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Platygonus sp. (Mammalia: Tayassuidae) in Uruguay (Raigón? Formation; Pliocene–early Pleistocene), comments about its distribution and palaeoenvironmental significance in South America

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This study provides the first record of *Platygonus* in Uruguay (Raigón? Formation, Pliocene–early Pleistocene; Canelones Department). The allocation to the Raigón Formation is tentative because the remains were found in a drill core. It is the oldest record of a tayassuid in Uruguay. The following morphological features clearly indicate that it belongs to *Platygonus*: simple premolars that are bicuspid, bunolophodont, mesodont and with an enamel cingulum surrounding the entire tooth. This is one of the largest forms among North American and South American *Platygonus.* The record of *Platygonus* in the Raigón Formation suggests arid or semi-arid climates, and, as do some associated birds and mammals, open or relatively open environments. A significant level of specific diversity of *Platygonus* in South America is recognized during the late Pliocene with the lowest diversity occurring during the early–middle Pleistocene.

Keywords: Tayassuidae; fossil peccaries; palaeoenvironments; South America

Introduction

The Tayassuidae (Mammalia, Artiodactyla) represents one of the first mammalian migrants to enter South America during the "Great American Biotic Interchange" (Webb 1985, 1991; Prevosti et al. 2006; Woodburne et al. 2006; Gasparini 2010; Woodburne 2010). However, the exact moment of their first arrival in South America is controversial. Several authors (Reig 1952; Kraglievich 1959; Prevosti et al. 2006; Woodburne 2010) place this in the middle Pliocene (*c.* 4–3.3 million years ago; late Chapadmalalan Age *sensu* Cione and Tonni 2005), in sediments outcropping in the southeastern coast of the Buenos Aires Province. In contrast, Campbell et al. (Campbell, Frailey, Heizler et al. 2000; Campbell, Frailey, Romero-Pittman 2000; Campbell et al. 2001) and more recently 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 of the Madre de Dios Formation outcropping in southeastern Peru. These authors report palaeomagnetic data combined with Ar^{40}/Ar^{39} data from volcanic ashes that indicate 9.5 million years ago for the basal levels and 3.0 million years ago for the upper levels in that Formation. Some tayassuid remains in Colombia are mentioned by Stirton

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(1947), tentatively referred to the Pliocene, but the chronological information on the bearing sediments is not accurate.

Three genera of Tayassuidae are recognized in South America: *Platygonus* Le Conte 1848 (middle Pliocene to early Pleistocene) with five extinct species; *Catagonus* Ameghino 1904 (late Pliocene? to Recent) with five species, only one of which is currently extant; and *Tayassu* Fischer 1814 (middle Pleistocene to Recent) with at least two extant species (Gasparini 2007).

A significant increase in the taxonomic diversity and abundance of tayassuid findings in South America occurs from the Pleistocene, particularly in Argentina, Brazil, Uruguay and Bolivia (Rusconi 1930; Paula Couto 1975; Ubilla et al. 2004; Gasparini 2007; Gasparini, Kerber et al. 2009; Gasparini and Ubilla 2009; Gasparini, Ubilla et al. 2009).

Numerous fossil remains of Tayassuidae have been found in the Quaternary of Uruguay, with controversial species assignments and whose stratigraphic provenance has received different interpretations. Until now, *Catagonus* and *Tayassu* were the only tayassuids that occurred in the palaeontological record of Uruguay (Rusconi 1952; Roselli 1976; Ubilla 1985, 2004; Ubilla et al. 2004; Gasparini 2007; Gasparini, Ubilla et al. 2009). Both tayassuids were recorded for the first time in sediments probably corresponding to the middle Pleistocene (Bonaerian Age *sensu* Cione and Tonni 2005), reaching the late Pleistocene to early Holocene (Lujanian Age *sensu* Cione and Tonni 2005).

The goals of this paper are, first, to present the oldest record of a tayassuid in Uruguay and the first of the genus *Platygonus* in the palaeontological record of this territory; and second, to assess the distributional and stratigraphic pattern of the genus *Platygonus* in South America and to analyse the climate–environmental significance of the studied material.

Geographical and stratigraphic context

The Raigón Formation outcrops essentially on the southwestern coast of Uruguay (San José Department), with thickness ranging from 4 to 5 m, reaching 30 to 67 m in the subsoil (Bossi 1966; Preciozzi et al. 1985; Spoturno, Oyhantçabal, Aubet et al. 2004; Spoturno, Oyhantçabal, Goso 2004). According to various interpretations, this formation may include distinct members, some formally defined (Bossi et al. 2009), and others identified by intraformational discontinuities (Tófalo et al. 2009). It is considered a fluvial-deltaic (Bossi 1966; Spoturno et al. 1993) or simply fluvial (Tófalo et al. 2009) unit, including channel-filled and floodplains facies involving swamp contexts. Its lithology includes green clay, fine and medium-grained white sands and conglomerate levels (Bossi 1966); some authors (Bossi et al. 2009; Tofalo et al. 2009) also include some paleosols at the top of the unit.

The Raigón Formation has been generally considered to be of Pliocene age, but the finding of certain Ensenadan mammals in it, such as *Catonyx tarijensis*, suggests that its deposition finished during the early Pleistocene (McDonald and Perea 2002). Currently, the biostratigraphic value of this taxon is disputed, given that the ages of the bearing levels are under discussion, particularly in Bolivia (Coltorti et al. 2006; Tonni et al. 2009). Palaeomagnetic studies performed in the coastal cliffs suggest its correspondence with the Gauss unit, with an age between 3.4 and 2.5 million years (Tófalo et al. 2009). From a palaeontological point of view, the background information for the Raigón Formation is scarce. In addition to *Catonix tarijensis*, cingulates

such as *Glyptodon* sp., *Plaxhaplous* sp. and *Doedicurus* sp.; notoungulates such as *Trigodon* and some Cardiatheriinae and Eumegamyinae rodents, including the largest known taxa, are recorded in the coastal outcrops (Francis and Mones 1966; Mones 1989; Rinderknecht and Blanco 2008). Large phorusrhacids (Tambussi et al. 1999) and, tentatively, anhingids (Rinderknecht and Noriega 2002) have been referred to this unit. In the area where the studied material comes from, near Sauce town (Canelones Department) (Figure 1), this unit occurs at subsurface level, with some of its thicker facies sometimes outcropping at the top part of the profiles in certain sites near major

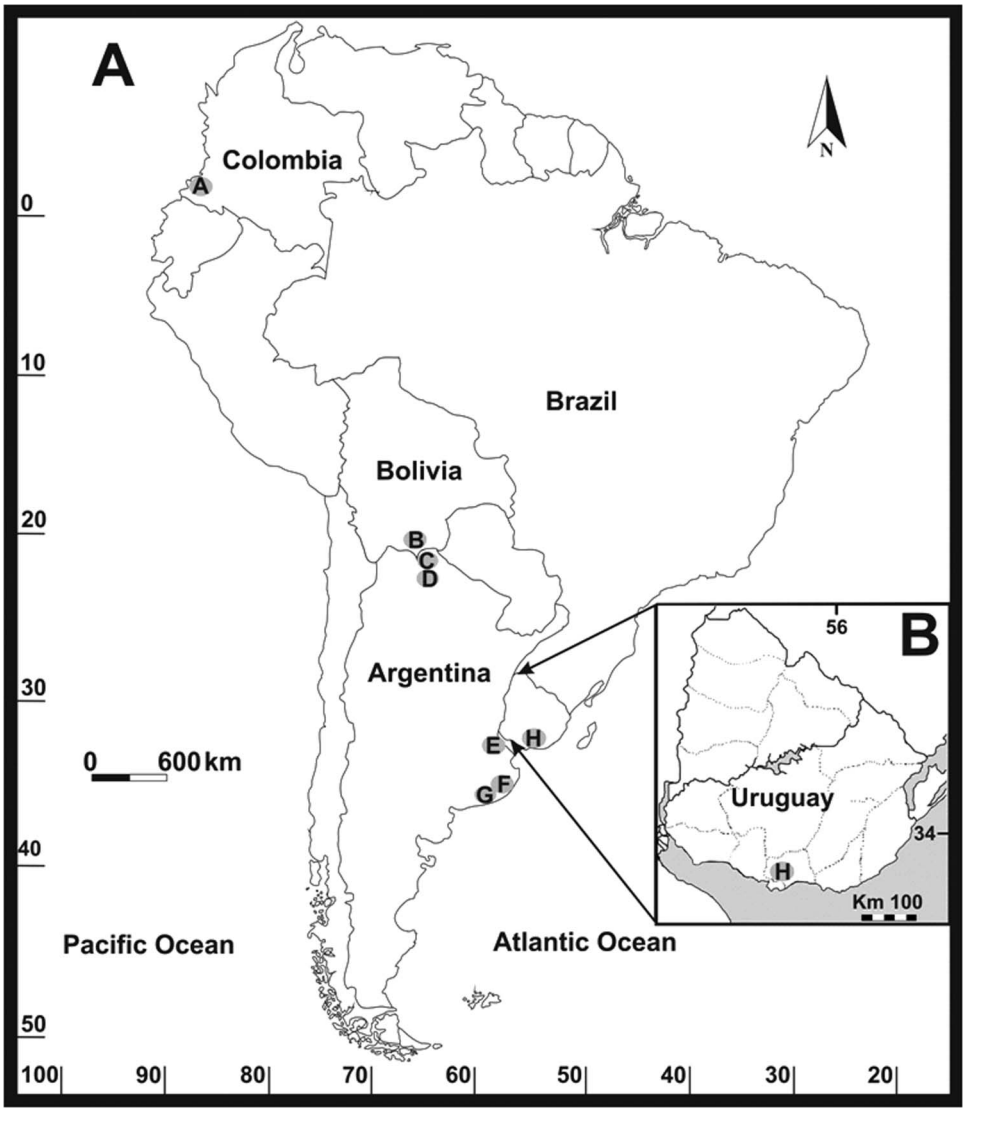

Figure 1. (A) Fossil record of the genus *Platygonus* in South America. A, Nariño locality; B, Tarija valley; C, Uquía, Jujuy Province; D, Esquina Blanca, Jujuy Province; E, Buenos Aires city; F, General Pueyrredón county; G, General Alvarado county; H, Canelones Department. (B) Geographical location of the FC-DPV-444. H, Canelones Department.

water courses. Even though the remains were collected from a green clay facies interleaved with sandy facies that are characteristic of the Raigón Formation, caution is taken to assign it to this unit because the remains were found in a drill core.

Materials and methods

Measurements were taken using Vernier callipers, with 0.01-mm accuracy; data are expressed in millimetres. The bivariate analysis was performed using PAST V.2.5 (Hammer et al. 2009).

Abbreviations of measurements used are: LPM4, maximum length of fourth upper premolar measured in a line parallel to the sagittal plane; APM4, maximum width of fourth upper premolar measured in a line perpendicular to the sagittal plane; Apm2, maximum width of second lower premolar measured in a line perpendicular to the sagittal line; Lpm2: maximum length of second lower premolar measured in a line parallel to the sagittal plane.

Abbreviations of Institutions used are: AMNH, American Museum of Natural History, New York, USA; 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", Ciudad Autónoma de Buenos Aires, Argentina; MLP, Museo de La Plata, Argentina; MMP, Museo Municipal de Mar del Plata, Buenos Aires, Argentina; UF, Florida Museum of Natural History, Florida University, Gainesville, FL, USA.

The following comparative materials were included in the bivariate analyses: *Platygonus* sp.: UF 57258, 53857, 62700, 66679, 66693, 62702, 66694; *Platygonus bicalcaratus*: UF 18187; *P. vetus*: UF 62613, 221238; *P. cf. P. vetus*: UF 63924, 67180; *P. cumberlandensis*: UF w/no. material, AMNH 27871; *P. compressus*: AMNH 45703, AMNHFLAG 6–90, 45724; *P. scagliai*: MMP(S) 156, MMP (M) 878, MLP w/no. material; *P. marplatensis*: MMP 199, MACN 19726; *P. chapadmalensis*: MMP (M) 246; *Platygonus* sp. MACN 5337, MMP 1617, 1212.

Systematic framework of South American Tayasssuidae

Little consensus has been reached regarding the systematics of fossil and extant South American Tayassuidae, owing to different factors: the dissimilar value assigned to certain characters by previous authors; the episodic nature of research efforts on this group; and the discovery of new fossil and extant taxa (Menegaz and Ortiz Jaureguizar 1995; Gasparini 2007 and literature cited therein).

Following the systematic review of Argentinean, Brazilian and Bolivian tayassuids by Rusconi (1930), different opinions about the taxonomic composition of the family and phylogenetic relationships of its members have been put forth (e.g. Pascual et al. 1966; Woodburne 1968; Wetzel 1977; Reig 1981; Marshall et al. 1984; Ortiz Jaureguizar and López Armengol 1984; Ortiz Jaureguizar and Prado 1986; Menegaz and Ortiz Jaureguizar 1995). The various classifications covered only a fraction of Tayassuidae diversity and many were intuitive schemes rather than being based on rigorous analysis of shared derived characters (e.g. Reig 1981, p. 41; Reig in Marshall et al. 1984, p. 21). This paper adopts the system proposed by Gasparini (2007), because this is the most current comprehensive review of the South American Tayassuidae.

Systematic palaeontology

Order **ARTIODACTYLA** Owen 1848
Suborder **SUIFORMES** Jaeckel 1911
Infraorder **SUOIDEA** Gray 1821
Family **TAYASSUIDAE** Palmer 1897
Subfamily **TYASSUINAE** Palmer 1897
Genus ***Platygonus*** Le Conte 1848: 103[1]

Synonymy

Hyops Le Conte 1848: 104.
Protochoerus Le Conte 1848: 105–106 (*Nomen dubium*).
Euchoerus Leidy 1853: 340.
Coyametla Duges 1887: 16.
Listriodon Ameghino 1904[2]: 76.
Mylohyus Rusconi 1930: 191–195 (*nec* Cope 1889: 134).
Argyrohyus Kraglievich 1959: 230.
Selenogonus Stirton 1947: 322.
Include *Antaodon* Ameghino 1886: 149.
Parachoerus Rusconi 1930: 150[3].
Brasiliochoerus Rusconi 1930: 160–163[3].
Type species: *Platygonus compressus* Le Conte 1848

Platygonus sp.

Studied material

Isolated teeth (PM4 and pm2) corresponding to a single individual FC-DPV-444 (Figure 2).

Geographic provenance

Near Sauce town, Canelones Department, Uruguay (Figure 1).

Stratigraphic provenance

Raigón? Formation (Pliocene to early Pleistocene). Assignation to this unit is doubtful because it comes from a drill core.

Description

Simple premolars, with two cusps, bunolophodont, mesodont and with a cingulum surrounding the entire tooth, corresponding to a large specimen.

[1]The first spelling was actually "*Platigonus"*, but there is sufficient indication that this was a misprint. The name is differently misprinted (*Platydonus*) in another paper by Le Conte, published almost simultaneously. *"Platygonus* is now universally used and may be retained" (Simpson 1945: 146) (see Mc Kenna and Bell 1997). See also the International Code of Zoological Nomenclature (1999), Articles 32 and 33.
[2] According to Mones (1986) *Listriodon* Von Meyer 1846
[3] Proposed as subgenus of *Platygonus*.

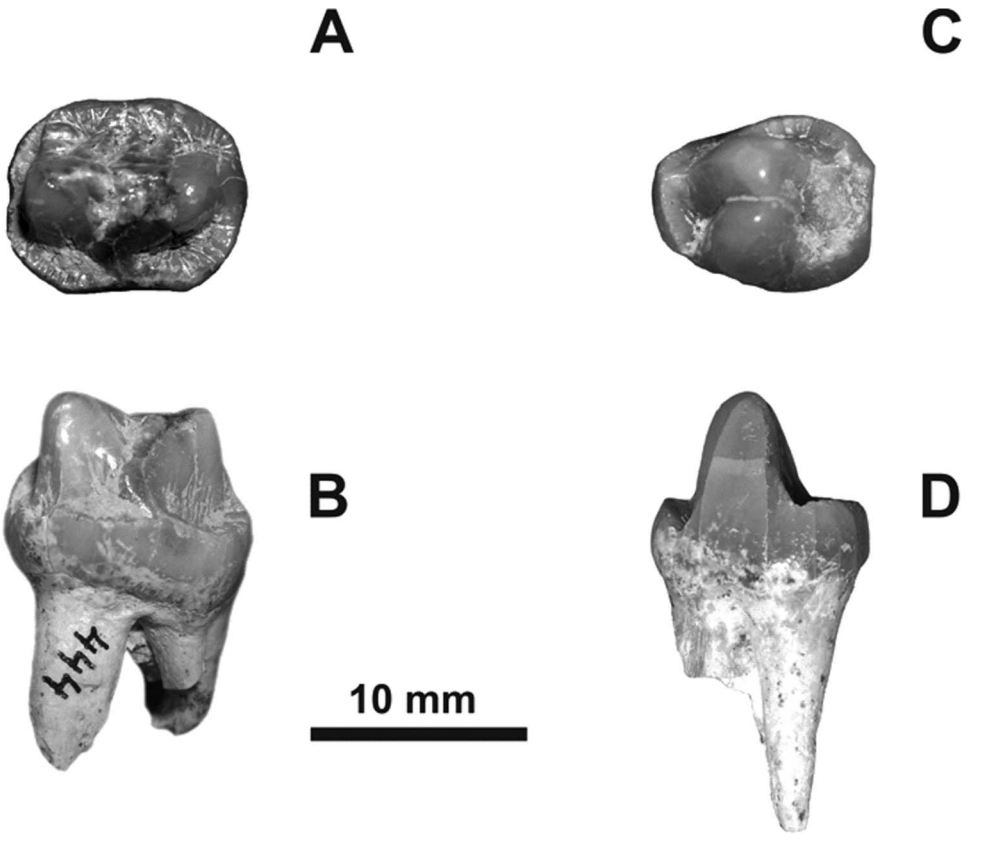

Figure 2. FC-DPV-444. (A,B) PM4: (A) occlusal view, (B) anterior view; (C,D) pm2: (C) occlusal view, (D) labial view. Scale bar 10 mm.

pm2 two-rooted and subtriangular in outline. Crown bears laterally paired major cusps and a low posterior heel. Each principal cusp subconical. Small anteroposteriorly flattened cingulum at anterior base of main cusps. Talonid bears worn central, transversely elongate accessory cuspule encircled by robust posterior cingulum.

PM4 with three roots, two labial, one lingual. This tooth subquadrate, transverse with only two major cusps anteroposteriorly compressed and almost forming a sharp-edged, transverse loph. This tooth wider than long.

Measurements

Measurements are listed in Table 1.

Comments

These isolated teeth have certain diagnostic morphological characters that allow us to determine the material as *Platygonus* sp. In particular, these are simple premolars with two major cusps, crown morphology is bunolophodont, crown height is mesodont and the enamel cingulum surrounds the entire tooth.

Table 1. Measurements (mm) with FC-DPV-444 and comparative materials included in the bivariate analysis.

Species	Collection number	LPM4	APM4	Lpm2	Apm2
Platygonus sp.	FC-DPV-444	12.44	15.3	10.65	8.8
Platygonus sp.	UF57258	11.31	13.93		
Platygonus sp.	UF53857	11.83	13.01		
Platygonus sp.	UF62700			11.44	7.60
Platygonus sp.	UF66679			11.19	8.25
Platygonus sp.	UF66693	12.06	14.23		
Platygonus sp.	UF62702	11.98	14.07		
Platygonus sp.	UF66694	11.17	12.43		
Platygonus bicalcaratus	UF18187	11.81	13.95		
Platygonus vetus	UF62613	10.50	14.06		
Platygonus vetus	UF221238	11.66	13.09		
Platygonus cf. P. vetus	UF63924	11.10	12.91		
Platygonus cf. P. vetus	UF67180	10.65	12.93		
Platygonus cumberlandensis	UF Unknown number	12.54		11.13	
Platygonus cumberlandensis	AMNH27871	11.97	13.87	10.78	8.88
Platygonus compressus	AMNH45703 type material	9.42	13.09		
Platygonus compressus	AMNHFLA6-90	10.89	13.91	9.22	6.95
Platygonus compressus	AMNH45724 type material			8.47	6.60
Platygonus scagliai	MMP (S) 156 type material	10.00	13.15	8.50	6.45
Platygonus scagliai	MMP (M) 878			9.85	
Platygonus scagliai	MLP Unknown number	11.15	13.70		
Platygonus marplatensis	MMP 199			7.40	4.85
Platygonus marplatensis	MACN 19726			7.25	5.00
Platygonus chapadmalensis	MMP (M) 246	10.25	13.75	9.00	6.50
Platygonus sp.	MACN 5337			8.60	5.80
Platygonus sp.	MMP 1617	11.55	14.00		
Platygonus sp.	MMP 1212	11.60	15.20	11.90	8.10

Notes: LPM4, maximum length of fourth upper premolar measured in a line parallel to the sagittal plane; APM4, maximum width of fourth upper premolar measured in a line perpendicular to the sagittal plane; Lpm2: maximum length of second lower premolar measured in a line parallel to the sagittal plane; Apm2, maximum width of second lower premolar measured in a line perpendicular to the sagittal line.

The development of mesodont and bunolophodont cheek teeth in *Platygonus* differs from the branquiodont and bunodont morphology observed in *Tayassu* and from the mesodont crown height and bunodont and "zygodont" cheek teeth (bunolophodont cheek teeth with higher and sharper cusps than in typical bunodont forms and fainter crests) observed in *Catagonus.* Besides this, the enamel cingulum never surrounds the entire tooth in *Catagonus* and *Tayassu* species; it develops on two or three sides (e.g. anterior, labial and posterior) of the teeth.

The crown configuration (presence of two principal cusps) of pm2 is similar to that observed in *Tayassu* species and in contrast to *Catagonus* species, which have only one major cusp. The presence of two major cusps on PM4 and its measurements clearly differ from *Catagonus* and *Tayassu* species, which have a molariform PM4, slightly longer than wide.

Taking into account the dental measurements of the material, it belongs to one of the largest tayassuids among the North American and South American *Platygonus* considered in the available comparative sample (see Tables 1, 2 and Figure 3), especially with regards to the absolute size of PM4 and width of pm2.

Table 2. Geographical and stratigraphical provenance of the FC-DPV-444 and comparative materials.

Collection no.	Geographical and stratigraphic provenance
FC-DPV-444	Uruguay, Canelones Department, near Sauce town; Raigón? Formation (Pliocene–early Pleistocene)
UF57258	USA, Florida, Inglis IA, Citrus; early Irvingtonian
UF53857	USA, Florida, Bartow Polk
UF62700	USA, Florida, Haile 21 A, Newberry Quad., Alachua; middle Irvingtonian
UF66679	USA, Florida, Haile 21 A, Newberry Quad., Alachua; Irvingtonian
UF66693	USA, Florida, Haile 21 A, Newberry Quad., Alachua; Irvingtonian
UF62702	USA, Florida, Haile 21 A, Newberry Quad., Alachua; Irvingtonian
UF66694	USA, Florida, Haile 21 A, Newberry Quad., Alachua; Irvingtonian
UF18187	USA, Florida, Inglis IA, Citrus
UF62613	USA, Florida, Haile 21A; late Irvingtonian
UF221238	USA, Florida, Haile 21 A, Alachua; early Irvingtonian
UF63924	USA, Florida, Leisey Shell Pit Ruskin Quad., Hillsborough; Irvingtonian
UF67180	USA, Florida, Leisey Shell Pit Ruskin Quad., Hillsborough; Irvingtonian
UF unknown	USA
AMNH27871	USA, Maryland, northwest of Cumberland; early Rancholabrean
AMNH45703 type	USA, Missouri, St Louis, Cherokee Cave; Pleistocene
AMNHFLA6-90	USA, Florida, Devil's Den Mine, Levy; Rancholabrean
AMNH45724 type	USA, Missouri, St Louis, Cherokee Cave; Pleistocene
MMP (S) 156 type	Argentina, Buenos Aires, Gral. Pueyrredón, southwest Lobería Stream, upper level of Barranca de Los Lobos "Formation"; Marplatan Age, Barrancoloban Subage
MMP (M) 878	Argentina, Buenos Aires, Gral. Pueyrredón, southwest Lobería Stream, upper level of Barranca de Los Lobos "Formation"; Marplatan Age, Barrancoloban Subage
MLP unknown	Argentina, Buenos Aires, Gral. Pueyrredón, between Lobería Stream and Punta Vorohué, San Andrés "Formation"; Marplatan Age, Sanandresian Subage
MMP 199	Argentina, Buenos Aires, Gral. Pueyrredón, Barranca de Los Lobos, Chapadmalal "Formation", layer 9; late Chapadmalalan Age
MACN 19726	Argentina, Buenos Aires, Gral. Pueyrredón, between Lobería Stream and Punta Vorohué, Chapadmalal "Formation"; Marplatan Age, Sanandresian Subage
MMP (M) 246	Argentina, Buenos Aires, Gral. Pueyrredón, Punta San Andrés; Marplatan Age, Vorohuan Subage
MACN 5337	Argentina, Jujuy, Uquía; Marplatan Age
MMP-M 1617	Argentina, Buenos Aires, Bajada Luna Roja, Vorohué; Marplatan Age
MMP 1212	Argentina, Buenos Aires, Gral. Alvarado, Cañada Chapar, Vorohué inferior; Marplatan Age

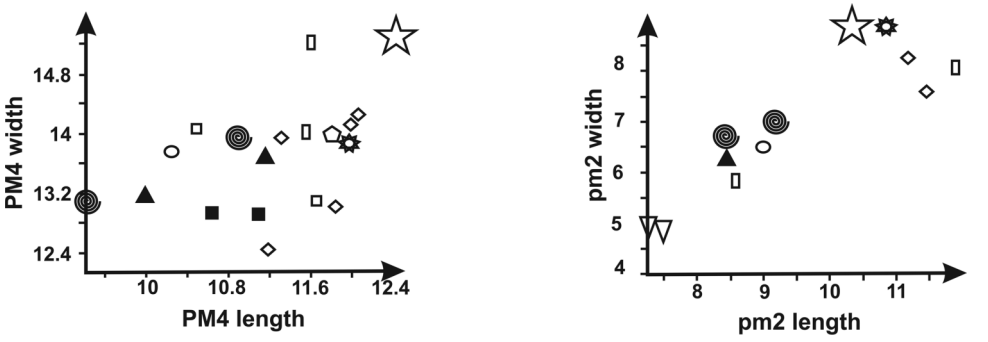

Figure 3. Bivariate diagram based on PM4 length/width and pm2 length/width of the FC-DPV-444 and comparative samples. FC-DPV-444 ☆; *Platygonus scagliai* ▲; *Platygonus chapadmalensis* ○; *Platygonus marplatensis* ▽; *Platygonus* sp. (South America) ▯; *Platygonus vetus* □; *Platygonus* cf. *P. vetus* ■; *Platygonus compressus* ◎; *Platygonus* sp. (North America) ◇; *Platygonus bicalcaratus* ⬠; *Platygonus cumberlandensis* ✲.

Discussion and conclusions

Distributional and stratigraphic pattern of the genus *Platygonus* in South America

In South America the genus *Platygonus* is represented by five extinct species (Gasparini 2007): *P. kraglievichi* Rusconi 1930; *P. scagliai* Reig 1952; *P. chapadmalensis* (Ameghino 1908); *P. marplatensis* Reig 1952; and *P. cinctus* (Ameghino 1886).

The oldest Tayassuidae record in South America is uncertain. Fossil remains of peccaries of indeterminate assignment have been collected from late Miocene sediments in Peru (see Campbell et al. 2010; Campbell 2010). 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 (Reig 1952; Kraglievich 1959; Prevosti et al. 2006; Gasparini 2007; Woodburne 2010). These earliest records correspond to Tayassuidae *indet.* (MMP-S 751) (Prevosti et al. 2006) and to *P. marplatensis* Reig 1952 (MMP-S 25 type, MACN 5420; MMP-S 200; 188, 199, 674; Reig 1952; Kraglievich 1959; Gasparini 2007) (Figure 1). These remains come from the Chapadmalal "Formation" (Barranca de Los Lobos, General Pueyrredón county, Buenos Aires Province, Argentina; see Kraglievich 1952). The species *P. chapadmalensis* (Ameghino 1908) (MACN 6637 type) (Chapadmalal region, General Pueyrredón county, Buenos Aires Province, Argentina), possibly represents another of the oldest records of South American tayassuids, but the chronological information for the bearing sediments is inaccurate (middle Pliocene?; see Ameghino 1908; Kraglievich 1952).

The greatest diversity of *Platygonus* species occurs during the late Pliocene (Marplatan Age *sensu* Cione and Tonni 2005) recorded mainly from Argentina, and also from Uruguay with the material studied here. In Argentina, *P. marplatensis* Reig 1952 (MACN 19725, 19726), *P. chapadmalensis* (Ameghino 1908) (MMP-S 246), *P. scagliai* Reig 1952 (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 recorded in Buenos Aires Province. These findings correspond to the first record of *P. scagliai* and in a reliable way to that of *P. chapadmalensis*. These species come from the coastal cliffs in the Chapadmalal area (Ameghino 1908; Reig 1952; Gasparini 2004, 2007) (Figure 1). The species *P. scagliai* appears in the Barranca de Los Lobos

"Formation" (Barrancaloban Subage) (Reig 1952) and in the San Andrés Formation (Sanandresian Subage) (Gasparini 2004, 2007). The species *P. marplatensis* appears in the Chapadmalal "Formation" (Marplatan Age, Sanandresian Subage) (Quintana 2002) and *P. chapadmalensis* has been recorded in the *Akodon (Akodon) lorenzinii* Biozone (Vorohuan Subage) (Gasparini 2007).

In the Jujuy Province (Argentina) (Figure 1), fossil peccaries have been exhumed from late Pliocene sediments (Marplatan Age): *P. kraglievichi* Rusconi 1930 (MACN 5341 type) and *Platygonus* sp. (MACN 5337, 5338, 5339, 5340), in Uquía locality; and *Platygonus* sp. (MLP 86-V-10-14), in Esquina Blanca locality (Rusconi 1930; Gasparini 2007; Reguero et al. 2007; Reguero and Candela 2008).

In Colombia (Cocha Verde, Nariño locality) (Figure 1), *Platygonus* sp. (unknown number MSGC; *Selenogonus nariñoensis sensu* Stirton 1947: 322; see discussion in Gasparini 2007) is recorded with uncertain stratigraphic provenance, because the only available information indicates that it comes from sediments tentatively assigned to late Pliocene without any specific data. In turn, Menegaz 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.

During the early to middle Pleistocene (Ensenadan Age *sensu* Cione and Tonni 2005; Soibelzon, Tonni et al. 2008), the findings of *Platygonus* in South America markedly decrease. They are recorded only in Buenos Aires Province, Argentina and in Tarija valley, Bolivia (Figure 1). It is precisely at this time that the only *Platygonus* species [*P. cinctus* (Ameghino 1886), MACN w/no. type (missing)] is recorded in the "toscas del río de La Plata", in the environs of Buenos Aires city (see Rusconi 1930; Soibelzon, Gasparini et al. 2008). This represents the youngest reliable record of the genus *Platygonus* in South America.

Fossil remains determined as *Platygonus* sp (MACN 10959, 525) have been found in sediments tentatively assigned to the early–middle Pleistocene and exposed in Miramar (General Alvarado county, Buenos Aires Province, Argentina; see Ameghino 1904; Rusconi 1930; Gasparini 2007) and Tarija valley (Bolivia; see Gasparini, Soibelzon, Zurita et al. 2010) (Figure 1). The age of the bearing sediments is uncertain as is their stratigraphic provenance.

In the south and southwest of Uruguay, tayassuid fossil remains have been found in the riversides of Las Limetas and El Caño creeks, near Colonia del Sacramento (see Rusconi 1952); and in Punta Chaparro, Soriano Department (see Roselli 1976). In central and northern Uruguay, tayassuid fossil remains have been found in the Sopas creek (Salto Department) (Ubilla 2004; Ubilla et al. 2004; Gasparini, Ubilla et al. 2009; Gasparini and Ubilla 2010); and in the Cuareim river, between the mouth of Cuaró and Tres Cruces river, Artigas Department (Ubilla 1985; Gasparini, Ubilla et al. 2009; Gasparini and Ubilla 2010). Sediments outcropping in the south and southwest region are tentatively considered to be of Bonaerian Age (Rusconi 1952; Gasparini 2007), whereas those exposed in the north and central region are of Lujanian Age (Sopas Formation: late Pleistocene to early Holocene; see Ubilla 1985, 2004; Ubilla et al. 2004; Gasparini, Ubilla et al. 2009; Gasparini and Ubilla 2010). Until now, *Catagonus* and *Tayassu* were the only tayassuid genera that were present in the palaeontological record of Uruguay (Rusconi 1952; Roselli 1976; Ubilla 1985, 2004; Ubilla et al. 2004; Gasparini 2007; Gasparini, Ubilla et al. 2009). The genus *Platygonus* is recorded for the first time in Uruguayan territory from the materials (FC-DPV-444) studied here. This finding expands its geographical range and could be the oldest record of

Tayassuidae in Uruguay. Despite the fact that the specimens were found in a core it is very likely that the material belongs to the Raigón Formation that is considered as Pliocene–early Pleistocene in age.

Ecological and anatomical considerations

The peccaries of the genus *Platygonus* were large mammals with some well-defined morphological features [e.g. orbits located in superior–posterior position and behind the M3 because of 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, among others] that allow it to be inferred that these animals were "runners", with diurnal habits, and lived in dry and relatively open environments (Guilday et al. 1971; Wetzel 1977; Menegaz and Ortiz Jaureguizar 1995; Gasparini 2007). In turn, the development of mesodont and bunolophodont cheek teeth and the lateral expansion of the angular process of the jaw providing greater surface for insertion of the lateral deep masseter muscle in *Platygonus* species, suggests a herbivorous diet and probably a foraging habit, although the possibility of a graminoid component in the diet cannot be dismissed (Menegaz and Ortiz Jaureguizar 1995). Dental microwear and isotopic analysis on North American *Platygonus* indicate a C_3 browser to mixed-feeder diet and under special conditions C_4 grasses (Feranec and MacFadden 2000; Feranec 2007; Schmidt 2008).

Preliminary studies have shown that in the last 3.3 million years, the South American Tayassuidae have maintained a relatively uniform body mass, ranging between 20 and 70 kg, with some exceptions [e.g. *Catagonus bonaerensis* (Ameghino 1904) and *Catagonus metropolitanus* Ameghino 1904; see Gasparini, Soibelzon, Soibelzon et al. 2010)]. Although these studies have not included all South American Tayassuidae species, it is worth remarking that the body mass of the South American *Platygonus* species varies between 30 and 70 kg (Gasparini, Soibelzon, Soibelzon et al. 2010). These preliminary analyses indicate that *Platygonus marplatensis* would be the largest taxon (63–66 kg) and *Platygonus scagliai* the smallest (37 kg).

The faunal changes that have taken place since the middle to late Pliocene could have been strongly influenced by the climate. Open and arid environments developed during glacial cycles, allowing the latitudinal expansion of *Platygonus* and *Catagonus*. Precisely during the early–middle Pleistocene (Ensenadan Age) the coexistence of *Catagonus* and *Platygonus* is recorded. Some of the main differences observed between the genera have adaptive value. For example, species of *Platygonus* have bunolophodont cheek teeth and show marked reduction of the lateral digits of the limbs, while *Catagonus* species have bunodont and/or "zygodont" cheek teeth and less reduction of the lateral digits on the limbs. These differences have been linked to a herbivorous diet and more specialized cursorial habit for *Platygonus* (e.g. Guilday et al. 1971; Wetzel 1977). When estimated body mass is also taken into account (Gasparini, Soibelzon, Soibelzon et al. 2010), it is possible to infer that species of *Catagonus* replaced those of *Platygonus* from the middle Pleistocene onwards, probably because of a reduction of the open environments to which *Platygonus* was better adapted. In turn, the alternation of these mainly arid or semi-arid and cold conditions with warmer and more humid short pulses would have allowed the posterior expansion of

Tayassu species. With regards to the prevailing climatic conditions during the deposition of the Raigón Formation, semi-arid, dry and cold climates with concentrated rainfall regimens have been postulated, which would explain the considerable development of coarse grain sizes (Preciozzi et al. 1985; Bossi and Navarro 1991; Panario and Gutiérrez 1999). Moreover, Tófalo and Morras (2009) have suggested humid conditions during the genesis of the Raigón Formation, whereas Tófalo et al. (2009) indicate that its final levels (palaeosoils) exhibit evidence of seasonal climate associated with C3 vegetation. Considering the morphological adaptations of *Platygonus* together with the associated environmental and climatic conditions, the presence of this genus supports those hypotheses that suggest arid or semi-arid climates and open or relatively open environments, at least for the basal and middle levels of this unit. Furthermore, some elements of the associated fauna, such as large phorusrhacid birds, dinomyid rodents and middle- and large-sized glyptodonts, could also support the existence of relatively open environments.

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