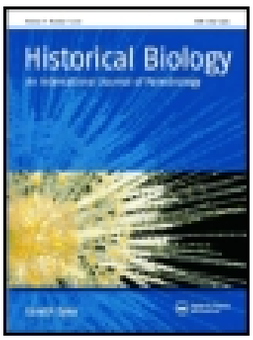

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Parachoerus carlesi (Mammalia, Tayassuidae) in the Late Pleistocene (northern Argentina, South America): paleoecological and palaeobiogeographic considerations

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ABSTRACT

The Tayassuidae is one of the first families of North American immigrant mammals that arrived into South America during the 'Great American Biotic Interchange'. They have been found associated with Late Cenozoic deposits mainly in Argentina and Brazil, but also in Uruguay, Bolivia, Colombia, Peru and Venezuela. Theirs records within Argentina come from the Pampean Region, Mesopotamia and north-central region. Here, we report the first record of *P. carlesi* with precise stratigraphic (26.630 ± 370 14C years BP, Late Pleistocene) data in Argentina, precisely from the Chacoan region. This specimen represents the most complete fossil material of this extinct species, increasing its morphological and morphometrical knowledge, and it provides relevant ecological and climatic information. From a palaeoenvironmental point of view, the fauna registered in this paleontological site, includes taxa mainly adapted to open or semi-open and arid or semi-arid environments. The bearing sediments and the peculiarities of the faunal assemblages, as well as the chronological data, allow confirming that arid and semiarid conditions, with scarce or absent vegetation cover were developed in this area of Argentina during the last part of MIS 3 and beginning of MIS 2. These environmental conditions favored the settlement of megamammals adapted to open environments.

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Artiodactyla; Chaco Province; absolute datings; Argentina; Late Pleistocene

Introduction

The Tayassuidae is one of the first families of North American immigrant mammals that arrived into South America during the 'Great American Biotic Interchange' (GABI) (Cione et al. 2015 and references cited therein). They have been found associated with Late Cenozoic deposits mainly in Argentina and Brazil, but also in Uruguay, Bolivia, Colombia, Peru and Venezuela (Rincón et al. 2009; Gasparini 2013; Montellano-Ballesteros et al. 2014; Parisi Dutra et al. 2017b).

The records of the family within Argentina come from the Pampean Region (Buenos Aires Province), Mesopotamia (Entre Ríos, Corrientes and Misiones provinces) and north-central region (Santiago del Estero, Santa Fe, Córdoba and Jujuy provinces) (Gasparini and Ferrero 2010; Gasparini et al. 2011, 2014; Gasparini 2013).

According to Gasparini (2007, 2013), three genera of Tayassuidae are recognized in South America: *Platygonus* Le Conte 1848; *Catagonus* Ameghino 1904; and *Tayassu* Fischer 1814. However, recently, Parisi Dutra et al. (2017a) recognized six genera in South America: *Platygonus*, *Catagonus*, *Tayassu*, *Pecari* Linnaeus 1758, *Brasiliochoerus* Rusconi 1930 and *Parachoerus* Rusconi 1930. They included within *Parachoerus* genus, the following species: *P. carlesi* (Rusconi 1930) and *P. wagneri* (Rusconi 1930). The species *P. wagneri* is recorded in Sopas Formation (Late Pleistocene; Artigas Department, Uruguay), in archaeological pre-Hispanic sites of Santiago del Estero Province (Argentina), and shows a current restricted geographical distribution inhabiting semi-arid thorny forests of dry Chaco in western Paraguay, south-eastern Bolivia and north-central Argentina (Gasparini et al. 2013; Torres et al. 2017). However, the species *P. carlesi* is only registered in Pleistocene sediments (middle Pleistocene *sic* Rusconi 1930) outcropping in Rio Dulce, Las Termas, Santiago del Estero Province.

In this contribution, we report the first record of *P. carlesi* with precise stratigraphic data in Argentina, precisely from the Chacoan region, an area where the paleontological knowledge is markedly scarce. In addition, this specimen represents the most complete fossil material of this extinct species, increasing its morphological and morphometrical knowledge. Thus, we extend the geographical distribution of this species, and discuss the climatic and paleoenvironmental aspects.

Geological and stratigraphic context

The paleontological site named 71 corresponds to residuary woods that recently have been affected by the implantation of

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crops and after that, by the removal of sediments for the brick manufacture (Figures 1 and 2). The exposed surface is 3 km^2 with three clearly delimited artificial cuts (eastern, center and western). It comprises alluvial sandy silts ('grandes abanicos fluviales', 'large alluvial fans', *sensu* Iriondo et al. 2000) reworked by aeolian processes. Two paleosols levels were identified at the exposed profile, corresponding to stabilization moments of the landscape.

Sediments overlying the upper paleosol correspond to Level 1; Level 2 was deposited between both paleosols, and Level 3 is below the lower paleosol (Figure 2). Level 2 was dated in 22.600 ± 380 (26.540–27.775 yr cal. BP.) and 24.010 ± 430 (28.361–29.413 yr cal. BP.) ^{14}C years BP (*Pomacea* sp.: LP 3141 and LP 3188, respectively); a similar specimen of Level 3 was dated in 26.630 ± 370 ^{14}C years BP (LP 3142; 30.878–31.734 yr cal. BP.) (Gasparini et al. 2016). The dates are stratigraphically consistent.

The faunal assemblage found at levels 2 and 3 correspond to *Glyptodon* sp., *Neosclerocalyptus* sp., *Equus (Amerhippus)* sp., and *Toxodon* sp. (Gasparini et al. 2016). At level 3 comes the specimen here presented (Figure 2).

Materials and methods

The specimen (S 71.2) examined is housed at the Museo Municipal de Charata, Charata locality, Chacabuco Department, Chaco Province, Argentina.

This paper adopts the classificatory system proposed by Parisi Dutra et al. (2017a). In the descriptions of the main cusps of lower premolars, the names 'protoconid', 'metaconid', 'hypoconid' and 'entoconid' in quotes are used to indicate topographical position, and not to infer homologies with the cusps of the molars, since there is no general agreement on this matter.

Radiocarbon analyses were made in the Radiocarbon Laboratory LATYR- Centro de Investigaciones Geológicas (CIG)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Universidad Nacional de La Plata (UNLP), La Plata, Argentina. The activity was measured by liquid scintillation spectrometry (LSC) with PerkinElmer Tri-Carb3170TR/SL and Packard Tri-Carb1050TR/LL equipment. Ages are in radiocarbon years before present (1950 AD)- denominated conventional radiocarbon age- corrected by isotopic fractionation with d13C values estimated by table (Stuiver and Polach 1977).

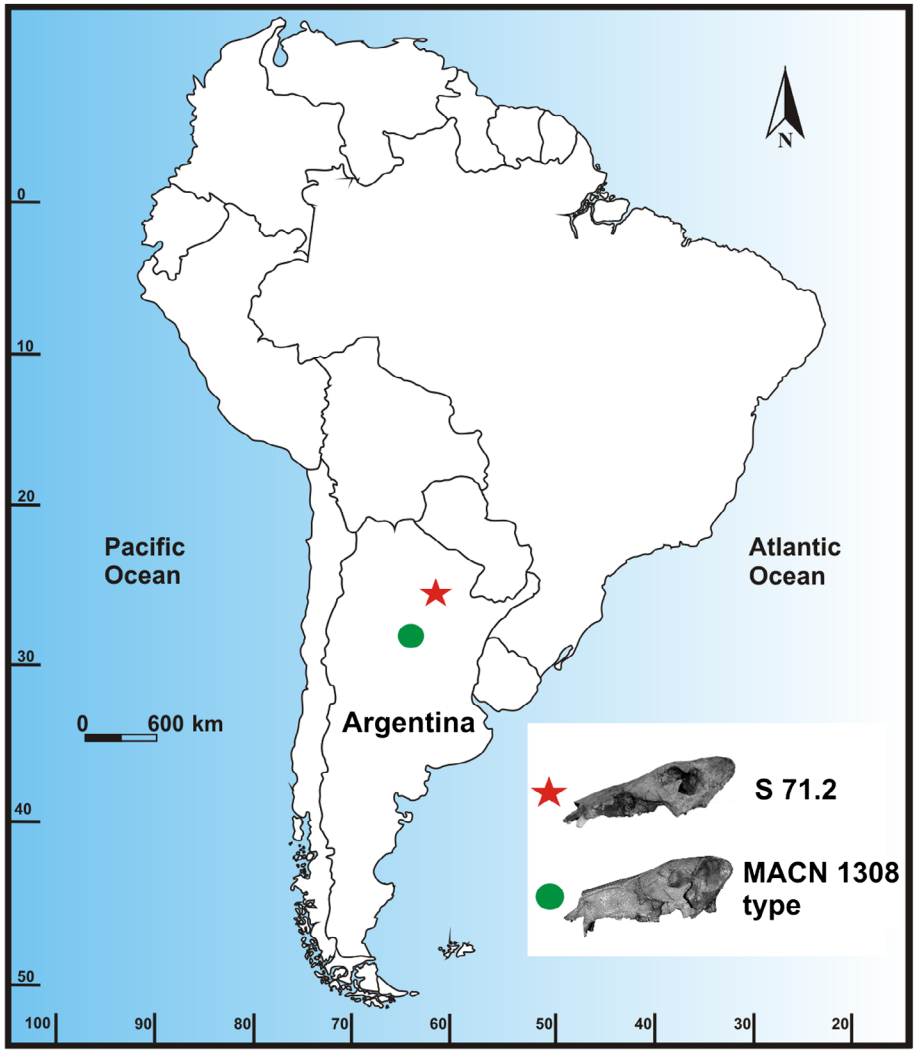

Figure 1. Paleontological record of *Parachoerus carlesi*. ★ S 71.2 specimen found at the paleontological site studied "71" (27°11´60´´S- 61°10´48´´W), Charata, Chacabuco, Chaco Province, Argentina. ● MACN 1308 type specimen found at Río Dulce Type locality, Las Termas, Santiago del Estero Province, Argentina.

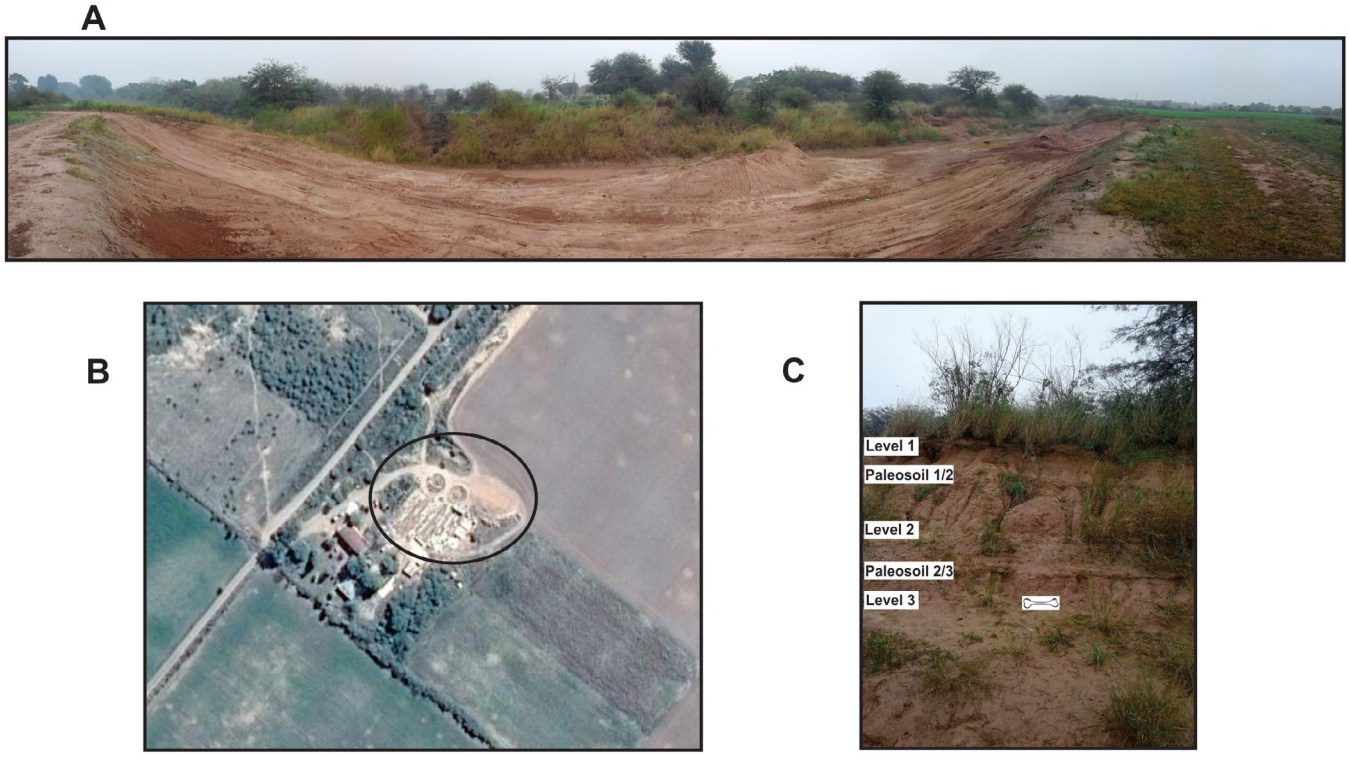

Figure 2. Paleontological site named '71'. (A) Panoramic view. (B) Aerial view; black circle indicates the paleontological outcrop. (C) Stratigraphical profile where the specimen of *P. carlesi* (S 71.2) was found.

The calibration for the terrestrial samples of the Southern Hemisphere is performed with the SHCal13.14c curve (Hogg et al. 2013) and the CALIB 7.0.4 program used in conjunction with Stuiver and Reimer (1993).

Institutional Abbreviations. MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Ciudad Autónoma de Buenos Aires, Argentina. MNHNP: Museo Nacional de Historia Natural del Paraguay, Asunción, Paraguay.

Measurements. *Skull*. AC: width of the skull: measured across the outer borders of frontal postorbital process; HAC: width of the zygomatic bar; LDPOSTC: length of the diastema from the mesial border of the alveolus of PM2 to the distal border of the alveolus of C; LDPREC: length of the diastema from the distal border of the alveolus of I to the mesial border of the alveolus of C; LP: palatal length, anterior margin of the premaxilla – back margin of the M3; LR: rostrum length, between the anterior point of the nasal and the anterior border of the orbits; LTC: maximum length of the skull: from the occipital region (lambdoidea crest) until the anterior margin of the premaxilla; DY: height of the jugal: measured at the middle of the orbit (crossing diagonally). *Mandible*: Lpostc: length of the diastema from the mesial border of the alveolus of pm2 to the distal border of the alveolus of c; Lmrh: length of the horizontal mandibular branch, from the distal alveolar margin of m3 until the mesial border of the symphysis; Hrmhm2: height of the horizontal mandible branch: measured at the level of the alveolus of m2; Hrmhm3: height of the horizontal mandible branch: measured at the level of the distal margin of the alveolus of m3; Hrmhm1: height of the horizontal mandible branch: measured at the level of the mesial margin of the alveolus of m1; Hrmhpm2: height of the horizontal mandible branch: measured at the level of the mesial margin of the alveolus of pm2. *Lower tooth series*: Hm2: Molar height, measured at the protoconid of the m2; Hm3: Molar height, measured at the protoconid of the m3; Lpm-m: length of the premolar-molar row, measured near the biting surface; Lm1–m3: length of the molar row, measured near the biting surface; Lpm2–pm4: length of the premolar row, measured near the biting surface; Lpm2: maximum length of premolar 2 in a parallel line to the sagittal plane; Apm2: maximum width of premolar 2 in a perpendicular line to the sagittal plane; Lpm3: maximum length of premolar 3 in a parallel line to the sagittal plane; Apm3: maximum width of premolar 3 in a perpendicular line to the sagittal plane; Lpm4: maximum length of premolar 4 in a parallel line to the sagittal plane; Apm4: maximum width of premolar 4 in a perpendicular line to the sagittal plane; Lm1: maximum length of molar 1 in a parallel line to the sagittal plane; Am1: maximum width of premolar 2 in a perpendicular line to the sagittal plane; Lm2: maximum length of molar 1 in a parallel line to the sagittal plane; Am2: maximum width of molar 2 in a perpendicular line to the sagittal plane; Lm3: maximum length of molar 3 in a parallel line to the sagittal plane; Am3: maximum width of molar 3 in a perpendicular line to the sagittal plane. Lc: length of lower canine; Ac: width of lower canine.

Measurements were taken using Vernier callipers, with 0.01 mm accuracy; data are expressed in millimeters.

Systematic palaeontology

Order Artiodactyla Owen 1838
Suborder Suiformes Jaeckel 1911
Infraorder Suoidea Gray 1821
Family Tayassuidae Palmer 1897

Subfamily Tayassuinae Palmer 1897
Genus *Parachoerus* Rusconi 1930
Type species. Parachoerus carlesi (Rusconi 1930)

Synonymy
Platygonus (Parachoerus) carlesi Rusconi 1930, p. 150–159, plates III, IV, V and VI.
Catagonus carlesi (Rusconi); Wetzel et al. 1975, p. 379–381
Catagonus carlesi (Rusconi); Wetzel 1977, 1–36 pp.
Catagonus carlesi (Rusconi); Gasparini 2007, 210 pp.
Parachoerus carlesi (Rusconi); Parisi Dutra et al. 2017a, 354 pp.

Type material

MACN 1308, an almost complete skull, without mandible.

Type locality and age

Río Dulce, Las Termas, Santiago del Estero Province, Argentina (Figure 1); Pleistocene (middle Pleistocene *sic* Rusconi 1930).

Remarks

Since Rusconi (1930) described the species, no other material has been assigned to *P. carlesi*. The collection number MACN 7013 used by Rusconi (1930), is an erroneous attribution. The correct number is MACN 1308 (Gasparini 2007).

Studied material

S 71.2 (Figure 3): An almost complete skull, lacking the basicranial and palatal region. The left canine and left I2 are present.

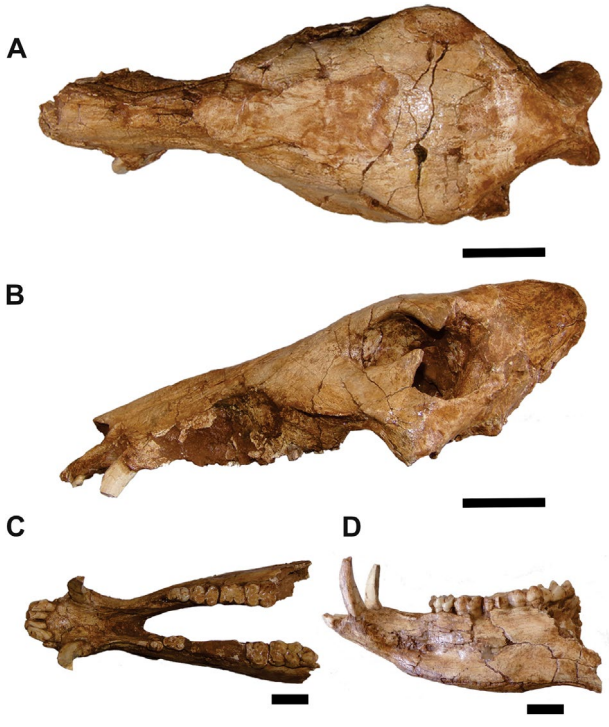

Figure 3. *Parachoerus carlesi*, S 71.2. Skull: (A) dorsal view, (B) lateral view. Mandible: (C) occlusal view, (D) lateral view. Scale bars: 5 cm (A, B), 2 cm (C, D).

An incomplete mandible, with a broken posterior portion in both vertical mandible branches. The fragment has an almost complete teeth series, lacking just the right i3, pm2, m3 and the left pm4 and m1.

Geographical and stratigraphical provenance

Paleontological site named '71' (27°11′60″S- 61°10′48″W), Charata locality, Chacabuco Department, Chaco Province, Argentina (Figures 1 and 2). Level 3: 26.630 ± 370 ^{14}C years BP (LP 3142; 30.878–31.734 yr cal. BP.), Late Pleistocene.

Description

Skull. An almost complete skull, lacking the basicranial and palatal region. The fronto- parietal surface has a slightly convex profile in lateral view. A preorbital depression is not present. The profile of the skull at the level of the frontal and nasal bones is straight. Well-marked nasal vein sulci are connecting with the anterior portion of the supraorbital sulci. The jugals are not expanded and the anterior part of the facial crest reaches the nasomaxillary suture in an almost 45 degrees. The facial muscles fossae are poorly excavated. The canine fossae have a high position (reaching or almost reaching the nasomaxillary suture). The orbits lie posteriorly in the skull; the anterior margin of the orbits is distinctly posterior to the last molar (at a distance less than the length of the molar series). The infraorbital process of zygomatic and the postorbital process of frontals are dorsal to the glenoid fossa (located posteriorly in relation to the pre glenoid process). A straight supra orbital sulci are present, but not well marked, probably because some reconstruct attempt. The postorbital processes of the frontals are downward inflected. The frontals have a concave surface above the orbits, and no depression on the medial portion of the parietals is present. The temporal crest has a concave shape and the parasagittal crests are thick and short. The occipital shield has a dorso ventral depression and the nuchal crests are ventrally convergent and in a higher position to the medial part of the supraoccipital.

A distinct basicranial flexure can be observed. In transverse section, the dorsum of the rostrum is convex, and in lateral view is straight. The nasal incision posteriorly extends behind the I2. Nasal sinuses and chambers are well developed. The lateral face of the maxillary is wide and flat. The left canine and left I2 are present.

Mandible. The postcanine diastema is short (greater than 30% of the length of the tooth row). An almost complete mandible with no vertical mandibular branch. The horizontal branches in both sides are straight anteroposteriorly. No post digastric sulcus is present, maybe because of the absence of the posterior portion of the mandible. A mandibular steep to pm2 is not present.

Lower teeth. Incisives 1 (left and right), 2 (left and right) and third incisor left are preserved. Both canines are also preserved. The left molars series are almost complete lacking the pm4 and m1. The right side lacks just the pm2 and m3.

The cheek teeth are bunodont and brachyodont.

Second lower premolar. Despite it is fragmented and incomplete, two main cusps and a flat and lower talonid can be distinguished. Besides that, a triangular outline can be differentiated.

Table 1. Measurements of S 71.2 specimen.

	S 71.2 (mm)
LTC	334 (approximately)
HAC	32
AC	117.3
LP	179 (approximately)
LR	181.6 (approximately)
Hm2	11
Hm3	15
DY	35
Lmrh	158.7
Hrmhm2	44
Hrmhm3	44.3
Hrmhm1	41.8
Hrmhpm2	37
LDPREC	33
LDPOSTC	21 (approximately)
LPM-M	98 (approximately)
Lpostc	40.2
Lpm2	9 (approximately)
Apm2	6.3
Lpm3	13.2
Apm3	8.2
Lpm4	17.4
Apm4	12
Lm1	14.7
Am1	12
Lm2	18.8
Am2	15.7
Lm3	26.4
Am3	14.7
Lpm-m	99.5 (approximately)
Lpm2-pm4	39.6 (approximately)
Lm1-m3	59.9
Lc	12
Ac	9.5

Third lower premolar. It is sub rectangular in outline, with four major cusps ('protoconid', 'metaconid', 'hypoconid' and 'entoconid'). The distal pair of principal cusps is smaller and lower than the mesial ones.

Fourth lower premolar. It is molariform; it has a rectangular outline in occlusal view, with four well-developed principal cusps.

First lower molar. It is badly worn; despite that, its rectangular outline can be observed.

Second lower molar. It is rectangular with two pairs of cusps developed, one in front of the other (protoconid-metaconid mesially and hypoconid-entoconid distally) separated by a labio-lingually orientated valley.

Third lower molar. It bears three lobes. The valley (as occur in the other lower molars) is narrow, deeper on both sides on the tooth and shallow in the middle of the crown. Besides that, it can be observed that the entoconid and hypoconid are not separated by accessories cusps. The third lobe has a complex pattern of accessory cusps.

Measurements. See Table 1.

Discussion

Anatomical comments

The material reassemble Tayassuidae for sharing the following characters: anterior portion of the facial crest reaching the naso-maxillary suture, the angle formed by the anterior portion of the facial crest and the molar series is about 45°, the origin of the muscles naso-labial elevator, superior labial and canine are well developed, forming a hollow surface and an enlargement of the cranium. A short post canine upper diastema and presence of accessories cusps in the lower premolar series referred the material to Tayassuini.

The material can be attributed to the genus *Parachoerus* by having a long-rostrum (with the anterior part of the orbits just behind the vertical plane of the posterior part of the M3), with the anterior portion of zygomatic arch's facial crest reaching the naso-maxillary and origin of facial muscles on the zygomatic arch with a hollow surface. Although the genus *Brasiliochoerus* presents some morphological similarities, the facial crests forming a 90° angle to reach the naso-maxillary suture, the wide occipital shield and the laterally inflected postorbital process of the frontals, can undoubtedly differ this genus to our material. The cranium and the mandible can be assigned to *Parachoerus carlesi* by having a greater canine fossa that extends to almost the naso-maxillary suture, an absence of a sagittal crest, and a brachyodont bunodont molars (Figure 3) instead of a small canine fossa, a sagittal crest extending to the frontals, and mesodont bunodont teeth with high crowns [referred as 'zygodont' by some authors (Gasparini 2007; Prothero and Grenader 2012; Gasparini et al. 2013)] that are exclusive features of *P. wagneri* (Figure 4).

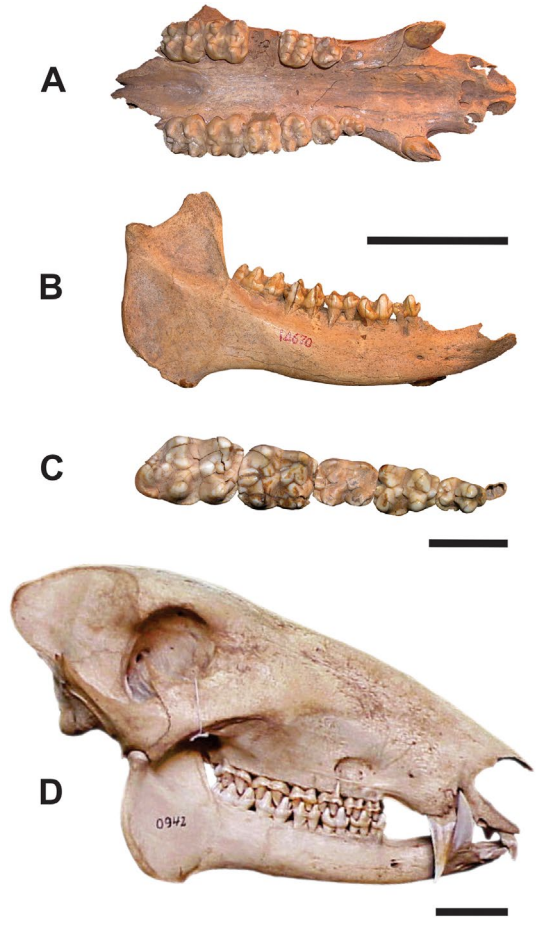

Figure 4. *Parachoerus wagneri*, MACN 14670 type: Pre-Hispanic deposits, Llajta Mauca (28°12′S, 63°05′W), Santiago del Estero Province, Argentina. Maxilla (A) palatal view. Mandible: (B) lateral view. Lower cheek teeth row: (C) occlusal view. MNHNP 0942: Recent, Dpto. Boquerón, Paraguay. Skull (D) lateral view. Scale bars: 6 cm (A, B), 2 cm (C), 3 cm (D).

Paleobiogeographic and paleoecological considerations

The knowledge about the paleontological record of the Chacoan region is markedly scarce and, mostly refers to paleontological collections of museums and/or fortuitous finds. Comparing Chaco and Santiago del Estero provinces (where *P. carlesi* is registered), we find certain differences and similarities taking into account fossil and living species of peccaries. In Recent times, the tayassuids are represented by three extant species in Chaco and Santiago del Estero provinces: *Tayassu pecari* (Link 1795), *Pecari tajacu* (Linnaeus 1758) and *Parachoerus wagneri* (Rusconi 1930). None of these species were registered in paleontological sites in Chaco Province. However, in Santiago del Estero Province, the species *P. carlesi*, *Tayassu cf. T. pecari* and *P. wagneri* are recorded; fossil remains of the last two species mentioned come from archaeological sites [Rusconi 1930; *ca* 1000 ^{14}C years BP (see Tonni 2006)]. The specimen referred to *P. carlesi* corresponds to the Holotype MACN 1308 and it was found in Pleistocene sediments (middle Pleistocene *sic* Rusconi 1930). Therefore, the new record presented in this contribution represents undoubtedly the first one of this species with precise stratigraphic data and extends its geographical distribution to northern Argentina (see Figure 2).

This genus has a series of features that allow some inferences on their habits: great development of nasal sinuses and chambers (which extend posteriorly below the orbits and dorsolaterally reaching the pterigoid processes); (b) postorbital process of the frontal bones lies behind the preglenoid process; (c) orbits located in a superior-posterior position and behind the M3 due to elongation of the rostrum; (d) infraorbital foramen located well anteriorly to the zygomatic arch; (e) possession of a distinct basicranial flexure and reduction of lateral digits in the limbs. In turn, this set of characters have led to infer that these animals were 'runners' and lived in open and arid or semi-arid environments (Guilday et al. 1971; Wetzel 1977; Menégaz and Ortiz Jaureguizar 1995; Gasparini 2007; Gasparini et al. 2011, 2013; Parisi Dutra et al. 2017b).

From a palaeoenvironmental point of view, the fauna registered in this paleontological site named '71' located in the Chaco Province (Argentina), includes taxa mainly adapted to open or semi-open and arid or semi-arid environments (e.g. *Glyptodon* sp., *Neosclerocalyptus*, *Equus* (*Amehippus*) sp., *P. carlesi*). *Toxodon* was also found at the same levels. It is worthy to mention that several authors have suggested that *Toxodon* was a mammal with amphibian habits, similar to hippopotamus (Bond et al. 1995; Archuby 1998). However, certain characters indicate markedly terrestrial habits, similar to those observed in current graviportal mammals such as elephants and rhinoceroses. Among these characteristics, the proportions of the femur and tibia, and the position of the skull (below the cross) can be mentioned (Fariña and Alvarez 1994). Additionally, *Toxodon* remains have been found not only in lacustrine deposits or floodplain areas but also in other aeolian deposits associated with fauna characteristics of semi-arid to arid conditions, such as in San Luis [e.g. southern region (Sayape dunes)] (Frenguelli 1931; Chiesa et al. 2015) and La Pampa provinces (e.g. Santa Rosa, Caleufú)(Montalvo et al. 2013; Tonni and Pasquali 2013).

The genus *Parachoerus* has a set of morphological features that are linked with a cursorial mode of life in open and arid or semi-arid environments. The bearing sediments and the particularities of the faunal assemblages, as well as the chronological data, allow confirming that arid and semiarid conditions, with scarce or absent vegetation cover were developed in this area of Argentina during the last part of MIS 3 and beginning of MIS 2. These environmental conditions favored the settlement of megamammals adapted to open environments.

Therefore, the finding of this specimen assigned to *P. carlesi* represents (a) the most complete fossil material of this extinct species, increasing its morphological and morphometrical knowledge; (b) the first record of this species with precise stratigraphic data [26.630 ± 370 ^{14}C years BP (30.878–31.734 yr cal. BP), Late Pleistocene] in Argentina, precisely from the Chacoan region, an area where the paleontological knowledge is markedly scarce; (c) the first fossil record of a Tayassuidae in the Chaco Province, extending the geographical distribution of the South American peccaries; and (d) it provides relevant ecological and climatic information.

Acknowledgements

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Disclosure statement

No potential conflict of interest was reported by the authors.

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