



Anais da Academia Brasileira de Ciências (2014) 86(4): 1641-1655
 (Annals of the Brazilian Academy of Sciences)
 Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
<http://dx.doi.org/10.1590/0001-3765201420140314>
www.scielo.br/aabc

Late Pleistocene carnivores (Carnivora: Mammalia) from a cave sedimentary deposit in northern Brazil

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Manuscript received on June 25; accepted for publication on July 29, 2014

ABSTRACT

The Brazilian Quaternary terrestrial Carnivora are represented by the following families: Canidae, Felidae, Ursidae, Procyonidae, Mephitidae and Mustelidae. Their recent evolutionary history in South America is associated with the uplift of the Panamanian Isthmus, and which enabled the Great American Biotic Interchange (GABI). Here we present new fossil records of Carnivora found in a cave in Aurora do Tocantins, Tocantins, northern Brazil. A stratigraphical controlled collection in the sedimentary deposit of the studied cave revealed a fossiliferous level where the following Carnivora taxa were present: *Panthera onca*, *Leopardus* sp., *Galictis cuja*, *Procyon cancrivorus*, *Nasua nasua* and *Arctotherium wingei*. Dating by Electron Spinning Resonance indicates that this assemblage was deposited during the Last Glacial Maximum (LGM), at least, 22.000 YBP. The weasel, *G. cuja*, is currently reported much further south than the record presented here. This may suggest that the environment around the cave was relatively drier during the LGM, with more open vegetation, and more moderate temperatures than the current Brazilian Cerrado.

Key words: carnivora, fossil record, Pleistocene, South America.

INTRODUCTION

The Brazilian Quaternary fossil deposits are mainly represented by karstic caves (Auler et al. 2003). The first studies of fossil mammals found in caves of South America were conducted from 1837 to 1844 by Peter Lund in Lagoa Santa, state of Minas Gerais, southeastern Brazil (Marchesotti 2011). As part of his research, Lund described the first fossil records of Carnivora from Brazil.

Since Lund, other findings of fossil carnivores have been made in Brazilian fossil deposits of Acre (Ranzi 2000), Bahia (Paula-Couto 1955, 1980, Cartelle and Hartwig 1996), Ceará (Gomide 1989, Gomide et al. 1987), Goiás (Moreira and Melo 1971), Mato Grosso (Cartelle and Hirooka 2005), Mato Grosso do Sul (Salles et al. 1999, Perini et al. 2009), Minas Gerais (Paula-Couto 1955, Cartelle 1994), Paraíba (Bergqvist 1993), Piauí (Guérin 1991), Rio Grande do Norte (Porpino et al. 2004, Araújo-Júnior and Porpino 2011) and Rio Grande do Sul (Rodrigues et al. 2004)

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(see Table I). However, the Quaternary carnivores of central and northern regions of Brazil are still poorly known. Conducting studies in those regions that include numerical dating and stratigraphy are critical to understand the Quaternary evolution of mammals in South America. On this context, we are reporting here new dated records of Quaternary carnivores from a karstic cave at northern Brazil.

ABBREVIATIONS

I1: upper first incisor; **I2**: upper second incisor; **I3**: upper third incisor; **C1**: upper canine; **P2**: upper second premolar; **P3**: upper third premolar; **P4**: upper fourth premolar; **i1**: lower first incisor; **i2**: lower second incisor; **i3**: lower third incisor; **p1**: lower first premolar; **p3**: lower third premolar; **p4**: lower fourth premolar; **m1**: lower first molar; **m2**: lower second molar.

UNIRIO-PM: Collection of fossil mammals, Laboratório de Mastozoologia at Universidade Federal do Estado do Rio de Janeiro.

REGIONAL AND GEOLOGICAL SETTINGS

The fossils described here were collected in 2011, 2012 and 2013 in a limestone cave named “Gruta do Urso”, at Aurora do Tocantins (-12,583; -46,516), state of Tocantins, northern Brazil. The geology of the studied area is still poorly understood. Online notes of Companhia de Pesquisa de Recursos Minerais (CPRM) report on the studied region, carbonate and terrigenous deposits of the Bambuí Group.

The excavation inside the cave was controlled in order to identify the stratigraphy of the deposit. Three stratigraphic levels were recognized: 1- A superficial carbonated layer that cements the top of the cave deposit; 2- A laminated reddish-grey loess-like sediment with granulometry from very thin to thin, with a thickness of 180 to 220 millimeters. Only the second layer (level 2) contained fossil remains. 3- A yellowish layer of thicker granulometry and containing several detached angular clasts that originated from the cave walls. This third level presents a thickness of 500 mm but it may vary according to the different sections of the cave.

MATERIALS AND METHODS

The material was identified by direct comparisons with specimens housed in the following collections: Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN/UFRJ); Museu de Ciências Naturais of the Pontifícia Universidade Católica de Minas Gerais, Minas Gerais, Brazil (PUC Minas); Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina (MLP); and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN). The identification was also based on descriptions found in the literature (Berman 1994, Seymour 1989, 2012, Yensen and Tarifa 2003).

The information on the geographical distribution of extant species was based on Wilson and Mittermeier (2009).

Electron Spinning Resonance (ESR) dating was performed on the specimen UNIRIO-PM 1027 (specimen L4) by the Physics Department of the Universidade de São Paulo (FFCLRP-USP; www.ffclrp.usp.br/departamentos/fisica). We chose to date only one specimen due to the fact that all carnivores were recovered from the same level (level 2). Therefore, this specimen is considered to be synchronic with the remaining specimens described here.

RESULTS

A total of 25 specimens, described hereafter, were identified within five families and six species of Carnivora (Table I).

The ESR dating of the specimen UNIRIO-PM 1027 (*Panthera onca*) resulted in 22,000 YBP, corresponding to the Lujanian Age (late Pleistocene - early Holocene). Additionally, the recovering of *Equus (Amerhippus) neogeus* – a species that biostratigraphically defines the Lujanian Age (see Cione and Tonni 1999) – also from level 2 gives further support to a late Pleistocene - early Holocene Age.

TABLE I

Fossil and recent species of Carnivora recorded in Brazil. RS-Rio Grande do Sul; PR-Paraná; SP- São Paulo; MG- Minas Gerais; MT- Mato Grosso; GO- Goiás; TO- Tocantins; PI-Piauí; BA- Bahia; SE- Sergipe; PB- Paraíba; CE- Ceará; RN- Rio Grande do Norte; AM- Amazonas. Adapted from Cartelle 1999. (*) – Doubtful record.

Species	TO	RS	PR	MS	SP	MG	MT	GO	PI	BA	SE	PB	CE	RN	AM
<i>Lycalopex vetulus</i>						X									
<i>Lycalopex gymnocercus</i>						X									
<i>Chrysocyon brachyurus</i>				X		X									
<i>Cerdocyon thous</i>	X					X	X	X	X	X		X		X	
<i>Theriodictis</i>			X			X									
<i>Dusicyon avus</i>			X			X									
<i>Protocyon troglodites</i>		X	X	X			X		X	X	X		X	X	
<i>Speothos pacivorus</i>						X									
<i>Speothos venaticus</i>						X				X					
<i>Arctotherium wingei</i>	X	*				X			X	X			X	X	
<i>Procyon cancrivorus</i>	X					X				X					
<i>Nasua nasua</i>	X					X				X					
<i>Eira barbara</i>						X		X		X					*
<i>Galictis cuja</i>	X														
<i>Galictis vittata</i>						X									
<i>Conepatus semistriatus</i>						X				X					
<i>Lontra longicaudis</i>						X									
<i>Pteronura brasiliensis</i>				X			X			X					
<i>Puma concolor</i>	X					X				X					
<i>Puma yagouaroundi</i>						X				X					
<i>Leopardus pardalis</i>						X				X					
<i>Leopardus tigrinus</i>						X				X				X	
<i>Leopardus wiedii</i>						X									
<i>Leopardus braccatus</i>	X			X											
<i>Leopardus geoffroyi</i>	X														
<i>Panthera onca</i>	X			X	X	X	X			X					
<i>Smilodon populator</i>		X		X	X	X	X		X	X	X		*	X	

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus 1758

Order CARNIVORA Bowdich 1821

Family FELIDAE Fischer 1817

Genus *Panthera* Oken 1816

Panthera onca (Linnaeus 1758)

(Fig. 1a and 2a; Table I)

New material. UNIRIO-PM 1026, left P4; UNIRIO-PM 1031, maxillary bone fragment with left P4; UNIRIO-PM 1027, maxillary bone fragment with P2 and P3; UNIRIO-PM 1053, right C1; UNIRIO-PM 1054, left C1; UNIRIO-PM 1028, second I2; UNIRIO-PM 1057, right third I3; UNIRIO-

PM 1029, right I3; UNIRIO-PM 1032, right I3; UNIRIO-PM 1043, right I3; UNIRIO-PM 1025, left jaw fragment with p3 and p4; UNIRIO-PM 1055, indeterminate canine; UNIRIO-PM 1056, indeterminate canine; UNIRIO-PM 1047, fragment of jaw without teeth.

Geographic and temporal provenance. “Gruta do Urso” cave (-12,583; -46,516), Lujanian (late Pleistocene - early Holocene).

Fossil record in South America. The first findings of *P. onca* in South America are from the Ensenadan (early to middle Pleistocene) at “Toscas del Río de La Plata”, Buenos Aires, Buenos Aires Province (Berman 1994 although discussed by

Soibelzon et al. 2008). Since then, the species was also recorded to the late Pleistocene to early Holocene of São Raimundo Nonato, Piauí (Faure et al. 1999); Campo Formoso and Ourlândia, Bahia (Lessa et al. 1998); Lagoa Santa, Minas Gerais (Cartelle 1999, Mayer 2011); Alto Ribeira, São Paulo (Ghilardi et al. 2011); Serra da Bodoquena, Mato Grosso do Sul, Brazil (Salles et al. 2006, Perini et al. 2009); La Carolina, Quito, Ecuador (Hoffstetter 1952, Román-Carrión 2012); Talara, Piura, Peru (Seymour 2010); Tarija (Tonni et al. 2009) and Ñuagapua, Chaco, Bolivia (Hoffstetter 1968, Coltorti et al. 2012); Sopas Formation, northern Uruguay (Ubilla et al. 2004); San Francisco, Córdoba Province, and Cañada Las Achiras, Entre Ríos, Argentina (Ferrero 2008, Cruz et al. 2012); Quebrada Quereo formation (Labarca and López 2006); Ultima Esperanza, Lava Field, Pali-Aike, and Tierra del Fuego, Chile (Martín et al. 2004, Massone and Prieto 2004, Martín 2008, Canto et al. 2010); Sierra de Perijá, Estado Zulia, Venezuela (Rincón 2006).

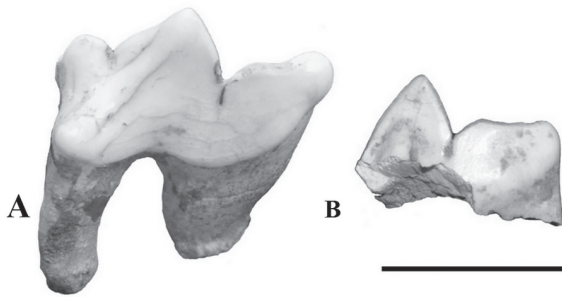


Figure 1 - A- *Panthera onca*, left P4 in labial view (UNIRIO-PM 1031). *Leopardus* sp., deciduous P3 in labial view (UNIRIO-PM 1048). Scale = 1cm.

Description. Upper second incisor (I2) – UNIRIO-PM 1028 is well preserved, however, it was not possible to distinguish it as left or right because of the similar morphology between right and left tooth. This tooth is larger than the upper first incisor. The root is mesiodistally compressed along its length. The crown extends laterally forming a

triangular form. The labial portion is convex and the lingual portion concave. On the lingual surface of the main cusp there is a deep horizontal groove (where the lower incisor occludes) and a rounded ridge centered at its base.

Upper third incisor (I3) – UNIRIO-PM1029 is a right upper incisor, with little wear on the crown apex, and laterally compressed roots. Both specimens are similar in size, but UNIRIO-PM 1032 is smaller. The right I3 UNIRIO-PM 1043 is the largest specimen among the material. Its crown is much worn with only a small band of enamel left, and the root is slender towards its apex. The tooth is compressed mesiodistally, and resembles a canine for having a conical main cusp. The labial side of the tooth is convex and the lingual side is slightly concave. On the lingual side, there is a narrow enamel crest that extends mesio-distally from the base of the crown to the apex of the main cusp; at this point a cusplet is developed. The distal side is straight and has a small groove where the lower canine occludes.

Upper canine (C) – The upper right canine UNIRIO-PM 1053 has moderate wear on its crown apex. The tooth is also fragmented at several parts of its crown and root. The other tooth, an upper left canine, UNIRIO-PM 1054, presents cracks on the root and on the upper half of the crown.

Maxillary bone – UNIRIO-PM 1027 is a left fragment of maxillary bone bearing the P2 and the P3. The P3 has two main cusps, where the mesial cusp is larger than the distal cusp. At the center of the base of the mesial cusp there is a small cusplet. The distal border of the crown ends with a transverse enamel ridge. The P2 is the smallest upper premolar and it is more developed mesiodistally than labiolingually, which forms a round shape. In occlusal view there is an enamel bridge.

Upper fourth premolar (P4) – The left P4 UNIRIO-PM 1031 is well preserved, and has a small fragment of maxillary bone preserved on its labial and lingual portions. The specimen UNIRIO-PM 1026 is

a left P4, also well preserved, but with some cracks on the root. The tooth has three roots, and the distal one is labio-lingually compressed and comprises the length of the metacone and half of the paracone. The mesiolabial root is positioned below the parastyle, lingually compressed and diagonally positioned. The third root is mesiolingually positioned below the protocone. The apex of this root bends towards the labial side. There are three cusps aligned at the labial border. The mesial cusp, the parastyle, is the smallest; the central cusp, the paracone, is the largest one followed by the distal cusp, the metacone. There is a shearing facet along the apex of all three cusps. The parastyle is conical, and the paracone is taller than the other two cusps being labiolingually compressed. The labial side of the paracone is convex and the lingual is flat. The labial portion of the metacone is also flat. The metacone presents a convex surface on the labial portion. The protocone is the smallest cusp, has round shape, and presents a punctiform projection at the apex which is positioned in front of the junction between the parastyle and the paracone.

Mandible – UNIRIO-PM 1025 is a right fragment of mandible with well preserved p3 and p4. The mandible is broken between the distal part of the p4 and the proximal portion of the mentonian foramen. Both teeth have similar morphology but the p4 is larger than the p3. On both teeth there is a main cusp which is bigger than the other ones, plus other two accessory cups. The distal accessory cusp is smaller than the mesial one. On both teeth there is also a large cingulum in distal portion.

Indet. canine – UNIRIO-PM 1056 is a well preserved root having only the crown's base. It was not possible to identify this canine as superior or inferior nor right or left. UNIRIO-PM 1055 is a worn root, which was also not possible to identify any further.

Remarks. UNIRIO-PM 1025, 1027, 1031, 1047, 1053, 1054, 1055 and 1056 were all found associated in the sediment. *Puma* is the most similar taxon to *Panthera* in size and morphology.

The canines of *Pa. onca* are markedly developed and robust. As in *Puma concolor*, the protocone of the P4 is placed on the lingual side of the crown (in front of the paracone-metacone boundary), but in *Pa. onca* the protocone of the P4 is proportionally larger and much more separated from the other two cusps. Also, the P4's parastyle is larger in *Pa. onca* in comparison to *Pu. concolor*. The p3 has a much more developed posterior cingulum in *Pa. onca*. Unlike *Pa. onca*, the P4 in *Pa. leo* has a cingulum around the parastyle. The p4 crown is much lower in *Pa. onca* than in *Pa. leo* which has an elongated principal cusp. The parastyle in P4 is less developed in *Pa. onca* than in *Smilodon*. In *Smilodon* all cusps are queued and mesiolabial cusps are absent. The upper canine of *Smilodon* is clearly broader and longer than the C1 of *Pa. onca*. Moreover, the canines of *Smilodon* are serrated on its lingual portion and comprised on its mesiodistal portion.

Genus *Leopardus* Gray 1842

Leopardus sp.

(Fig. 1b)

New material. UNIRIO-PM 1048, left dP3.

Geographic and temporal provenance. "Gruta do Urso" cave (-12,583; -46,516), Lujanian (late Pleistocene to early Holocene).

Description. Upper fourth premolar (P4) – The left P4 UNIRIO-PM 1048 is broken on the parastyle and protocone and also has missing roots. The paracone is triangular and higher than the metacone. The apex of the metacone is almost straight. The base of the crown in labial view goes up towards the end of the metacone. The labial portion is concave and folds to the inside where the metacone connects the paracone.

Remarks. The specimen is represented by a deciduous tooth. The paracone and metacone are straight on its lingual portion while its cusps are convex in shape. In a permanent tooth, the paracone

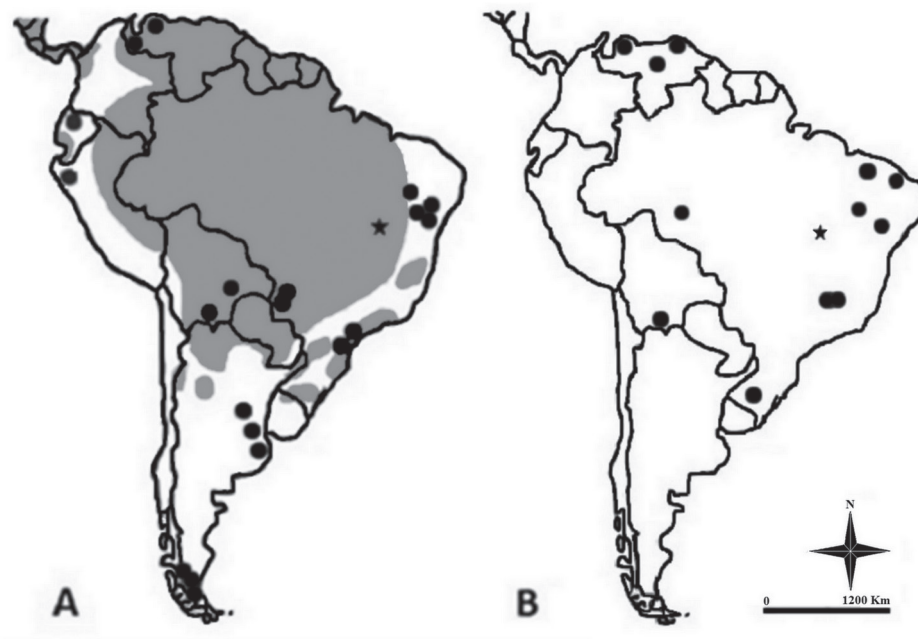


Figure 2 - Maps with the current distributions in South America (in grey; adapted of Wilson and Mittermeier 2009) and fossil record in South America (black dots): **A** - *P. onca* (Faure et al. 1999, Lessa et al. 1998, Cartelle 1999, Mayer 2011, Ghilardi et al. 2011, Salles et al. 2006, Perini et al. 2009, Hoffstetter 1952, Román-Carrión 2012, Seymour 2010, Tonni et al. 2009, Hoffstetter 1968, Coltorti et al. 2012, Ubilla et al. 2004, Ferrero 2008, Cruz et al. 2012, Labarca and López 2006, Martín et al. 2004, Massone and Prieto 2004, Martín 2008, Canto et al. 2010, Rincón 2006, Oschenius 1980); **B** - *A. wingei* (Paula-Couto 1960, Guérin 1991, Cartelle 1994, 1998, Trajano and Ferrarezzi 1994, Lessa et al. 1998, Soibelzon 2002, 2004, 2012, Soibelzon et al. 2005, Ribeiro et al. 2003). (★) – Aurora do Tocantins caves.

has a pyramidal form and the cusps are aligned at the labial edge. The deciduous P3 is smaller than in *Puma* and *Panthera*. However, the dental morphology of the dP3 is similar to *Leopardus pardalis*, *Leopardus wiedii* and *Leopardus tigrinus*. For that reason the specimen UNIRIO-PM 1048 is identified only by genus level.

Family URSIDAE Fischer 1817

Genus *Arctotherium* Bravard 1857

Arctotherium wingei Ameghino 1902

(Fig. 3a and 2b; Table I)

New material. UNIRIO-PM 1033, right I3; UNIRIO-PM 1060, upper incisor indet.; UNIRIO-PM 1021, right C; UNIRIO-PM 1020, left c; UNIRIO-PM 1019, right p1.

Geographic and temporal provenances. “Gruta do Urso” cave (-12,583; -46,516) Lujanian (late Pleistocene to early Holocene).

Fossil record in South America. Late Pleistocene of Tarija, Bolivia; Monagas and Muaco, Venezuela (Soibelzon 2004, Soibelzon et al. 2005, Soibelzon and Rincón 2007); Bahia, Brazil (Lessa et al. 1998); Ubajara, Ceará, Brazil (Trajano and Ferrarezzi 1994); São Raimundo Nonato, Piauí, Brazil (Guérin 1991); Rio Grande do Norte, Brazil (Cartelle 1994, 1998); Lagoa Santa, Minas Gerais, Brazil (Paula-Couto 1960); Lapa da Escrivantina, Prudente de Moraes, Minas Gerais, Brazil, (Soibelzon 2002); Rio Grande do Sul, Brazil (Ribeiro et al. 2003).

Description. **Upper third incisor (I3)** –The right I3 UNIRIO-PM 1033 is well preserved and

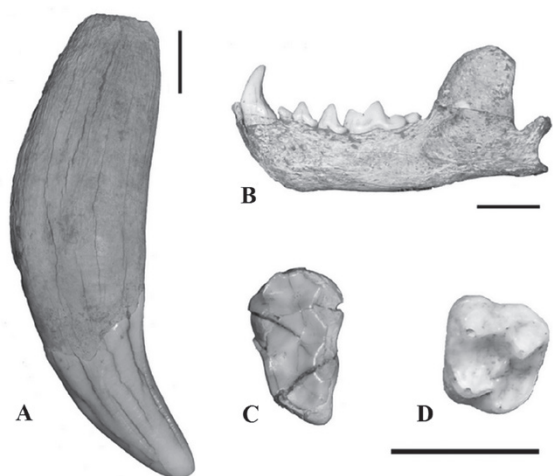


Figure 3 - A- *Arctotherium wingei*, lower right canine in lingual view (UNIRIO-PM 1020). *Galictis cuja*, left dentary in labial view (UNIRIO-PM 1007). *Procyon cancrivorus*, right m2 in occlusal view. *Nasua nasua*, left M1 in occlusal view. Scales = 1cm.

has a deep groove where the tooth occludes with the lower tooth. The tooth is labio-lingually compressed from the root apex to halfway up the crown. The crown has a large central cusp, conically shaped on its base and mesiodistally curved. The crown is convex on labial view, straight on distal view, and concave on mesiolingual view.

Upper incisor indet. – UNIRIO-PM 1060 has the root broken on its apex. The crown is well preserved with little wear. The root is mesiodistally compressed, and larger on the mesial and distal view than on the lingual and labial view. The crown has a triangular form in all views. There is a groove on the occlusal area.

Upper canine (C) – The right canine UNIRIO-PM 1021 is well preserved, having few cracks and little wear on the crown. It is a large tooth in both length and width. The crown is conical and slightly labiolingually compressed, and delimited by two enamel crests that are present along the whole length of the crown. The root is long, laterally compressed and gets thinner towards its apex. The mesial part of the root is concave and the distal part is convex.

Lower canine (c) – The left canine UNIRIO-PM 1020 is shorter and thinner than its upper correspondent. The crown has little wear and some cracks are present along the whole tooth. The root is bent and longer than the crown. The crown is also bent and has the same crests as the upper canine.

Remarks. All specimens belong to one individual adult specimen. UNIRIO-PM 1020 and UNIRIO-PM 1021 were found associated, and are proportional in size. The occlusion is also perfect between them. *A. wingei* is the only species known for the late Pleistocene of northern South America (Brazil, Bolivia and Venezuela). The exception is the record of *A. tarijense* to Tarija, Bolivia, in sediments presumed to be younger than early Pleistocene (see Soibelzon et al. 2005, Soibelzon and Rincón 2007). *A. wingei* is the smallest species of *Arctotherium* and even though size is not considered a good taxonomic character for bears, the difference between *A. wingei* and the other species is so conspicuous (Soibelzon and Tarantini 2009) that we decided to use it in association with other anatomical characters described in the next segment.

The canines of *A. wingei* are markedly curved labio-lingually. The upper canine is very similar between species of *Arctotherium*, differing mainly in size. The canine of *A. wingei* is the smallest among the species. The lower canine of *A. wingei* presents two enamel ridges as in *A. angustidens* and *A. tarijense*, while in *A. vetustum* and *A. bonariense* there are three ridges. The upper third incisor is the largest incisor of the upper tooth row; it is caniniform, with a high laterally compressed crown. The main cusp is morphologically similar to that of the I2, the mesial ridge is broader and longer than the distal ridge, and there is no enamel bulge between them. In *A. vetustum*, the distal ridge is very small and the mesial ridge is small, while in *A. angustidens* and *A. tarijense* both ridges are large. The total of observed characters leads us to assign the following specimens as *A. wingei*.

Family MUSTELIDAE Fischer, 1817

Genus *Galictis* Bell 1826

Galictis cuja (Molina 1782)

(Fig. 3b and 4a; Table I)

New material. UNIRIO-PM 1001 is represented by a right and a left dentary. On the right dentary the coronoid and condylar processes are absent. Only the p4 and m1 are present, and only the alveoli of

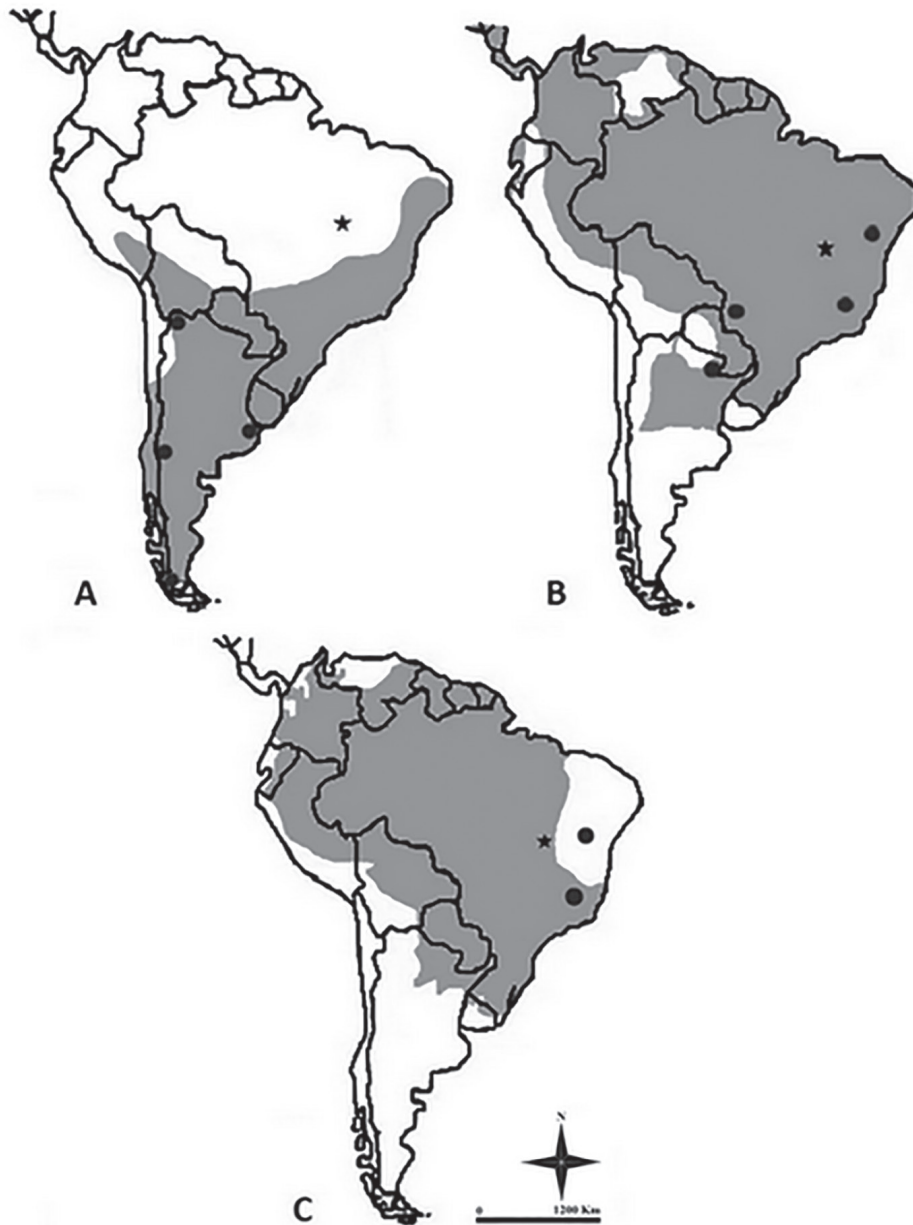


Figure 4 - Maps with current distribution in South America (in grey; adapted from Wilson and Mittermeier 2009) and fossil record in South America (black dots): **A** - *G. cuja* (Prevosti in litt, Distel 1986, Mazzanti and Quintana 2001); **B** - *P. cancrivorus* (Paula-Couto 1970, Lessa et al. 1998, Salles et al. 2006, Soibelzon et al. 2010); **C** - *N. nasua* (Berta and Marshall 1978, Paula Couto 1970, Cartelle 1999). (★) – Aurora do Tocantins caves.

the incisors, canine, p3 and m2 are preserved. The left dentary has i3, c, p2, p3, p4, m1 and m2 present and no tooth is worn.

Geographic and temporal provenance. “Gruta do Urso” cave (-12,583; -46,516), Lujanian (late Pleistocene to early Holocene).

Fossil record in South America. The species is recorded from late Pleistocene to early Holocene of Cueva de Milodón, Magallanes, Chile; Chenque Haichol, Argentina (Massoia 1992); Cueva Tixi, Buenos Aires, Argentina (Mazzanti and Quintana 2001); El Manantial, Provincia Rio Negro, Argentina (Yensen and Tarifa 2003) and Cueva III of Huachichocana, Provincia Jujuy, Argentina (Distel 1986).

Description. **Dentaries** – UNIRIO-PM 1001 left dentary has its angular process preserved but the coronoid and condylar processes are broken. The labial portion is broken at the same height as the p4. The material has cracks all over its surface. The mandibular foramen is preserved. The right dentary is broken horizontally at the coronoid process. The fracture was made during the collection of the material, but it was possible to reunite and glue all parts. The angular portion of the condylar process is broken on its lingual portion. Five mentalis foramina and the mandibular foramen are present.

Third lower incisor (i3) – The crown is straight and quadrangular on labial view.

Lower canine (c) – The base of the crown is large and gets thinner towards its apex. The tooth is curved, where the labial portion is convex and the lingual portion is concave.

Third lower premolar (p3) – There is only one conical cusp. A thick cingulum is present in front of the mesial margin of the p4.

Fourth lower premolar (p4) – This tooth is bigger than the p3 but it is very similar in form to the p3. The enamel is elongated behind the single cusp, flexing markedly at the lingual margin of the tooth, while the labial margin is straight. The tooth is placed diagonally on the tooth row.

First lower molar (m1) – The protoconid is straight. There is a thick cingulum at the talonid margin. The metaconid is absent.

Second lower molar (m2) – This molar is smaller than the m1, subcircular in form and has an enamel crest along the crown. The tooth is placed on the tooth row higher than the other teeth, next to the coronoid process.

Remarks. The genus *Galictis* is found throughout zoological collections with identifications that have been switched back and forth between *G. cuja* and *G. vittata*. The only dental characteristic that distinguishes *G. cuja* and *G. vittata* is the presence of a metaconid on the m1 of *G. vittata*. Apart from that, both species are very similar, except in size, where *G. cuja* is smaller than *G. vittata*. Both hemimandibles described here were found at approximately the same place in the cave, but in two different years. These dentaries have similar proportions and their symphyses are well preserved so that they fit together. Therefore, we consider that these dentaries belong to the same individual.

Family PROCYONIDAE Gray 1825

Genus *Procyon* Storr 1780

Procyon cancrivorus (Cuvier 1798)

(Fig. 3c and 4b; Table I)

New material. UNIRIO-PM 1007, right m2.

Geographic and temporal provenance. “Gruta do Urso” cave (-12,583; -46,516), late Pleistocene to early Holocene.

Fossil record in South America. The species is recorded from late Pleistocene to early Holocene of Argentina (Soibelzon et al. 2010); Lagoa Santa, Minas Gerais, Brazil (Paula-Couto 1970); Bahia, Brazil (Lessa et al. 1998); Serra da Bodoquena, Alto Ribeira, Brazil (Salles et al. 2006).

Description. **Lower second molar (m2)** – The right m2 UNIRIO-PM 1007 is markedly worn and it probably belonged to an older individual. The mesiodistal length is bigger than the labiolingual length. The distal edge is narrow and triangular. The mesial edge is broad and rounded. The trigonid and

the talonid have similar dimensions. The metaconid and the hypoconid are absent and it is only possible to identify their bases. The base of the protoconid is almost the same length of the trigonid. The base of the metaconid is about half the size of the base of the protoconid. The base of the hypoconid is similar in length to the base of the protoconid, and is placed behind the mesiodistal portion of the tooth, aligned to the main axis. The entoconid is placed parallel to the mesiodistal portion of the base of the hypoconid. A cristid connects diagonally the base of the hypoconid and the entoconid. The mesial root and part of the enamel on the base of the crown are absent. The material has some cracks on both crown and root.

Remarks. The specimen of *Procyon cancrivorus* described here represents the first potential late Pleistocene record of the species to Brazil (for more details see Rodriguez et al. 2013).

Genus *Nasua* Storr 1780

Nasua nasua (Linnaeus 1766)

(Fig. 3d and 4c; Table I)

New material. UNIRIO-PM 1320 left M1.

Geographic and temporal provenance. "Gruta do Urso" cave (-12,583; -46,516), Lujanian (late Pleistocene to early Holocene).

Fossil record in South America. The species is recorded at the late Pleistocene of Tarija, Bolivia (Berta and Marshall 1978); late Pleistocene-Holocene of Minas Gerais, Brazil (Paula Couto 1970) and Bahia, Brazil (Cartelle 1999).

Description. **Upper first molar (M1)** – Three roots are present: two thin roots on labial position, which are mesiodistally compressed, and one large root of pyramidal form on lingual position. The crown is quadrangular, and longer labio-lingually than mesiodistally. There are four cusps of pyramidal form. The paracone is the largest cusp placed at the mesiolabial portion of the crown. This cusp is connected with the metacone and the protocone by a thin enamel crest. The metacone is placed at the distolingual portion of the crown.

Remarks. Usually the M1 has a more rounded outlined crown than the material described here, which has a quadrangular outlined crown. A more rounded outlined crown was also observed in the specimens MNRJ 3075, MNRJ 13518 and MNRJ 32431 housed at the Department of Mammalogy of the Museu Nacional/Universidade Federal do Rio de Janeiro, Brazil. Also, the tooth is worn on the labial portion of the crown. Maybe this wear was caused by friction with upper teeth and/or bad occlusion. *Bassaricyon gabbii* has only one lingual cusp on the M1. *Bassariscus astutus* and *Bassariscus sumichrasti* have differences in form, number of cusps and form of these cusps, and resembles the M1 of Canidae. In *Procyon cancrivorus* the metacone is more centralized than in *Nasua nasua*, and presents a large mesiolabial cingulum that is not present in *N. nasua*. On the described material, the M2 is the tooth more similar with *Pr. Lotor*. However, some differences are recognizable between both taxa, such as lingual cusp larger and more centralized in *Pr. lotor* than in *N. nasua*. An other important difference is the presence of two accessory cusps in *N. nasua*. Also, the M1 of *Pr. lotor* has a lingual cingulum that is not present in *N. nasua*.

Family CANIDAE Fischer von Waldheim 1817
Canidae indet.

New material. UNIRIO-PM 1321, right mandible fragment with canine.

Geographic and temporal provenance. "Gruta do Urso" cave (-12,583; -46,516); Lujanian (late Pleistocene to early Holocene).

Description. **Mandible fragment** – UNIRIO-PM 1321 is broken behind the mentonian foramen. The mandibular symphysis is long and goes from the incisors to the p2 alveoli. On the mesial portion of the mandible the alveoli of the incisors are also broken. The canine is the only preserved tooth. Its crown is conical and curved towards the distal portion of the tooth. There are two enamel crests, one on

the lingual portion and another on the mesial portion, which occludes with the upper third incisive. The crown is fissured perpendicularly to the mandible.

Remarks. The specimen was compared with *Lycalopex vetulus*, *Lycalopex gymnocercus* and *Cerdocyon thous*, due to the dental morphology similarity of these species to our material. The intraspecific variation and similarity of teeth between Canidae taxa have prevented us to identify our specimen beyond family level.

DISCUSSION

The fossil assemblage of “Gruta do Urso” cave includes the greatest diversity of Pleistocene Carnivora found in association at the same site in South America (Table I). The stratigraphic control applied, assured that all fossils came from the same level. Therefore, this assemblage can be recognized as part of an ancient mammalian community.

Previous studies in Brazilian caves gathered fossil diversity data from a number of caves or merged information from several localities (e.g. Cartelle 1999, Lessa et al. 1998) treating this collection of taxa of different spatial origins as a single ancient ecological community. Moreover, most fossils were found laying over the sediment (out of stratigraphic context), or no stratigraphic control was made during the excavation. In addition, there is also no taphonomic analysis nor numerical dating procedures in those previous studies to assure that all specimens were from the same locality and stratigraphic level. Therefore, these collections might represent artificial assemblages as a result of great temporal and spatial mixture. Although only one dating was performed on the fossils here described, the stratigraphic controlled survey performed at “Gruta do Urso” cave indicates that this assemblage has so far the highest Carnivora diversity for the late Pleistocene of South America.

Nowadays, South America is the continent which has the highest diversity of extant Carnivora

(Van Valkenburgh 1988), but during the Pleistocene this diversity was even greater. Many of the South American extant taxa were already present in the continent during the late Pleistocene, and co-existed with species that became extinct during the late Pleistocene-Holocene boundary (Prevosti and Soibelzon 2012). Therefore, several extant South American carnivores are survivors of the late Pleistocene/Holocene extinctions. The conditions that allowed the survival of those taxa are still unknown, mainly because their fossil records are scarce. However, it appears to be partially related to their medium to small body masses.

Among the extant carnivores which are also recorded to the South American Pleistocene, the best known species from biostratigraphic context and geographic distribution is *Panthera onca*. Today, *Pa. onca* is also the largest living South American carnivore. Yet, large Pleistocene extinct carnivores such as *Arctotherium*, *Smilodon* and several taxa of Canidae are also well documented on the fossil record (Soibelzon and Prevosti 2007). The lack of information regarding the fossil record of middle to small-sized Pleistocene Carnivora of South America might lead to the idea of rarity. However, the common usage of survey techniques such as picking that evidence larger fossils (complete or fragmented) may help to support the assumption that smaller carnivore taxa were scarce. Furthermore, this scarcity of middle to small-sized Carnivora in South American Pleistocene deposits can be also a consequence of taphonomic bias (Soibelzon and Prevosti 2007). This would also explain their absence or scarcity in tropical regions (Soibelzon and Prevosti 2007).

Among the Carnivora taxa of Aurora do Tocantins, *Arctotherium wingei* is the only species that was completely extinct by the late Pleistocene (Soibelzon and Rincón 2007). This is the smallest (Soibelzon and Tartarini 2007) and the most herbivore (Figueirido and Soibelzon 2009) species of *Arctotherium*. The fossil record presented here represents the first fossil of *A. wingei* from Brazil

with accurate stratigraphic procedure, since older findings (e.g. the materials from Minas Gerais) were described without stratigraphic context (see Soibelzon et al. 2005).

The described remains of *Galictis cuja* correspond to the first record of this species to northern Brazil, as well as the first record at lower latitudes of South America. The mustelid *G. cuja* is currently distributed from southern Peru to Argentina, except for southern Patagonia (Fig. 4a). Nowadays, *Galictis cuja* inhabits the drier Cerrado (Savanna) and Caatinga (Deserts and Xeric Shrublands) biomes of northeast Brazil, the Atlantic Forest throughout the eastern seaboard, and the pampas grassland towards the south (Bornholdt 2012). Therefore, it is possible that the extinction of *G. cuja* in northern Brazil was the result of environmental changes occurred during the end of Pleistocene.

The felid *Panthera onca*, and the procyonids *Procyon cancrivorus* and *Nasua nasua* are present today throughout all Brazilian territory, but the fossil records of the last two are more infrequent. These species may inhabit several habitats, such as dry and wet rainforests. They are common in gallery forests and areas close to freshwater, such as swamps, margins of rivers and mangroves (Handley 1976, Schaller 1983, Mondolfi 1986, Emmons 1990). Today, the jaguar *Pa. onca* is occasionally found in arid environments, but always nearby water sources (Wilson and Mittermeier 2009). It seems that the ability of *Pa. onca* to inhabit arid places is not that uncommon, since they occur in arid regions of Mexico and southwestern North America today. Also, late Pleistocene fossil records of jaguars indicate environmental plasticity across much of North and South America. Thus, their current geographic distribution is not necessarily a reflection of their potential range. Other fossils found in “Gruta do Urso” cave are also known for their association to freshwater resources: the

sigmodontid rodent *Holochilus sciureus* (Pardiñas et al. 2011); the boiid snake *Eunectes murinus* (the anaconda; Hsiou et al. 2013); and the caiman from the subfamily Caimaninae. Although *Pa. onca* and *Pr. cancrivorus* currently occur on the studied area, this does not imply that the region was climatically stable since the Pleistocene. Although these species exhibit great environmental plasticity, we can only infer that their presence in the area during the time of deposition indicates freshwater sources nearby the caves.

Hence, the fossil assemblage recovered from “Gruta do Urso” cave indicates that the different climatic conditions and ecosystems might have existed during the late Pleistocene. Those changes probably produced the local extinction of *G. cuja* and the extinction of *A. wingei*.

ACKNOWLEDGMENTS

We would like to thank the following curators: João Alves and Sergio Maia Vaz (Museu Nacional-UFRJ), Castor Cartelle (Museu PUC-Minas), Marcelo Regueiro (Museo de La Plata), Itati Olivares (Museo de La Plata) and Alejandro Kramartz (Museo Argentino Bernardino Rivadavia) for granting us access to the zoological and paleontological collections. Also, we appreciate all technical and logistic support provided during expeditions by Municipality of Aurora de Tocantins, Mr. Wagner Moura and the Sociedade Brasileira de Espeleologia. The authors also thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (401812/2010-3, Edital MCT/CNPq N° 32/2010 - Fortalecimento da Paleontologia Nacional / Edital 32/2010 - Faixa B and 552975/2011, Apoio a Projetos de Pesquisa / Chamada MCTI/CNPq N° 23/2011 - Apoio Técnico para Fortalecimento da Paleontologia Nacional), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), ANPCyT (PICT 0804), CONICET (PIP 0436) and UNLP (PI 11/N645) for financial support.

RESUMO

Os Carnívora terrestres do Quaternário brasileiro são representados pelas seguintes famílias: Canidae, Felidae, Ursidae, Procyonidae, Mephitidae e Mustelidae. Sua recente história evolutiva na América do Sul está associada com o soerguimento do Istmo do Panamá, que possibilitou o Grande Intercâmbio Biótico das Américas (GIBA). Aqui apresentamos novos registros fossilíferos de Carnívora encontrados em uma caverna no município de Aurora do Tocantins, Tocantins, norte do Brasil. A coleta com controle estratigráfico no depósito sedimentar da caverna estudada revelou um nível fossilífero onde os seguintes taxa de Carnívora estão representados: *Panthera onca*, *Leopardus sp.*, *Galictis cuja*, *Procyon cancrivorus*, *Nasua nasua* e *Arctotherium wingei*. A datação por Ressonância Eletrônica de Spin indica que essa assembléia foi depositada durante o Último Máximo Glacial (UMG), há pelo menos 22.000 Ma. O furão, *G. cuja* é atualmente registrado mais longe do sul do continente que o registro apresentado aqui. Isto pode sugerir que o ambiente próximo à caverna era relativamente mais seco durante o UMG, com vegetação mais aberta, e temperaturas mais moderadas que o atual Cerrado Brasileiro.

Palavras-chave: carnívora, registro fossilífero, Pleistoceno, América do Sul.

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