



CARNIVORES (MAMMALIA, CARNIVORA) FROM THE QUATERNARY OF SERRA DA BODOQUENA, MATO GROSSO DO SUL, BRAZIL ¹

(With 4 figures)

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ABSTRACT: A report on fossil remains of carnivores from the Quaternary of Serra da Bodoquena (Mato Grosso do Sul, Brazil), recovered from two limestone flooded caves, is presented. A total of six species could be identified belonging to three carnivore families, namely Felidae (*Smilodon populator*, *Panthera onca*, *Leopardus braccatus*), Canidae (*Procyon troglodytes*, *Chrysocyon brachyurus*) and Mustelidae (*Pteronura brasiliensis*), a mosaic of extinct and extant species presumably related to the Holo-Pleistocene fauna of the region. These findings support in part previous suggestions of a paleoecological scenario of open savannas rich in wetlands for the Quaternary environment of Serra da Bodoquena.

Key words: Mammalia. Carnivora. Quaternary. Serra da Bodoquena. Underwater Caves.

RESUMO: Carnívoros (Mammalia, Carnivora) do Quaternário da Serra da Bodoquena, Mato Grosso do Sul, Brasil.

Uma primeira apreciação relativa aos fragmentos fósseis de carnívoros do Quaternário da Serra da Bodoquena (Mato Grosso do Sul, Brasil) é apresentada. A amostra analisada foi recuperada em duas cavernas submersas e, presumivelmente, representam depósitos de origem associada ao intervalo entre Pleistoceno inferior e o Holoceno. Esta hipótese é corroborada pela megafauna de mamíferos associada. Seis espécies puderam ser identificadas, compreendendo três famílias de Carnívora: Felidae (*Smilodon populator*, *Panthera onca*, *Leopardus braccatus*), Canidae (*Procyon troglodytes*, *Chrysocyon brachyurus*) e Mustelidae (*Pteronura brasiliensis*), retratando, assim, um mosaico de espécies recentes e extintas da fauna de carnívoros que compõem a região. Estes achados suportam parcialmente sugestões anteriores de um cenário paleoecológico de savanas ricas em áreas úmidas para o Quaternário da Serra da Bodoquena.

Palavras chave: Mammalia. Carnivora. Quaternário. Serra da Bodoquena. Cavernas Submersas.

INTRODUCTION

The fossil record of carnivores is relatively scarce in Brazil. First reports arose in the mid-19th century, with descriptions of the Pleistocene fauna from the limestone caves of Lagoa Santa (Minas Gerais, Southeastern region) by Peter Lund (PAULA COUTO, 1953). Since then, new discoveries have been made in the Southern (RODRIGUES *et al.*, 2004; OLIVEIRA *et al.*, 2005), Southeastern (CARTELLE, 1994,

1999), and Northeastern (LESSA *et al.*, 1998; CARTELLE, 1999; DANTAS *et al.*, 2005) regions of the country. Apart from occasional reports from Goiás (MOREIRA & MELO, 1971), Mato Grosso (CARTELLE & HIROOKA, 2005), and Acre (RANZI, 2000), the carnivore paleofauna from the North and Central regions of Brazil remains largely unknown. Here we present a report on fossil remains of carnivores from the Quaternary of Serra da Bodoquena, Mato Grosso do Sul.

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GEOLOGICAL SETTING AND ASSOCIATED FAUNA

The Serra da Bodoquena is located in the southeastern part of the Mato Grosso do Sul State, harboring the municipalities of Jardim, Bonito, Bela Vista, Porto Murtinho, and Bodoquena (Fig.1). A full description of its geological and phytogeographic setting can be found in BOGGIANI *et al.* (1999) and SALLES *et al.* (2006).

Few studies concerning the Quaternary period have been conducted in the region, such as those of ALMEIDA (1965), MENDES (1957), LINO *et al.* (1984), GNASPINI *et al.* (1994), and AYUB *et al.* (1996). There are hundreds of caves in the Serra da Bodoquena karst, but no more than fifty were formally described and/or mapped (LINO *et al.*, 1984; GNASPINI *et al.*, 1994; AYUB *et al.*, 1996).

Fossil carnivores were recovered from two underwater caves, Japonês (21°35'63"S, 56°39'59"W) and Nascente do Formoso (21°15'35"S, 56°38'26"W). All specimens presumably range from latest Pleistocene to Holocene; efforts to date related fossil material from these caves have been hindered by unsuccessful attempts to extract collagen from the bones. Numerous other fossils mammals, typical of the South American Quaternary, are found in the clayey sedimentary layers associated with the carnivore fragments here described (SALLES *et al.*, 2006), such as: xenarthrans (*Dasypus*, *Euphractus*, *Propaopus*, *Pampatherium*, *Glossotherium*, *Myloodonopsis*, *Eremotherium*, and *Glyptodon*), horses (*Equus*), tapirs (*Tapirus*), mastodons (*Stegomastodon*), deer (*Mazama* and *Ozotoceros*), peccaries (*Tayassu*), llamas (*Paleolama*), and members of South American endemic ungulate orders (*Macrauchenia* and *Toxodon*).

TAXONOMY

Identifications were based on comparisons with fossil and recent material mainly belonging to the mammal collections of the Museu

Nacional (MN), Rio de Janeiro, and Museu de Zoologia, Universidade de São Paulo, Brazil. Measurements were taken with 0.02x150mm digital calipers and are shown in table 1.

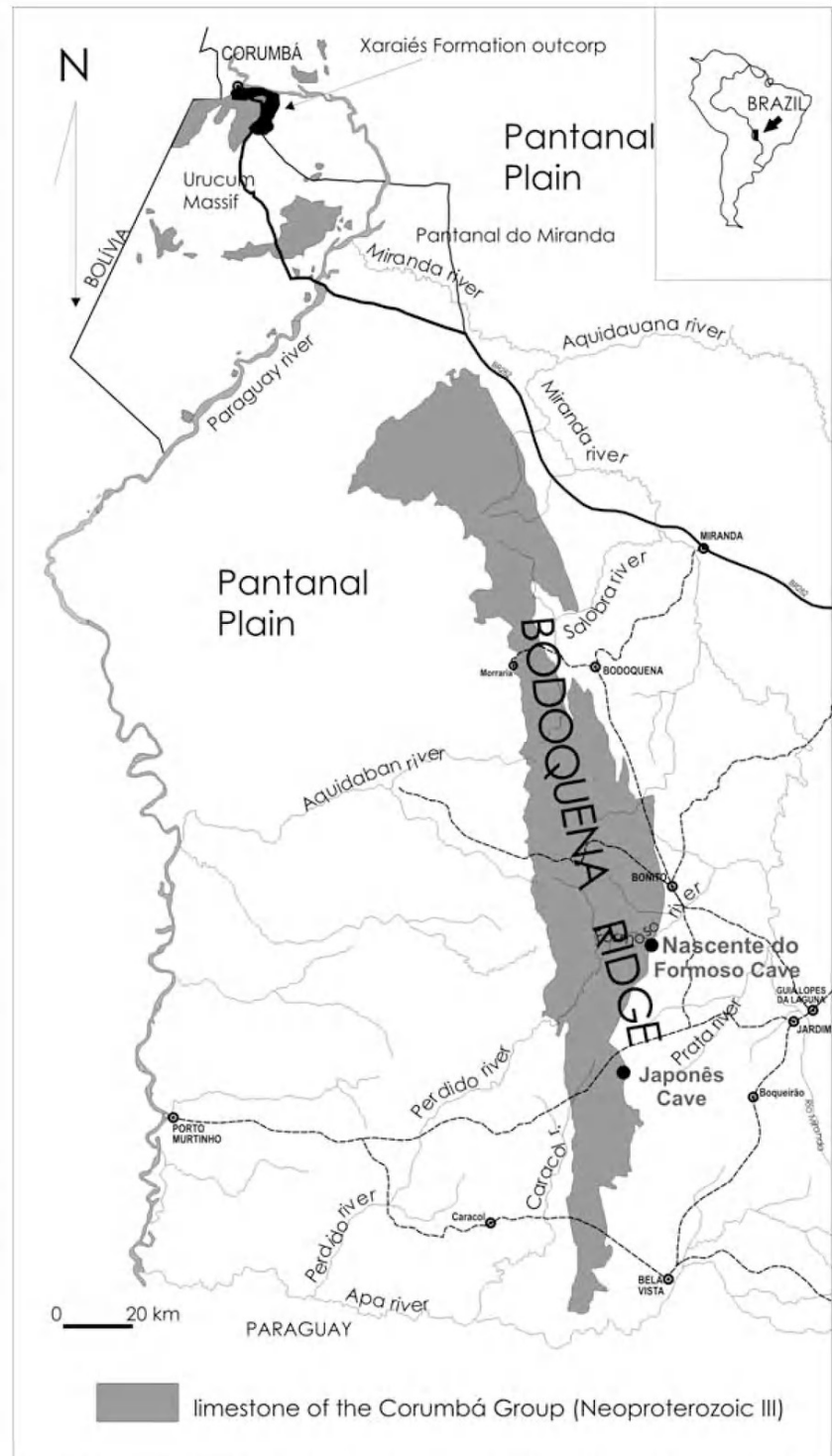


Fig.1- Map of the Serra da Bodoquena region (Mato Grosso do Sul, Central Brazil), indicating the location of the two fossiliferous limestone caves explored: Japonês and Nascente do Formoso.

The taxonomy of recent species follow, as standard references, WILSON & REEDER (2005) and for extinct species McKENNA & BELL (1997) and PAULA COUTO (1979).

FAMILY FELIDAE GRAY, 1821

Smilodon populator Lund, 1842

RESULTS

Eight bone fragments that could be attributed to Carnivora were recovered from Japonês Cave and one fragment from Nascente do Formoso Cave. There is a total of six species belonging to three families.

Referred material and description: MN 56851, an incomplete first cervical vertebra, and MN 56852, a fragment of right mandible with pm4 and root of m1 (Figs 2.A and 2.B, respectively). The atlas lost the right transverse process, and the left transverse process is heavily worn, lacking most of the anterior surface of the wing plate. The anterior and posterior articular processes (especially on the left side) are easily

TABLE 1: Measurements taken from carnivore fossil material.

SPECIES	MEASUREMENTS	SPECIMENS
<i>Smilodon populator</i> (Fig.2A)	Atlas	MN 56851
	Width at the anterior articular surface	7.87
	Length at anterior and posterior notches	3.30
<i>Smilodon populator</i> (Fig.2B)	Right mandible	MN 56852
	Maximum length of m1	2.85
	Height of the crown of m1	2.16
<i>Panthera onca</i> (Fig.2C)	Left femur	MN 56853
	Width of the shaft	2.42
	Width of the trochlea	2.26
	Width at the condyles	5.27
<i>Leopardus braccatus</i> (Fig.2D)	Left humerus	MN 56854
	Maximum length	11.98
	Width of the shaft	0.84
	Width of the articular head	1.61
	Width of the trochlea	1.47
	Width at the condyles	2.12
<i>Procyon troglodytes</i> (Fig.3A)	Right humerus	MN 56858
	Width of the trochlea	2.31
	Width at the condyles	3.37
<i>Chrysocyon</i> sp. (Fig.3B)	Left humerus	MN 56859
	Width of the shaft	1.7
	Width at the condyles	3.56
<i>Chrysocyon brachyurus</i> (Fig.3C)	Left tibia	MN 56856
	Width of the shaft	1.64
	Width at the condyles	2.31
<i>Chrysocyon brachyurus</i> (Fig.3D)	Right humerus	MN 56857
	Width of the shaft	1.52
	Width of the trochlea	2.44
	Width at the condyles	3.15
<i>Pteronura brasiliensis</i> (Fig.4)	Right mandible	MN 56855
	Depth of the mandible (at the posterior end of root of m1)	2.34
	Maximum length of m1	2.03
	Height of the crown of m1	1.03

All measurements are in cm.

distinguished, as is the foramen transversarium. The fragment of the right mandible is well preserved, but broken at the anterior portion where the posterior margin of the mental foramen can be distinguished. At the broken posterior margin, the alveolus and partial portion of the root of m1 can be observed. The pm4 is cracked, however intact, and is preceded by a diastema. The aligned paraconid, protoconid, and two accessory cusps are clearly distinguished, composing the cutting blade of the tooth.

Comments: The cervical vertebra belongs to a large cat, and is readily comparable with fossil material of *S. populator*. The mandible fragment is also comparable with a cast of the mandible of *S. populator*, and the absence of pm3 leaves no doubt about its identification. The presence of *S. populator* in Serra da Bodoquena has been previously indicated (SALLES *et al.*, 2006), but no description of the material was given. Although not abundant, remains of *S. populator* are widespread among Quaternary deposits of Brazil (MOREIRA & MELO, 1971; PAULA COUTO, 1979; CARTELLE, 1999; DANTAS *et al.*, 2005), and adjacent countries (CARTELLE, 1999; PRADO *et al.*, 2001). *Smilodon* was first described from the Pleistocene of Brazil (Lagoa Santa) and is among the last saber-toothed cat genera to become extinct, disappearing from North and South America around 10,000y.a. (TURNER, 1997). The South American species *S. populator* was the largest of the genus, perhaps attaining 300kg. It probably preyed on large mammals typically found in the South American Pleistocene, using its strong forequarters to subjugate, and saber-like teeth to kill the prey.

Panthera onca (Linnaeus, 1758)

Referred material and description: MN 56853, distal portion of a broken left femur (Fig.2C). Although broken near the distal end, the fragment is well preserved, and a long and cylindrical shaft can be distinguished, that widens towards the extremity. A pair of parallel, similar-sized ridges surround the articular surface of the trochlea. Its posterior face is flattened, and a deep intercondyloid fossa is present.

Comments: The bone clearly belongs to an adult large-sized cat, and based on comparisons with recent and fossil material it was assigned to *Panthera onca*. Clear diagnostic features are hard to find, but overall size and shape allow a positive identification. Other candidates, like *Smilodon populator*, possess a much larger, robust femur, and the similar-sized femur of *Puma concolor* has more

gracile proportions. *Panthera onca* fossils have been occasionally reported from the Pleistocene of Minas Gerais and Bahia (LESSA *et al.*, 1998; CARTELLE, 1999). The jaguar is typically found in both forests and savannahs, usually near fresh water (NOWAK, 1999). Sightings of the species are still widespread and quite common in the region (CÁCERES *et al.*, 2007).

Leopardus braccatus (Cope, 1889)

Referred material and description: MN 56854, a complete left humerus (Fig.2D). The shaft is long, slender, and with a slight spiral twist. The deltoid tuberosity is well marked, and the head is long and curved posteriorly. The coronoid and oleocranon fossae communicate through the supratrochlear foramen, and there is a large supracondyloid foramen. The supracondyloid ridge is well marked and extends along the distal portion of the shaft. The medial epicondyle is separated from the main body of the distal end of the bone, where a grooved and asymmetrical trochlear surface is distinguished.

Comments: The humerus morphology conforms to that of a small cat. Size and shape comparisons with many South American species, such as *Leopardus braccatus*, *L. pardalis* (Linnaeus, 1758), *L. tigrinus* (Schreber, 1775), *L. wiedii* (Schinz, 1821), *Puma yaguaroundi* (É. Geoffroy Saint-Hillaire, 1803), and *Felis catus* (Linnaeus, 1758) (MN612) suggest its identification as *L. braccatus*. The position and shape of the supratrochlear foramen is the best evidence supporting this identification. *L. braccatus* was originally included in the *Leopardus colocolo* complex, but the taxonomic review of GARCIA-PEREA (1994) divided this "super-species" into three: *L. braccatus* from Western Brazil, Paraguay, and Uruguay; *L. colocolo* from Chile; and *L. pajeros* from Argentina, Bolivia, Chile, Ecuador, and Peru. Nevertheless, recent molecular evidence does not support this taxonomical arrangement, indicating *L. colocolo* as the only valid species (Eizirik, pers.comm.). The material cited by PRADO *et al.* (2001) as *Oncifelis colocolo* (Molina, 1782) to the Quaternary of the Pampean Region in Argentina probably refers to *L. pajeros* (*sensu* Garcia-Perea), therefore, the humerus described here is taken as the first fossil record of the branch *L. braccatus*. *Leopardus braccatus* is still extant in the region (CÁCERES *et al.*, 2007). Although also occupying forested habitats, it is chiefly an open habitat species, commonly found in Cerrado, Pantanal, and Chaco (OLIVEIRA & CASSARO, 2005).

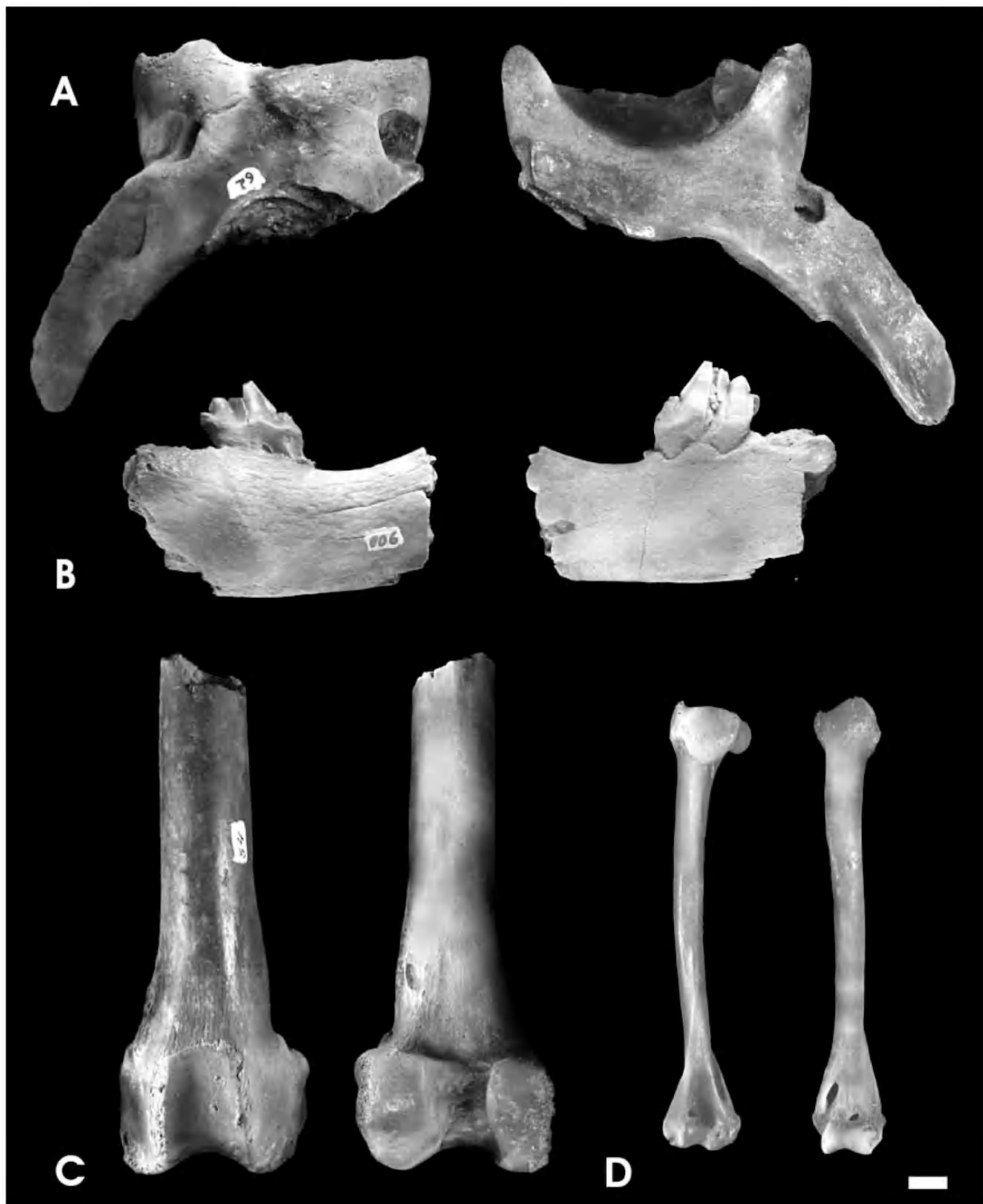


Fig.2- Felidae: (A) dorsal and ventral views of MN 56851, a first cervical vertebra of *Smilodon populator*; (B) labial and lingual views of MN 56852, a right mandible of *Smilodon populator*; (C) anterior and posterior views of MN 56853, a left femur of *Panthera onca*; (D) posterior and anterior views of MN 56854, a left humerus of *Leopardus braccatus*. Scale bar = 1cm.

FAMILY CANIDAE GRAY, 1821

Protocyon troglodytes (Lund, 1838)

Referred material and description: MN 56858, the distal portion of a broken right humerus (Fig.3A). A supracondyloid ridge and a small supratrochlear foramen are distinguished. The trochlear surface is oblique, with a relatively shallow synovial fossa, and a ridge is distinctly marked on the articular surface. The epicondyles are prominent.

Comments: The humerus clearly belongs to a large canid, and readily compares to fossil material of *Protocyon troglodytes*, a hypercarnivorous canid that occurred in open environments of the Late Pleistocene in Brazil, Bolivia, and Ecuador (PREVOSTI *et al.*, 2005). Remains of this species are widespread in Brazil, occurring in the states of Piauí, Ceará, Paraíba, Rio Grande do Norte, Bahia, Minas Gerais, Paraná, and Rio Grande do Sul (CARTELLE & LANGGUTH, 1999; OLIVEIRA *et al.*, 2005; PREVOSTI *et al.*, 2005). Weighting 16-25kg, *P. troglodytes* probably formed packs, actively pursuing medium-sized prey (CARTELLE & LANGGUTH, 1999; PREVOSTI *et al.*, 2005).

Chrysocyon sp.

Referred material and description: MN 56859, the distal portion of a broken left humerus (Fig.3B). Its articular portion is relatively narrow, and the shaft appears long and slender. A weak supracondylar ridge and a large supratrochlear foramen are present. The trochlear surface is heavily worn, and its medial portion is broken, making it difficult to distinguish features.

Comments: The general morphology of this distal fragment of humerus is similar to that observed in *Chrysocyon brachyurus*. In spite of that, the fragment differs from all examined humeri (including fossil and recent *C. brachyurus*) by possessing a proximal portion of the oleochroneon fossae that is so shallow that it is nearly absent, with the posterior end of the shaft occupying most of its space. For this reason, a positive specific identification is not possible with the material at hand, and it is provisionally assigned to *Chrysocyon* sp.

Chrysocyon brachyurus (Illiger, 1815)

Referred material and description: MN 56856, a left tibia, and MN 56857, a nearly complete right humerus (Figs.3C, 3D, respectively), both lacking the proximal articular parts. The shaft of the humerus is long and slender, and the supracondyloid ridge is well marked.

A large supratrochlear foramen connects the coronoid and the deep oleocranon fossae. The distal portion is relatively narrow, with an asymmetrical trochlear surface and deep synovial fossae. The shaft of the tibia is long and slender, and slightly curved. On the anterior face a short but prominent tibial crest can be distinguished, and the posterior portion is compressed. The distal portion is relatively small, with the medial malleolus detached and slightly curved inwards.

Comments: The specimens compare readily with recent *Chrysocyon brachyurus*. Maned wolves are mainly solitary canids that inhabit grasslands and scrub forests of the Cerrado and Chaco of central South America (DIETZ, 1985). *Chrysocyon brachyurus* is previously known from fossils in the Pleistocene of Minas Gerais (PAULA COUTO, 1979), and is still widespread and relatively common in the region (CÁCERES *et al.*, 2007).

FAMILY MUSTELIDAE FISHER, 1817

Pteronura brasiliensis (Gmelin, 1788)

Referred material and description: MN 56855, a right mandible fragment with complete m1, alveolus of m2, and partial alveolus of pm4 (Fig.4). The bone is broken at both ends and worn especially on the lingual face, with the inferior margin of the masseteric fossa visible at its posterior extremity. The small, single-rooted, alveolus of m2 is clearly distinguished posterior to the m1 and is located just anterior to the ascent of the coronoid process. The impression of the pm4 roots are exposed on the anterior portion of the mandible. The m1 is complete and unworn, with five cusps. The triangular shaped paraconid, protoconid and metaconid, surround a strait, lingually open trigonid basin. The talonid basin is also open lingually, with a short hypoconid and entoconid, connected by a high labial cristid. The alignment of the paraconid, protoconid, hypoconid and entoconid forms a trenchant blade typical of carnivorans.

Comments: The specimen is virtually undistinguishable when compared to recent *Pteronura brasiliensis* (MN 42965). Giant otters are found mainly in slow-moving rivers and creeks within forests, swamps, and marshes (NOWAK, 1999). This is the second fossil record of giant otter, the other being a humerus and first upper molar from the Pleistocene of the adjoining state of Mato Grosso (CARTELLE & HIROOKA, 2005). This species also occurs in the contemporaneous fauna of the region (CÁCERES *et al.*, 2007).



Fig.3- Canidae: (A) anterior and posterior views of MN 56858, a right humerus of *Protocyon troglodytes*; (B) anterior and posterior views of MN 56859, a left humerus of *Chrysocyon* sp.; (C) anterior and posterior views of MN 56856, a left tibia of *Chrysocyon brachyurus*; (D) anterior and posterior views of MN 56857, a right humerus of *C. brachyurus*. Scale bar = 1cm.

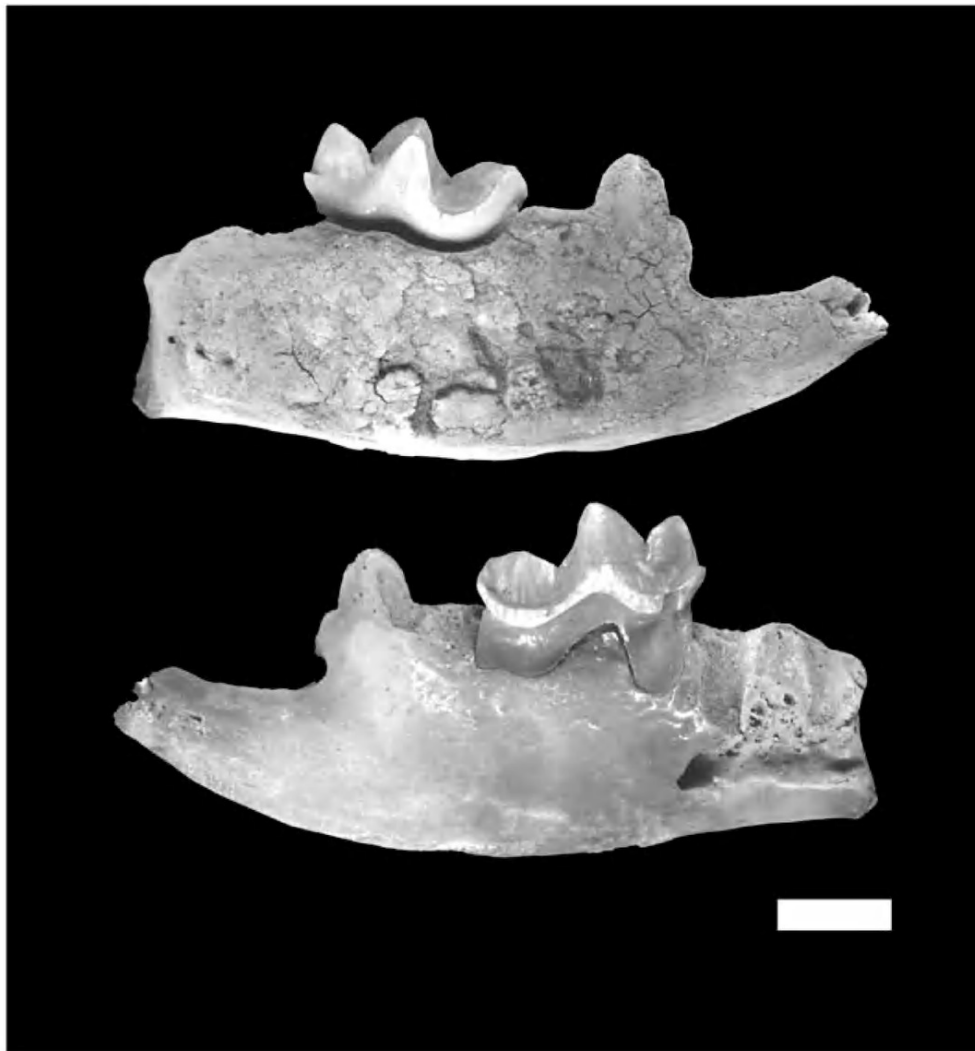


Fig.4- Mustelidae. Lingual and labial views of MN 56855, a right mandible of *Pteronura brasiliensis*. Scale bar= 1cm.

DISCUSSION

A mosaic of extant and extinct species composes the fossil carnivore fauna of the Quaternary of Serra da Bodoquena. There are still doubts about the antiquity of the material, but the association with the extinct mammalian megafauna, and the similarities in appearance and preservation strongly suggest a Late Pleistocene-Holocene age; *P. onca*, *L. braccatus*, *C. brachyurus* and *P. brasiliensis* are still extant in the region (CÁCERES *et al.*, 2007).

Paleoecological reconstructions that depicted the late Quaternary environment of Serra da Bodoquena as an open savanna rich in wetlands (SALLES *et al.*, 2006) are supported, in part, by its carnivore fauna. *Leopardus braccatus* and *C. brachyurus* are

currently typically encountered in open vegetation regions, such as Campos and Cerrados (NOWAK, 1999; OLIVEIRA & CASSARO, 2005), and *P. brasiliensis* is a semi-aquatic species, found in large rivers and marshes (NOWAK, 1999), currently abundant in the Pantanal region adjacent to Serra da Bodoquena. Large predators, such as *S. populator* and *P. troglodytes*, probably occur in association with the high diversity of herbivorous mammals typical of the South American Pleistocene, also recorded for the Bodoquena Karst (SALLES *et al.*, 2006).

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