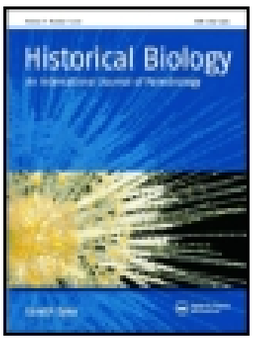

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Fossil peccaries of Late Pleistocene/Holocene (Cetartiodactyla, Tayassuidae) from underwater caves of Serra da Bodoquena (Mato Grosso do Sul State, Brazil)

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ABSTRACT

New records of *Catagonus stenocephalus* and *Tayassu pecari* are reported from the karst of Serra da Bodoquena, located at a south-western portion of Brazil near the border with Paraguay. Skull and lower jaw fragments at different stages of mineralisation were retrieved from two limestone underwater caves, Japonês and Nascente do Formoso, associated with clay and sand deposits with no retrievable stratigraphy. C14 dating of fossil mammals from these caves was attempted, but so far no success was achieved, but the inferred age for the associated paleofauna of these caves is Late Pleistocene and Holocene. The morphology of these fossil peccaries, from the most south-western known population in Brazil, is detailed and paleoecological implications are considered.

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KEYWORDS
Tayassuidae; peccary; quaternary; South American; Central Brazil; morphology

Introduction

The Tayassuidae (Mammalia, Cetartiodactyla) has an extensive fossil record in South America. They have been found associated with Late Cenozoic deposits in Argentina, Brazil, Uruguay, Bolivia, Colombia, Peru and Venezuela (Rincón et al. 2009; Gasparini 2013; Montellano-Ballesteros et al. 2014). The diversity and abundance of fossil findings of tayassuids in South America are greater during the Pleistocene than in Pliocene and Holocene epochs. They experienced a remarkable decrease in diversity near the Pleistocene–Holocene boundary (Gasparini 2013), and only two genera (*Catagonus* and *Tayassu*) and three extant species are representing the current family's diversity (see Gasparini 2013; Gasparini et al. 2014).

The greater portion of the diversity and abundance of fossil species of tayassuids in South America is concentrated in Argentina, where, according to Gasparini (2007), three genera with twelve species of Tayassuidae are recognised. In contrast, in Brazil, there are records of three species only (Gasparini, Kerber et al. 2009; Avilla et al. 2013; Gasparini 2013): *Tayassu pecari* (Link, 1795), *Tayassu tajacu* (Linnaeus, 1758) and *Catagonus stenocephalus* (Lund in Reinhardt, 1880). Curiously enough, Brazil is the only South American country where peccaries fossil remains are often found associated with cave deposits (Avilla et al. 2013; Gasparini 2013); in Argentina, there is only one cave record (i.e. *Platygonus* sp.in Olavarría locality, Buenos Aires Province; see De los Reyes et al. 2014).

This article aims to (1) describe the tayassuid fossil records from two underwater caves from Serra da Bodoquena and Mato Grosso do Sul State, Brazil; and (2) discuss the palaeoecological implications of these findings.

Geological setting and associated fauna

The Serra da Bodoquena (19°48′–22°16′S, 56°32′–57°24′W) is located in the south-eastern part of the Mato Grosso do Sul State, comprising the municipalities of Jardim, Bonito, Bela Vista, Porto Murtinho and Bodoquena (Figure 1). A full description of its geological and phytogeographic settings can be found in Boggiani and Coimbra (1995) and Sallun Filho et al. (2004). Few studies concerning the Quaternary period have been conducted in the region, highlighting those of Almeida (1965), Mendes (1957), Lino et al. (1984), Gnaspini et al. (1994) and Ayub et al. (1996).

Fossil tayassuids were recovered from two underwater caves: Caverna do Japonês (21°35′63″S, 56°39′59″W) and Nascente do Formoso (21°15′35″S, 56°38′26″W). The fossils were manually collected on the cave floor through diving and then sorted out in the laboratory (Salles et al. 2006). The material from these flooded caves, displaying significantly different levels of mineralisation, probably represents a mixed assemblage from different horizons, presumably ranging from Late Pleistocene to Holocene, but so far attempts to directly date associated fossil material have proved fruitless. Numerous other fossil mammals, typical of the South American Quaternary, were found in these two caves, such as xenarthrans (*Dasypus*, *Euphractus*, *Propaopus*,

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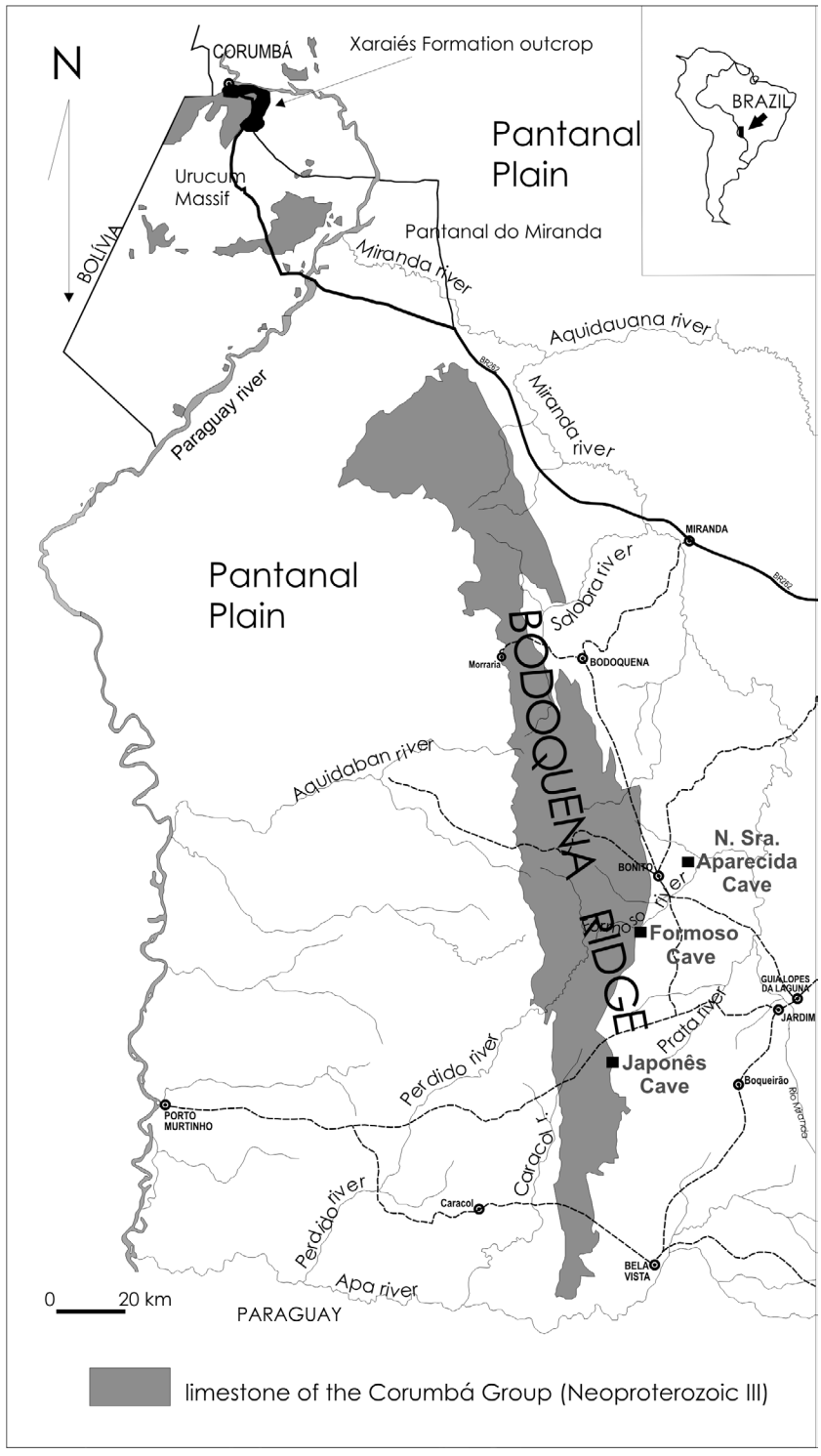

Figure 1. Map of the Serra da Bodoquena region (Mato Grosso do Sul, Central Brazil), indicating the location of Japonês and Nascente do Formoso caves.

Pampatherium, *Glossotherium*, *Mylodonopsis*, *Eremotherium* and *Glyptodon*), carnivores (*Smilodon*, *Panthera*, *Leopardus*, *Chrysocyon*, *Protocyon* and *Pteronura*), horses (*Equus*), tapirs (*Tapirus*), mastodons [*Stegomastodon* = *Notiomastodon sensu* Mothé et al. (2011, 2012)], deer (*Mazama* and *Ozotoceros*), llamas (*Paleolama*) and members of South American endemic ungulate orders (*Macrauchenia* and *Toxodon*) (Salles et al. 2006; Perini et al. 2009, 2011).

Materials and methods

Abbreviations

PM: upper premolar cheek series; M: upper molar cheek series; pm: lower premolar cheek series; m: lower molar cheek series.

pm3: third lower premolar; pm4: fourth lower premolar; m1: first lower molar; m2: second lower molar; m3: third lower

molar; PM3: third upper premolar; dPM4: deciduous fourth upper premolar; PM4: fourth upper premolar; M1: first upper molar; M2: second upper molar; M3: third upper molar.

Lpm4: maximum mesio-distal length of pm4; Wpm4: maximum labio-lingual width of pm4; Lm1: maximum mesio-distal length of m1; Wm1: maximum labio-lingual width of m1; Lm2: maximum mesio-distal length of m2; Wm2: maximum labio-lingual width of m2; Lm3: maximum mesio-distal length of m3; Wm3: maximum labio-lingual width of m3; LPM3: maximum mesio-distal length of P3; WPM3: maximum labio-lingual width of P3; LPM4: maximum mesio-distal length of P4; WPM4: maximum labio-lingual width of P4; LM1: maximum mesio-distal length of M1; WM1: maximum labio-lingual width of M1. Hpm2: height of the dentary at pm2 level; Hm1: height of the dentary at m1 level; Har: height of the dentary at the beginning of the ascending ramus; WPC: width of the parasagittal crests; FPO: Width of the frontal bone at level of the posterior margin of the orbits; PWM1: Width of the palatine bone at the level of the anterior portion of the M1.

The specimens examined are deposited in the mammal collection of the Museu Nacional – UFRJ, Rio de Janeiro, Brazil. Measurements were taken using Vernier callipers, (0.01 mm accuracy) and data are expressed in millimetres (Supplemental Material).

Herein, we adopt the taxonomical arrangement proposed by Gasparini (2007), which is, currently, the most throughout review of the South American Tayassuidae.

In the descriptions of the main cusps of the premolars, the recognition of the paracone, metacone, protocone and hypocone simply indicates topographical position, not implying that any hypothesis of serial homologies, related to the molar's cusps, is advocated. As understood, those serial homologies are yet subject matters under debate (Rusconi 1929, Wetzel 1977, Mones 1979, Gasparini 2001).

Systematic paleontology

Order Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997
Suborder Suiformes Jaeckel, 1911
Infraorder Suoidea Gray, 1821
Family Tayassuidae Palmer, 1897
Subfamily Tayassuinae Palmer, 1897
Genus *Tayassu* G. Fischer de Waldheim, 1814
Tayassu pecari (Link, 1795)

Chronology and geographic distribution in South America

Middle Pleistocene to Holocene in Argentina, Brazil and Uruguay; current distribution ranging from northern Argentina to south-eastern Mexico (Gasparini 2013).

Geographical and stratigraphical provenances

Caverna do Japonês and Nascente do Formoso, both being underwater limestone caves from the karstic region associated with Bodoquena plateau, are located at the Mato Grosso do Sul State, Brazil. Age ranges from Late Pleistocene to Holocene.

Referred material and description

MN 57456 (Figure 2), a partial maxillary and palatine bone with complete molar series and left PM 3–4; MN 57457 (Figure 3), a nearly complete mandible with complete molar series and right pm4; MN 57458 (Figure 2), a partial right mandible with pm4–m2 and an isolate m3.

MN 57456 has a longitudinal medial sulcus in the palatine; the posterior portion of the buccinator sulcus can be observed at the left side of the material. The cheek teeth are bunodont and brachyodont. The PM3 is subquadrangular, bearing three major cusps (paracone, protocone and metacone) on the trigon area and a smaller one (hypocone) on the talon. The cingulum is well defined on the mesial and distal sides. The lingual side is slightly convex but the labial is straight, not showing the typical quadrangular outline of molars. The PM4 is molariform, quadrangular and larger than the PM3. It has four major cusps very similar in size; however, the hypocone is slightly less developed than the other cups. The paracone and metacone are located primarily labially to the protocone and hypocone, respectively. The cingulum is well developed in the mesial and distal sides.

Measurements

LPM3: 10,04; WPM3: 11; LPM4: 11,49; WPM4: 10,66; LM1: 15,59; WM1: 12,63; LM2: 15,42; WM2: 14,76; LM3: 14,39; WM3: 13,94; PWM1: 19,62.

The vertical mandibular rami of MN 57457 are damaged, but the horizontal rami are almost intact. The molar series is complete, but only the right pm4 is present. The anterior portion of the mandibular symphysis is also missing. The ascending ramus does not overlap the m3 in lateral view. There is no step to pm2 alveolus, notice, however, that several modern specimens of *T. pecari* also lack this structure. The cheek teeth are bunodont and brachyodont. The pm4 is molariform, having a quadrangular outline in occlusal view, with four well-developed principal cusps. The entoconid and hypoconid are separated by two accessories cusps. The m1 and m2 have a quadrangular online in occlusal view, with only mesial and distal cingula developed. The entoconid and hypoconid are not separated by accessories cusps. The m3 has a posterior constriction, resulting in different widths between the anterior and posterior portions. A mesial cingulum is present, but the posterior, lingual and labial cingula are absent. The third lobe is well developed and has a complex pattern of accessory cusps.

Measurements

Lpm4: 12,41; Wpm4 9,43; Lm1:13,95;Wm1: 11,84; Lm2:14,94; Wm2:14,34; Lm3: 21,78; Wm3: 13,50; Hpm2: 33,53; Hm1: 37,84; Har: 41.

MN 57458 consists of a very fragmentary right mandible, with only partial teeth series preserved. The cheek teeth are bunodont and brachyodont. The pm4 is molariform with a subquadrangular outline in occlusal view. The principal cusps are well developed with accessory cups separating the entoconid and hypoconid. The m1 and m2 have a quadrangular outline, with the mesial and distal cingula well developed. Labial and lingual cingula are absent. The entoconid and hypoconid are not separated by accessory cusps. The m3 do not have labial, lingual or distal cingula, but a mesial cingulum is present. The entoconid

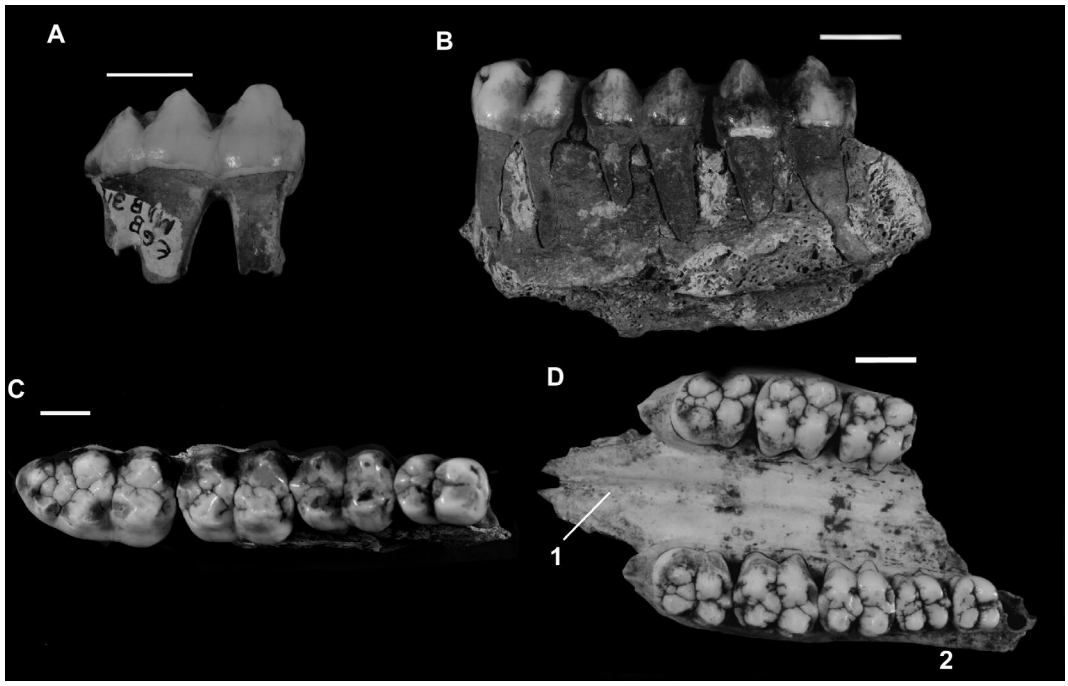

Figure 2. Fragments of *Tayassu pecari*: A, B – MN57458, lateral view of partial right mandible with pm4-m2 and isolated m3; C – MN57458, Occlusal view; D – MN57456, partial maxillary and palatine bone with complete molar series and left PM3-PM4. 1 – Presence of the longitudinal medial sulcus in the palatine bone; 2 – a well-developed buccinator sulcus.

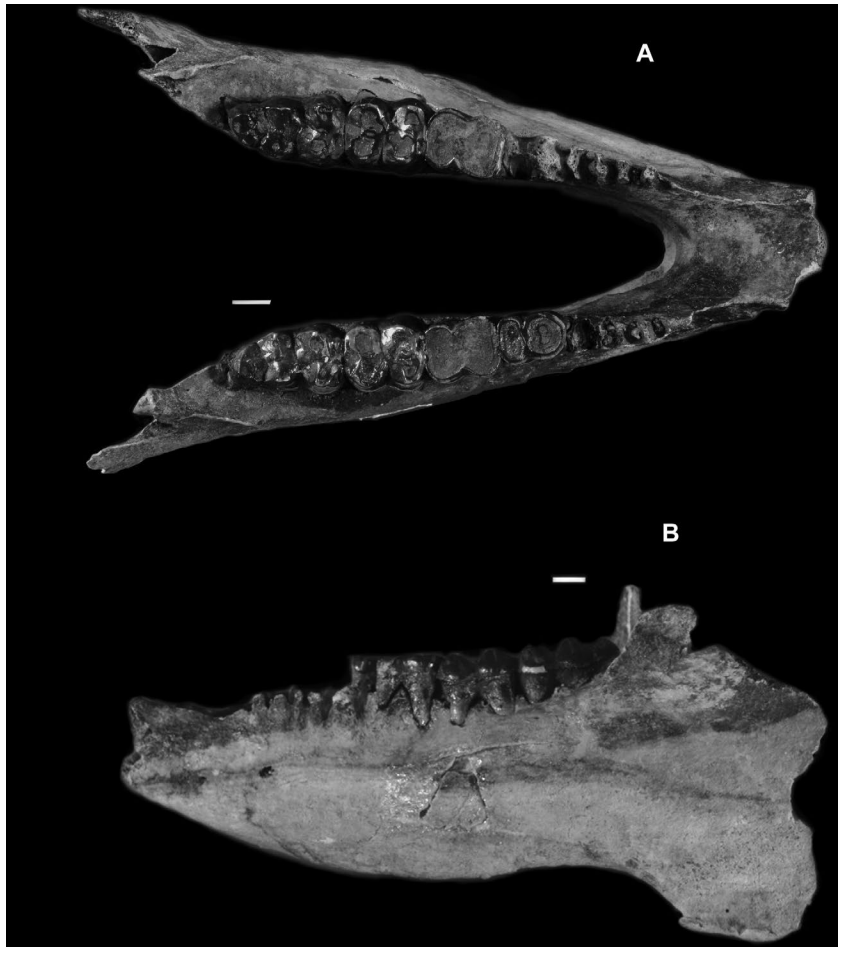

Figure 3. Fragments of *Tayassu pecari*: A – MN57457, a nearly complete mandible with complete molar series and right pm4, Occlusal view; B – MN57457, lateral view.

and hypoconid are also not separated by accessory cusps. The third lobe is complex with multiple accessory cusps. The m3 has a posterior constriction, resulting in different widths between the anterior and posterior portions.

Measurements

Lpm4: 13,66; Wpm4:10,50; Lm1: 16,23; Wm1: 12,01; Lm2:18,83; Wm2:14,97; Lm3:25,41; Wm3:15,73.

Remarks

According to Gasparini (2007), the morphological features that allow us to determine these specimens such as *T. pecari* are the following: (i) the brachyodont and bunodont conditions of the crown; (ii) the molariform shape of PM3 and PM4; the marked size reduction of the hypocone in PM3, being slightly smaller than the three major cusps of PM4; and (iii) the relatively well developed mesial and distal portions of the cingulum. Here, it is added two more diagnostic features: the presence of the longitudinal medial sulcus in the palatine bone and a well-developed buccinator sulcus.

Genus *Catagonus*Ameghino, 1904

Catagonus stenocephalus (Lund in Reinhardt, 1880)

Chronology and geographic distributions in South America

Middle Pleistocene to Holocene in Argentina, Brazil, Uruguay and Bolivia (Avilla et al. 2013).

Geographical and stratigraphical provenances

Caverna do Japonês and Nascente do Formoso, both being underwater limestone caves from the karstic region associated with Bodoquena plateau, are located at the Mato Grosso do Sul State, Brazil. Age ranges from Late Pleistocene to Holocene.

Referred material and description

MN 57459 (Figure 4), a fragment of skull (part of frontal, parietal and occipital bones) and MN 57460 (Figure 4), a fragment of maxillary with dPM4-M1 in both sides.

MN 57459 includes the frontal, parietal and part of the occipital bones. The frontal bone has a convex surface above the orbits and on the nasal suture. The postorbital processes of the frontal bone are less downward inflected. The supraorbital sulci are deep and straight to the nasal bones. There is no visible lacrimal foramen, and the lacrimal bone is not exposed in the anterior portion of the orbits, in lateral view. A very shallow depression is observed in the medial part of the parietal bone. The temporal crest has a concave shape and the parasagittal crests are thick and short. The occipital bone has a wide surface, with ventral oriented parallel nuchal crests.

Measurements

WPc: 20,23; FPO: 107,61; Total length as preserved: 158,30.

MN 57460 has both deciduous PM4 and the M1 with no marked wear in both sides. The teeth are bunodont and brachyodont. The dPM4 is molariform with four well-developed principal cusps and, below the dPM4, both permanent PM4 are visible. The M1 is a typical quadrangular molar with four well-developed principal cusps and several accessories cusps in the medial part. A mesial cingulum is present.

Measurements

LM1: 16,10; WM1: 13,76; PWM1:20,48.

Remarks

Despite the fact that the material is quite fragmented, the assignment to *C. stenocephalus* is unequivocally sustained by several morphological features preserved in the material such as (i) the shape of the occipital bone (wider than the other Tayassuinae); (ii) the thickness of the parasagittal crests (thicker than the other Tayassuinae); (iii) the orientation of the supra orbital sulcus (straight to the nasal bones as in *T. pecari*); and (iv) the well-developed hypocone in dPM4.

According to Gasparini (2007), *C. stenocephalus* has a bunodont and mesodont cheek teeth. In comparison with another Tayassuinae with mesodont crown such as *Platygonus* sp and *C. wagneri,* the crown of *C. stenocephalus* does not have the same height of the others. So, we propose that the height of the crown of *C. stenocephalus* should be considered as brachyodont instead of mesodont.

In the skull cap, the frontal, parietal and the supraoccipital bones display several diagnostic characters that allow the identification of this specimen as *C. stenocephalus*: a less downward inflected postorbital processes of the frontal bone when compared to other tayassuids, a shallow depression on the medial part of the parietal bone, the concave shape of the temporal crests, the width of the parasagittal crest and the supraoccipital shield. The postorbital processes of the frontal bones are more laterally oriented in *C. stenocephalus* than on the other species of peccaries registered in the Brazilian Quaternary (e.g. *T. pecari*, *T. tajacu*). The presence of this feature results in a wider and flattened forehead, implying in more concave temporal crests instead of a straighter shape as in *T. pecari*, or convex as in *T. tajacu*. A shallow depression is present in the medial part of the parietal bones just in frontal of the parasagittal constriction. This feature is exclusive of *C. stenocephalus*, having an inflated shape in *T. pecari* and flattened in *T. tajacu*. The thick parasagittal crests are also exclusive of *C. stenocephalus*. The supraoccipital shield in *T. pecari* and *T. tajacu* has a deep dorsoventral depression with the nuchal crests in a higher position, while *C. stenocephalus* has a flat surface, with the nuchal crests in almost the same level of the medial part of the supraoccipital. The skull cap is also more robust than in *T. pecari* and *T. tajacu.*

Discussion

Distributional and stratigraphic patterns of Catagonus stenocephalus and Tayassu pecari in South America

The species *Catagonus stenocephalus* is a medium-to-large size extinct tayassuid recorded from Middle to Late Pleistocene in South America (Avilla et al. 2013). It is known from several localities in Argentina (Buenos Aires Province; Gasparini 2004, 2007, 2013; Avilla et al. 2013), Uruguay (Sopas Formation, Salto

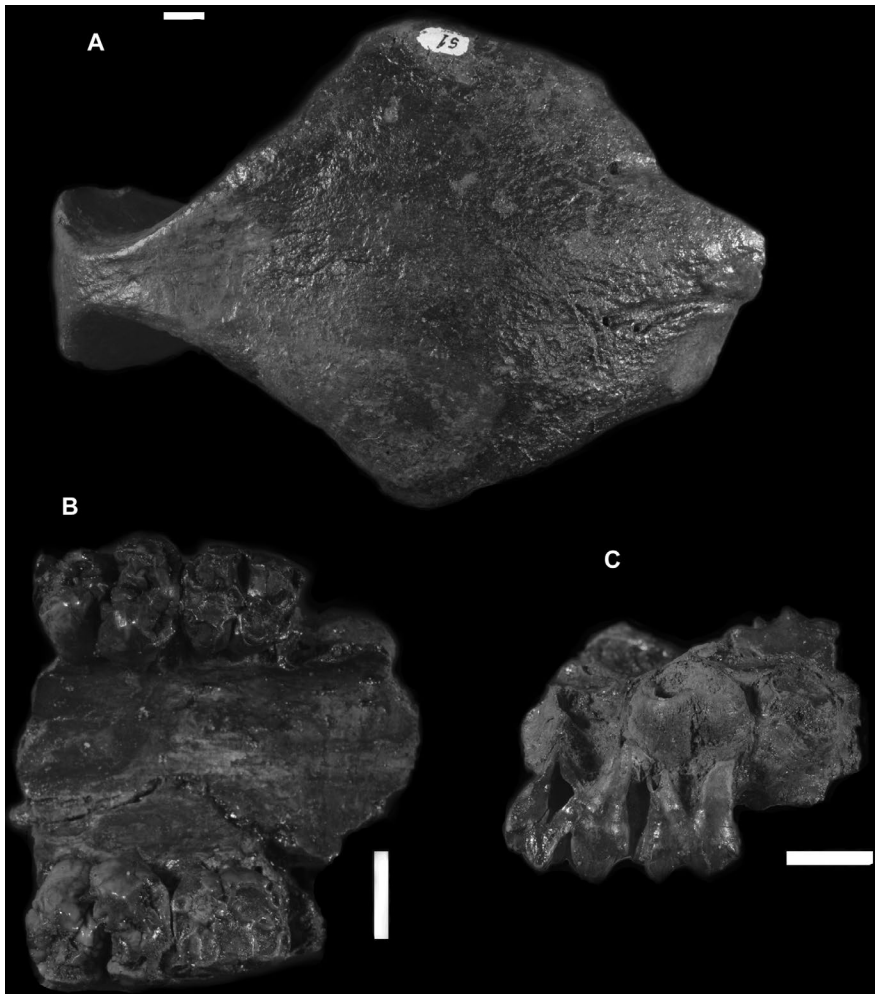

Figure 4. Fragments of *Catagonus stenocephalus*: A – MN57459, fragments of skull, upper view; B, C – MN57460, fragment of maxillary with dPM4-M1 in both sides.

Department; see Gasparini, Ubilla, et al. 2009; Gasparini and Ferrero 2010) and Brazil (Touro Passo Formation, municipality of Uruguaiana (Gasparini, Kerber, et al. 2009); Lagoa Santa, Minas Gerais State (Winge 1906; Fonseca 1979; de Paula Couto 1975, 1981); Gruta dos Moura cave, Tocantins State (Avilla et al. 2013)). An additional record of *Catagonus cf. stenocephalus* is known from Late Pleistocene sediments outcropping in Gruta do Vale do Ribeira, Paraná State (Dias da Silva et al. 2010). It is also known from the Tarija Valley, Bolivia (Gasparini et al. 2010); unfortunately, the ages of these sediments are uncertain (tentatively Late Pleistocene, see Soibelzon et al. 2011).

The species *Tayassu pecari* is a small- to medium-sized extant tayassuid, widely distributed from northern Argentina to south-eastern Mexico (Pautasso 2008; Gasparini et al. 2011, 2014). Despite its large geographical range, its fossil record is scarce; it is recorded from Middle Pleistocene to Holocene in South America. It is known from several localities in Argentina [Buenos Aires Province (Gasparini 2013; Gasparini et al. 2014); Corrientes Province (Gasparini and Zurita 2005); Misiones Province (Tonni 2004); and Santa Fe Province (Gasparini et al. 2011)], Brazil [Lagoa Santa (Fonseca 1979), and Lapa do Dragão (Parisi Dutra et. al. 2010), Minas Gerais State; Rio Grande do Sul and Mato Grosso do Sul states (de Paula Couto 1975); Gruta do Vale do Ribeira, Paraná State (Dias da Silva et al. 2010); Aurora do Tocantins, Tocantins State (Müller et al. 2013); Gruta Toca Fria, Iuiú and Malhada, Bahia State (Dantas et al. 2013); and Piauí, Ceará and Amazonas states (Rancy 1999; Faure et al. 1999)] and Uruguay (Sopas Formation, Salto Department (Gasparini, Ubilla et al. 2009; Gasparini and Ferrero 2010)). In Argentina, records of *Tayassu* cf. *pecari* appear in Santiago del Estero Province (Rusconi 1930; Kraglievich and Rusconi 1931; Tonni 2006). Recently, Montellano-Ballesteros et al. (2014) mentioned fossil remains of the white-lipped peccary in sediments outcropping in Venezuela (Monagas, Falcón, Anzoategui and Zulia states); however, the age of the bearing sediments is not accurate (probably Late Pliocene-early Holocene).

During the Quaternary (Pleistocene and Holocene), the fossil record of tayassuids suggests a possible coexistence of *Catagonus* and *Platygonus* during Early-to-Middle Pleistocene in the Pampean Region (mainly in Buenos Aires Province, Argentina), similar to that registered during the Pleistocene in Bolivia (Tarija valley). In turn, the palaeontological information raises the possibility of coexistence of *Catagonus* and *Tayassu* during Middle Pleistocene to earliest Holocene in the Pampean Region (mainly in Buenos Aires Province, Argentina), similar to that registered during Late Pleistocene in the Argentine Mesopotamian, northern Uruguay, Minas Gerais and, with the specimens here described, in Mato Grosso do Sul (Brazil). This

last relationship can also be observed during the Holocene of Santiago del Estero Province (Argentina), and presently in the Great Chaco (see Gasparini 2013).

Ecological considerations

The species *T. pecari* has a wide distribution in the Neotropics, being well adapted to tropical and subtropical rainforests, but it may also be present in arid environments, such as the Venezuelan savannas, xerophilous woodland of the eco-region of Dry Chaco and the tropical dry forest of Costa Rica (Wetzel 1977; Mayer and Brandt 1982; Nowak and Paradiso 1983; Oliver 1993; Gasparini and Zurita 2005). Throughout its entire geographic distribution, they range altitudinally from sea level to over 1900 m (see Gasparini et al. 2014 and references cited therein). However, despite its wide geographical distribution, its preferred habitat is the tropical rainforest lowland. White-lipped peccaries are omnivores, feeding on fruits, nuts, vegetation, and small amounts of animal matter (Altrichter and Boaglio 2004).

On the other hand, the species *C. stenocephalus* has certain morphological features (see Gasparini, kerber et al. 2009, and literature cited therein) that allow to infer that these animals were 'runners', and lived in dry and relatively open environments, and that they had a herbivorous and foraging diet. The occurrence of these species is in agreement with previous paleoecological reconstructions of the late Quaternary environment of Serra da Bodoquena as an open savanna rich in wetlands (Salles et al. 2006; Perini et al. 2009).

The climatic changes that occurred during the Late Pleistocene, responsible for the decrease of open areas, may have caused the extinction of *C. stenocephalus*. However, the broad ecological tolerance of *Tayassu pecari* enabled this species survival during this changing environment, and it still remains as part of the extant mammalian fauna of central Brazil.

Acknowledgements

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