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The Chacoan peccary, *Catagonus wagneri* (Mammalia, Tayassuidae), in the late Pleistocene (northern Uruguay, South America): paleoecological and paleobiogeographic considerations

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Catagonus wagneri has the most restricted geographical distribution among extant Tayassuidae and inhabited semi-arid thorny forests of dry Chaco in Paraguay, Bolivia and Argentina. Until now, *C. wagneri* has only been recorded in archaeological, pre-Hispanic deposits from the Santiago del Estero Province, Argentina. A new partially complete skull from the Sopas Formation (Late Pleistocene; Uruguay) is identified as *C. wagneri*. This is the only fossil record of the species which extends its biochron until the late Pleistocene, and the first one substantially far from its current range; the first fossil record of the species in Uruguay; the most complete fossil material of the species; and it provides relevant ecological and climatic information. According to the ecological and climatic available information of *C. wagneri*, the presence of this mammal in the late Pleistocene of northern Uruguay indicates a warm climate and arid to semi-arid environments. Even though not associated with the fossil remains of *C. wagneri*, some mammals included in the sedimentary levels of the Sopas Formation also suggest arid to semi-arid environments. Climatic changes, in particular in the late Pleistocene and Holocene, could be invoked to explain modifications of its geographic range.

<http://zoobank.org/ECF04BCF-8246-4F11-AAB8-5FAA9F437BDA>

Keywords: Argentina; Bolivia; Uruguay; Paraguay; Pleistocene; *Catagonus*

Introduction

Wetzel et al. (1975) reported a new living species of peccary in the Chaco of South America and assigned this new form to the genus *Catagonus* Ameghino, 1904 and to the species *Platygonus wagneri* Rusconi, 1930. This species has been only known by the description of Rusconi (1930), in archaeological pre-Hispanic sites from Santiago del Estero Province of Argentina (ca. 1000 ¹⁴C years BP; see Tonni 2006). Consequently, it was believed to be extinct until was discovered by Wetzel et al. (1975) and extensively described in Wetzel (1977).

Catagonus wagneri – commonly known as Chacoan peccary, taguá or chanco quimilero – shows a current restricted geographical distribution (Figure 1) and inhabits semi-arid thorny forests of dry Chaco in western Paraguay, south-eastern Bolivia and northern Argentina (Mayer and Wetzel 1986; Gasparini et al. 2006).

It belongs to a clade – the Tayassuidae – that first expanded their range into North America from Eurasia (Wright 1998; Hulbert 2001; Prothero 2009) and then extended into South America during the ‘Great American Biotic Interchange’ becoming one of the first North American mammalian immigrants (Gasparini 2011).

In addition to the genus *Catagonus* Ameghino, 1904 (late Pliocene? early Pleistocene to Recent), recent systematic studies recognised in South America the genus *Platygonus* Le Conte, 1848 (middle Pliocene to early Pleistocene) and *Tayassu* Fischer, 1814 (middle Pleistocene to Recent) (Gasparini 2007). In particular for the genus *Catagonus*, five species are considered: *C. metropolitanus* Ameghino, 1904; *C. bonaerensis* (Ameghino, 1904); *C. carlesi* (Rusconi, 1930); *C. stenocephalus* (Lund in Reinhardt, 1879–1880) and *C. wagneri* (Rusconi, 1930).

The oldest record of the genus *Catagonus* is represented by the extinct species *C. metropolitanus* in the early Pleistocene (Jaramillo event chron C1r1n; 1.07 and 0.98 Ma; see Soibelzon et al. 2008) from deposits in the Buenos Aires City (Argentina). However, *Catagonus* sp. was registered from sediments tentatively referred by Gasparini (2007) to the lower part of the Barranca de Los Lobos Formation (late Pliocene), southern Buenos Aires Province. If the stratigraphical location of this specimen is confirmed, it should be considered in fact as the oldest record of the genus in South America (Gasparini 2011). With the exception of *C. wagneri*, the remaining species of the genus *Catagonus* became extinct during the Pleistocene.

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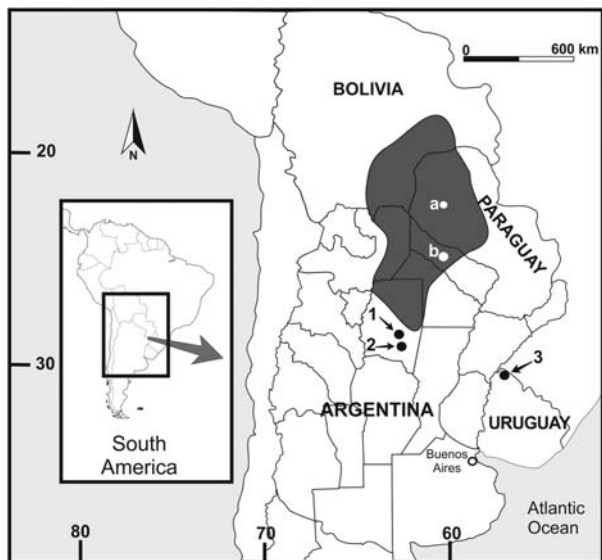


Figure 1. Archaeological and paleontological sites where fossil remains of *C. wagneri* were found and current range. (1) Llajta Maüca archaeological site, 15 km north-west of Melero, Santiago del Estero Province. (2) Tulip-Loman archaeological site, near Icano, Santiago del Estero Province, 45 km south of Llajta Maüca. (3) Paleontological site in the Cuareim river, Artigas Department, Uruguay. (a) Mariscal Estigarribia, Boquerón Department, Paraguay. (b) Las Lomitas, Formosa Province, Argentina. Grey area: current range of *C. wagneri*.

A partially complete skull of a peccary, which we identified as the chacoan peccary *C. wagneri*, was found in sediments of the Sopas Formation (late Pleistocene) that outcrops in northern Uruguay (Ubilla et al. 2004, 2011); this is the oldest and in fact the only fossil record for the species.

The goals of this paper are as follows: (1) to perform a description of the only fossil record of *C. wagneri* and (2) to assess the distributional and stratigraphical pattern of this species in South America and to analyse its climate-environmental significance.

Geographical and stratigraphic context

The Sopas Formation (Late Pleistocene) has up to 15 m high sections and is characterised by brownish mudstones, sandy to silty levels and occasionally conglomerates. In some places, paleosols can be observed. It occurs quite frequently as carbonate as dust, pulverulent and concretionary. It outcrops in river and creek banks in northern Uruguay and yields different types of fossils (ichnofossils, woods, molluscs and vertebrates) (Martínez and Rojas 2004; Ubilla et al. 2004, 2011; Verde et al. 2007). According to a biostratigraphic information and absolute ages (radiocarbonic and thermoluminescence dates), a late Pleistocene age (pre-Last Glacial Maximum) is recognised. It is biostratigraphically correlated with the Lujanian Stage (Late Pleistocene–Early Holocene; Ubilla et al. 2004).

The mammals are dominant in the fossiliferous assemblage. Until now, ca. 45 mammal genera have been found, including the typical extinct terrestrial herbivorous megamammals of South America (glyptodonts, ground sloths, toxodonts, litopterns, horses and large llamas) and extant herbivorous (tapirs, peccaries, deer and some guinea pigs), as well some fresh-water mammals (river otters, tapirs, rat-marsh, coypus and capybaras). Predators are well represented by extant and extinct felids (jaguar, mountain lion, an ocelote-like and the saber-tooth cat) and also by large extinct canids including hypercarnivorous forms (Ubilla et al. 2004, 2011; Ubilla 2008; Prevosti et al. 2009).

According to the fossil content, various habitats were present (lacustrine and fluvial context, open/semi-open environments as riparian forest and open woodland to savanna and grassland), and some mammals are related today to tropical/subtropical conditions (Ubilla et al. 2004, 2010). It is noteworthy that in the Sopas Formation three species of peccaries have been found (Gasparini et al. 2009) with important paleoecological connotations.

Materials and methods

Institutional Abbreviations – MACN: Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ Buenos Aires, Argentina; MHD-P: Museo Histórico Departamental de Artigas, Uruguay; MLP: Museo de La Plata, Argentina; MNHNP: Museo Nacional de Historia Natural de Paraguay, Asunción, Paraguay.

Measurements. Skull. AH: maximum width of ‘snout’: measured across the outer borders of the alveoli of canine (C); AMH: maximum width of ‘snout’: measured from the outer borders of paracanine’s process to that on the other side of the jaw; AP: palatal width: measured between Pm4 and M1; HAC: width of the zygomatic bar; HAN: height of the nasal openings; 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 (lambda/lambda crest) until the anterior margin of the premaxilla. **Upper tooth series:** AC: width of C; LC: length of the permanent canine; 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.

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

This paper adopts the classificatory system proposed by Gasparini (2007) because this is the most current integrative review of the South American Tayassuidae. In the descriptions of the main cusps of maxillary premolar, 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).

A total of 58 complete and incomplete adult specimens of the three extant peccaries were used for morphological comparisons: *C. wagneri* ($n = 21$), *Tayassu pecari* ($n = 15$) and *T. tajacu* ($n = 22$) (Table 1). It was registered for each specimen [operational taxonomic unit (OTU)], 28 multistate quantitative characters corresponding to skulls and upper teeth (see the measurements list above). Descriptive statistics of these taxa are included in Table 2.

To perform the multivariate analysis, we selected an ordination method and a cluster analysis. Principal component analysis (PCA) was selected because it has the advantage of indicating the relative contribution of each character to each vector. PCA was based on the Pearson product-moment correlation coefficient (Michener and Sokal 1957).

To obtain the phenogram, the similarity of each possible OTU pair has been quantified using the ‘Squared Euclidean Distance’ coefficient. The similarity between all the OTUs was represented by an UPGMA phenogram (Sokal and Michener 1958). Distortion among phenogram and the data was calculated using the correlation coefficient (CCC) (Sokal and Rohlf 1962). Values equal to or higher than 0.80 are considered to be indicators of slight distortion (see Crisci and López Armengol 1983; Sokal 1986).

Multivariate analysis was performed using Past V.2.5 (Hammer et al. 2009).

Systematic paleontology

Order **Cetartiodactyla** Montgelard, Catzefflis and Douzery, 1997

Suborder **Suiformes** Jaeckel, 1911

Infraorder **Suoidea** Gray, 1821

Family **Tayassuidae** Palmer, 1897

Subfamily **Tayassuinae** Palmer, 1897

Genus *Catagonus* Ameghino, 1904

Type species. *C. metropolitanus* Ameghino, 1904

C. wagneri (Rusconi, 1930)

Synonymy

Platygonus (Parachoerus) carlesi wagneri Rusconi, 1930: 231–238.

Parachoerus carlesi wagneri Kraglievich and Rusconi, 1931: 553–564.

Platygonus (Parachoerus) wagneri Rusconi, 1948: 231.

C. wagneri Wetzel, Dubois, Martin and Myers, 1975: 379–380 (see Wetzel and Crespo 1975: 25–26; Wetzel 1977: 1–36).

Type material

Partial skull and mandible, MACN 14670.

Type locality

Pre-Hispanic deposits, Argentina, Santiago del Estero Province, Llajta Mauca (28°12'S, 63°05'W) (Figure 1).

Study material

Partially complete skull: MHD-P-9 (Figure 2).

Geographical and stratigraphical provenance

Cuareim River, between the Cuaró and Tres Cruces creeks (30°16'47.60"S 57°12'4.87"W). Sopas Formation, Late Pleistocene; Artigas Department, Uruguay (Ubilla 2004) (Figure 1).

Description

As usually occur in fossils of the Sopas Formation, the material is externally covered by carbonaceous impregnation.

Skull. The dorsal surface of the parietal–frontal region is convex. The anterior edge of the orbit clearly lies behind the posterior margin of M3 (at a distance less than the molar series length). The rostrum has a markedly convex lateral profile. The dorsal surface of the nasals is transversely convex. A distinct basicranial flexure is remarkable. The

Table 1. Specific signature, collection data and acronyms, relative ages, sex and locality of specimens used in multivariate analysis.

Specific signature	Collection number	Relative ages	Sexual dimorphism	Locality
1 <i>C. wagneri</i>	MHD-P-9	Adult	Unknown	Cuareim river, Artigas, Uruguay; Sopas Formation, Late Pleistocene
2 <i>C. wagneri</i>	MNHNP 0943	Adult	Female	Dpto. Boquerón, Paraguay; Recent
3 <i>C. wagneri</i>	MNHNP 1216	Adult	Female	Dpto. Boquerón. 60 km from Neuland. Estancia Gran Siete, Paraguay; Recent
4 <i>C. wagneri</i>	MNHNP 0948	Adult	Female	Dpto. Boquerón. Estancia Waldbrunner. 25 km S from Colonia Neuland, Paraguay; Recent
5 <i>C. wagneri</i>	MNHNP 0941	Adult	Female	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay
6 <i>C. wagneri</i>	MNHNP 0949	Adult	Female	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay; Recent
7 <i>C. wagneri</i>	MNHNP 0947	Adult	Female	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay; Recent
8 <i>C. wagneri</i>	MNHNP 0951	Adult	Female	Dpto. Boquerón. Estancia San Ramón, 48 km W from Colonia Neuland, Paraguay; Recent
9 <i>C. wagneri</i>	MACN 36-695	Adult	Female	Salta: Agua Linda, near Dragones, Argentina; Recent
10 <i>C. wagneri</i>	MNHNP 0942	Adult	Male	Dpto. Boquerón, Paraguay; Recent
11 <i>C. wagneri</i>	MNHNP 0937	Adult	Male	Dpto. Boquerón, Estancia Ganadera, 48 km from Colonia Neuland, Paraguay; Recent
12 <i>C. wagneri</i>	MNHNP 0944	Adult	Male	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay; Recent
13 <i>C. wagneri</i>	MNHNP 0935	Adult	Male	Dpto. Boquerón. Estancia Paraíso, 48 km from Colonia Neuland, Paraguay; Recent
14 <i>C. wagneri</i>	MNHNP 0945	Adult	Male	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay
15 <i>C. wagneri</i>	MNHNP 0952	Adult	Male	Dpto. Boquerón. Fortín Tte. Acosta. Estancia Los Caminantes, Paraguay; Recent.
16 <i>C. wagneri</i>	MNHNP 0946	Adult	Male	Dpto. Boquerón. Estancia Ganadera. 48 km W from Colonia Neuland, Paraguay; Recent
17 <i>C. wagneri</i>	MACN 36-719	Adult	Male	Salta: Dragones, Argentina; Recent
18 <i>C. wagneri</i>	MLP 25.III.02.2	Adult	Unknown	Chaco. Dep. Gral. Guemes, Puerto San Alfonso, Argentina; Recent
19 <i>C. wagneri</i>	MLP 25.III.02.3	Adult	Unknown	Chaco. Dep. Gral. Guemes, Puerto San Alfonso, Argentina; Recent
20 <i>C. wagneri</i>	MLP 25.III.02.4	Adult	Unknown	Chaco. Dep. Gral. Guemes, Puerto San Alfonso, Argentina; Recent
21 <i>C. wagneri</i>	MACN 14670 type	Adult	Unknown	Santiago del Estero, Llajta Maitca, 15 km NW Melero, Argentina; prehispanic epoch
<hr/>				
1 <i>T. pecari</i>	MACN 1073	Adult	Unknown	Misiones, Argentina; Recent
2 <i>T. pecari</i>	MACN 49-340	Adult	Unknown	Misiones, Aguará-í river, 30 km Pto. Bemberg, Argentina; Recent
3 <i>T. pecari</i>	MACN 49-342	Adult	Unknown	Misiones, Aguará-í river, 30 km Pto. Bemberg, Argentina; Recent
4 <i>T. pecari</i>	MACN 48-350	Adult	Male	Misiones, Aguará-í Guazú river, Argentina; Recent
5 <i>T. pecari</i>	MACN 3-55	Adult	Unknown	Santa Fe, Colonia Mocolí, Argentina; Recent
6 <i>T. pecari</i>	MNHNP 0977	Adult	Female	Dpto. Boquerón, Estancia Paraíso, 48 km from Colonia Neuland, Paraguay; Recent
7 <i>T. pecari</i>	MNHNP 0986	Adult	Unknown	Dpto. Nueva Asunción, Transchaco route 15 km notheastern Agrochaco, Paraguay; Recent
8 <i>T. pecari</i>	MACN 39-422	Adult	Unknown	Chaco: Las Palmas and El Perdido; Recent
9 <i>T. pecari</i>	MACN 25-57	Adult	Unknown	Bolivia: Río Beni; Recent
10 <i>T. pecari</i>	MACN 35-32	Adult	Unknown	Jujuy and Formosa; Recent
11 <i>T. pecari</i>	MACN 32-97	Adult	Unknown	Bolivia; Recent
12 <i>T. pecari</i>	MNHNP 1179	Adult	Unknown	Dpto. Presidente Hayes, Reserva Laguna Porá, Paraguay; Recent
13 <i>T. pecari</i>	MNHNP 2219	Adult	Unknown	Paraguay; Recent
14 <i>T. pecari</i>	MNHNP 0979	Adult	Female	Dpto. Boquerón, Estancia Paraíso, 58 km W Colonia Neuland, Paraguay; Recent
15 <i>T. pecari</i>	MNHNP 0991	Adult	Unknown	Dpto. Boquerón, 80 km N de Mcal Estigarribia, Aguada Verde, Paraguay; Recent
<hr/>				
1 <i>T. tajacu</i>	MACN 36-722	Adult	Unknown	Salta, Dragones, Argentina; Recent
2 <i>T. tajacu</i>	MACN 49-319	Adult	Female	Misiones, Aguará-í river, 30 km Pto. Bemberg, Argentina; Recent
3 <i>T. tajacu</i>	MACN 36-696	Adult	Unknown	Salta, Dragones, Argentina; Recent
4 <i>T. tajacu</i>	MACN 35-31	Adult	Unknown	Jujuy and Formosa, Argentina; Recent
5 <i>T. tajacu</i>	MACN 36-705	Adult	Unknown	Salta, Dragones, Argentina; Recent
6 <i>T. tajacu</i>	MACN 50-130	Adult	Male	Dto. Santa Cruz, Bolivia; Recent
7 <i>T. tajacu</i>	MACN 45-27	Adult	Unknown	Paraguay; Recent

8	<i>T. tajacu</i>	MACN 36-690	Adult	Unknown	Salta: Agua Linda, from 15 km of Dragones, Argentina; Recent
9	<i>T. tajacu</i>	MACN 30-13	Adult	Unknown	Chaco, El Zapallar, Argentina; Recent
10	<i>T. tajacu</i>	MACN 36-716	Adult	Unknown	Salta, Dragones, Argentina; Recent
11	<i>T. tajacu</i>	MACN 20-811	Adult	Unknown	San Luis, Dpto. Junín, Quebrada de Cautana, Argentina; Recent
12	<i>T. tajacu</i>	MACN 30-397	Adult	Male	Salta, Argentina; Recent
13	<i>T. tajacu</i>	MLP 8.X.97.4	Adult	Unknown	Formosa, Argentina; Recent
14	<i>T. tajacu</i>	MLP 17.V.02.2	Adult	Unknown	Salta: Agua Linda, from 15 km of Dragones, Argentina; Recent
15	<i>T. tajacu</i>	MLP 17.V.02.1	Adult	Unknown	Salta: Agua Linda, from 15 km of Dragones, Argentina; Recent
16	<i>T. tajacu</i>	MACN 36-712	Adult	Unknown	Salta, Dragones, Argentina; Recent
17	<i>T. tajacu</i>	MACN 36-694	Adult	Unknown	Salta: Agua Linda, from 15 km of Dragones, Argentina; Recent
18	<i>T. tajacu</i>	MACN 36-697	Adult	Unknown	Salta, Dragones, Argentina; Recent
19	<i>T. tajacu</i>	MACN 45-20	Adult	Female	Pto. Casado, Paraguay; Recent
20	<i>T. tajacu</i>	MNHNP 2211	Adult	Unknown	Presidente Hayes, Estancia Tres Marias km39, 21°14'66"S and 59°33'95"W, Paraguay; Recent
21	<i>T. tajacu</i>	MNHNP 1901	Adult	Unknown	Dpto. Concepción, Parque Nacional Serranía, San Luis, Paraguay; Recent
22	<i>T. tajacu</i>	MNHNP 1202	Adult	Unknown	Dpto. Tarija, 29 km south-eastern Villa Montes, Bolivia; Recent

diastema postcanine is short (its length is greater than the 30% of the cheek teeth length). At the anterior part of the skull, the nasal incision almost posteriorly extends to the anterior edge of the canine buttresses. The nasal sinuses and chambers are well developed. The lateral face of the maxillary is broad and poorly excavated. The ventrolateral face of the maxillary zygomatic process is poorly excavated as the fossa for the *dilatator naris lateralis* muscle, and the fossa does not extend anteriorly beyond the infraorbital foramen. The zygomatic processes do not expand laterally. The latero-external face of the jugal is plane. A pair of deep and well-defined supraorbital canals on the skull's dorsal surface extends from the frontals, become lateral in the nasals and then passes anteriorly to the nasal aperture. The anterior opening of the infraorbital foramen is almost halfway between the orbit and the tip of the premaxilla, lying above PM4. The transverse shape of the opening is ovoid and oriented vertically along its longest axis.

Upper tooth series. The crown height of the cheek teeth is mesodont and the morphology is zygodont (bunolophodont cheek teeth with higher and sharper cusps than in typical bunodont forms and fainter crests).

Incisors. The material studied here has a complete left I1, an incomplete right I1 and both I2 alveoli. There is no evidence of an I3. The I1 is large, its anterior surface is rounded, the lingual surface is nearly flat and the lingual cingulum is robust.

Canines. They are large and are represented by its basal portion.

PM1. The PM1 is absent in this specimen.

PM2. This tooth is represented by basal portion; despite its incomplete preservation, its triangular outline can be distinguished; its anteroposterior diameter is greater than the transverse diameter.

PM3. This tooth is subquadrangular. It has three major cusps ('paracone,' 'protocone' and 'metacone') and a smaller cusp ('hypocone'). The cingulum is well defined on the anterior, labial and posterior sides. The lingual face is slightly convex unlike the labial face, which is flat. Due to the fact that the lingual side is convex, it does not show the typical quadrangular outline of molars.

PM4. It is molariform, nearly large as the first molar. This tooth is quadrangular and larger than the PM3. It has four major cusps very similar in size; however, the "hypocone" is slightly less developed than the remaining cusps. The cingulum is developed in the anterior, labial and posterior sides.

M1. This molar is quadrangular in outline, with two pairs of cusps (paracone- protocone anterior and metacone- hypocone posterior, respectively) separated by a valley. The valley is clearly narrow and its depth seems to be slightly higher on both sides of the tooth and lower in the middle of the valley. The anterior and posterior cingulum is interrupted at the mid-point by cuspules. As in the other maxillary cheek

Table 2. Comparative measurements of the three extant tayassuids.

	<i>C. wagneri</i>				<i>T. pecari</i>				<i>T. tajacu</i>			
	R	X	SD	N	R	X	SD	N	R	X	SD	N
LTC	266–308	282.20	10.46	20	249–266.5	256.96	5.86	15	193–222	212.07	7.04	22
HAC	28.5–46	35.42	5.66	20	23.8–38.8	28.62	3.43	15	19.75–28	23.35	2.16	22
AH	55.15–64.35	58.72	2.32	21	52.7–66.45	57.70	3.78	15	41.7–53.65	47.16	3.23	22
AMH	56.4–67.75	61.90	3.56	21	56.25–70	62.17	3.73	15	45.2–70	55.28	5.28	22
AC	88–106.5	96.30	5.83	17	85.55–100.25	92.33	4.07	15	61.6–85.15	74.34	5.09	22
LP	157–177	164.26	5.21	20	155–165	158.71	2.70	14	121–137	130.47	4.04	22
AP	24.8–35.7	29.01	2.54	20	25.55–31.8	30.33	1.65	15	15.85–29.5	26.03	2.74	22
LR	169.34–197	183.87	5.99	20	145–163	152.51	4.43	15	108–131	121.08	5.42	22
HAN	17.62–29.55	26.54	2.69	17	21–25	22.57	1.26	15	17.65–20.6	18.90	0.79	22
LDPREC	14.3–22.25	18.57	1.95	20	18.75–22.3	20.83	1.24	15	14–19.2	16.64	1.40	22
LDPOSTC	20.2–27.65	23.16	1.70	21	22.85–30.5	25.78	2.13	15	13.4–21.75	17.91	2.34	22
LPM-M	85.25–95.65	91.34	3.15	12	73.7–84.35	78.93	2.69	14	62.65–71.75	66.75	2.89	22
LPM2-PM4	33.25–38.26	35.70	1.57	11	29.8–33.35	31.93	0.94	15	24.8–29.9	27.28	1.46	22
LM1-M3	46.35–60	54.53	3.06	18	42.85–51	47.09	1.94	14	36.45–42	39.47	1.71	22
LPM2	9.4–12.3	10.66	0.87	12	8.8–10.65	9.44	0.50	15	6.75–9.3	8.16	0.58	22
AMP2	8.0–10.0	9.16	0.60	12	8.45–9.45	8.83	0.34	15	5.55–9	7.66	0.74	22
LPM3	11–13.8	12.25	0.66	18	9.25–11.5	10.65	0.55	15	8.2–10.35	9.24	0.64	22
APM3	11.9–14.5	12.64	0.77	18	10.1–11.25	10.64	0.31	15	8.15–10.9	9.72	0.72	22
LPM4	12.7–16	13.91	0.76	21	10.7–12.65	11.88	0.49	15	9.35–10.9	10.03	0.42	22
APM4	13.5–16.3	14.58	0.61	21	10.9–12.45	11.70	0.36	15	9.55–12.3	10.83	0.64	22
LM1	10.6–18.8	15.47	1.72	21	12.35–15.6	14.16	0.83	15	10.45–12.85	11.67	0.66	22
AM1	13.34–16.55	15.15	0.70	21	12.85–13.8	13.35	0.28	15	9.55–13.9	11.26	0.92	22
LM2	17–22.25	19.18	1.15	21	14.8–17.15	16.27	0.67	15	12.65–15	13.79	0.65	22
AM2	15.45–21.9	18.37	1.23	21	13.55–15.65	14.82	0.50	15	11.45–15.2	12.56	0.86	22
LM3	18.45–22.35	20.51	1.02	21	14.55–18	16.90	1.05	14	11.8–16.3	14.38	1.01	22
AM3	14.73–20	18.09	1.20	19	13.7–14.9	14.21	0.46	14	10.5–13.15	11.83	0.65	22
LC	12.65–16.2	14.54	0.90	18	14.3–17.3	16.14	1.00	11	10.8–15.15	12.92	1.22	22
AC	8.2–10.7	9.64	0.55	18	7.55–11.2	9.64	1.04	11	5.95–10.4	8.21	1.19	22

Notes: R, range; X, mean; SD, standard deviation; N, sample size.

teeth, a cingulum on the labial side is continuous with the cingulum of the anterior and posterior sides.

M2. This tooth is quadrangular and much wider and longer than the M1. The width of this tooth is larger than that of M3. In this tooth, there are a couple of accessory cusps in the valley that separates the two pairs of main cusps, a smaller cusp in front of the previous pair and another cusp in the labial side of the valley intimately related to the labial cingulum. Pronounced cuspules occur medially at the anterior and posterior borders of this tooth. The cingulum surrounds the anterior, labial and posterior sides.

M3. The last upper molar is subquadrangular in outline. The two anterior cusps have a greater width and separation than the posterior pair. The third lobule of this tooth has a simple configuration of the crown. In its posterior portion, there is a crenulated cingulum almost as wide as the tooth, where several small accessory cusps can be recognised. The cingulum basal surrounds the anterior, labial and posterior margins of the tooth.

Measurements. LTC: 305.00; HAC: 30.76; AH: 56.95; AMH: 66.89; AC: 106.50; LP: 168.37; AP: 27.16; LR: 169.34; HAN: 17.62; LDPREC: 19.77; LDPOSTC: 23.18; LPM-M: 93.10; LPM2-PM4: 38.26; LM1-M3: 56.12; LPM2: 11.21; APM2: 8.44; LPM3: 12.54; APM3: 12.38;

LPM4: 14.47; APM4: 14.38; LM1: 15.79; AM1: 13.34; LM2: 18.31; AM2: 15.45; LM3: 20.34; AM3: 14.73; LC: 16.20; AC: 9.94.

Multivariate analysis

In the phenogram (Figure 3) two groups were identified at the similarity level of 17.80. In the first group, two subgroups were identified at a similarity level of 9.50: one composed by specimens of *C. wagneri* and the fossil material from Uruguay and the other by the sample of *T. pecari*. The second group includes all the specimens of *T. tajacu*. CCC reach a value of 0.8721.

The PCA (Figure 4) shows the same groups observed in the phenogram. The first two principal components encompass 78.535% of the total variance (PCI: 70.221 and PCII: 8.314). The three living species of peccaries occupy different locations in the multidimensional space involved and can be clearly identified. The fossil specimen from the late Pleistocene of northern Uruguay is included inside the group of the species *C. wagneri* as well the type material of this species.

The PCI had significant representation for characters: palatal length, anterior margin of the premaxilla – back

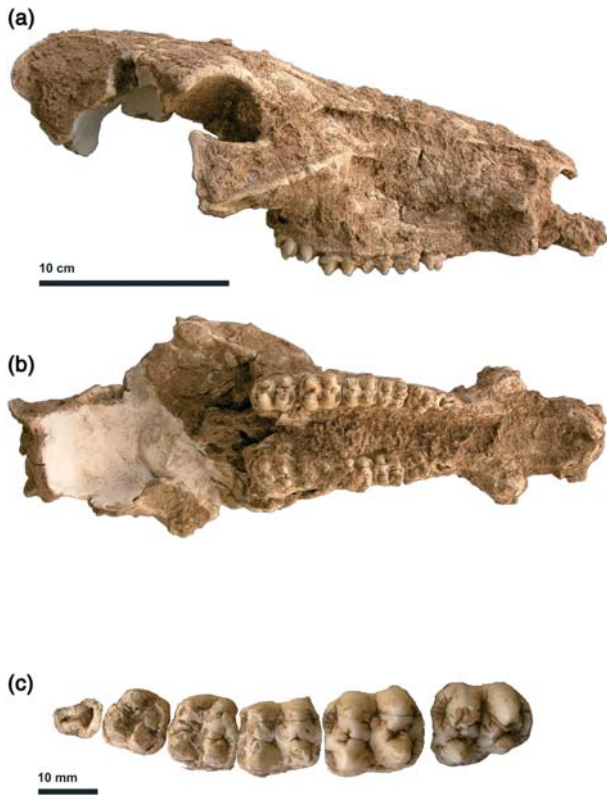


Figure 2. Specimen assigned to *C. wagneri*: MHD-P-9: (a) Lateral view. (b) Palatal view. (c) Occlusal view of right P2-M3 series.

margin of the M3 (LP = 0.96), rostrum length, between the anterior point of the nasal and the anterior border of the orbits (LR = 0.95), and length of the molar row, measured near the biting surface (LM1–M3 = 0.91). These characters separate *C. wagneri* and *T. pecari* from *T. tajacu*. The PCII had significant representation for characters: rostrum length, between the anterior point of the nasal and the anterior border of the orbits (LR = 0.82), height of the nasal openings (HAN = 0.78), maximum length of molar 1 in a parallel line to the sagittal plane (LM2 = 0.77) and maximum width of molar 2 in a perpendicular line to the sagittal plane (AM2 = 0.76). These features separate *C. wagneri* from *T. pecari*. It can be arguably assumed that the size is influencing at the PCI and certain aspects related to the shape for the PCII.

The quantitative data confirm the observed scale of measurement (*C. wagneri* > *T. pecari* > *T. tajacu*) (see Table 2).

It is noteworthy to mention that although the multivariate analysis was performed considering few characters, every extant species were distinguished from each other and the fossil from the late Pleistocene of northern Uruguay clearly integrates the group of *C. wagneri*.

Discussion

Anatomical comparisons with South and North American *tayassuids*

The MHD-P-9 specimen from the Sopas Formation has many diagnostic characters that have allowed us to determine the material as *C. wagneri*. In particular, the nasal incision almost posteriorly extends to the anterior edge of the canine buttresses (is located well posterior to I2); the rostrum has a markedly convex lateral profile; in transverse section, the dorsum of the rostrum is broadly rounded; 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 nasal sinuses and chambers are well developed; the lateral face of the maxillary is broad and poorly excavated; the crown height is mesodont and the crown morphology is zygodont; a molarisation is evident in the PM3 and PM4; the third lobule of M3 has a simple configuration of the crown and the measurements are in the range of *C. wagneri* (see Table 2). In turn, the quantitative analysis performed (PCA and cluster) reinforces the proposition that the fossil material from the late Pleistocene of northern Uruguay belongs to the species *C. wagneri*. Certainly, in both types of analysis it was clearly included in the comparative sample of the living Chacoan peccary.

The species *C. wagneri* does not develop laterally expanded zygomatic processes; however, most late Miocene, Pliocene and Pleistocene North American species [e.g. *Prosthennops crassigenis* Gidley, 1904, *Mylohyus elmorei* (White, 1942), *Platygonus cumberlandensis* Gidley, 1921 and *C. brachydonatus* (Dalquest and Mooser, 1980) and among others] developed large laterally flaring zygomatic processes. The degree of development of those processes varies between the mentioned North American taxa. Miocene species such as *Prosthennops crassigenis* and *Mylohyus elmorei* display very remote processes limiting the rostral region resembling ‘wings’ arriving in some cases to change from a lateral-horizontal projection to a lateral-vertical projection. Conversely, the others of the mentioned Pliocene and Pleistocene species developed zygomatic processes laterally extended, but without reaching the high development and complexity of the oldest species already mentioned. Similarly, during Tertiary and the Quaternary of North America, several genera and species of Tayassuidae are recorded with zygomatic processes not expanded sideways and almost upright (e.g. *Perchoerus* Leidy, 1869b; *Hesperhys* Douglass, 1903; *Dyseohyus* Stock, 1937; *Mylohyus nasutus* Leidy, 1869a; *Platygonus compressus* Le Conte, 1848). None of the South American tayassuids (fossil and extant) has developed such zygomatic ‘wings’, being restricted to North American species.

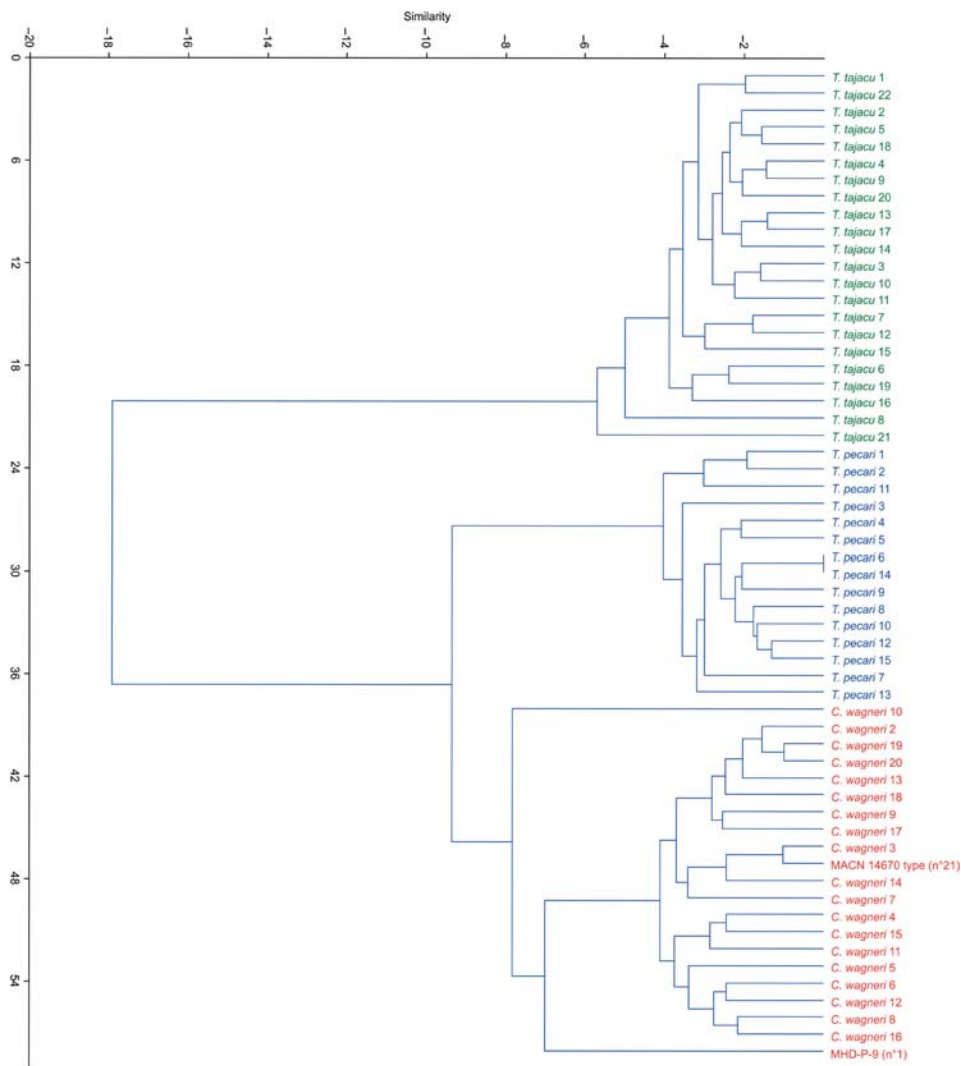


Figure 3. Phenogram. Cluster analysis including samples of the three living species of South America and studied fossil materials.

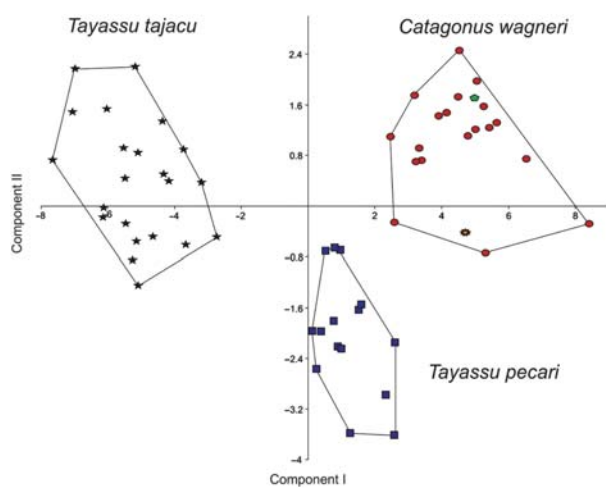


Figure 4. PCA: *T. pecari*, *T. tajacu*, *C. wagneri*: Type material MACN 14670, MHD-P-9.

The South American species *C. wagneri* and *C. carlesi*, and the North American tayassuids *Platygonus compressus*, *Platygonus cumberlandensis* and *Mylohyus elmorei* and the American *T. pecari* (Link, 1795) have the most posterior lateral margin of the nares (= narial notch) located well posterior to I2. In one of the most ancient species of tayassuids, *Perchoerus pristinus* (Cope, 1888) (late Eocene–early Miocene; North America), and in the American species, *T. tajacu* (Linnaeus, 1758), the narial notch is broader, not so deep, and falls above the posterior part of I2. In *T. pecari*, the narial notch differs from both extant species *T. tajacu* and *C. wagneri* in being acuminate.

The dorsal surface of the parietal–frontal region in *C. wagneri* is convex. This feature is shared with *Catagonus* (e.g. the North American species *C. brachyodontus*; and *C. carlesi* and *C. stenocephalus* between the South American taxa) and *Tayassu* (*T. tajacu* and *T. pecari*). In contrast, the

genus *Platygonus* [e.g. *Platygonus cumberlandensis* and *Platygonus compressus* between North American forms and *Platygonus scagliai* Reig, 1952 and *Platygonus chapadmalensis* (Ameghino, 1908) between South American taxa] developed a flat skull dorsal surface.

The rostrum has a markedly convex profile in *C. wagneri*. This character is shared with *C. stenocephalus* among the South American tayassuids, and with *Platygonus compressus* and *Perchoerus pristinus* among North American representatives. The rostrum has a slightly concave profile in *T. pecari*; the rostrum in *T. tajacu*, and in the South American species *Platygonus scagliai* and *Platygonus chapadmalensis* has a slightly convex profile or a straight one. The configuration of the lateral face of the maxillary is very similar to that of *C. stenocephalus*.

In the transverse section, the dorsum of the rostrum of *C. wagneri* is broadly rounded. This character is shared with the genera of *Catagonus*, *Platygonus* and *Prosthennops* and with the species *Perchoerus pristinus* and *T. tajacu*. The species *T. pecari* is the only South American taxa which has a flat transverse rostrum; certain North American genera and species have developed such characteristics [e.g. *Mylohyus*, *Dyseohyus*, *Hesperhys pinensis* and *Perchoerus rostratus* (Cope, 1888)].

The anterior edge of the orbit in *C. wagneri* lies clearly behind the posterior margin of M3. This feature is shared with species of *Catagonus*, *Platygonus*, *Prosthennops*, *Dyseohyus* and in *Perchoerus rostratus*. In contrast, *Tayassu* Fischer, 1814, and the North American *Hesperhys* and *Perchoerus pristinus* have the anterior margins of their orbits above the M2 or M3.

In both *T. pecari* and *T. tajacu*, the ventrolateral face of the maxillary zygomatic process is deeply excavated as the fossa for the *dilator naris lateralis muscle* (as described for *T. tajacu* by Woodburne 1968), and the fossa extends anteriorly above the opening of the infraorbital foramen. The species *C. wagneri*, *C. carlesi* and *Platygonus compressus* differ markedly from *Tayassu* in having only a shallow, short fossa not extending anteriorly beyond the infraorbital foramen.

Although the material lacks the occipital region, it is easy to observe that the basicranial flexure is remarkable, as occurring in *Platygonus*, *Catagonus*, *Prosthennops* and *Mylohyus* genera; this character is absent in *Tayassu*.

In *Catagonus* and *Platygonus*, the orbits lie posteriorly in the skull; the anterior margin of the orbits is distinctly posterior to the last molar; and the postorbital process of the zygomatic is dorsal to the glenoid fossa. Although the studied material lacks the glenoid fossa, it can be interpreted that this morphological feature was developed on it. However, in *Tayassu*, the anterior margin of the orbits lies above either the M2 or M3, and the postorbital process of the zygomatic is well anterior to the preglenoid process. Thus, in *Catagonus* and *Platygonus* the eyes are

set posteriorly behind a much longer rostrum, whereas in *Tayassu*, eyes are more anteriorly positioned behind a shorter rostrum.

Like in *Catagonus*, *Platygonus*, *Prosthennops* and *Mylohyus* but differing from *Tayassu*, the nasal sinuses and chambers are well developed.

The postcanine diastema length varies between North and South American tayassuids. The North American genus *Mylohyus* has an extremely long postcanine diastema (the postcanine diastema length is larger than the 80% of the cheek teeth length). A long postcanine diastema (more than the 50% of the cheek teeth length) is observed in *Platygonus* [except the South American *Platygonus kraglievichi* (Rusconi, 1930), *Prosthennops* and *C. brachyodontus*]; a short postcanine diastema (greater than the 30% of the cheek teeth length) is observed in the North American species *Dyseohyus stirtoni* Woodburne, 1969 and *Platygonus kraglievichi*, *C. wagneri*, *C. bonaerensis*, *C. carlesi*, *C. stenocephalus*, *T. pecari* and *T. tajacu* among the South American taxa; and an extremely short postcanine diastema (less than the 30% of the cheek teeth length) is observed in the ancient North American species *Hesperhys pinensis* Matthew, 1907, *Perchoerus pristinus*, *Perchoerus rostratus* and *Perchoerus probus* (Leidy, 1856) (Gasparini 2007).

The location of the infraorbital foramen almost halfway between the orbit and the tip of the premaxilla differs from *Tayassu* where the opening is in the posterior third of the rostrum.

The tayassuids have steadily upper incisors 1 and 2. In general, the I1 is larger than the I2, and the second has sharper crests than the first one. The presence of I3 is not constant among the family. Hence, a trend towards its reduction and subsequent absence in South American extinct taxa can be appreciated (Gasparini 2007). The I3 is common in older genus of Tayassuidae, such as *Dyseohyus* (early–middle, late? Miocene; North America), *Hesperhys* (early Miocene–early Pliocene; North America) and *Perchoerus* (early Eocene–early Miocene; North America). Some North American peccaries (e.g. some species of *Prosthennops*) have a rudimentary I3. In contrast, in South American tayassuids the I3 is absent (Gasparini 2007).

The development of mesodont crown height and zygodont dental morphology in *C. wagneri* differs from the mesodont and bunolophodont morphology observed in *Platygonus* and from the braquiodont and bunodont cheek teeth observed in *Tayassu*. Certain species of *Catagonus* also developed bunodont cheek teeth (e.g. *C. carlesi*, *C. metropolitanus*, *C. bonaerensis* and *C. stenocephalus*). Besides this, the enamel cingulum developed in three sides of the teeth in *C. wagneri* is similar to that observed in *Tayassu* and differs with *Platygonus* in which teeth the enamel cingulum surrounds the entire teeth.

The PM1 is typically lost in North and South American tayassuids, except in a few, very ancient genera

(e.g. *Perchoerus* and *Hesperhys*). The PM2 in *C. wagneri* is triangular in outline; in contrast, this tooth in *Platygonus* has equal diameters; in *Tayassu*, this tooth is roughly triangular in shape.

A molariform PM3 is found in *Mylohyus*, *Prosthennops* and *C. brachyodontus* among North American taxa, and *C. metropolitanus* and *C. stenocephalus* among South American species. This morphology is also present in the extant *C. wagneri* and *T. pecari*; however, the main difference in the degree of molarisation in these last taxa mentioned is the differential development of the 'hypocone' in the PM3. In turn, it differs from *Platygonus* whose PM3 has two major cusps, transversely arranged, and a complete cingulum surrounding the entire teeth.

The molarisation evident in the PM4 of *C. wagneri* (in which the 'hypocone' is less developed than the rest of the main cusps) is also observed in *T. pecari* among living species, and in *C. bonaerensis*, *C. carlesi* and *C. brachyodontus*. In contrast, taxa which have four principal cusps with equal development include *C. metropolitanus* and *C. stenocephalus* (among South American forms) and in North American *Prosthennops* and *Mylohyus* species. This is in contrast to *Platygonus*, which has much smaller PM4 with only two major cusps.

The M3 lacks the distinct posterior constriction in transverse width that occurs in *Tayassu*, *Mylohyus* and most *Platygonus* and *Prosthennops*. The appearance of posterior taper is accentuated in *Mylohyus*, *Tayassu* and *Platygonus* by the presence of a posterior lobe or heel as contrasted with the truncated M3 of *Catagonus* and *Prosthennops*.

Paleoecological and paleobiogeographic considerations

At present, *C. wagneri* is endemic of the dry Chaco in western Paraguay, south-eastern Bolivia and northern Argentina (Figure 1; Wetzel and Crespo 1975; Wetzel 1977; Mayer and Brandt 1982; Mayer and Wetzel 1986; Redford and Eisenberg 1992; Gasparini et al. 2006). It inhabits in areas of rainfall between 800 mm (Mariscal Estigarribia, Paraguay; see Figure 1) and 80 mm (Las Lomitas, Argentina; see Figure 1), concentrated in summer months, and high temperatures (mean annual temperature over 24°C) (Oliver and D'Huart 1996; Altrichter and Boaglio 2004; Gasparini et al. 2011).

It is noteworthy that the chacoan peccary is in many aspects more like the extinct *Platygonus* than the other living peccaries. These aspects are, among others, the orbits located in superior-posterior position and behind the M3 due to elongation of the rostrum, great development of nasal sinuses and chambers (which extend posteriorly below the orbits and dorsolaterally reaching the pterygoid processes), infraorbital foramen located well anteriorly to the zygomatic arch; a distinct basicranial flexure, reduction of the lateral digits in the limbs. In turn, these features are

linked with a cursorial mode of life in open and arid or semi-arid environments (Guilday et al. 1971; Wetzel 1977; Menégaz and Ortiz Jaureguizar 1995; Gasparini 2007).

The chacoan peccary has a diet mainly based on the tender parts of cacti, but also feeds on roots, flowers and fruits. At the same time, they lick and eat mineral-rich soil, natural salt marshes and nests. Occasionally, they consume carrion and small mammals. These are mammals with a wide tolerance to long periods without water. They are territorial animals and live in very small groups ranging from 2 to 10 individuals (Mayer and Brandt 1982; Oliver and D'Huart 1996).

In a pre-Hispanic site (late Holocene; see Tonni 2006) of Santiago del Estero (northern Argentina), *C. wagneri* is associated with mammals that indicate arid or semi-arid conditions (e.g. *Lama guanicoe*, *Myrmecophaga tridactyla*) as well chacoan vegetation (Kraglievich and Rusconi 1931; Rusconi 1948).

The Sopas Formation yields some mammals living today under tropical to subtropical conditions with riparian forest and fluvial environments (coendu, river-otter, tapirs, capybaras, rat-marshs), as well as arid to semi-arid environments (a vicugna-like camelid, some guinea pigs like *Microcavia*). According to the ecological and climatic available information of *C. wagneri*, the presence of this mammal in the late Pleistocene of northern Uruguay indicates a warm climate and arid to semi-arid environment. Even though not associated with the fossil remains of *C. wagneri*, some mammals included in the sedimentary levels of the Sopas Formation also suggest arid to semi-arid environments. Nevertheless, in others outcrops of this unit there are mammals related to subtropical climates and to fluvial and riparian forest that could imply that different climatic processes have been registered in this unit. But, are the current restricted geographic distribution and the highly specialised ecological adaptations of *C. wagneri* representatives of those that were prevalent in the late Pleistocene of northern Uruguay? What processes could be invoked in order to explain the change of their geographic distribution from late Pleistocene to Recent?

An arguable explanation implies to accept that during the arid phases of the Pleistocene and Holocene, *C. wagneri* had a wider geographic range, whereas during humid phases – similar to the present phases – it has survived in a scrub-thorn refuge.

A different interpretation implies to assume that *C. wagneri* had in the past wider ecological adaptations in terms of trophic role than in the Recent. Under such circumstances, its current specialised mode of life could be in fact an individual response to the result of the mammal communities "reorganisation" due to climatic changes and reordering of the biomes in the transition Holocene to Recent. Further studies are needed in order to test this hypothesis.

Previous to this contribution, the oldest fossil record of this species dates to pre-Hispanic deposits (ca. 1000 ¹⁴C years BP) from the Santiago del Estero Province, Argentina, very close to the current distribution of *C. wagneri*. These records (MACN 14670 type, MACN 1467, 14672 and 14673) correspond to fragmentary skull and mandible remains.

Therefore, the finding in the Sopas Formation (northern Uruguay) of the specimen MHD-P-9 assigned to *C. wagneri* represents (a) the only fossil record of the species which extends its biochron until the late Pleistocene, and the first record substantially far from its current range; (b) the first fossil record of the species in Uruguay; (c) an almost complete fossil material of the species; and (d) it provides relevant ecological and climatic information.

Besides that, it is important to mention that in the same unit (Sopas Formation) another two species of peccary (*C. stenocephalus* and *T. pecari*) have been recently found, with high probability of spatial and temporal coexistence despite having been collected in different locations (Gasparini et al. 2009). A fourth species (e.g. *C. bonaerensis* in A° las Limetas, Colonia de Sacramento, southern Uruguay; see Gasparini 2007) is added to the paleontological record, but with unclear temporal relationship with the others (Late Pleistocene?). Therefore, if a similar age of this last taxon could be confirmed, this situation gives the species of Uruguay a distinctive character: that four species of Tayassuidae were present at the same time in this area of South America.

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