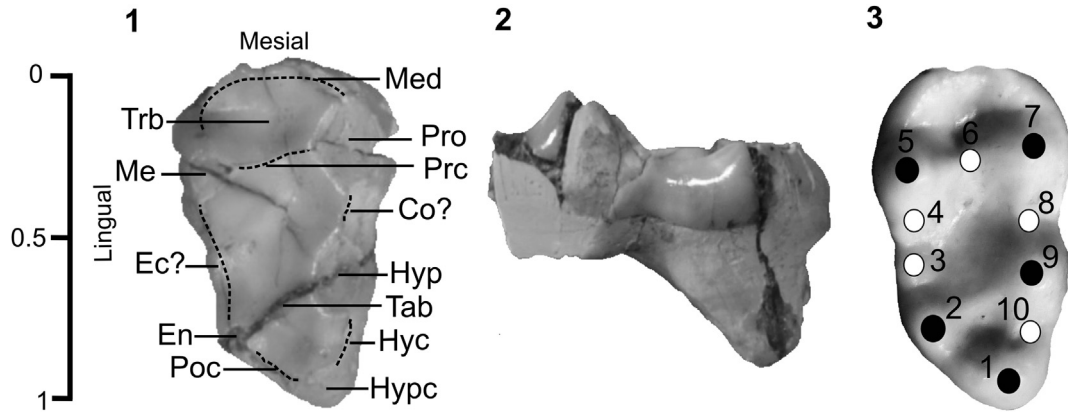


Fig. 2. UNIRIO-PM 1007 1. Occlusal view of m2 showing nomenclature of cusps and cristids. Co: Cristida obliqua (8), Ec?: Entocristid? (3) and (4), En: Entoconid, Hyc: Hypocristid (10), Hyp: Hypoconid (9), Hypc: Hypoconulid (1), Me: Metaconid (5), Med: Mesial edge, Poc: Postcristid, Pro: Protoconid (7), Prc: Protocristid (6), Tab: Talonid basin and Trb: Trigonid basin. Dashed lines indicate cristids. 2. Lateral view. 3. Second lower molar of a modern *P. cancrivorus* showing 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.

Figure C). The two species showed slight overlap along this axis (Fig. 3) with *P. cancrivorus* presenting a greater range of variation. The second relative warp (RW2) explained 21.89% of the variation, and both species were widely overlapping along this axis (Fig. 3). RW2 is primarily associated with shape changes of the trigonid; toward more positive RW2 values, the trigonid cusps are closer together and more separated from those of the talonid, while toward negative values, the trigonid cusps are more separated from each other. The individual UNIRIO-PM 1007 fell well within the

morphospace occupied by *P. cancrivorus*. The regression analysis showed very low influence of size on the overall shape of m2 (3.09% of shape variation explained by size, $p < 0.05$).

Discrimination between *P. lotor* and *P. cancrivorus* was highly significant (Wilks' $\lambda = 0.47$, $F = 35.80$, $p < 0.001$). The average accuracy obtained was 84.9%, with somewhat larger percentage for *P. lotor* (87.9% vs. 81.9% for *P. cancrivorus*). The specimen UNIRIO-PM 1007 was classified as *P. cancrivorus* with a posterior probability ≥ 0.99 .

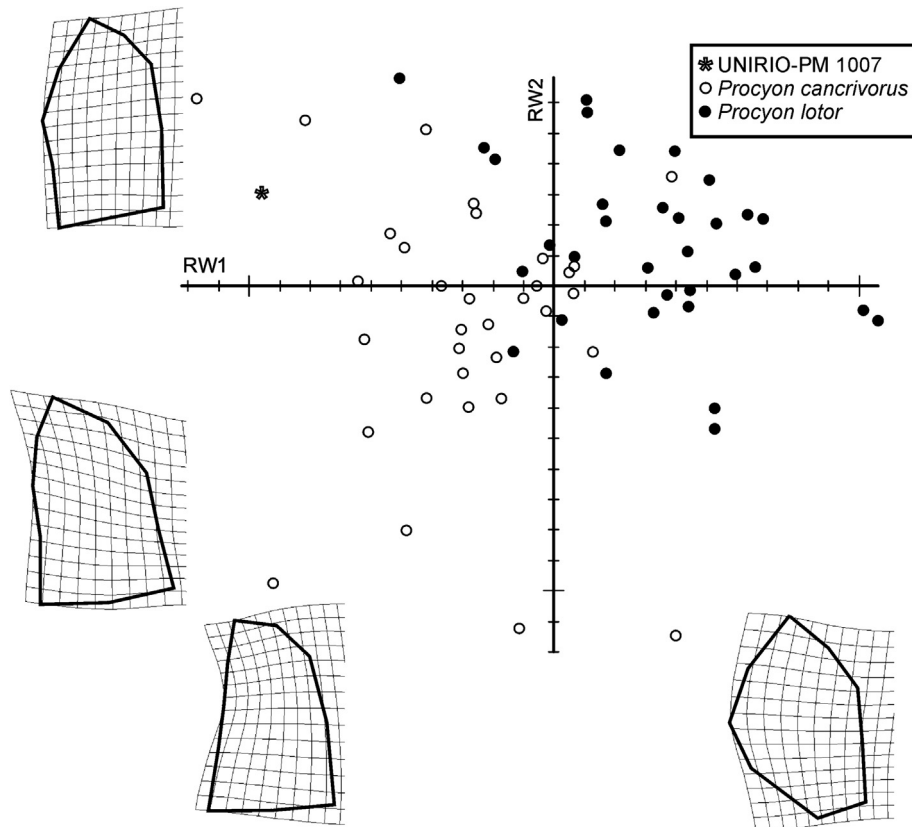


Fig. 3. Morphospace of relative deformations on the second lower molar (relative warps, RW) and deformation diagrams showing the extremes of variation for each RW. Morphospace represented by the first two relative deformations (RW1 and RW2).

3.2. Systematic palaeontology

Class Mammalia Linnaeus, 1758.
 Order Carnivora Bowdich, 1821.
 Family Procyonidae Gray, 1825.
 Genus *Procyon* Storr, 1780.
Procyon cancrivorus (Cuvier, 1798).

Type species: *P. lotor* (Linnaeus, 1758).

Referred specimen: Lower second molar (m2) UNIRIO-PM 1007. From “Gruta do Urso”, Aurora do Tocantins (Tocantins, Brazil; Fig. 1A). Late Pleistocene.

3.2.1. Description

The tooth is heavily worn, especially the cusps, which probably indicates that it is from an older individual. Mesiodistal length is greater than labiolingual length. Greatest mesiodistal length is 11.5 mm and greatest labiolingual width is 7.2 mm. The distal border is triangular and narrow, while the mesial border is broader and rounded. Talonid and trigonid lengths are similar. The base of the protoconid occupies almost the entire trigonid area. The diameter of the metaconid is about half of that of the protoconid. The hypoconid and protoconid have similar length, but the former is positioned mesiodistally relative to the latter. The entoconid is parallel to the mesiodistal portion of the hypoconid, and a narrow valley diagonally connects the hypoconid and entoconid.

3.3. Description of the geology and age of the deposits

The material comes from a limestone cave (“Gruta do Urso”) at 12°35'0.08" S and 46°30'58.39" W, Aurora do Tocantins (Tocantins, Brazil; Fig. 1A). The specimen was found in a thick sediment layer that fills the corridor of the cave (Fig. 1B).

From a geological perspective, the limestones of the Aurora do Tocantins region belong to the Speleological Province of the Bambuí Group, where the largest number of caves in Brazil has been found (Zampaulo and Ferreira, 2009). The geology of the area is poorly studied. Online notes by the CPMR (Companhia de Pesquisa de Recursos Minerais) on the geology of the municipality of Aurora do Tocantins report carbonate deposits of the Bambuí Group, which is Neoproterozoic in age (CPRM, 2006). The lower portion of the Bambuí Group is represented by the Sete Lagoas Formation, composed of thick deposits of pelite, calcarenite and dolomite bearing stromatolite. The Sete Lagoas Formation is overlain by siltstone and laminar siltstone of the Serra de Santa Helena Formation. These carbonate rocks lie beneath the dark, organic-rich calcarenite and marl of the Lagoa do Jacaré Formation that represent the upper portion of the Bambuí Group. Overlying the Bambuí Group are Cretaceous sediments of the Urucua Formation. The fossil bearing level (deposited inside the cave) is composed of laminated reddish-gray (5YR5/2) loess-like sediment.

The age of the deposit is indicated by the taxa: *Propraopus* cf. *grandis* Ameghino (1881), *Pampatherium* cf. *typum* Ameghino (1875), *Pachyarmatherium* cf. *brasiliense* Porpino et al. (2009) and *Xenorhinotherium bahiense* Cartelle and Lessa (1988) occurring at the same stratigraphic level indicate a Late Pleistocene age for the deposit (Cartelle, 1999). The remaining taxa represented at this stratigraphic level are species alive today (e.g. *Panthera onca* Linnaeus, 1758) and do not further constrain the age of the deposit. The inferred age of Gruta do Urso is consistent with the other known eastern Brazilian caves which are also Late Pleistocene (Auller et al., 2009).

4. Discussion and conclusions

The present results highlight the usefulness of morphometric analyzes for the study and taxonomic assignation of isolated

molars. While the assignment of the specimen to *P. cancrivorus* was unequivocal in this case, our analyzes reveal the existence of overlapping morphologies and considerable intraspecific variation, which should be taken into account. In this sense, ongoing studies (S.G.R, L.H.S. and C.C.M.) are analyzing such intra- and interspecific variation for different types of cheek teeth (all upper and lower premolars and molars) in order to determine their relative usefulness for species recognition.

This is the first record of *P. cancrivorus* in stratigraphic context in Brazil and the second one for South America (Soibelzon et al., 2010). These two records support the idea that *Procyon* entered South America during the Late Pleistocene. This is compatible with the hypothesis that procyonids invaded South America twice (as postulated by Patterson and Pascual (1968), Webb (1985) and Soibelzon, 2011 among others), the first time at the end of the Tertiary (Late Miocene) when *Cyonasua* and *Chapadmalania* are first recorded (see Berman, 1994; Soibelzon and Prevosti, 2007; Soibelzon, 2011) and then during the Late Pleistocene when *P. cancrivorus* has its two first records (see Soibelzon et al., 2010 and the record described here). *Nasua* probably invaded South America during the Late Pleistocene too, but such a proposal cannot be tested at this time given the lack of stratigraphic context for its records (Berta and Marshall, 1978). On the other hand, Koepfli et al. (2007) postulated that due to the divergence times between sisters groups (e.g. *Nasua narica* and *Nasua nasua* diverged ca. 7–8 mya, during the Late Miocene, *P. cancrivorus* and *P. lotor* diverged ca. 5–5.7 mya), they should be recorded in South America earlier than Late Pleistocene.

Interestingly, the first invading procyonids (*Cyonasua*, recorded from Late Miocene to Early Pleistocene) were more carnivorous than those that entered South America later (*Bassaricyon*, *Nasuella*, *Potos*, *Procyon*, and *Nasua*, Late Pleistocene to Recent) as inferred from their molar morphology (Kays, 2009; Soibelzon, 2011). This dietary shift (and consequently ecological niche change) could have been the result of the peculiar evolution of the carnivore guild in South America; although a similar trend could be observed on North American procyonids. Other mammalian predators recorded in South America by the Late Tertiary were the Sparassodonta (Metatheria) that became extinct by the Late Pliocene (Forasiepi et al., 2007 and literature cited therein), while placental carnivorans started to be recorded at the latest Pliocene (when canids and mustelids appear). However, the diversification of Carnivora (represented by the first record of Ursidae, Felidae, Mephitidae, Lutrinae and large canids) occurred in the Early Pleistocene.

Therefore, while procyonids were the only placental carnivorans in South America, they were diverse and, according to their molar morphology, seem to have occupied a much more predatory niche than today. Nevertheless, when other placental carnivorans arrived these early forms became abruptly extinct. Remarkably, when Late Pleistocene–Recent taxa (e.g. *P. cancrivorus*, *Potos flavus*, *N. nasua*) joined the South American carnivoran guild, their niche was quite different from the one that had been occupied by fossil taxa for almost 6 Ma.

Acknowledgments

We would like to thank Anselmo Rodrigues, Wagner Moura and the staff of the Sociedade Brasileira de Espeleologia, who invited us to participate in the speleological expedition to Tocantins and gave us logistic help. We appreciate all help from the group involved in the prospection and collection of the material. We also thank Itati Olivares, Sérgio Maia, David Flores, Eugenia Arnaudo, Andres Pautasso, Darrin Lunde, and Linda Gordon for allowing us to study the collections under their care; and Dimila Mothé for drawing the map in Fig. 1A. To Dr. Baskin and anonymous reviewer that help us to improve the ms with valuable suggestions. The authors also thank

CNPq (401812/2010-3, Edital MCT/CNPq n° 32/2010 – Fortalecimento da Paleontologia Nacional/Edital 32/2010), ANPCyT (PICT 0804 and 1744), CONICET (PIP 0436 and 0270) and UNLP (PI 11/N645 and 11/N568) for financial support.

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