



The Tayassuidae (Mammalia, Artiodactyla) from the Quaternary of Entre Ríos Province. A palaeofaunal review in Argentina

Germán M. Gasparini, La Plata and Brenda S. Ferrero, Diamante

With 2 figures

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Abstract: The Tayassuidae has a wide geographic distribution and stratigraphic record during the Quaternary of South America. Three genera of Tayassuidae (*Platygonus*, *Catagonus* and *Tayassu*) are recognized in this continent. Argentina has the greatest diversity and abundance of fossil tayassuids in South America. In the Argentine Mesopotamian, the oldest tayassuid records are from the late Pleistocene of Corrientes and Entre Ríos provinces, and from an archaeological site in the Holocene of Misiones Province. This paper aims to: 1) describe the tayassuid materials found in the Pleistocene in Entre Ríos Province; 2) review and update the palaeontological record of the family in the Mesopotamian region during the Quaternary; and 3) check the geographic and stratigraphic distribution in South America, specially in Argentina, of the tayassuids from the Mesopotamian region. The palaeontological evidence indicates that in this area, *Tayassu* and *Catagonus*, the latter for the first time, are registered only in late Pleistocene sediments. Furthermore, the record of *Tayassu* and *Catagonus* during the late Pleistocene in Entre Ríos Province reflects a faunistic difference in comparison with the extant mammal fauna. Today, in the Mesopotamian region, *T. pecari* and *T. tajacu* are part of the mammalian fauna of Misiones Province. In the north of Corrientes Province there is possibly the most austral record of *T. pecari*. *Catagonus* reaches its most southern distribution in the north of Santiago del Estero and the northeast of Tucumán; therefore at present this tayassuid does not inhabit the Argentine Mesopotamian.

Key words: *Catagonus*, *Tayassu*, Argentine Mesopotamian, geographic distribution, biostratigraphy, Pliocene, Pleistocene, Holocene, South America.

1. Introduction

The families Tayassuidae and Suidae (Mammalia, Artiodactyla) may have differentiated from their common ancestor in the late Eocene in Eurasia; this can be inferred from the distribution of their oldest fossil records (ROMER 1966). Younger records suggest that the Tayassuidae may have migrated to North America, where they reached their greatest diversity

(see SAVAGE & RUSSELL 1983; GASPARINI 2007). From there they have migrated to South America during the “Great American Biotic Interchange” (GABI). They represent one of the first mammalian immigrants from North America, after procyonids (Carnivora) and cricetid rodents (PREVOSTI et al. 2006; WOODBURN et al. 2006; GASPARINI 2007, and bibliographies cited therein). The oldest fossil tayassuid in South America dates to the beginning of the late

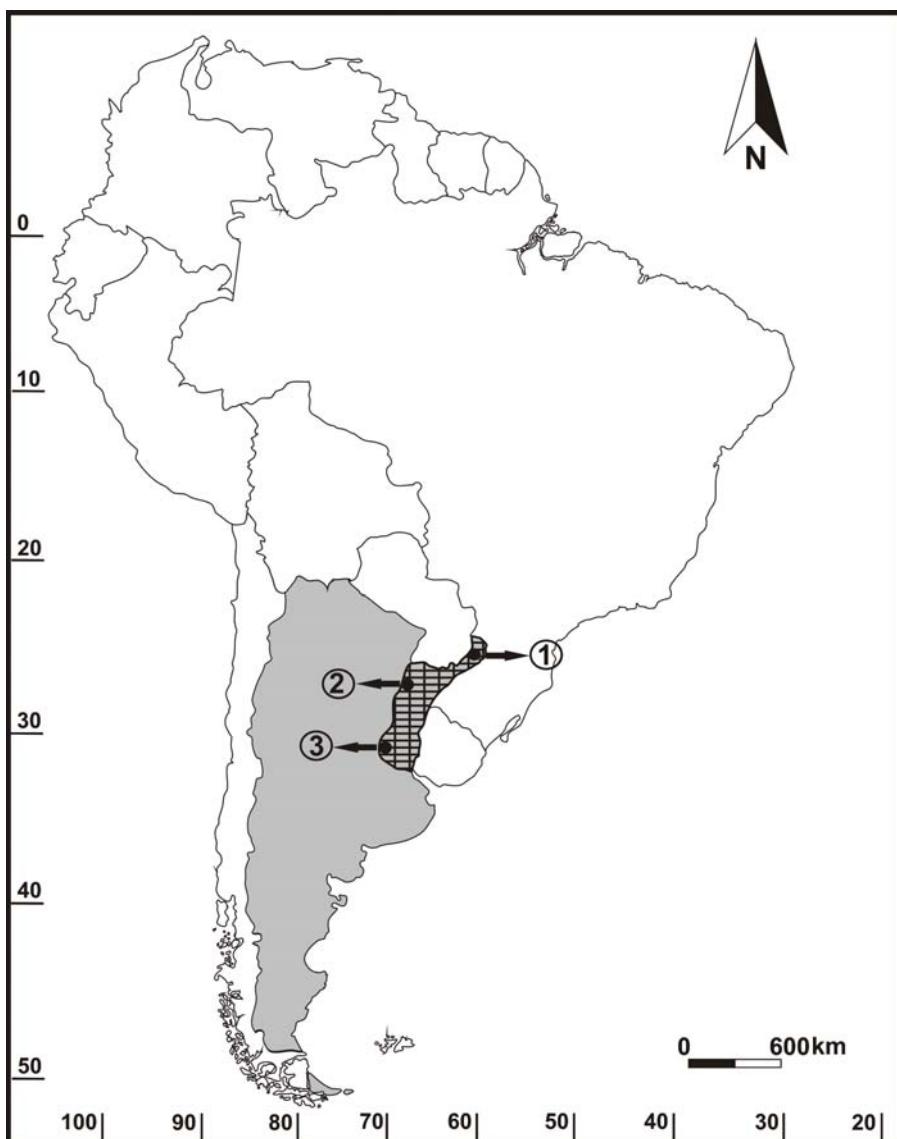


Fig. 1. Location map of the palaeontological sites in the Argentine Mesopotamian. Mesopotamian region; (1) Panambí, an archaeological site (Holocene), Oberá Department, Misiones Province; (2) Yupoí Formation (late Pleistocene), Toropí Stream, Corrientes Province; (3) “Arroyo Feliciano Formation” (late Pleistocene), Ensenada Stream, Entre Ríos Province.

Chapadmalalan (middle Pliocene, 3.3-4 Ma; PREVOSTI et al. 2006).

The greatest generic and specific diversity of Tayassuidae in South America derives from the sediments exposed in central-eastern Argentina. The family has also been found in Brazil, Uruguay, Bolivia and Colombia; together with doubtful records from Peru (RUSCONI 1930, 1952; STIRTON 1947; PAULA COUTO 1975, 1981; MENEGAZ & ORTIZ JAUREGUIZAR

1995; RANCY 1999; CAMPBELL et al. 2000a, 2000b, 2001; MARTINS & OLIVEIRA 2003; UBILLA 2004; UBILLA et al. 2004; GASPARINI 2007).

Three genera of Tayassuidae are recognized in South America: *Platygonus* LE CONTE, 1848 (middle Pliocene to early Pleistocene); *Catagonus* AMEGHINO, 1904 (late Pliocene? to Recent), and *Tayassu* FISCHER, 1814 (middle Pleistocene to Recent) (GASPARINI 2007). In the Mesopotamia region, *Tayassu pecari* (LINK,

1795) has been recorded in the Yupoí Formation (late Pleistocene), Toropí Stream, Corrientes Province (GASPARINI & ZURITA 2005) and in Panambí, an archaeological site (Holocene), Oberá Department, Misiones Province (TONNI 2004); and *?Prosthenops* GIDLEY, 1904 in “Arroyo Feliciano Formation” (late Pleistocene), Ensenada Stream, Entre Ríos Province (GASPARINI et al. 2002).

At present, tayassuids are distributed in the American continent from south-western USA to north-central Argentina (MAYER & BRANDT 1982; REDFORD & EISENBERG 1992; NOWAK 1999; PARERA 2002; GASPARINI 2002, 2007; GASPARINI et al. 2005, 2006) and they are represented by at least two genera and three species: *Tayassu tajacu* (LINNAEUS, 1758), *T. pecari* (LINK, 1795) and *Catagonus wagneri* (RUSCONI, 1930) (GASPARINI 2007 and bibliographies cited therein).

This paper aims to: 1) describe the tayassuid materials found in the Pleistocene in Entre Ríos Province; 2) review and update the palaeontological record of the family in the Mesopotamian region during the Quaternary; and 3) check the geographic and stratigraphic distribution in South America, especially in Argentina, of the tayassuids from the Mesopotamian region.

2. Geographic and stratigraphic context

The Argentine Mesopotamian comprises a large region between the Paraná and Uruguay rivers and includes Entre Ríos, Corrientes and Misiones Provinces (Fig. 1). The specimens here studied come from Entre Ríos Province, from sediments of the “Arroyo Feliciano Formation” (IRIONDO et al. 1985). This Formation constitutes the fluvial valley filling deposited during a prolonged humid period during the late Pleistocene. This unit is composed partly of light green silt, clearly friable clay, with interlayers of quartzose very fine sand and partly of clay silt. These deposits form the highest terrace that occurs in the majority of the rivers and streams of Entre Ríos Province (IRIONDO et al. 1985; IRIONDO 1996). These deposits become smaller and scarcer towards the north of the province. From a biochronological point of view, according to the associated mammals, the “Arroyo Feliciano Formation” corresponds to the base of the Lujanian (CIONE & TONNI 1999, 2005; NORIEGA et al. 2004; FERRERO & NORIEGA, in press).

3. Previous studies of the Tayassuidae

There has been little consensus in the systematics of fossil and extant South American Tayassuidae. This is due to many factors: the different values assigned to certain characters by previous authors; the episodic nature of investigations of this group; and the discovery of new taxa, both fossil and extant (MENEGAZ & ORTIZ JAUREGUIZAR 1995; GASPARINI 2007 and literature cited therein).

After the systematic review of Argentinean, Brazilian and Bolivian tayassuids by RUSCONI (1930), divergent opinions about the taxonomic composition of the family and phylogenetic relationships of its members can be found (e.g. PASCUAL et al. 1966; WOODBURN 1968; WETZEL 1977; REIG 1981; MARSHALL et al. 1984; ORTIZ JAUREGUIZAR & LÓPEZ ARMENGOL 1984; ORTIZ JAUREGUIZAR & PRADO 1986; MENEGAZ & ORTIZ JAUREGUIZAR 1995). The various classificatory proposals cover only a fraction of Tayassuidae diversity and many are intuitive schemes rather than being based on rigorous analysis of shared derived characters (e.g. REIG 1981: 41; REIG in MARSHALL et al. 1984: 21).

This paper adopts the system proposed by GASPARINI (2007), since this is the most recent integral review of the South American Tayassuidae.

4. Materials and methods

Measurements were taken using digital callipers, with 0.01 mm accuracy; data have been expressed in millimetres. In order to calculate the relative ontogenetic age of the examined units, MARGARIDO et al. (2007) method was used to. This method establishes age classes using the sequence and pattern of tooth eruption.

The stratigraphic references correspond to the schemes of CIONE & TONNI (1999, 2005) and SOIBELZON (2008).

Abbreviations of measurements: Ac: width of lower canine; Am3: width of m3; Hmrmv: height of the vertical ramus from the basal point of the angular process to coronoïd; Hrmhm2: height of the mandible in front of m2, measured on the labial side; Hrmhm1: height of the mandible in front of m1; Hrmhm3: height of the mandible at the level of the most posterior part of the alveolus of the m3 (labial side); Lam2: length of alveolus m2; Lam3: length of alveolus m3; Lc: length of the lower canine; Lcm3: maximum length from the condyle to the anterior margin of the m3; Lm3: length of m3; m: lower molar; Wam2: width of alveolus m2; Wam3: width of alveolus m3.

Institutional abbreviations: CICYTTP-PV: Centro de Investigaciones Científicas y de Transferencia de Tecnología a la Producción-CONICET, Diamante, Entre Ríos, Argentina; MLP: Museo de La Plata, Argentina.

5. Systematic palaeontology

Order Artiodactyla OWEN, 1848
 Suborder Suiformes JAECKEL, 1911
 Infraorder Suoidea GRAY, 1821
 Family Tayassuidae PALMER, 1897

Genus *Catagonus* AMEGHINO, 1904

Type species: *Catagonus metropolitanus* AMEGHINO, 1904.

Catagonus sp.

Fig. 2A-C

Studied material: Partial right mandible, CICYTTP-PV- M-1-107; collected by Prof. RAÚL KEMER.

Geographic provenance and age: Ensenada Stream, Diamante Department, Entre Ríos Province, Argentina. "Arroyo Feliciano Formation" (late Pleistocene); Lujanian Age.

Description: The mandible is broken in front of pm4. It has a simple unerupted m3 in situ. Despite its incomplete state, the most posterior part of the jaw is interpreted as the condyle.

The angular process projects forwards as far as the front of the m3 and it does not project laterally as in the South American species *Tayassu pecari*, *Tayassu tajacu* and *Catagonus wagneri* and in the North American *Perchoerus pristinus* (COPE, 1888), *Hesperhyus DOUGLASS*, 1903, *Dyseohyus stirtoni* WOODBURNE, 1969 and *Mylohyus nasutus* (KINSEY, 1974). In *Platygonus* species and some of the North American genera *Prosthennops* and *Mylohyus* (COPE, 1889), a greater degree of lateralization, which increases the insertion surface of the masticatory muscle, is observed. The South American *Catagonus stenocephalus* (LUND in REINHARDT, 1880) possesses a bony rim round the posterior end of the ascending ramus with a slight lateral tendency. It is not considered to be a typical lateral projection, a characteristic which is observed in the North American *Platygonus compressus* LE CONTE, 1848.

The ascending ramus lies behind the m3 as in the majority of the Tayassuidae, with the exception of *Tayassu*, *Prosthennops*, *Dyseohyus* STOCK, 1937 and *Hesperhyus*.

The coronoid process has a rounded contour, directed upwards and backwards. These features are characteristic of Tayassuidae with the exception of *Platygonus scagliai* (REIG, 1952) that possesses a forwarders inclined coronoid process (see GASPARINI 2007).

The third lower molar is mesodont in height and bunodont in morphology. In its anterior face there exists a crenulated cingulum including almost the entire width of the tooth. The main cusps of these teeth are distinguished from those of *Tayassu* by their greater height, sharpness and limited anteroposterior extension. The first pair of anterior cusps (metaconid and protoconid) is slightly wider than the posterior pair (hypoconid and entoconid). Behind both

characteristic lobes, the tooth presents a complex third lobe in which more than four cusps of similar size are observed. It is important to emphasize that a simple third lobe (with a unique dominant cusp, which can be accompanied by a pair of smaller cusps; see GASPARINI 2007) is observed in *Catagonus wagneri* and species of the genera *Hesperhyus* and *Platygonus* (with the exception of *P. chapadmalensis* (AMEGHINO, 1908) where it is reduced). However, *Tayassu*, *Prosthennops*, *Mylohyus*, *Perchoerus probus*, *Catagonus brachydontus* (DALQUEST & MOOSER, 1980), *Catagonus bonaerensis* (AMEGHINO, 1904) and *C. stenocephalus* (LUND in REINHARDT, 1880) possess a third lobe with a complex configuration.

Relative age of specimen (MARGARIDO et al. 2007): juvenile/ young adult.

Measurements: Lcm3: 64.7mm; Hmrvm: 77.7 mm; Hrmhm2: 28.9 mm; Hrmhm1: 31.4 mm; Hrmhm3: 44.65 mm; Lm3: 22.95 mm; Am3: 12.05 mm.

Remarks: The material CICYTTP-PV- M-1-107 was originally referred to *?Prosthennops* by GASPARINI et al. (2002). On that occasion the authors raised doubts about their systematic allocation which they based on the work of RUSCONI (1930), MONES (1986) and MENEGAZ & ORTIZ JAUREGUIZAR (1995), among others. The mandible fragment is incomplete; hence the observation of the diagnostic character of the South American species of Tayassuidae is difficult. According to the most recent systematic adjustment of South American Tayassuidae (GASPARINI 2007), the main morphologic and morphometric characters that allow us to identify the material as *Catagonus* sp. are the following: the posterior edge of the condyle is located further backwards in comparison to the posterior margin of the mandible; the angular process does not project laterally; the crown height is mesodont; the cheek teeth morphology is bunodont; the m3 has a third well-developed lobe with several accessory cusps behind the two main lobes; and the tooth and mandible measurement agree with those of the genus *Catagonus*.

cf. *Catagonus* sp.

Fig. 2D, E

Studied material: Partial left mandible, CICYTTP-PV- M-1-108; collected by DANIEL DIEDERLE.

Geographical provenance and age: Ensenada Stream, Diamante Department, Entre Ríos Province, Argentina. "Arroyo Feliciano Formation" (late Pleistocene); Lujanian Age.

Description: The partial mandible corresponds to the region of the m2-m3. It has no teeth. The alveoli indicate a bunodont cheek teeth morphology and considering their relative size, it is inferred that this material would belong to *Catagonus*. The height of this fragment is within the range of measurements observed in *Catagonus*. Its systematic allocation is doubtful due to its incomplete preservation.

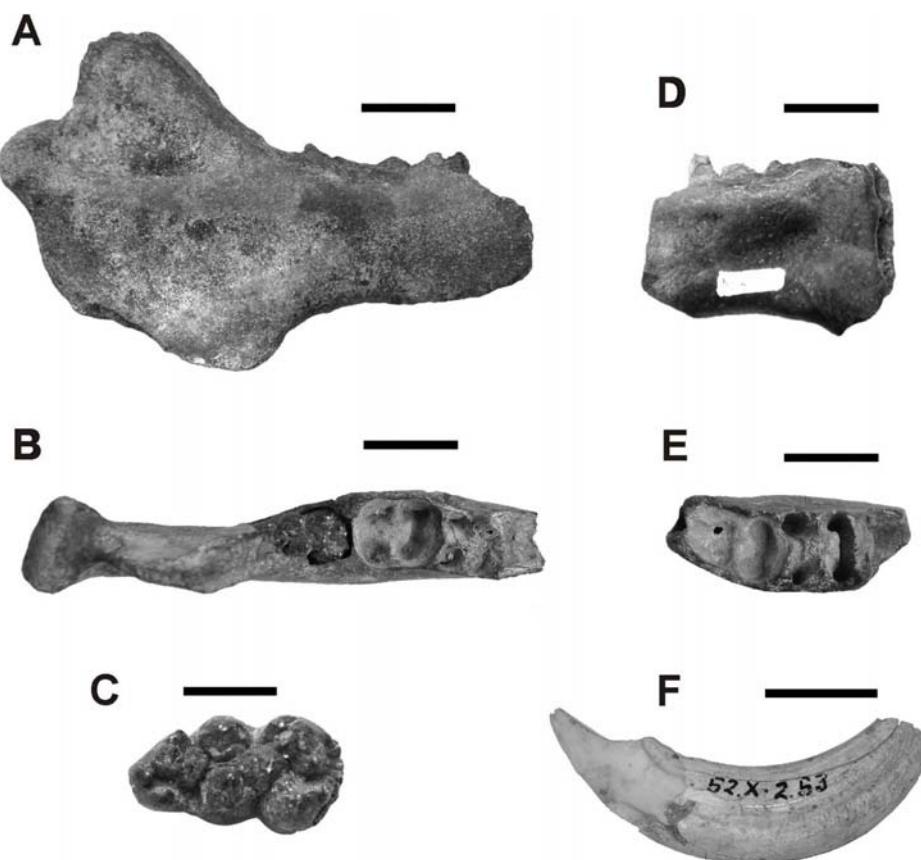


Fig. 2. *Catagonus* sp. (CICYTTP-PV-M-1-107). **A** – partial right mandible in labial view. **B** – occlusal view. **C** – m3 in occlusal view. Cf. *Catagonus* sp. (CICYTTP-PV-M-1-108). **D** – partial left mandible in labial view. **E** – occlusal view. *Tayassu* sp. (MLP 52-X-2-53). **F** – lower canine in lingual view. – Scale bar: A, B, D, E, F: 20 mm; C: 10 mm.

Measurements: Hrmhm2: 33.8 mm; Lam2: 14.55 mm; Lam3: 21.7 mm; Wam2: 17.07 mm; Wam3: 16.64 mm.

Genus *Tayassu* FISCHER, 1814

Type species: *Tayassu pecari* (LINK, 1795).

Tayassu sp.
Fig. 2F

Studied material: Lower canine, MLP 52-X-2-53.

Geographical provenance and age: Ensenada Stream, Diamante Department, Entre Ríos Province, Argentina. Age unknown.

Description: Despite the incomplete state of the apex of the canine, this tooth is interpreted it was sharp and longitudinally curved. This tooth is short and robust. The

posterior surface of the tip has a developed almost flat wear facet produced by contact with the anterior surface of the upper canine.

Measurements: Lc: 14.45 mm; Ac: 8.44 mm.

Remarks: The material (MLP 52-X-2-53) differs from the thin and elongated canine observed in *Platygonus* and *Catagonus*.

6. Discussion

Argentina has the greatest diversity and abundance of fossil tayassuids in South America. Three genera are present in Buenos Aires Province (*Platygonus*, *Catagonus* and *Tayassu*) (GASPARINI 2007). There are also records of *Platygonus* in Jujuy Province; of *Catagonus* in Santiago del Estero Province; and of

Tayassu in Córdoba, Corrientes and Misiones Provinces (see GASPARINI 2007 and the bibliographies cited therein).

Catagonus is one of the two genera of tayassuids present in the Mesopotamian region. The oldest record of *Catagonus* in South America is from sediments possibly referred to the Barranca de Los Lobos Formation (lower part of the Formation), near the mouth of the Lobería Stream (Buenos Aires Province) and assigned to the late Pliocene (early Marplatian) (see GASPARINI 2007).

In South America, during the early to middle Pleistocene, *Catagonus* [*Catagonus* sp., *C. metropolitanus* AMEGHINO, 1904 and *C. stenocephalus* (LUND)] is recorded only in Argentina, being frequently found in the “toscas del río de La Plata” (the environs of Buenos Aires city) and in the cliff to the southeast of Buenos Aires Province.

From the middle Pleistocene to early Holocene *Catagonus* is recorded in several localities in Brazil, Uruguay and Bolivia. Within Argentina, *C. stenocephalus*, *C. bonaerensis* and *Catagonus* sp. have been registered in several localities in the north, east and southeast of Buenos Aires Province. *C. carlesi* is recorded in Santiago del Estero Province (GASPARINI 2007 and the bibliographies cited therein).

For the first time, *Catagonus* is recorded in the Mesopotamian region, by the materials described here (CICYTTP-PV-M-1-107 and CICYTTP-PV-M-1-108), collected from sediments of the “Arroyo Feliciano Formation” (late Pleistocene) in Entre Ríos Province.

During the Holocene, the diversity and the quantity of tayassuid findings in South America are lower; there are no reports of *Catagonus* from the palaeontological record of the Mesopotamian region. However, for the first time records of *C. wagneri* appear in archaeological deposits of Santiago del Estero (RUSCONI 1930; KRAGLIEVICH & RUSCONI 1931; RUSCONI 1948; WETZEL et al 1975; WETZEL & CRESPO 1975; WETZEL 1977). Radiocarbon ages between 730 +/- 60 (GIF 2309) and 530 +/- 90 (GIF 2310) radiocarbon years BP have been obtained (1200-1400 AD) (TONNI 2006).

Tayassu is the second genus of tayassuid found in the Mesopotamian region. In South America, it is registered from the middle Pleistocene to the Present. A few *Tayassu* fossils are reported in Brazil and Uruguay (GASPARINI 2007).

The geographical distribution of *Tayassu* in Argentina during middle Pleistocene to early Holocene is confined to Córdoba (*Tayassu* sp.) and Buenos

Aires Provinces (*Tayassu* sp., *T. tajacu*, *T. pecari*) (GASPARINI 2007). In the Mesopotamian region *Tayassu* is registered in sediments of the late Pleistocene (ca. 50-35 ka; see TONNI et al 2005), in Corrientes Province, (*T. pecari*; see GASPARINI & ZURITA 2005); and in Entre Ríos Province on the basis of the material described in this contribution (MLP 52-X-2-53).

In the Holocene of South America, there are few records of *Tayassu*. In Buenos Aires Province, the teeth originally referred to *Tayassu* sp. (CIONE & TONNI 1978) and soon after assigned as *T. pecari* (GASPARINI & SOIBELZON 2003), which came from archaeological site Islas Las Lechiguanas I, confirms the presence of tayassuids in the Pampean region during the Holocene. There is thus a faunistic difference from the extant mammal fauna of the Delta of Paraná. The age of the level from which these remains were found is 2,740 +/- 80 and 2,550 +/- 90 years BP radiocarbon (lapse 2,926 - 2,759 and 2,755 - 2475 years cal BP respectively) (GASPARINI & SOIBELZON 2003). KRAGLIEVICH & RUSCONI (1931) attributed some remains to *Tayassu* cf. *T. pecari* found in an indigenous tumulus of the Chaco region in Santiago del Estero Province. In the Mesopotamian region, the only record of the genus corresponds to *T. pecari* dug from the archaeological site Panambí (Department of Oberá, Misiones) (TONNI 2004). The fauna from this archaeological site includes mammal species that still occur in the area (*Alouatta* sp., *Procyon cancrivorus*, *Mazama* sp., *Mazama rufina*, and *Tapirus terrestris*) (TONNI 2004). The level of the remains was dated to 920 +/- 70 years BP radiocarbon (LP-176), (732-925 years cal BP, 1.025-1.218 AD) (TONNI 2004). There are travellers' stories making reference to the presence of “peccaries” inhabiting the Mesopotamian and Pampean regions up to (middle of the 18th century) the present locality of Balcarce in Buenos Aires Province and possibly further south (GALLIARI et al. 1991).

Today the geographic distribution of the tayassuid species within Argentina is restricted to the central-north region. Among the living tayassuid species, *T. tajacu* has the most southernly range (north of Córdoba, San Luis and the northeast of Mendoza Provinces) (BÁRQUEZ et al. 1991; REDFORD & EISENBERG 1992; PARERA 2002; GASPARINI et al. 2006; GASPARINI 2007). *T. pecari* reaches its most southern distribution in the north of Santiago del Estero, and possibly north of Corrientes and Santa Fe (BAKER 1974; HALL 1981; MAYER & BRANDT 1982; MAYER & WETZEL 1987; REDFORD & EISENBERG

1992; GASPARINI et al. 2006; GASPARINI 2007). *C. wagneri* inhabits the west of Chaco and Formosa, east of Salta and Jujuy, north of Santiago del Estero and the northeast of Tucumán (OLROG et al. 1976; WETZEL & CRESPO 1975; WETZEL 1977; MAYER & BRANDT 1982; MAYER & WETZEL 1986; REDFORD & EISENBERG 1992; GASPARINI et al. 2006; GASPARINI 2007).

From the ecological and biogeographic point of view, *Catagonus* inhabits dry and relatively open environment. *Catagonus wagneri* is endemic to the semi-arid thorny forests of the Dry Chaco (GASPARINI et al. 2006; GASPARINI 2007). However, *Tayassu* inhabits wooded, warm and humid environment; hence it is found in subtropical forests (Paranaense and Yungas eco-region), forests and savannahs of the Humid Chaco, and xerophilous woodland of the ecoregion of Dry Chaco (GASPARINI et al. 2006; GASPARINI 2007). *T. tajacu* also inhabits the ecoregion of Monte de Sierras and Bolsones. Despite its geographical preferences, the presence of the two *Tayassu* does not allow us to infer the prevailing environmental conditions (GASPARINI 2007 and references cited therein).

7. Conclusions

The partial mandibles (CICYTTP-PV- M-1-107 and CICYTTP-PV- M-1-108) constitute the first fossil record of *Catagonus* sp. in the Mesopotamian region, in late Pleistocene sediments. Moreover, the record of *Tayassu* sp. (MLP 52-X-2-53) in the southwest of Entre Ríos Province together with the report of *T. pecari* in Toropí Stream in Corrientes Province provide further evidences of the presence and distribution of *Tayassu* in the Mesopotamian region during the late Pleistocene.

Furthermore, the record of *Tayassu* and *Catagonus* during the late Pleistocene in Entre Ríos Province reflects a faunistic difference from extant mammal fauna. Today, in the Mesopotamian region, *T. pecari* and *T. tajacu* are part of the mammalian fauna of the subtropical forests of Misiones Province. In the north of Corrientes there is possibly the most austral record of *T. pecari*. *Catagonus* reaches its southernmost distribution in the north of Santiago del Estero and the northeast of Tucumán; therefore at present this tayassuid does not inhabit the Argentine Mesopotamian.

On the basis of previously available evidence, the palaeontological record indicates that in the Mesopotamian region, *Catagonus* and *Tayassu* among the South American tayassuids are registered solely and

essentially in late Pleistocene sediments. So far, the only material reported in the Mesopotamian region that could be determined to the specific level *Tayassu pecari* were found in the late Pleistocene of Corrientes Province and in the Holocene of Misiones Province.

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Addresses of the authors:

GERMÁN M. GASPARINI, División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, UNLP, Paseo del Bosque s/n 1900, La Plata, Argentina. CONICET;
e-mail: chinogasparini@yahoo.com.ar

BRENDA S. FERRERO, Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante-CONICET, Materi y España, 3105 Diamante, Entre Ríos, Argentina;
e-mail: brendaferreiro@yahoo.com.ar