Journal of South American Earth Sciences 42 (2013) 39–46

Contents lists available at SciVerse ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

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

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ARTICLE INFO

Article history:
Received 27 January 2012
Accepted 5 October 2012

Keywords:
Tayassuidae
Late Pleistocene
Semi-arid
South America
Brazil

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.

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-ligual 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; MCPU-PV, Museu de Ciencias 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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http://dx.doi.org/10.1016/j.jsames.2012.10.001

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 de 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.

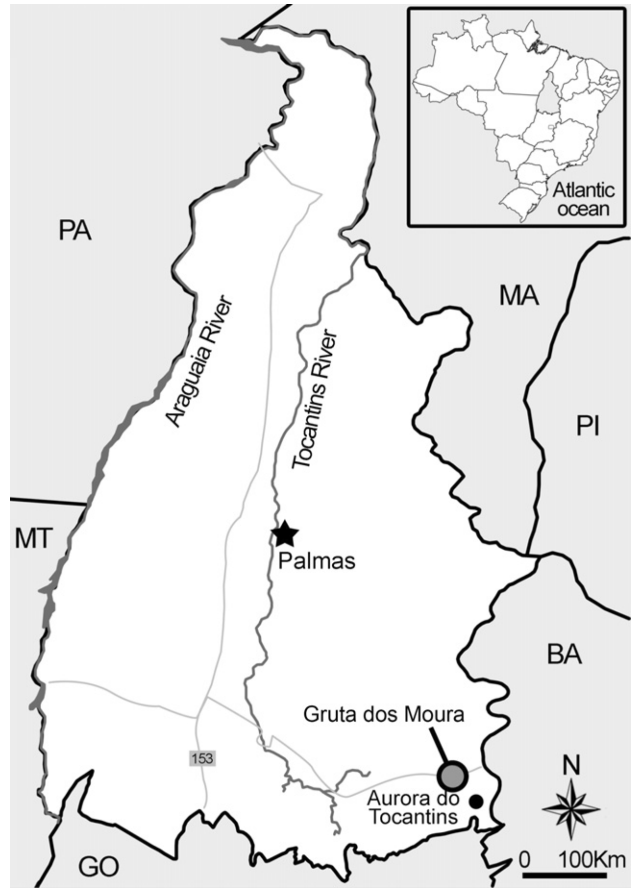

Fig. 1. Location map. At the right top corner, the map of Brazil showing Tocantins state in gray, and the larger map shows Tocantins State in white, emphasizing the study area (12°42′47″ S/46°24′28″ W).

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 de 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 Urucuia 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 calcilutites 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

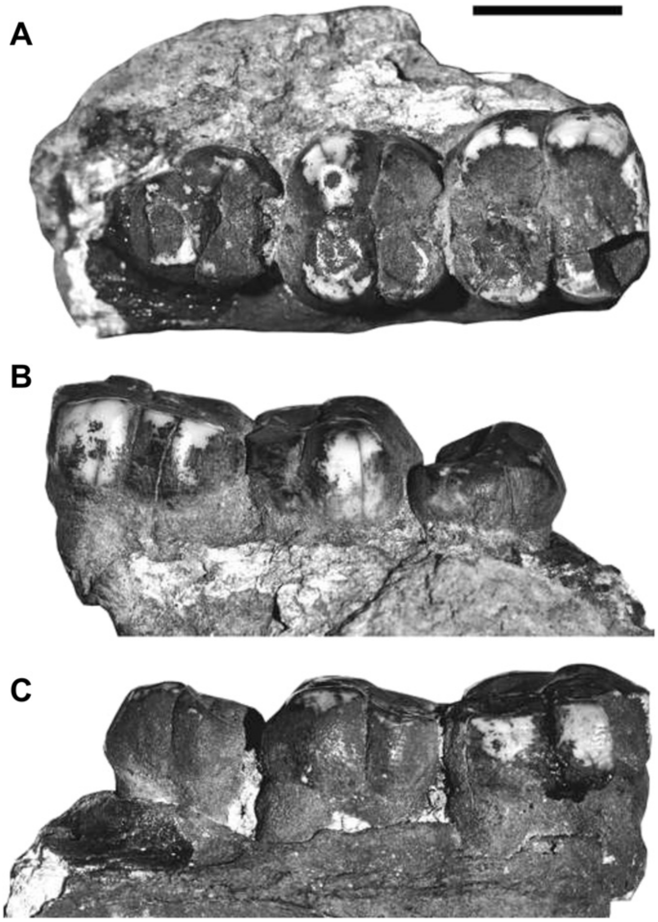

Fig. 2. Right maxillary fragment of *Catagonus stenocephalus* (UNIRIO – PM 1006) described here. (A): Occlusal view; (B): Lingual view; (C): Labial view. Scale bar = 10 mm.

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 Urucuia 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 coraloids, 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
Catagonus stenocephalus	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 Escrivaninha, 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 Escrivaninha, 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 (Bauermann 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
Catagonus cf. *stenocephalus*	UFPR 0118 PV	Partial skull	Gruta do Vale do Ribeira, between Adrianópolis and Doutor Ulysses, Paraná, Brazil	Late Pleistocene	Drier and colder than today/mixed C_3 and C_4 grassland (Saia, 2006)

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).

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

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 (Jaeckel, 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 oclussal 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.

Acknowledgments

The field trips which resulted in the collection of the specimen were made possible by the financial support of the Conselho Nacional de desenvolvimento Científico e Tecnológico (401812/2010-3, Edital MCT/CNPq n° 32/2010 – Fortalecimento da Paleontologia Nacional/Edital 32/2010) and the Universidade Federal do Estado do Rio de Janeiro; GMG and LHS also thank CONICET (PIP 0436) and ANPCyT (PICT) for financial support. We also thank the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia": Museo de Arqueología y Ciencias Naturales de Salto, Uruguay; Museo Municipal de Ciencias Naturales "Carlos Ameghino", Mercedes, Argentina; Museu de Ciencias da PUCRS, Geology and Palaeontology Laboratory, Uruguaiana, Brazil; Museo Municipal de Ciencias Naturales de Mar del Plata, "Lorenzo Scaglia", Argentina; Museo Nacional de Paleontología y Antropología, Tarija, Bolivia; Departamento de Geología, Universidade Federal do Paraná, Curitiba, PR, Brazil; Zoologisk Museum, Copenhagen, Denmark for providing material for analysis.

References

Ameghino, F., 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. Anales de la Sociedad Científica Argentina 58, 1–188.
Auler, A.S., 1999. Karst Evolution and Palaeoclimate of Eastern Brazil. Ph.D. thesis. School of Geographical Sciences, University of Bristol.
Auler, A.S., Smart, P.L., Wang, X., Piló, L.B., Edwards, R.L., Cheng, H., 2009. Cyclic sedimentation in Brazilian caves: mechanisms and palaeoenvironmental significance. Geomorphology 106, 142–153.
Avilla, L.S., Winck, G.R., Francisco, V.M.R., Gil, B.B., Granhen, A., Costa, D.G., 2007. A Fauna de Morcegos Fósseis como Ferramenta na Caracterização de Paleoambientes Quaternários. Anuário do Instituto de Geociências 30, 19–26.
Baffa, O., Kinoshita, A., Figueiredo, A.M.G., Brunetti, A., Ginesu, S., 2006. ESR dating of an ancient goat tooth from Nuoro, Sardinia, Italy. Radiation Protection Dosimetry 119 (1–4), 446–449.
Bauermann, S.G., Behling, H., Macedo, R.B., 2009. Biomas regionais e evolução da paisagem no Rio Grande do Sul com base em paleopalinologia. In: Ribeiro, A.M., Bauermann, S.G., Scherer, C.S. (Eds.), Quaternário do Rio Grande do Sul e Integrando Conhecimentos. Sociedade Brasileira de Paleontologia, Porto Alegre, pp. 81–93.
Blackwell, B.A.B., Gong, J.J.J., Skinner, A.R., Blais-Stevens, A., Nelson, R.E., Blickstein, J.I.B., 2010. ESR dating pleistocene barnacles from BC and Maine: a new method for tracking sea level change. Health Physics 98 (2), 417–426.
Behling, H., 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecolgy 177, 19–27.
Brain, C.K., 1995. The influence of climatic changes on the completeness of the early hominid record in Southern African caves, with particular reference to Swartkrans. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 451–458.
Brennan, B., Rink, W., Rule, E., Schwarcz, H., Prestwich, W., 1999. The ROSY ESR dating program. Ancient TL 17, 45–53.
Brook, G.A., Cowart, J.B., Brandt, S.A., Scott, L., 1997. Quaternary climatic change in southern and eastern Africa during the last 300 ka: the evidence from caves in Somalia and the Transvaal region of South Africa. Zeitschrift fur Geomorphologie. Supplementband 108, 15–48.
Campbell, K.E., 2010. Recalibrating the Great American Faunal Interchange. In: Vizcaino, S.F., Bargo, S. (Eds.), X Congreso Argentino de Paleontología y Bioestratigrafía y VII. Latinoamericano de Paleontología, La Plata, pp. 141–142.
Campbell, K.E., Prothero, D., Romero-Pittman, L., Hertel, F., Rivera, N., 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. Journal of South American Earth Sciences 29, 619–626.
Companhia de Pesquisa de Recursos Minerais (CPRM), 2006. Rochas Carbonáticas do Grupo Bambuí na região Nordeste do Estado de Goiás. Available from: http://www.cprm.gov.br/publique/cgi/cgilua.exe/sys/start.htm?infoid=261&sid=32 (accessed 5.12.2010).
Cione, A.L., Tonni, E.P., 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean area. In: Rabassa, J., Salemme, M. (Eds.), Quaternary of South America and Antarctic Peninsula, 12, pp. 22–51.
Cione, A.L., Tonni, E.P., 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. In: De Barrio, R.E., Etcheverry, R.O., Caballé, M.F., Llambias, E. (Eds.), Geología y Recursos Minerales de la Provincia de Buenos Aires, XVI Congreso Geológico Argentino, La Plata, 9, 183–200.
Dardene, M.A., 1978. Síntese sobre a estratigrafia do Grupo Bambuí no Brasil Central 30° Congresso Brasileiro de Geologia. Sociedade Brasileira de Geologia, Recife. 597–610.
Dardene, M.A., Walde, H.H.G.., 1979. A estratigrafia dos Grupos Bambuí e Macaúbas no Brasil Central. In: 1° Simpósio de Geologia de Minas, Sociedade Brasileira de Geologia, Belo Horizonte, 43–54.
Dias da Silva, D., Sedor, F.A., Oliveira, E.V., 2010. A presencia de Catagonus e Tayassu (Artiodactyla, Tayassuidae) no Pleistoceno do Estado do Paraná, Brasil. In: Silva, R.C., Avilla, L.S. (Eds.), 7° Simpósio Brasileiro de Paleontologia de Vertebrados. Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro. 112.
Fischer, G., 1814. Zoognosia Tabulis Synopticus Illustrata. Pt. III. Nicolai Sergeidis Vsevolozsky, Moscow. 732.
Fonseca, J.S., 1979. Taiassuídeos do Pleistoceno de cavernas calcárias de Minas Gerais. Master thesis, Universidade Federal do Rio Grande do Sul, Instituto de Geociencias.
Gasparini, G.M., 2001. Morfología dentaria comparada entre *Tayassu pecari* y *Tayassu tajacu* (Tayassuidae, Artiodactyla, Mammalia). Ameghiniana 38, 33R.

Gasparini, G.M., 2004. Presencia de Tayassuidae en la Formación San Andrés (Plioceno tardío) en la región costera de Argentina central. Ameghiniana 41 (4), 47–48.

Gasparini G.M., 2007. Sistemática, biogeografía, ecología y bioestratigrafía de los Tayassuidae (Mammalia, Artiodactyla) fósiles y actuales de América del Sur, con especial énfasis en las especies fósiles de la provincia de Buenos Aires. Ph.D. Thesis, Universidad Nacional de La Plata, Argentina.

Gasparini, G.M., 2010. Los Tayassuidae (Mammalia, Artiodactyla) fósiles de América del Sur: aspectos ecológicos y biogeográficos. In: Silva, R.C., Avilla, L.S. (Eds.), 7° Simpósio Brasileiro de Paleontologia de Vertebrados. Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, p. 138.

Gasparini, G.M., 2011. Records and stratigraphical ranges of South American Tayassuidae (Mammalia, Artiodactyla). Journal Mammalian Evolution. http://dx.doi.org/10.1007/s10914-011-9172-z. Available online at: http://www.springerlink.com/content/18016m413x823325/.

Gasparini, G.M., Ortiz Jaureguizar, E., Carlini, A.A., 2006. Familia Tayassuidae. In: Bárquez, R.M., Díaz, M.M., Ojeda, R.A. (Eds.), Los Mamíferos de Argentina: Sistemática y distribución. Publicación Especial de la Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Mendoza, pp. 114–115.

Gasparini, G.M., Kerber, L., Oliveira, E., 2009a. *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Tayassuidae) in the Touro Passo Formation (Late Pleistocene), Rio Grande do Sul, Brazil. Taxonomic and palaeoenvironmental comments. Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 254 (3), 261–273.

Gasparini, G.M., Soibelzon, E., Zurita, A.E., Miño-Boilini, A.R., 2010a. A review of the Quaternary Tayassuidae (Mammalia, Artiodactyla) from the Tarija Valley, Bolivia. Alcheringa. An Australasian Journal of Palaeontology 1, 7–20.

Gasparini G.M., Soibelzon E., Soibelzon L.H., Zurita A.E., Scarano A.C., Hertel M.F., 2010b. Estimación de la masa corporal de los tayasuidos (Mammalia, Artiodactyla) fósiles de América del Sur. XXIII Jornadas Argentinas de Mastozoología, 42.

Gasparini, G.M., Ubilla, M., 2010. Primeros ungulados inmigrantes norteamericanos: los Tayassuidae (Mammalia, Artiodactyla) del Cuaternario de Uruguay. In: Silva, R.C., Avilla, L.S. (Eds.), 7° Simpósio Brasileiro de Paleontologia de Vertebrados. Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, p. 89.

Gasparini, G.M., Ubilla, M., 2011. *Platygonus* sp. (Mammalia, Tayassuidae) in Uruguay (Raigón? Fm.; Pliocene-early Pleistocene), comments about its distribution and palaeonvironmental significance in South America. Journal of Natural History 45 (45–46), 2855–2870.

Gasparini, G.M., Ubilla, M., Tonni, E.P., 2009b. Tres especies de tayasuidos (*Catagonus wagneri, C. stenocephalus* y *Tayassu pecari*) en el Pleistoceno tardío del norte de Uruguay (Fm. Sopas). Ameghiniana 46 (4), 80.

Gray, J.E., 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15, 296–306.

Ikeya, M. (Ed.), 1993. New Applications of Electron Paramagnetic Resonance. Dating, Dosimetry and Microscopy. World Scientific, Singapore, Singapore, pp. 67–138.

Jaeckel, O.M.J., 1911. Eine Übersicht über die fossilen und lebenden Formen. Die Wirbeltiere. Gebrüder Bornträger. 252 p.

Jones, R.L., Hasson, H.C., 1985. Mineral Licks, Geophagy, and Biochemistry of North American Ungulates. Iowa State University Press, Ames.

Kerber, L., Kinoshita, A., Jose, F.A., Figueiredo, A.M.G., Oliveira, E.V., Baffa, O., 2011. Electron spin resonance dating of the southern Brazilian Pleistocene mammals from Touro Passo Formation, and remarks on the geochronology, fauna and palaeoenvironments. Quaternary International 245 (2), 201–208.

Kinoshita, A., Brunetti, A., Avelar, W.E.P., Mantelatto, F.L.M., Simões, M.G., Fransozo, A., Baffa, O., 2002. ESR dating of a subfossil shell from Couve Island, Ubatuba, Brazil. Applied Radiation and Isotopes 57 (4), 497–500.

Kinoshita, A., Karmann, I., William da Cruz, J.F., Graeff, C.F.O., Baffa, O., 2005a. K-band ESR spectra of calcite stalagmites from southeast and south Brazil. Applied Radiation and Isotopes 62 (2), 247–250.

Kinoshita, A., Magnólia Franca, A., Augusto Costa de Almeida, J., Figueiredo, A.M.G., Nicolucci, P., Graeff, C.F.O., Baffa, O., 2005b. ESR dating at K and X band of northeastern Brazilian megafauna. Applied Radiation and Isotopes 62 (2), 225–229.

Kinoshita, A., Figueiredo, A.M.G., Felice, G.D., Lage, M.C.S.M., Guidon, N., Baffa, O., 2008. Electron spin resonance dating of human teeth from Toca da Santa shelter of São Raimundo Nonato, Piauí, Brazil. Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms 266 (4), 635–639.

Kinoshita, A., Jose, F.A., Sundaram, D., Paixão, J.S., Soares, I.R.M., Figueiredo, A.M.G., Baffa, O., 2011. Electron spin resonance dating of teeth from Western Brazilian megafauna – preliminary results. Radiation Measurements 46 (9), 842–846.

Link, D.H.F., 1795. Beiträge zur Naturgeschichte. Rostock and Leipzig 2, 1–126.

Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 1. Laurentii Salvii, Stockholm. 1–824.

Lopes, R.P., Oliveira, L.C., Figueiredo, A.M.G., Kinoshita, A., Baffa, O., Buchmann, F.S., 2010. ESR dating of pleistocene mammal teeth and its implications for the biostratigraphy and geological evolution of the coastal plain, Rio Grande do Sul, southern Brazil. Quaternary International 212 (2), 213–222.

Mascarenhas, S., Filho, O.B., Ikeya, M., 1982. Electron spin resonance dating of human bones from Brazilian shell-mounds (Sambaquís). American Journal of Physical Anthropology 59 (4), 413–417.

Mayer, J.J., Wetzel, R.M., 1986. Catagonus wagneri. Mammalian Species 259, 1–5.

Mones, A., 1979. Los dientes de los vertebrados. Una introducción a su estudio. Dirección General de Extensión Universitaria. División Publicaciones y Ediciones. Universidad de la República. Departamento de Paleontología, Museo Nacional de Historia Natural; Departamento de Paleontología, Facultad de Humanidades y Ciencias, Montevideo, Uruguay.

Montgelard, C., Catzeflis, F., Douzery, E., 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. Molecular Biology and Evolution 14 (5), 550–559.

Morrone, J.J., 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands, based on panbiogeographic and cladistic analyses of the entomofauna. Annual Review of Entomology 51, 467–494.

Nabel, P.E., Cione, A., Tonni, E.P., 2000. Environmental changes in the Pampean area of Argentina at the Matuyama–Brunhes (C1r–C1n) Chrons boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 162, 403–412.

Nihei, S.S., De Carvalho, C.J.B., 2007. Systematics and biogeography of *Polietina* Schnabl & Dziedzicki (Diptera, Muscidae): neotropical area relationships and Amazonia as a composite area. Systematic Entomology 32, 477–501.

Pascual, R., Ortiz-Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. Journal of Human Evolution 19, 23–60.

Palmer, A.N., 1991. Origin and morphology of limestone caves. Geological Society of America Bulletin 103, 1–21.

Palmer, T.S., 1897. Notes on the nomenclature of four genera of tropical American mammals. Proceedings of the Biological Society of Washington 11, 173–174.

Parizzi, M.G., Salgado-Laboriau, M.L., Kohler, H.C., 1998. Genesis and environmental history Lagoa Santa, southeastern Brazil. The Holocene 8 (3), 311–321.

Paula Couto, C., 1975. Mamíferos fósseis do Quaternário do sudeste brasileiro. Boletim Paranaense de Geociências 33, 89–132.

Paula Couto, C., 1981. On an extinct peccary from the Pleistocene of Minas Gerais. Iheringia Série Geología, Porto Alegre 6, 75–78.

Prado, D.E., Gibbs, P.E., 1993. Patterns of species distribution in the dry seasonal Forest South America. Annals of the Missouri Botanical Garden 80, 902–927.

Prescott, J.R., Hutton, J.T., 1994. Cosmic ray contributions to dose rates for luminescence and ESR dating: large depths and long-term time variations. Radiation Measurements 23 (2/3), 497–500.

Prevosti, F., Gasparini, G.M., Bond, M., 2006. On the systematic position of a specimen previously assigned to Carnivora from the Pliocene of Argentina and its implication for the Great American Biotic Interchange. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 242 (1), 133–144.

Prieto, A.R., 2000. Vegetational history of the Late glacial–Holocene transition in the grasslands of eastern Argentina. Paleogeography, Paleoclimatology, Palaeecology 157, 167–188.

Prieto, A.R., Blasi, A.M., Francesco, C.D., de Fernandéz, C., 2004. Environmental history since 11,000 14C yr B.P. of the northeastern Pampas, Argentina, from alluvial sequences of the Luján River. Quaternary Research 62, 146–161.

Redford, K.H., Eisenberg, J.F., 1992. Order Artiodactyla. In: Redford, K.H., Eisenberg, J.F. (Eds.), Mammals of the Neotropics. The Southern Cone. University of Chicago Press, Chicago, pp. 229–252.

Reinhardt, J., 1879–1880. De i de brasilianske knoglehuler fundne Navlesvin- Arter. Videnskabelige Meddlelser fra den Naturhistorike Forening I, Kjøbenhavn, 271–301.

Roig-Juñent, R., Domínguez, M.C., Flores, G.E., Mattoni, C., 2006. Biogeographic history of South American arid lands: a view from its arthropods using TASS analysis. Journal of Arid Environments 66, 404–420.

Rusconi, C., 1929. Anatomía craneodental de los tayassuinos vivientes. Anales Sociedad Científica Argentina 107 (66–82), 177–242.

Rusconi, C., 1930. Las especies fósiles argentinas de pecaríes y sus relaciones con las del Brasil y Norteamérica. Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia" 36, 121–241.

Saia, S.E.M.G., 2006. Reconstrução paleoambiental (vegetação e clima) no Quaternário tardio com base em estudo multi/interdisciplinar no Vale do Ribeira (sul do Estado de São Paulo). Ph.D. thesis, Universidade de São Paulo.

Salis, S.M., Silva, M.P., Mattos, P.P., Silva, J.S.V., Pott, V.J., Pott, A., 1993. Fitossociologia de remanescentes de floresta estacional decídua em Corumbá, Estado do Mato Grosso do Sul. Brasil. Revista Brasileira de Botânica 27 (4), 671–684.

Soibelzon, E., 2008. Los Mamíferos del Ensenadense (Pleistoceno Inferior-Medio) del Este de la Región Pampeana, con énfasis en los Xenarthra. Bioestratigrafía, diversidad y correlaciones biogeográficas. Ph.D. thesis, Universidad Nacional de La Plata.

Soibelzon, E., Soibelzon, L., Rodriguez Bualó, S., Pérez, M., Avilla, L., Zurita, A., Miño Boilini, A., Gasparini, G.M., Alcaraz, A., 2011. Los mamíferos del Pleistoceno del valle de Tarija (Bolivia): diversidad y paleoambientes. IV Congreso Latinoamericano de Paleontología de Vertebrados. San Juan.

Stehli, F.G., Webb, S.D., 1985. The Great American Biotic Interchange. Springer Press, NewYork. 550.

Stirton, R.A., 1947. A rodent and a peccary from the Cenozoic of Colombia. Compilación de Estudios Geológicos Oficiales en Colombia 7, 317–324.

Ubilla, M., 2004. Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. Proceedings of the Geologists Association 115, 1–11.

Ubilla, M., Perea, D., Aguilar, C.G., Lorenzo, N., 2004. Late Pleistocene vertebrates from northern Uruguay: tools for biostratigraphic, climatic and environmental reconstruction. Quaternary International 114, 129–142.

Verde, M., Ubilla, M., Jiménez, J.J., Genise, J.F., 2007. A new earthworm trace fossil from paleosols: aestivation chambers from the Late Pleistocene Sopas Formation of Uruguay. Palaeogeography, Palaeoclimatology, Palaeoecology 243, 339–347.

Voglino, D., Pardiñas, U.F.J., 2005. Roedores sigmodontinos (Mammalia: Rodentia: Cricetidae) y otros micromamíferos pleistocénicos del norte de la provincia de Buenos Aires (Argentina): reconstrucción paleoambiental para el Ensenadense cuspidal. Ameghiniana 42 (1), 1–18.

Webb, S.D., 1985. Late Cenozoic mammal dispersals between the Americas. In: Stehli, F.G., Webb, S.D. (Eds.), The Great American Biotic Interchange. Plenum Press, pp. 357–386.

Webb, S.D., 1991. Ecogeography and the Great American Interchange. Paleobiology 17, 266–280.

Wetzel, R.M., 1977. The Chacoan peccary, *Catagonus wagneri* (Rusconi). Bulletin of the Carnegie Museum of Natural History 3, 1–36.

Woodburne, M.O., Cione, A.L., Tonni, E.P., 2006. Central American provincialism and the Great American Biotic Interchange. In: Carranza-Castañeda, O., Lindsay, E.H. (Eds.), Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange, 4. Universidad Nacional Autónoma de México, Instituto de Geología y Centro de Geociencias, Publicación Especial, pp. 73–101.

Woodburne, M.O., 2010. The great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution 17 (4), 245–264.

Zampaulo, R.A., Ferreira, R.L., 2009. Terrestrial cave invertebrate diversity in nine caves in the municipality of Aurora do Tocantins (TO). In: 30° Congresso Brasileiro de Espeleologia. Sociedade Brasileira de Espeleologia, Montes Claros. Available from: http://www.sbe.com.br/anais30cbe/30cbe_267274.pdfhttp://www.sbe.com.br/anais30cbe/30cbe_267-274.pdf (accessed 5.12.2010).