



The northernmost record of *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Cetartiodactyla) and its palaeoenvironmental and palaeobiogeographical significance

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ABSTRACT

During fieldwork carried out in January 2009 at Aurora do Tocantins (Tocantins State, northern Brazil), we recovered a fragmentary right maxilla (UNIRIO-PM 1006) of *Catagonus stenocephalus* from a sedimentary deposit of presumed late Pleistocene age in a karstic cave. This paper aims to: (1) provide the first record of *C. stenocephalus* in the northern region of Brazil (and consequently, also the northernmost one); (2) update the geographic distribution of *C. stenocephalus*; (3) present a date for the specimen; and (4) discuss the palaeoenvironmental and palaeobiogeographical implications of the finding. The species *C. stenocephalus* (Lund) is known from the Bonaerian (middle Pleistocene) and Lujanian (late Pleistocene to earliest Holocene) ages in Argentina, Uruguay, Brazil and Bolivia. The new record presented here extends the geographical distribution of *C. stenocephalus* more than 1000 km north from the former northernmost record (caves of Lagoa Santa region). Peccaries of the genus *Catagonus* have several morphological features associated with cursorial habits in relatively open and dry environments. The new distributional range of *C. stenocephalus* is coincident with the Chacoan subregion, characterized by dry climates and open areas. As the studied material comes from the top of the carbonate layer, this may suggest that the deposition of the *C. stenocephalus* remains described here is synchronous with the onset of a wetter climate phase. This argument is also in accordance with the datation results, around 20 ky BP, just after the last glacial maximum. This increasingly wet climate, which may also be related to the climatic changes that occurred during the late Pleistocene/early Holocene, could be a factor in the extinction of *C. stenocephalus* in South America.

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Abbreviations: Dental terminology: PM1, first upper premolar; PM2, second upper premolar; PM3, third upper premolar; PM4, fourth upper premolar; Measurements: LPM2, maximum mesio-distal length of the second upper premolar; APM2, maximum labio-lingual width of second upper premolar; LPM3, maximum mesio-distal length of third upper premolar; APM3, maximum labio-lingual width of third upper premolar; LPM4, maximum mesio-distal length of fourth upper premolar; APM4, maximum labio-lingual width of fourth upper premolar. Institutions; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; Buenos Aires, Argentina; MACN-S, Museo de Arqueología y Ciencias Naturales de Salto, Uruguay; MCA, Museo Municipal de Ciencias Naturales “Carlos Ameghino”; Mercedes, Argentina; MCPV, Museu de Ciências da PUCRS; Geology and Palaeontology Laboratory, Uruguaiana, Brazil; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia” Argentina; MNPA-V, Museo Nacional de Paleontología y Antropología, Tarija, Bolivia; UFPR PV, Departamento de Geología, Universidade Federal do Paraná, Curitiba; PR, Brazil; ZMK, Zoologisk Museum; Copenhagen, Denmark.

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1. Introduction

The rise of the Panamanian Isthmus, dated around 3 Ma before present, resulted in an overland connection between the Americas (Webb, 1985; Woodburne, 2010). This intercontinental “land bridge” opened a two-way migration route between South and North America where the biota dispersed. This biogeographic event, the Great American Biotic Interchange (GABI), heavily influenced the evolution and composition of the Quaternary-Recent mammalian fauna of the Americas (Jones and Hasson, 1985; Stehli and Webb, 1985; Woodburne, 2010).

The Tayassuidae (Mammalia, Cetartiodactyla) represent one of the first mammalian clades that entered South America during the GABI (Webb, 1991; Prevosti et al., 2006; Woodburne et al., 2006; Gasparini, 2010; Woodburne, 2010). The exact timing of their arrival in South America is controversial, however, with some authors placing it in the late Miocene (see Campbell, 2010; Campbell et al., 2010) and others in the middle Pliocene (Gasparini and Ubilla, 2011; Gasparini, 2011).

According to Gasparini (2007), the South American Tayassuidae includes three genera: *Platygonus* Le Conte, 1848 (middle Pliocene to early Pleistocene) with five species; *Tayassu* Fischer, 1814 (middle Pleistocene to Recent) with two extant species; and, *Catagonus* Ameghino, 1904 (late Pliocene? to Recent) with five species (four extinct and one extant).

The family has an extensive fossil record in South America and has been found in sediments exposed in Argentina, Brazil, Uruguay, Bolivia, Colombia, and Peru (Stirton, 1947; Paula Couto, 1975, 1981; Ubilla, 2004; Ubilla et al., 2004; Gasparini et al., 2009a,b, 2010a; Campbell, 2010; Campbell et al., 2010; Gasparini and Ubilla, 2011; Gasparini, 2011).

In Brazil, tayassuids are represented by two genera: *Tayassu* [*T. pecari* (Link, 1795) and *T. tajacu* (Linnaeus, 1758)] and *Catagonus* [*C. stenocephalus* (Lund in Reinhardt, 1880)]. The species *C. stenocephalus* is known from the southern [Rio Grande do Sul (Gasparini et al., 2009a); possibly in Paraná (Dias da Silva et al., 2010)] and southeastern [Minas Gerais (Fonseca, 1979; Paula Couto, 1975, 1981)] regions of Brazil.

The South American tayassuids experienced a remarkable decrease (~75%) in their diversity near the Pleistocene-Holocene boundary (Gasparini, 2007; Gasparini, 2011). Only two genera (*Catagonus* and *Tayassu*) and three species survived this boundary. Living members are widely distributed throughout the Americas, from the southwestern United States to north-central Argentina (Gasparini et al., 2006).

During fieldwork carried out in January 2009 at Aurora do Tocantins (Tocantins State, northern Brazil, Fig. 1), we recovered a fragmentary right maxilla (UNIRIO-PM 1006, Fig. 2A–C) of *Catagonus stenocephalus* from a sedimentary deposit of presumed late Pleistocene age in a karstic cave (see Locality, Geology and Age).

This paper aims to: (1) provide the first record of *C. stenocephalus* in the northern region of Brazil (and consequently, also the northernmost in South America); (2) revise the geographic distribution of *C. stenocephalus*; (3) present a date for the specimen; and (4) discuss the palaeoenvironmental and palaeobiogeographical implications of the finding.

2. Locality, geology and age

The specimen under study comes from a thick carbonate deposit in the main room of a limestone cave, Gruta dos Moura, at Aurora do Tocantins (12°42'47" S and 46°24'28" W), Tocantins State, northern Brazil (Fig. 1). Access to the plateaus occurs mainly through vicinal roads and paths that cut the vegetation. Currently, the region is situated mainly within the Cerrado biome.

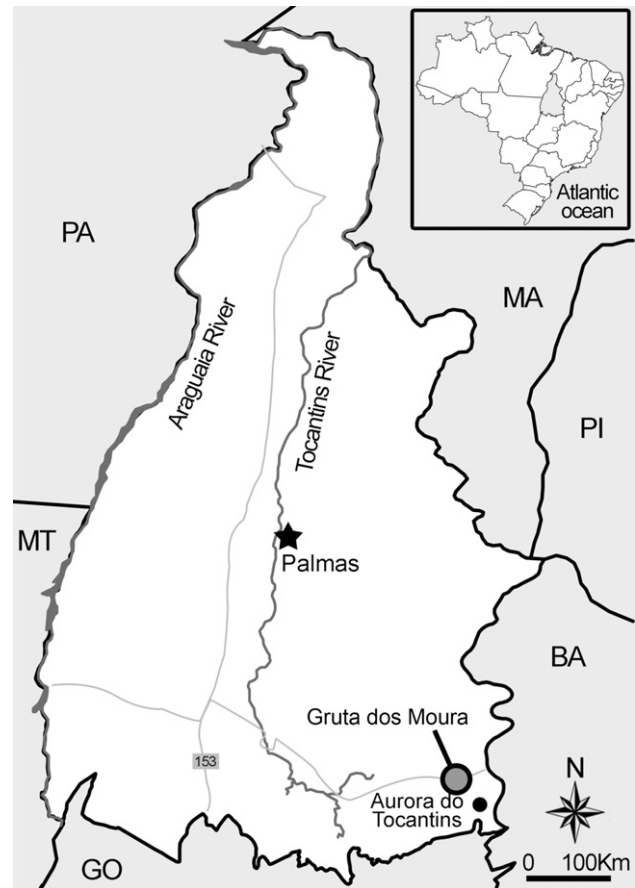


Fig. 1. Location map. At the right top corner, the map of Brazil showing Tocantins state in gray, and the larger map shows Tocantins State in white, emphasizing the study area (12°42'47" S/46°24'28" W).

The carbonate rocks in the region of Aurora do Tocantins constitute part of the Speleological Province of the Bambuí Group, where a large number of caves have been found (Zampaulo and Ferreira, 2009). The geology of the study area is still poorly understood. The predominant rocks in the region are rhythmic limestones and siltstones from the Paraopeba Subgroup of Neoproterozoic age, although alluvial deposits might occur locally (Dardene, 1978; Dardene and Walde, 1979).

Online notes from the Serviço Geológico do Brasil (CPRM, 2006) on the geology of the municipality of Aurora do Tocantins report carbonates and terrigenous deposits. The lower portion is represented by the Sete Lagoas Formation, which is composed of thick deposits of mudstones, limestone and dolomites, and siltstone of the Serra de Santa Helena Formation. This carbonate-terrigenous conjunction of rocks is superimposed by dark calcarenites and marls, with organic material from the Lagoa do Jacaré Formation. Superimposed over the Bambuí Group are the Cretaceous sediments of the Urucua Formation. The cave Gruta dos Moura, as well as other caves in the region, was developed mainly in the limestones of Lagoa do Jacaré Formation, that consist in slightly weathered dark gray metacalcarenites, massive or with horizontal lamination, with sparry calcite (generally in veins), micritic calcite, ooids and small amounts of silica. Interbedded metacalcarenites, mudstones and calcilitites can also occur.

The limestones often form plateaus that rise from the rest of the terrain and comprise a partially active karst system. Most caves occur above the ground level in high portions of the plateaus. The caves originated during a period of formation of karst relief in

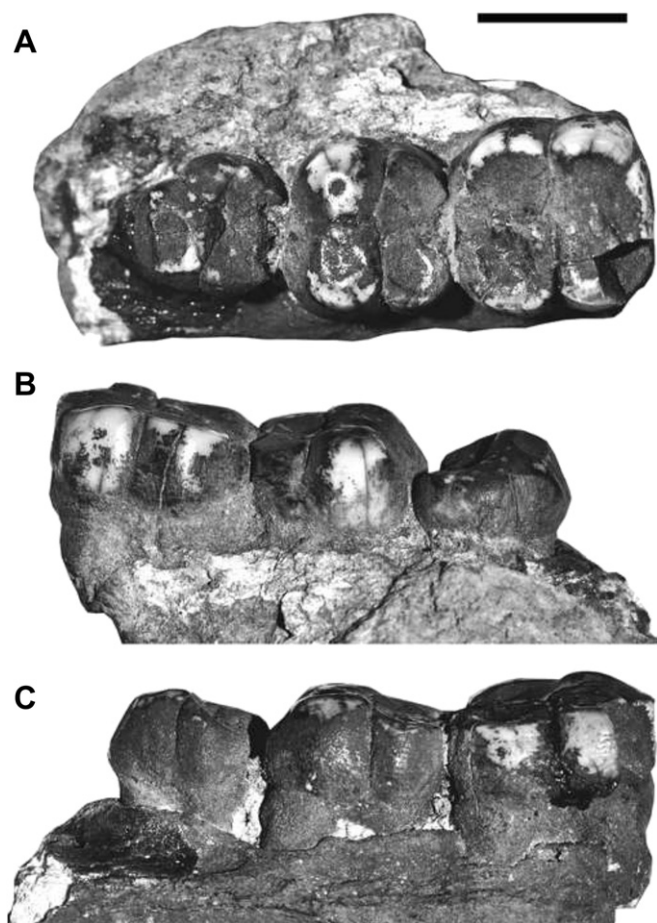


Fig. 2. Right maxillary fragment of *Catagonus stenocephalus* (UNIRIO – PM 1006) described here. (A): Occlusal view; (B): Lingual view; (C): Labial view. Scale bar = 10 mm.

which the rocks that now compose the plateaus were below the ground level. The current outcrops were developed by the differential erosion of the limestones and the erosive retraction of the Urucua sandstones which once covered the region and today occur to the east of the study area.

The Gruta dos Moura is an epigenic, solutional, ramiform to network cave with some branchwork passages (sensu Palmer, 1991) and great vertical and horizontal development. The entire length of the cave has not yet been completely mapped. It originated in a phreatic zone and was later invaded and enlarged by vadose water. There is a notable difference between upper and lower levels. The higher levels show galleries and fissures with many speleothems, including travertines, draperies, stalactites, stalagmites and coralloids, showing a higher activity of vadose waters. The fossils were found in the lower levels, which consist of phreatic passages and rooms with few speleothems. Slightly consolidated sedimentary deposits outcrop at these levels, composed of massive, very fine to coarse, immature and poorly sorted sands with clayey matrix. In some parts of the cave a relict carbonate precipitation layer is observed that is rich in millimeter- to centimeter-sized fragments of bones and teeth. This layer, which is thicker than 1 meter in some points, seems to have covered the sedimentary deposits in a period of decreased sedimentation and stagnation of water flow, causing the precipitation of carbonates and concentration on the sediment. The herein studied fossils come from the carbonate layers.

The occurrence of sedimentary deposits covered by carbonate layers is also observed in many other caves in the region of Aurora

do Tocantins, corresponding to a larger event of increased humidity, causing changes in the pattern of recharge from the land surface and consequently in the entire environment. These layers are of metric thickness in several caves, showing that the event was temporally and geographically significant and not a result of changes in the cave morphology. The same kind of depositional features was studied by Auler et al. (2009) in caves of Minas Gerais and Bahia states. They identified three processes (clastic sediment input, erosion and calcite deposition) that are linked to distinct palaeoenvironmental and climatic conditions.

The episodes of clastic input are related to a drier climate, sparse vegetation and intense sediment yield due to runoff, while the precipitation of calcite and growth phases of speleothems is related to wetter conditions (Auler, 1999; Brain, 1995; Brook et al., 1997). Sediment erosion inside caves would be interpreted as intermediate climatic conditions, not wet enough for speleothem deposition and not dry enough to allow sediment transport into caves (Auler et al., 2009).

In this work, Electron Spin Resonance (ESR) spectroscopy was employed to date the *Catagonus stenocephalus* teeth. ESR dating has been successfully used to date fossil samples including human teeth (Kinoshita et al., 2008), deposits of karst system (Kinoshita et al., 2005a), shells (Kinoshita et al., 2002; Blackwell et al., 2010), bones from Samaquis (Mascarenhas et al., 1982) and megafauna teeth (Kinoshita et al., 2005b; Baffa et al., 2006; Lopes et al., 2010; Kinoshita et al., 2011; Kerber et al., 2011). Since the age estimated of samples in the present study is within the range of ages that can be determined by dating ESR (Ikeya, 1993), this method is suitable for use.

3. Materials and methods

The specimen (UNIRIO-PM 1006) examined is housed at the paleontological collection of the Laboratório de Mastozoologia of the Universidade Federal do Estado do Rio de Janeiro, Brazil.

Measurements were taken with digital calipers with 0.01 mm accuracy; all measurements are in millimeters.

In the descriptions of the main cusps of premolars, the names “paracone”, “metacone”, “protocone” and “hypocone” in quotes, are used to indicate topographical position, and not to infer serial homologies with the cusps of the molars, since there is no general agreement on this matter (Rusconi, 1929; Wetzel, 1977; Mones, 1979; Gasparini, 2001).

This paper adopts the taxonomy proposed by Gasparini (2007) since this is the most current comprehensive review of the South American Tayassuidae.

The materials of *C. stenocephalus* mentioned here are listed in Table 2.

The chronostratigraphic/geochronologic units used herein (Marplatan, Ensenadan, Bonaerian and Lujanian) follow the usage by Woodburne et al. (2006) (also see Cione and Tonni, 1999, 2005; Soibelzon, 2008).

3.1. ESR dating experiments

The soils attached to tooth were saved to determination of radioisotopes concentration. Then the tooth was initially washed with water and subsequently submitted to thermal treatment by freezing

Table 1
Radioisotopes concentration in enamel, dentine and soil determined by neutron activation analysis.

Sample	U (ppm)	Th (ppm)	K (%)
Enamel	0.048 ± 0.001	<0.01	<0.075
Dentine	5.72 ± 0.06	0.32 ± 0.02	<0.075
Soil	1.4 ± 0.1	2.27 ± 0.09	0.12 ± 0.05

Table 2
Specimens of *Catagonus stenocephalus* from several localities in South American and covering most of its geographical and stratigraphical range. Data on climatic/environment interpretations mainly based on palynological analysis and faunal associations.

Specific signature	Collection number	Material	Geographical provenance	Age/Stage	Climatic/environment interpretations
<i>Catagonus stenocephalus</i>	MACN 10083	Upper cheek teeth series and postcranial	Samborombón river, Buenos Aires, Argentina	Lujanian	Subhumid to humid grassland, xerophytic woodland plants decreased notably (Prieto, 2000; Prieto et al., 2004)
	ZMK 8617 (Holotype)	Partial mandible	"Gruta Lapa da Escrivantina, No. 11", Lagoa Santa, Minas Gerais, Brazil	Lujanian	Drier and colder than today/subtropical grassland (Parizzi et al., 1998; Behling, 2002)
	ZMK 8638 (Holotype)	Skull	"Gruta Lapa da Escrivantina, No. 11", Lagoa Santa, Minas Gerais, Brazil	Lujanian	Drier and colder than today/subtropical grassland (Parizzi et al., 1998; Behling, 2002)
	MCPU-PV 029	Partial skull	Touro Passo Stream, Uruguaiana, Rio Grande do Sul, Brazil	Touro Passo Formation, Lujanian	Dry and cold/grassland associated with forest areas next to water bodies (Bauerermann et al., 2009; Kerber et al., 2011)
	MACN-S-10	Skull	Arroyo Cañas, Salto, Paso de Cañas, Uruguay	Sopas Formation, Lujanian	Dry and cold/grassland (Ubilla et al., 2004; Verde et al., 2007)
	MCA 2001	Skull and postcranial	Frías Stream, Mercedes, Buenos Aires, Argentina	Bonaerian	Drier and colder conditions than today/grasslands (Nabel et al., 2000)
	MACN 7000	Upper cheek teeth series and postcranial	Malacara Stream, Gral. Alvarado, Buenos Aires, Argentina	Lujanian	Drier and colder conditions than today/grasslands (Voglino and Pardiñas, 2005; Nabel et al., 2000)
	MMP 41	Skull	Gral. Pueyrredón, Mar del Plata, Buenos Aires, Argentina	Lujanian	
	MNPA-V 1450	Partial skull	Tarija Valley, Bolivia	Pleistocene	No information
	<i>Catagonus cf. stenocephalus</i>	UFPR 0118 PV	Partial skull	Gruta do Vale do Ribeira, between Adrianópolis and Doutor Ulysses, Paraná, Brazil	Late Pleistocene

in liquid nitrogen and defrosting at room temperature to detach the enamel from dentine. The enamel was treated in acid solution (HCl) 1:10 in ultrasonic bath for extraction of layers of both sides of approximately 250 µm. After drying, the enamel was ground manually in an agate mortar until the particles reached a diameter $\varphi < 0.5$ mm. Ten aliquots of about 70 mg were irradiated with different doses, ranging from 0 to 50 Gy in Cobalt-60 irradiator at IPEN. The spectra were recorded in a Jeol FA200 X-Band spectrometer.

The intensity of peak-to-peak signal dosimetric g_{\perp} was used to construct the dose–response curve. The equivalent dose (D_e) was determined by fitting with exponential function (1) (Ikeya, 1993).

$$I = I_0 \left\{ 1 - e^{-\left[\frac{D + D_e}{D_0} \right]} \right\} \quad (1)$$

where I is the ESR signal intensity, D , the dose, and I_0 and D_0 are the intensity and dose at saturation.

The concentration of uranium, thorium and potassium of enamel, dentine and soil were determined by neutron activation analysis (NAA). The conversion of D_e into age was made using the ROSY ESR Dating software (Brennan et al., 1999). The water content in soil was considered 10% and the value of 78 µGy/year was adopted for cosmic ray dose rate, taking into account the latitude, longitude and altitude (386 m) and the depth where the samples were collected (8 m) (Prescott and Hutton, 1994).

4. Systematic Palaeontology

Order Cetartiodactyla (Montgelard et al., 1997)
Suborder Suiformes (Jaekel, 1911)
Infraorder Suoidea (Gray, 1821)
Family Tayassuidae (Palmer, 1897)
Subfamily Tayassuinae (Palmer, 1897)
Genus *Catagonus* (Ameghino, 1904)
Catagonus stenocephalus (Lund in Reinhardt, 1880)

4.1. Studied material

UNIRIO-PM 1006 is represented by a right maxillary fragment with complete PM2–PM4 series (Fig. 2) from Gruta dos Moura, at Aurora do Tocantins (12°42'47" S and 46°24'28" W), Tocantins State, northern Brazil, late Pleistocene.

4.2. Description

According to the new systematic scheme of South American Tayassuidae (Gasparini, 2007), the morphological features, and/or a combination of them, that allow to determine this specimen as *Catagonus stenocephalus* are the following: the crown morphology is bunodont; the crown height is mesodont; the PM3 and PM4 are molariform; the "hypocone" is well-developed in PM3–4; the PM3 has a subquadrangular outline and the measurements are in the range of *C. stenocephalus*. The crowns of preserved teeth are very worn, indicating an adult individual.

The outline of PM2 is subtriangular in occlusal view. The crown has a complex configuration due to the presence of four cusps of various sizes. The largest cusp is located mesially on the mesio-distal axis of the tooth. Behind it, and on the lingual side, there is a less-developed cusp and further along the lingual side is a pair of very small cusps. The cingulum is basal and continuous.

The PM3 is subquadrangular and readily differentiated from the typical quadrangular outline of the molars, since the lingual side is slightly convex rather than straight. Despite significant wear, the PM3 reveals four well-developed cusps ("paracone", "protocone", "metacone" and "hypocone"). The cingulum is well defined on the mesial, lingual and distal sides.

The PM4 is quadrangular and larger than the PM3. It has four main well-defined cusps ("paracone", "protocone", "metacone" and "hypocone"). The cingulum is developed on the mesial, labial and distal sides.

Measurements LPM2: 10 mm; APM2: 9.3 mm; LPM3: 10.45 mm; APM3: 12.25 mm; LPM4: 12.3 mm; APM4: 13.25 mm.

4.3. Comparisons

The genus *Platygonus* develops a mesodont crown height as occurs in the studied material but it differs in the dental morphology (it has simpler premolars, with only two cusps labiolingually aligned, bunolophodont teeth, and an enamel cingulum completely surrounding premolars and molars). The genus *Tayassu* has a bunodont cheek teeth morphology as it is observed in the studied material but it develops a different crown height condition (braquiodont).

A bunodont cheek teeth morphology with a mesodont crown height are observed in some *Catagonus* (e.g., *C. metropolitanus* (Ameghino, 1904), *C. carlesi* (Rusconi, 1930), *C. bonaerensis* (Ameghino, 1904) and *C. stenocephalus*). Specimens of *C. wagneri* (Rusconi, 1930) develop also a bunodont cheek teeth but with a “zygodont” (bunolophodont cheek teeth with higher and sharper cusps than in typical bunodont forms and fainter crests) crown morphology.

A molariform PM3 is found in *C. metropolitanus*, *C. stenocephalus*, *C. wagneri* and *Tayassu pecari*; however, the “hypocone” is less developed in the two later species. The species *C. metropolitanus* differs in having a typical quadrangular outline instead of the subquadrangular outline observed in the material studied here; and the PM3 of *C. metropolitanus* is larger than that of *C. stenocephalus*. In turn, PM3 of *T. tajacu* presents only three main cusps (“paracone”, “metacone” and “protocone”).

The degree of molarization (presence of four main well-defined cusps and a quadrangular outline) observed in the PM4 of *C. stenocephalus* is equivalent to that of *C. metropolitanus*, and greater than that observed in all other South American tayassuids [e.g., *C. carlesi*, *C. bonaerensis* and *C. wagneri*; the “hypocone” is less developed than the other major cusps]. However, *C. metropolitanus* has a PM4 larger than *C. stenocephalus*; moreover, *C. metropolitanus* is considered the biggest South American species of *Catagonus* (see Gasparini, 2007; Gasparini et al., 2010b).

5. Results and discussion

Table 1 shows the concentration of uranium, thorium and potassium of enamel, dentine and soil obtained by NAA.

The fitting of dose–response curve with Eq. (1) results in $D_e = (9.4 \pm 0.6)$ Gy. The conversion of D_e in ages results in age of 20 ± 2 ka, which is in accordance with *C. stenocephalus* chronostratigraphic distribution.

The peccary *Catagonus stenocephalus* (Lund) is recorded from the Bonaerian (middle Pleistocene) and Lujanian (late Pleistocene to earliest Holocene) ages in Argentina, Uruguay, Brazil and Bolivia (Table 2 and Fig. 3).

In Argentina it is known from various localities in Buenos Aires Province (Gasparini, 2004, 2007) (MACN 10083, MCA 2001, MMP 41; see Table 2 and Fig. 3). It is important to mention that we reanalyzed the fossil records of this species, particularly the available information of MMP 41 (see Table 2). We propose that the first record of *C. stenocephalus* corresponds to the Bonaerian instead of Ensenadan (early Pleistocene to middle Pleistocene) as previously considered (see Gasparini et al., 2009a).

The species *C. stenocephalus* is also known from northwestern Uruguay (Sopas Formation, Salto Department; MACN-S-10; Gasparini et al., 2009b; Gasparini and Ubilla, 2010) and from extremely southeastern Brazil at the Touro Passo Formation (municipality of Uruguaiana; MCPU-PV 029 – Gasparini et al., 2009a), and in the caves of Lagoa Santa region, Minas Gerais State (ZMK 8638, 8617; Fonseca, 1979; Paula Couto, 1975, 1981) (Table 2 and Fig. 3). It is also known from the Tarija Valley in southern Bolivia (MNPA-V 1450; Gasparini et al., 2010a); unfortunately, the

age of these sediments is undetermined (most probably late Pleistocene, see Soibelzon et al., 2011). An additional record of *Catagonus* cf. *C. stenocephalus* (UFPR 0118 PV) is known from late Pleistocene sediments outcropping in Gruta do Vale do Ribeira, Paraná State, southeastern Brazil (Dias da Silva et al., 2010).

The new record presented here extends the geographical distribution of *C. stenocephalus* more than 1000 km north from the former northernmost record (caves of Lagoa Santa region).

Peccaries of the genus *Catagonus* have several morphological features associated with cursorial habits in relatively open and dry environments (e.g., orbits located in posterodorsal position and behind the M3 due to elongation of the rostrum, pronounced development of nasal sinuses and chambers, infraorbital foramen located anteriorly to the zygomatic arch, a distinct basicranial flexure, and reduction of the lateral digits of the limbs; Wetzel, 1977; Gasparini et al., 2009a, 2010a).

The new distributional range of *C. stenocephalus* is coincident with the Chacoan subregion, defined by Morrone (2006) (Fig. 3). The Chacoan subregion is considered a monophyletic unit in cladistic biogeographic studies formed during the late Tertiary (Morrone, 2006; Nihei and De Carvalho, 2007), probably late Miocene (Pascual and Ortiz-Jaureguizar, 1990; Roig-Juñent et al., 2006). This subregion represents the “savannah corridor” or “diagonal of open formations” (Salis et al., 1993; Morrone, 2006; Avilla et al., 2007), which acted as a barrier separating the continuous ancestral forest formation (represented by the Paraná and southeastern Amazonia subregions of the Neotropical region; see Prado and Gibbs, 1993;



Fig. 3. Geographical and temporal range of *Catagonus stenocephalus*, *Catagonus* cf. *stenocephalus* and *Catagonus wagneri* and the Chacoan subregion limits (dashed line). *C. stenocephalus*: middle Pleistocene (Bonaerian), black star; late Pleistocene to earliest Holocene (Lujanian), black circle; Pleistocene, black diamond. Biochronological data for *C. cf. stenocephalus*: late Pleistocene, black cross. *C. wagneri*: Holocene, number 1; late Pleistocene, number 2; current distribution, dark gray area.

Morrone, 2006; Nihei and De Carvalho, 2007) and producing allopatric speciation events.

The Chacoan subregion is characterized by dry climates and open areas and includes four Neotropical biomes (provinces *sensu* Morrone, 2006): Pampa, Chaco, Cerrado and Caatingas. The species *C. stenocephalus* is recorded in Pleistocene deposits of every Chacoan (subregion) biome, with the exception of the Caatingas (Fig. 3), although a bias in the fossil record is not discarded. Consequently, we consider here *Catagonus stenocephalus* as an endemic taxon of the Chacoan subregion. This could be confirmed by the distribution of the extant *Catagonus wagneri* (Chacoan peccary), which is endemic to the Chacoan subregion (Fig. 3), inhabiting semi-arid thorny forests of Dry Chaco in western Paraguay, southeastern Bolivia and northern Argentina (Mayer and Wetzel, 1986; Redford and Eisenberg, 1992; Gasparini et al., 2006).

Moreover, the ancestral Chacoan subregion would have been a dry open area, may be a grassland (Roig-Juñent et al., 2006), inhabited by *C. stenocephalus* during the Pleistocene (Fig. 3). The datation of *C. stenocephalus* here resulted is in accordance to a period of humidity increased after the Last Glacial Maximum, when this large region was possibly divided into the present Chacoan subregion provinces (Pampa, Chaco, Cerrado and Caatinga). Thus, some of the ancestral Chacoan subregion limits could be traced analyzing the fossil record of *C. stenocephalus* (Table 2 and Fig. 3) and other taxa with similar ecological requirements.

Some preservational aspects relative to the record of *Catagonus stenocephalus* at Gruta dos Moura cave should be considered for a better understanding of it is timing and environmental significance. In view of the fact that the material was found in a carbonate layer that capped clastic deposits, there are two possible but opposing scenarios:

- (A) The material fossilized under wet environmental conditions that promoted deposition of carbonates or,
- (B) The material was reworked from older sedimentary deposits.

As the material is fragmentary, one could argue that its stratigraphic position is a result of reworking processes. This would be expected if the osteological material came from outside the cave. Thus, in this case, we cannot determine with certainty the origin of the osteological material of *C. stenocephalus* preserved at Gruta dos Moura. As sediment erosion is related to intermediate conditions between wet and dry climate (Auler, 1999; Brain, 1995; Brook et al., 1997), a brief erosive phase may have occurred before the deposition of carbonate. Therefore, any reworked material from sedimentary deposits should be preserved at the base of the carbonate layer, since its formation provides a stabilization of erosion inside the cave. As the studied material comes from the top of the carbonate layer, this may suggest that the deposition of the *C. stenocephalus* remains described here is synchronous with the onset of a wetter climate phase. This increasingly wet climate, which may also be related to the climatic changes that occurred at the late Pleistocene/early Holocene, could be responsible for the extinction of *C. stenocephalus* in South America.

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