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Records and Stratigraphical Ranges of South American Tayassuidae (Mammalia, Artiodactyla)

Germán Mariano Gasparini

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Abstract Tayassuidae represent one of the first mammalian immigrants that entered South America during the “Great American Biotic Interchange.” However, the exact moment of its arrival for the first time in South America is controversial. Three genera are recognized in South America: *Platygonus*, *Catagonus*, and *Tayassu*. This paper aims to: (1) review the paleontological record of the South American Tayassuidae and update it; and (2) discuss its geographical and stratigraphical distribution pattern in South America. The genus *Platygonus* (middle Pliocene to early Pleistocene) is registered in Argentina, Uruguay, Colombia, and Bolivia; *Catagonus* (late Pliocene? to Recent) in Argentina, Uruguay, Brazil, and Bolivia; and *Tayassu* (middle Pleistocene to Recent) in Argentina, Uruguay, and Brazil. *Platygonus* and *Catagonus* have adaptations to dry and relatively open environments; in contrast, *Tayassu* is adapted mainly to humid climates and woodland and forest environments. The faunal changes that took place since the middle-late Pliocene could have been strongly influenced by climate. Open and arid environments developed during the glacial cycles, allowing the latitudinal expansion of *Platygonus* and *Catagonus*. Considering ecological and anatomical information, it is possible to infer that *Platygonus* species were replaced by those of *Catagonus* since the middle Pleistocene, probably due to a reduction of the open environments to which *Platygonus* species were better adapted. The alternation of these mainly arid or semiarid,

cold conditions with warmer and more humid short pulses would have allowed the posterior expansion of *Tayassu* species. According to phylogenetic analysis and chronological as well as geographical evidence, *Platygonus* and *Catagonus* represent two Tayassuidae lineages that originated in North America and then migrated to South America. This migration would have occurred on more than one occasion and with different taxa. Evidence indicates that *Tayassu* represents a lineage that differentiated in the Southern Hemisphere and then migrated to North America.

Keywords Peccaries · Great American Biotic Interchange · *Platygonus* · *Catagonus* · *Tayassu* · Pliocene · Pleistocene · Holocene · Paleobiogeography range

Introduction

The family Tayassuidae (Mammalia, Artiodactyla) entered North America from Eurasia (Wright 1998; Hulbert 2001; Prothero 2009) and, then extended its range into South America during the “Great American Biotic Interchange” (GABI). However, the exact moment of its arrival for the first time in South America is controversial. Several authors (Reig 1952; Kraglievich 1959; Prevosti et al. 2006; Woodburne 2010) cite tayassuids for the first time in the middle Pliocene (ca. 4–3.3 Ma) in sediments outcropping on the southeastern coast of Buenos Aires Province, Argentina. In contrast, Campbell (2010) and Campbell et al. (2010) mention two indeterminate forms of extinct peccaries, among other mammals of Nearctic origin (e.g., gomphotheres, tapirs), coming from the basal levels (9.5 Ma.) of Madre de Dios Formation outcrops in southeastern Peru (Madre de Dios Department). Another possible Tertiary tayassuid record

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comes from Colombia, but the chronological information about the bearing sediments of those remains is not accurate (Stirton 1947).

The Tayassuidae (commonly known as peccaries or javelinas) had a great taxonomic diversity and a wide geographic distribution in the past. There are records of tayassuids [i.e., Tayassuinae sensu McKenna and Bell (1997)] in Asia (late Eocene); North America (late Eocene to Holocene); Central America (late Miocene to Holocene); and South America (middle Pliocene to Holocene) based on the studies of McKenna and Bell (1997), Gasparini (2007), and works cited therein. The greatest generic and specific diversity of Tayassuidae in South America derives from sediments exposed in Argentina. The family has also been found in Brazil, Uruguay, Bolivia, Colombia, and Peru (Rusconi 1930; Stirton 1947; Rusconi 1952; Paula Couto 1975, 1981; Rancy 1999; Ubilla 2004; Ubilla et al. 2004; Gasparini 2007; Gasparini et al. 2009a, b, 2010b; Campbell 2010; Campbell et al. 2010). However, in the modern fauna, tayassuids have a lower generic and specific diversity, and they are distributed in the American continents from the southwestern USA to north-central Argentina (Mayer and Brandt 1982; Redford and Eisenberg 1992; Gasparini et al. 2005, 2006).

This paper aims to: (1) review the paleontological record of the South American Tayassuidae and update it; and (2) discuss its geographical and stratigraphical distribution pattern in South America.

Systematics of South American Tayassuidae

According to Gasparini (2007), three genera of Tayassuidae are recognized in South America: *Platygonus* Le Conte, 1848, with five extinct species; *Catagonus* Ameghino, 1904, with five species, one of them actually extant; and *Tayassu* Fischer, 1814, with two extant species.

The following species of tayassuids are recognized in South America:

Genus *Platygonus* Le Conte, 1848: *Platygonus kraglievichi* Rusconi, 1930; *Platygonus scagliai* Reig, 1952; *Platygonus marplatensis* Reig, 1952; *Platygonus chapadmalensis* (Ameghino, 1908); and *Platygonus cinctus* (Ameghino, 1886).

Genus *Catagonus* Ameghino, 1904: *Catagonus metropolitanus* Ameghino, 1904; *Catagonus bonaerensis* (Ameghino, 1904); *Catagonus carlesi* (Rusconi, 1930); *Catagonus stenocephalus* (Lund in Reinhardt, 1880); and *Catagonus wagneri* (Rusconi, 1930).

Genus *Tayassu* G. Fischer de Waldheim, 1814: *Tayassu pecari* (Link, 1795); and *Tayassu tajacu* (Linnaeus, 1758).

Materials and Methods

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

The materials studied are in Tables 1 and 2. The geographical location of the paleontological and archaeological sites mentioned in this contribution, are showed in Fig. 1.

Abbreviations of Institutions. CICYTTP-PV: Centro de Investigaciones Científicas y de Transferencia de Tecnología a la Producción-CONICET, Diamante, Entre Ríos, Argentina; CPR: colección paleontológica Roselli, Uruguay; Ctes-PZ UNNE: Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; FC-DPV: colección Paleontología de Vertebrados de la Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; MACN-S: Museo de Arqueología y Ciencias Naturales de Salto, Uruguay; MCA: Museo Municipal de Ciencias Naturales “Carlos Ameghino,” Mercedes, Argentina; MCN.P: Museo de Ciencias Naturales do SCB, Universidade Federal do Paraná, Curitiba, Brazil; MCPV: Museu de Ciências da PUCRS, Geology and Palaeontology Laboratory, Uruguaiana, Brazil; MDC: Museo Departamental de Colonia, colección Dr. Bautista Rebuffo, Uruguay; MFA-PV: Museo Provincial de Ciencias Naturales “Florentino Ameghino,” Palaeontología de Veterebrados, Santa Fe, Argentina; MHD-P: Museo Histórico Departamental de Artigas, Uruguay; MLP: Museo de La Plata, Buenos Aires, Argentina; MMH: Museo Municipal de Ciencias Naturales, Monte Hermoso, Argentina; MMP: Museo Municipal de Ciencias Naturales de Mar del Plata, “Lorenzo Scaglia,” Argentina; MNPA-V: Museo Nacional de Paleontología y Antropología, Tarija, Bolivia; MSGC: Museo del Servicio Geológico, Bogotá, Colombia; UFPR PV: Departamento de Geología, Universidade Federal do Paraná, Curitiba, PR, Brazil; ZMK: Zoologisk Museum, Copenhagen, Denmark.

Results and Discussion

Distributional and Stratigraphical Ranges of Tayassuidae in South America

Although peccaries represent one of the first North American mammalian immigrants that migrated to South America during the “Great American Biotic Interchange” (Prevosti et al. 2006; Woodburne et al. 2006; Gasparini 2010; Woodburne 2010), its oldest fossil record in South America is controversial. Fossil remains of tayassuids of

Table 1 Description of the materials included in this contribution

Collection number	Material
MMP-S 25 type	Partial mandible
MACN 5420	Lower premolars 3-4
MMP-S 200	Partial skull
MMP-S 188	Partial mandible
MMP-S 199	Partial mandible
MMP-S 674	Partial mandible
MACN 19725	Partial mandible
MACN 19726	Partial mandible
MACN 6637 type	Lower molar 1
MMP-S 246	Skull
MMP-S 156 type	Skull
MMP-M 878	Partial skull
MMP-S 553	Partial mandible
MACN 5341 type	Partial mandible
MACN s/n° type (missing)	Upper molar
MMP 1139	Mandible
MMP-S 556	Lower canine
MLP 92-IV-1-1	Upper molar 3
MMP 1212	Skull
MMP-M 1617	Isolated upper teeth
MACN 5337	Partial mandible
MACN 5338	Partial mandible
MACN 5339	Partial skull
MACN 5340	Partial mandible
MLP 86-V-10-14	Partial mandible and isolated bones
FC-DPV-444	Isolated upper and lower premolar
s/n° MSGC	Partial mandible
MACN 10959	Lower isolated teeth
MACN 525	Lower molar 2
MACN 850 a and b type	Partial maxillary
ZMK 8638 and 8617 type	Skull and partial mandible, respectively.
MMP 41	Skull
MCA 2001	Skull and postcranial
MACN 7000	Upper cheek teeth series and postcranial
MACN 10083	Upper cheek teeth series and partial skull
MACN-S-10	Skull
MCPU-PV 029	Partial skull
MNPA-V 1450	Partial skull
UFPR 0118 PV	Partial skull
MACN 1308 type	Partial skull
MACN 2440 type	Isolated upper and lower teeth
MDC 1345	Partial mandible
MACN 14670 type	Partial skull and mandible
MHD-P-9	Partial skull
MACN 14671	Partial mandible
MACN 14672	Partial maxillary
MACN 14673	Partial skull

Table 1 (continued)

Collection number	Material
MMP 972	Partial skull
s/n° Henning collection	Upper molar 2
MACN 5239	Partial maxillary
MACN 5242	Lower molar 3
MACN 8849	Partial isolated molar
CICYTTP-PV-M-1-107	Partial mandible
CICYTTP-PV-M-1-108	Partial mandible
MDC 398	Partial mandible
MMP-S 707	Partial skull
MMH 186	Partial mandible
MACN 6182	Partial isolated molar
MLP 52-X-3-62	Partial skull
MCN.P.1123	Partial mandible and postcranial
MACN 10512	Partial mandible
MACN 6427	Lower molar
MACN 10465	Partial mandible and maxillary
MACN 7114	Partial skull
Ctes-PZ UNNE 1599	Upper premolar 2
Ctes-PZ UNNE 1603	Upper molar 3
Ctes-PZ UNNE 3562	Lower premolars 2-4
MFA-PV 1172	Isolated cheek teeth
FC-DPV-1057	Upper cheek teeth series
MCN.P.1124	Skull
MLP s/n°	Upper premolar 3-4 and molar 1
MACN 6183	Isolated lower premolar 2-3
MLP 52-XI-5-2	Metacarpals
MLP 60-VI-16-1	Partial mandible
MACN 7003	Astragalus and vertebrae
MACN 5234	Partial mandible
FCS.CLAA.82	Ulnacubito
LDS-01	Lower premolar 4
LDS-80	Partial mandible
MLP 52-X-2-53	Lower canine
CPR 557	Partial mandible
MMP- S 751	Maxillary fragment
MLP 268	Partial mandible
MACN 10896	Partial mandible
MLP 64-VI-9-1	Phalange
MLP 64-VI-9-8	Phalange
MLP 92-XI-28-5	Upper isolated molar
MLP 92-XI-28-1	Upper isolated molar

indetermined systematic assignation have been collected from late Miocene sediments in Peru (see Campbell et al. 2010; Campbell 2010). In contrast, the oldest unquestionable records of fossil tayassuids in Argentina date back to the beginning of the middle Pliocene in the southeast of Buenos Aires Province. These earliest records correspond

Table 2 Materials studied: taxa, collection number, geographical and stratigraphical provenance

Taxa	Collection number	Geographical and stratigraphical provenance
<i>Platygonus marplatensis</i>	MMP-S 25 type	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, layer 3, Chapadmalal "Formation"; middle Pliocene
	MACN 5420	Argentina, Buenos Aires, Gral. Alvarado, Barranca de Los Lobos, Chapadmalal "Formation", NE Miramar; middle Pliocene
	MMP-S 200	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, Chapadmalal "Formation", layer 9; middle Pliocene
	MMP-S 188	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, Chapadmalal "Formation", layer 9; middle Pliocene
	MMP-S 199	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, Chapadmalal "Formation", layer 9; middle Pliocene
	MMP-S 674	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, Chapadmalal "Formation", layer 9; middle Pliocene
	MACN 19725	Argentina, Buenos Aires, Gral. Pueyrredón, between Lobería Stream and Punta Vorohué, Chapadmalal "Formation"; late Pliocene
	MACN 19726	Argentina, Buenos Aires, Gral. Pueyrredón, between Lobería Stream and Punta Vorohué, Chapadmalal "Formation"; late Pliocene
	MACN 6637 type	Argentina, Buenos Aires, Gral. Pueyrredón, Chapadmalal; middle Pliocene?
	MMP-S 246	Argentina, Buenos Aires, Gral. Pueyrredón, Punta San Andrés, Vorohué inferior; late Pliocene
	MMP-S 156 type	Argentina, Buenos Aires, Gral. Pueyrredón, SW Lobería Stream, upper level of Barranca de Los Lobos "Formation"; late Pliocene
	MMP-M 878	Argentina, Buenos Aires, Gral. Pueyrredón, SW Lobería Stream, upper level of Barranca de Los Lobos "Formation"; late Pliocene
<i>Platygonus kraglievichi</i>	MMP-S 553	Argentina, Buenos Aires, Gral. Alvarado, Miramar, SW Punta Vorohué, upper level of Barranca de Los Lobos Formation; late Pliocene
	MACN 5341 type	Argentina, Jujuy, Uquía; late Pliocene
	MACN s/n° type	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	MMP 1139	Argentina, Buenos Aires, Gral. Pueyrredón, Arroyo Seco, Vorohué inferior; late Pliocene.
	MMP-S 556	Argentina, Buenos Aires, Gral. Pueyrredón, between Punta Lobería and Punta San Andrés, Vorohué, layer I; late Pliocene
	MPL 92-IV-1-1	Argentina, Buenos Aires, Gral. Alvarado, Miramar, Vorohué? Formation, inferior layer; late Pliocene?
	MMP 1212	Argentina, Buenos Aires, Gral. Alvarado, Cañada Chapar, Vorohué inferior; late Pliocene.
	MMP-M 1617	Argentina, Buenos Aires, Bajada Luna Roja, Vorohué; late Pliocene
	MACN 5337	Argentina, Jujuy, Uquía; late Pliocene
	MACN 5338	Argentina, Jujuy, Uquía; late Pliocene
	MACN 5339	Argentina, Jujuy, Uquía; late Pliocene
	MACN 5340	Argentina, Jujuy, Uquía; late Pliocene
<i>Catagonus metropolitani</i>	MPL 86-V-10-14	Argentina, Jujuy, Esquina Blanca; late Pliocene
	FC-DPV-444	Uruguay, near Sauce town, Canelones, Raigón? Formation; Pliocene-early Pleistocene
	s/n° MSGC	Colombia, Cocha Verde, Nariño; late Pliocene?
	MACN 10959	Argentina, Buenos Aires, Gral. Alvarado, Miramar; early-middle Pleistocene
	MACN 525	Bolivia, Tarija valley; early-middle Pleistocene?.
	MACN 850 a type	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	MACN 850 b type	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	ZMK 8638 type	Brazil, "Gruta Lapa da Escrivania, N° 11", Lagoa Santa, Minas Gerais; late Pleistocene.
	ZMK 8617 type	Brazil, "Gruta Lapa da Escrivania, N° 11", Lagoa Santa, Minas Gerais; late Pleistocene.
	MMP 41	Argentina, Buenos Aires, Gral. Pueyrredón, NNE Mar del Plata, Miramar Formation; early-middle Pleistocene
	MCA 2001	Argentina, Buenos Aires, Mercedes, Frías Stream; middle Pleistocene

Table 2 (continued)

Taxa	Collection number	Geographical and stratigraphical provenance
	MACN 7000	Argentina, Buenos Aires, Gral. Alvarado, Malacara Stream; middle Pleistocene
	MACN 10083	Argentina, Buenos Aires, Samborombón river; late Pleistocene-earliest Holocene
	MACN-S-10	Uruguay, Paso de Cañas, Arroyo Cañas, Salto, Sopas Formation; late Pleistocene
	MCPU-PV 029	Brazil, Touro Passo Stream, Uruguaiana, Rio Grande do Sul, Touro Passo Formation; late Pleistocene
	MNPA-V 1450	Bolivia, Tarija valley; Pleistocene
<i>cf. C. stenocephalus</i>	UFPR 0118 PV	Brazil, Paraná, between Adrianópolis and Doutor Ulysses, Gruta do Vale do Ribeira; late Pleistocene
<i>Catagonus carlesi</i>	MACN 1308 type	Argentina, Santiago del Estero, Dulce river, Las Termas; Pleistocene (middle Pleistocene sic Rusconi 1930)
<i>Catagonus bonaerensis</i>	MACN 2440 type	Argentina, Buenos Aires, Capital Federal; late Pleistocene- earliest Holocene
	MDC 1345	Uruguay, 50 km N Colonia del Sacramento; middle Pleistocene?
<i>Catagonus wagneri</i>	MACN 14670 type	Argentina, Santiago del Estero, Llajta Maica, 15 km NW Melero; prehispanic epoch
	MHD-P-9	Uruguay, Cuareim river, Artigas, Sopas Formation; late Pleistocene
	MACN 14671	Argentina, Santiago del Estero, Llajta Maica, 15 km NW Melero; prehispanic epoch
	MACN 14672	Argentina, Santiago del Estero, Tulip-Loman, near Icano; prehispanic epoch
	MACN 14673	Argentina, Santiago del Estero, Llajta Maica, 15 km NW Melero; prehispanic epoch
<i>Catagonus</i> sp.	MMP 972	Argentina, Buenos Aires, Gral. Pueyrredón, SW Lobería Stream, Barranca de Los Lobos Formation, inferior layer; late Pliocene?
	s/n Henning collection	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	MACN 5239	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	MACN 5242	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	MACN 8849	Argentina, Buenos Aires, Arrecifes del río de La Plata; early-middle Pleistocene
	CICYTTP-PV-M-1-107	Argentina, Entre Ríos, Ensenada Stream, Diamante; "Arroyo Feliciano Formation", late Pleistocene
	CICYTTP-PV-M-1-108	Argentina, Entre Ríos, Ensenada Stream, Diamante; "Arroyo Feliciano Formation", late Pleistocene
	MDC 398	Uruguay, Arroyo de Las Limetas, 50 km N Colonia del Sacramento; middle Pleistocene?
	MMP-S 707	Argentina, Buenos Aires, San Antonio de Areco; middle Pleistocene
<i>Tayassu tajacu</i>	MMH 186	Argentina, Buenos Aires, Monte Hermoso; middle Pleistocene- earliest Holocene
	MACN 6182	Argentina, Buenos Aires, Gral. Pueyrredón, Corrientes Stream, Mar del Plata; middle Pleistocene- earliest Holocene
	MLP 52-X-3-62	Argentina, Buenos Aires, Gral. Pueyrredón, Punta Porvenir, Mar del Plata; middle Pleistocene- earliest Holocene
	MCN.P.1123	Brazil, Paraná, between Adrianópolis and Doutor Ulysses, Gruta do Vale do Ribeira; late Pleistocene
<i>Tayassu pecari</i>	MACN 10512	Argentina, Buenos Aires, Quequén, Lobería; late Pleistocene- earliest Holocene
	MACN 6427	Argentina, Buenos Aires, Gral. Pueyrredón, Punta Piedras, Mar del Plata; late Pleistocene-earliest Holocene
	MACN 10465	Argentina, Buenos Aires, Gral. Alvarado, del Moro Stream, Miramar; late Pleistocene-earliest Holocene
	MACN 7114	Argentina, Buenos Aires, Gral. Alvarado, Punta Hermengo, Miramar; middle Pleistocene
	Ctes-PZ UNNE 1599	Argentina, Corrientes, Toropí Stream, 10 km S Bella Vista, Yupoí Formation; late Pleistocene
	Ctes-PZ UNNE 1603	Argentina, Corrientes, Toropí Stream, 10 km S Bella Vista, Yupoí Formation; late Pleistocene
	Ctes-PZ UNNE 3562	Argentina, Corrientes, Toropí Stream, 10 km S Bella Vista, Yupoí Formation; late Pleistocene

Table 2 (continued)

Taxa	Collection number	Geographical and stratigraphical provenance
	MFA-PV 1172	Argentina, Santa Fe, San Martín, Las Petacas, Tezanos Pinto Formation; middle Pleistocene-earliest Holocene
	FC-DPV-1057	Uruguay, Arroyo Sopas, Salto, Sopas Formation; late Pleistocene
	MCN.P.1124	Brazil, Paraná, between Adrianópolis and Doutor Ulysses, Gruta do Vale do Ribeira; late Pleistocene
	MLP s/n°	Argentina, Buenos Aires, archaeological site Islas Las Lechiguanas I, layer 3; Holocene
<i>Tayassu</i> sp.	MACN 6183	Argentina, Buenos Aires, General Pueyrredón, Punta Porvenir, Mar del Plata; middle Pleistocene-earliest Holocene
	MLP 52-XI-5-2	Argentina, Buenos Aires, Gral. Alvarado, Punta Hermengo, Miramar; middle Pleistocene
	MLP 60-VI-16-1	Argentina, Buenos Aires, La Granja, La Plata; Age unknown
	MACN 7003	Argentina, Buenos Aires, Gral. Alvarado, Malacara Stream; middle Pleistocene
	MACN 5234	Argentina, Córdoba; late Pleistocene-earliest Holocene
	FCS.CLAA.82	Argentina, Buenos Aires, Tandil, archaeological site Campo Laborde; Holocene
	LDS-01	Brazil, Minas Gerais, archaeological site Lapa do Dragão, layer 3; Holocene
	LDS-80	Brazil, Minas Gerais, archaeological site Lapa do Dragão, layer 3; Holocene
<i>Tayassu</i> sp.	MLP 52-X-2-53	Argentina, Entre Ríos, Ensenada Stream, Diamante; Age unknown
	CPR 557	Uruguay, Punta Chaparro, Soriano, Libertad? Formation; middle-late Pleistocene
Tayassuinae indet.	MMP- S 751	Argentina, Buenos Aires, Gral. Pueyrredón, Baliza Caniú, Chapadmalal Formation, layer 3; middle Pliocene
	MLP 268	Argentina, Buenos Aires, Coronel Pringles, Bajo San José; early-middle Pleistocene?
	MACN 10896	Argentina, Buenos Aires, Gral. Alvarado, Miramar; early-middle Pleistocene
	MLP 64-VI-9-1	Argentina, Buenos Aires, Gral. Alvarado, Malacara Stream, Miramar; middle Pleistocene?
	MLP 64-VI-9-8	Argentina, Buenos Aires, Gral. Alvarado, Malacara Stream, Miramar; middle Pleistocene?
	MLP 92-XI-28-5	Argentina, Buenos Aires, Gral. Alvarado, Centinela del Mar; late Pleistocene
	MLP 92-XI-28-1	Argentina, Buenos Aires, Gral. Pueyrredón, Camet Norte; late Pleistocene

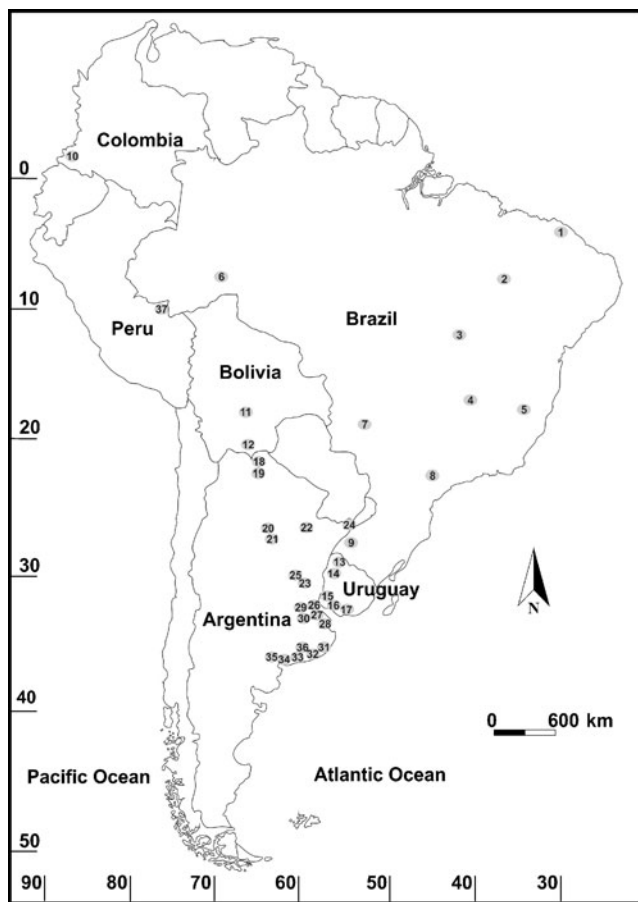


Fig. 1 Location map of the archaeological and paleontological sites. **Brazil:** 1 Ceará State; 2 Piauí State; 3 Tocantins State; 4 Minas Gerais State (archaeological site Lapa do Dragao); 5 Minas Gerais State (Lagoa Santa locality); 6 Amazonas State; 7 Mato Grosso do Sul State; 8 Paraná State; 9 Rio Grande do Sul State. **Colombia:** 10 Nariño locality. **Bolivia:** 11 Potosí city; 12 Tarija valley. **Uruguay:** 13 Artigas Department; 14 Salto Department; 15 Soriano Department; 16 Colonia Department; 17 Canelones Department. **Argentina:** Jujuy Province: 18 Esquina Blanca locality; 19 Uquía locality. Santiago del Estero Province: 20 Melero locality; 21 Icano locality. Corrientes Province: 22 Bella Vista locality. Entre Ríos Province: 23 Diamante Department. Misiones Province: 24 Panambí archaeological site. 25 Santa Fe Province: San Martín Department. Buenos Aires Province: 26 Delta of Paraná river (archaeological site Islas Las Lechiguanas); 27 Capital Federal city; 28 La Plata city; 29 San Antonio de Areco county; 30 Mercedes county; 31 General Pueyrredón county; 32 General Alvarado county; 33 Lobería county; 34 Monte Hermoso county; 35 Coronel Pringles county; 36 Tandil county (archaeological site Campo Laborde). **Perú:** 37 Madre de Dios Department

to Tayassuinae indet. (MMP-S 751) (Prevosti et al. 2006) and to *P. marplatensis* (MMP-S 25 type; MACN 5420, MMP-S 200, MMP-S 188, MMP-S 199, MMP-S 674). These remains come from the Chapadmalal “Formation” exposed in Barranca de Los Lobos (General Pueyrredón county, Buenos Aires Province, Argentina; see Kraglievich 1952). The species *P. chapadmalensis* (MACN 6637 type) from the Chapadmalal region (General Pueyrredón county, Buenos Aires Province, Argentina) possibly represents

another one of the oldest records of South American tayassuids, but the chronological information for the bearing sediments is not accurate (middle Pliocene?; see Ameghino 1908; Kraglievich 1952).

Fossils Records During the Late Pliocene The greatest specific diversity of *Platygonus* is recognized during this time period in South America; they are registered mainly in Argentina, Uruguay, and possibly in Colombia.

In Argentina, *P. marplatensis* (MACN 19725, MACN 19726), *P. chapadmalensis* (MMP-S 246), *P. scagliai* (MMP-S 156 type, MMP-M 878, MMP-S 553) and *Platygonus* sp. (MMP 1139, MMP-S 556, MLP 92-IV-1-1, MMP 1212, MMP-M 1617) are registered in Buenos Aires Province. The species *P. scagliai* and certainly *P. chapadmalensis* are registered for the first time in South America. These three species come from the coastal cliff in the Chapadmalal region (General Pueyrredón and General Alvarado counties), in the southeastern Buenos Aires Province (Ameghino 1908; Reig 1952; Gasparini 2004, 2007). In Jujuy Province, fossil remains of peccaries have been exhumed from late Pliocene sediments of two localities. The species *P. kraglievichi* (MACN 5341 type) and *Platygonus* sp. (MACN 5337, MACN 5338, MACN 5339, MACN 5340) are registered in Uquía locality; and *Platygonus* sp. (MLP 86-V-10-14) is recorded in Esquina Blanca locality (Rusconi 1930; Gasparini 2007; Reguero et al. 2007; Reguero and Candela 2008).

Coming from sediments possibly referred to Barranca de Los Lobos Formation (lower part of the formation; late Pliocene?), exposed in southern Buenos Aires Province, a skull (MMP 972) identified as *Catagonus* sp. was found. This specimen could be the oldest record of the genus in South America; however, its stratigraphic provenance is uncertain.

In Uruguay (Canelones Department), *Platygonus* sp. (FC-DPV-444) is registered in the Raigón? Formation (Pliocene- early Pleistocene; see Gasparini and Ubilla 2009). This finding represents the only record of the genus in Uruguay, and the oldest one of the family in Uruguayan territory.

In Colombia (Cocha Verde, Nariño locality), *Platygonus* sp. (unknown number MSGC) is registered with uncertain stratigraphic provenance. This record is considered doubtful, because the only available information indicates that it comes from sediments tentatively assigned to late Pliocene without any specific data (see Stirton 1947). In turn, Menégaz and Ortiz Jaureguizar (1995), considering the hypotheses of Kraglievich (1959: 233–234) and Reig (1981: 41), suggest a lower to middle Pliocene age for those bearing sediments.

Fossils Records During the Early To Middle Pleistocene During this period of time, the findings of *Platygonus* fossils in

South America markedly decrease and, *Catagonus* is recorded unquestionably for the first and only time in Argentina.

The genus *Platygonus* is recorded only in Buenos Aires Province, Argentina and in the Tarija valley, Bolivia. It is precisely in this period of time when the only known *Platygonus* species [*P. cinctus*, unknown number MACN type (missing)] is recorded in the “toscas del río de La Plata,” in the environs of Buenos Aires city (see Soibelzon et al. 2008). This represents the youngest reliable record of the genus *Platygonus* in South America.

Fossil remains determined as *Platygonus* sp. have been found in the coastal cliffs in Miramar city (MACN 10959, General Alvarado county, Buenos Aires Province, Argentina; see Rusconi 1930; Gasparini 2007) and in the Tarija valley (MACN 525, Bolivia; see Gasparini et al. 2010b). However, the age of the bearing sediments of both records is uncertain (early to middle Pleistocene?) as is their stratigraphic provenances.

During this period of time, the genus *Catagonus* is recorded in Argentina; precisely, *C. metropolitanus* (MACN 850 a and b type) and *Catagonus* sp. (unknown number Henning collection, MACN 5239, MACN 5242, MACN 8849) are registered in the “toscas del río de La Plata” (the environs of Buenos Aires city) (Soibelzon et al. 2008). In turn, *C. stenocephalus* (MMP 41) and *Tayassuinae* indet. (MLP 268, MACN 10896) are recorded in the coastal cliffs in the southeast of Buenos Aires Province.

Fossils Records During the Middle Pleistocene to Earliest Holocene The greatest specific diversity and abundance of *Catagonus* is documented during this time in South America (e.g., Argentina, Brazil, Uruguay, and Bolivia); in the middle Pleistocene, the genus *Tayassu* appears for the first time in the South American fossil record.

In Argentina, *C. stenocephalus* [MCA 2001 (see Gasparini 2004), MACN 7000, MACN 10083], *C. bonaerensis* (MACN 2440 type), *Catagonus* sp. (MMP-S 707), *T. tajacu* (MMH 186, MACN 6182, MLP 52-X-3-62), *T. pecari* (MACN 10512, MACN 6427, MACN 10465, MACN 7114), *Tayassu* sp. (MACN 6183, MLP 52-XI-5-2, MLP 60-VI-16-1, MACN 7003), and *Tayassuinae* indet. (MLP, 64-VI-9-1, MLP 64-VI-9-8, MLP 92-XI-28-5, MLP 92-XI-28-1) have been recorded in several localities in the northern, eastern, and southeastern Buenos Aires Province. In the Mesopotamian region, *Catagonus* sp. (CICYTTP-PV-M-1-107, CICYTTP-PV-M-1-108) is known from sediments of the “Feliciano Stream Formation” (late Pleistocene) outcropping in Entre Ríos Province (Gasparini and Ferrero 2010); *T. pecari* (Ctes-PZ UNNE 1599, Ctes-PZ UNNE 1603, Ctes-PZ UNNE 3562) is documented from sediments of the Yupoi Formation (late Pleistocene) in Corrientes Province (Gasparini and Zurita 2005); and

Tayassu sp. (MLP 52-X-2-53) is recorded in Entre Ríos Province (Gasparini and Ferrero 2010). In the central region of Argentina, *C. carlesi* (MACN 1308 type) is registered in Santiago del Estero Province (middle Pleistocene? sic Rusconi 1930); *T. pecari* (MFA-PV 1172) is known from sediments of the Tezanos Pinto Formation (late Pleistocene to earliest Holocene) outcropping in Santa Fe Province (Gasparini et al. 2011); and *Tayassu* (MACN 5234) sp. in Córdoba Province.

In Uruguay, four species of *Tayassuinae* are recorded. Specifically, in the Sopas Formation [$>45,000$ RCYBP; $43,500 \pm 3600$ and $58,300 \pm 7400$ CALYBP (TL dates); see Ubilla 2004] that outcrops in the central and northern region, the species *C. wagneri* (MHD-P-9) (Artigas Department), *C. stenocephalus* (MACN-S-10) and *Tayassu pecari* (FC-DPV-1057) (Salto Department) are registered (Gasparini et al. 2009a, b, 2010a, b; Gasparini and Ubilla 2010). In turn, in the southern region, the species *Tayassu* sp. (CPR 557) (Libertad Formation?, middle- late Pleistocene, Soriano Department; see Roselli 1976; Gasparini 2007), *C. bonaerensis* (MDC 1345), and *Catagonus* sp. (MDC 398) (middle Pleistocene?, Colonia Department; see Rusconi 1952; Gasparini 2007) are recorded.

In Brazil, *Catagonus* and *Tayassu* species are registered in the fossil record. Thus, during the late Pleistocene, *C. stenocephalus* is registered in Lagoa Santa (ZMK 8638 and 8617 type; Minas Gerais State; see Fonseca 1979; Paula Couto 1975, 1981); in sediments of Touro Passo Formation outcropping in the Touro Passo Stream (MCPV-PV 029; Uruguaiana, Rio Grande do Sul State; see Gasparini et al. 2009a, b); and in Gruta dos Moura (Aurora de Tocantins, Tocantins State; see Avilla et al. 2010). In turn, *Catagonus* cf. *C. stenocephalus* is known from late Pleistocene sediments outcropping in Gruta do Vale do Ribeira (UFPR 0118 PV; Paraná State; see Dias da Silva et al. 2010). There are records of *T. pecari* in Lagoa Santa (late Pleistocene; Minas Gerais State) (Fonseca 1979); in Rio Grande do Sul, Mato Grosso do Sul (Paula Couto 1975); in Gruta do Vale do Ribeira (late Pleistocene; Paraná State; MCN.P.1124; see Dias da Silva et al. 2010); and in Piauí, Ceará and Amazonas states (Rancy 1999). The species *T. tajacu* is recorded in Lagoa Santa (late Pleistocene; Minas Gerais State; see Fonseca 1979); in Ceará State (Fonseca 1979); and in Gruta do Vale do Ribeira (late Pleistocene; Paraná State; MCN.P.1123; see Dias da Silva et al. 2010).

It is notable that in Bolivia, there are records of *C. stenocephalus* (MNPA-V 1450) in Tarija valley; and *Tayassuinae* indet. (without reference material or repository) in Potosí Department and Ñaupua Formation (see Gasparini et al. 2010b). However, the ages of the bearing sediments of Bolivian records are wide (Pleistocene) and their stratigraphic provenances are unknown (see Gasparini et al. 2010b).

Fossils Records During the Holocene The diversity and the abundance of tayassuids records in South America markedly decrease during this period, registering in Argentina mainly, and Brazil.

In Argentina, records of *C. wagneri* (MACN 14670 type, MACN 14671, MACN 14672, MACN 14673) and *Tayassu* cf. *T. pecari* appear in archaeological sites from Santiago del Estero Province [Rusconi 1930; ca. 1000 RCYBP (see Tonni 2006)]. In Buenos Aires Province, *T. pecari* (unknown number MLP) is documented from the archaeological site “Islas Las Lechiguanas I”; the age of the level from which these remains were found is 2.740 \pm 80 and 2.550 \pm 90 years BP ^{14}C (2.926–2.759 and 2.755–2475 years cal BP respectively; see Gasparini and Soibelson 2003). In turn, *Tayassu* sp. (FCS.CLA.A.82) is recorded in the archaeological site “Campo Laborde”, located in the upper basin of Tapalqué Creek (ca. 9700 and 6700 years BP ^{14}C ; see Politis and Messineo 2008). In the Argentine Mesopotamian, *T. pecari* is cited in the archaeological site Panambí (Department of Oberá, Misiones Province); the level of the remains was dated to 920 \pm 70 years BP radiocarbon (LP-176), (732–925 years cal BP, 1.025–1.218 AD) (Tonni 2004).

In the Holocene of Brazil, a very few remains of tayassuids are registered. Recently, Parisi Dutra et al. (2010) mentioned some remains of *Tayassu* sp. (LDS-01, LDS-80) from the archaeological site Lapa do Dragão (Minas Gerais State). The level where those remains were found was dated to ca. 2100 years BP.

Records in Recent Times According to Gasparini (2007), Tayassuidae are represented by three extant species: *T. pecari*, *T. tajacu*, and *C. wagneri*. However, a new extant species of even-toed ungulate from the Brazilian Amazonia was recently reported (Van Roosmalen et al. 2007). The systematic position (generic and specific levels) of this “giant” peccary (sensu Van Roosmalen et al. 2007) is uncertain according to the systematics presented here.

The species *T. tajacu* has the largest geographic distribution, recorded from north-central Argentina to southwestern USA; *T. pecari* has a more restricted distribution, recorded from north-central Argentina to southern Mexico. Finally, *C. wagneri* is endemic to the Great Chaco of Argentina, Paraguay, and Bolivia (Mayer and Brandt 1982; Redford and Eisenberg 1992; Gasparini et al. 2006).

Ecological and Anatomical Considerations

The peccaries of *Platygonus* and *Catagonus* were large-sized mammals with some morphological features (e.g., orbits located in posterodorsal position and behind the M3

due to elongation of the rostrum, great development of nasal sinuses and chambers, a distinct basicranial flexure, reduction of the lateral digits in the limbs) supporting the inference that these animals lived in dry and relatively open environments (Guilday et al. 1971; Wetzel 1977; Menégaz and Ortiz Jaureguizar 1995; Gasparini et al. 2010a, b). In contrast, *Tayassu* has certain morphological characters (e.g., orbits located anterior to the posterior border of the M3 due to shortening of the rostrum, poor development of nasal sinuses and chambers, a poor basicranial flexure, development of the lateral digits in the limbs) that indicate that they are adapted mainly to humid climates and woodland and forest environments. However, the presence of *Tayassu* is insufficient to infer environmental conditions, because of its extensive geographic range and ecological tolerances (Menégaz and Ortiz Jaureguizar 1995; Gasparini and Zurita 2005; Gasparini 2007). In turn, preliminary studies have shown that in the last 3.3.Ma, the South American Tayassuidae have maintained a relatively uniform body mass, ranging between 20 and 70 kg, with some exceptions [e.g., *C. bonaerensis* and *C. metropolitanus*; (see Gasparini et al. 2010a)].

Conclusions

The family Tayassuidae is recorded in South America from middle Pliocene to Recent times. However, if the systematic assignment of the remains coming from the Madre de Dios Formation outcropping in southeastern Peru is verified, the first arrival in South America would be older (late Miocene).

There are fossils records of *Platygonus* (middle Pliocene to early Pleistocene) in Argentina, Uruguay, Bolivia, and Colombia; *Catagonus* (late Pliocene?, early Pleistocene to Holocene) in Argentina, Uruguay, Brazil, and Bolivia; and *Tayassu* (middle Pleistocene to Holocene) in Argentina, Uruguay, and Brazil.

On the basis of what was exposed before, Argentina has the greatest diversity and abundance of South American tayassuids species. Brazil and Uruguay have an interesting diversity and a great abundance of fossil records. In turn, in the Pampean region (mainly in Buenos Aires Province, Argentina) and in southern Uruguay, the three South American genera of peccaries are registered.

The *Platygonus* species recognized in South America are: *P. marplatensis* [middle to late Pliocene; Argentina (Buenos Aires Province)]; *P. chapadmalensis* [middle? to late Pliocene; Argentina (Buenos Aires Province)]; *P. kraglievichi* [late Pliocene; Argentina (Jujuy Province)]; *P. scagliai* [late Pliocene; Argentina (Buenos Aires Province)]; and *P. cinctus* [early to middle Pleistocene; Argentina (Buenos Aires Province)].

The *Catagonus* species recognized in the South American fossil record are: *C. metropolitanus* [early to middle Pleistocene; Argentina (Buenos Aires Province)]; *C. bonaerensis* [late Pleistocene to earliest Holocene; Argentina (Buenos Aires Province) and Uruguay (Colonia Department)]; *C. carlesi* [middle Pleistocene?; Argentina (Santiago del Estero Province)]; *C. stenocephalus* [early Pleistocene to earliest Holocene; Argentina (Buenos Aires Province), Brazil (Minas Gerais, Rio Grande do Sul, Tocantins and possibly Paraná states), Bolivia (Tarija valley), and Uruguay (Salto Department)]; and *C. wagneri* [late Pleistocene to Holocene; Argentina (Santiago del Estero Province) and Uruguay (Artigas Department)].

The *Tayassu* species distinguished in the South American fossil record are: *T. tajacu* [middle Pleistocene to earliest Holocene; Argentina (Buenos Aires Province) and Brazil (Minas Gerais, Ceará and Paraná states)]; and *T. pecari* [middle Pleistocene to Holocene; Argentina (Buenos Aires, Santa Fe, Corrientes, Misiones and possibly Santiago del Estero provinces), Brazil (Minas Gerais, Rio Grande do Sul, Mato Grosso do Sul, Piauí, Ceará, Amazonas and Paraná states), and Uruguay (Salto Department)].

During the end of the Tertiary (middle-late Pliocene), *Platygonus* is the only tayassuid that undoubtedly was present in South America. However, if the age of the bearing sediments of the specimen 972 MMP is verified (lower part of the Barranca de Los Lobos formation, late Pliocene?), this would correspond to the oldest record of *Catagonus* in South America. This could indicate the possible coexistence of *Catagonus* and *Platygonus* during this time interval in Buenos Aires Province, Argentina.

During the Quaternary (Pleistocene and Holocene), evidence of possible coexistence has been registered in South America. The fossil record of tayassuids suggests a possible coexistence of *Catagonus* and *Platygonus* during the early to middle Pleistocene in the Pampean Region (mainly in Buenos Aires Province, Argentina), similar to that recorded during the Pleistocene in Bolivia (Tarija valley). In turn, the paleontological information raises the possible coexistence of *Catagonus* and *Tayassu* during the middle Pleistocene to earliest Holocene in the Pampean Region (mainly in Buenos Aires Province, Argentina), similar to that registered during the late Pleistocene in the Argentine Mesopotamian, in Minas Gerais (Brazil), and in northern Uruguay. The last relationship mentioned can also be observed during the Holocene in Santiago del Estero Province (Argentina), and actually in the Great Chaco.

The faunal changes that took place since the middle-late Pliocene could have been strongly influenced by climate. Open and arid environments developed during the glacial cycles, allowing the latitudinal expansion of *Platygonus* and *Catagonus*. Certain shared anatomical features linked to the type of diet and habit, together with body mass, make

it possible to infer that *Platygonus* species were replaced by those of *Catagonus* since the middle Pleistocene, probably due to a reduction of the open environments to which *Platygonus* species were better adapted. In turn, the alternation of these mainly arid or semiarid and cold conditions with warmer and more humid short pulses would have allowed the posterior expansion of *Tayassu* species.

According to phylogenetic analysis and chronological as well as geographical evidence, *Platygonus* and *Catagonus* represent two Tayassuidae lineages that originated in North America and then migrated to South America. This migration would have occurred on more than one occasion and with different taxa. Evidence indicates that *Tayassu* represents a lineage which differentiated in the Southern Hemisphere and then migrated to North America.

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