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## Original article

# First continental vertebrates from the marine Paraná Formation (Late Miocene, Mesopotamia, Argentina): Chronology, biogeography, and paleoenvironments<sup>☆</sup>

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## ABSTRACT

First records of continental vertebrates from the upper levels of the Paraná Formation (Late Miocene) at La Juanita locality, Entre Ríos Province (Mesopotamia, Argentina), are reported and evaluated from chronological, paleobiogeographical, and paleoenvironmental perspectives. Among caviomorph rodents, caviids, hydrochoerids, and the extinct octodontoid *Plesiacaechimys* are described. The pamphathiid *Scirrotherium* sp. and a phoenicopterid bird are identified. A “pre-Huayquerian” age (older than 8.7 Ma) is proposed for the fossil bearing levels. The “Paranense Sea”, one of the most widespread Middle-Late Miocene Atlantic transgressions that covered southern South America, is interpreted as an important geographical barrier promoting vicariance of the *Plesiacaechimys* lineage. Cavioids recovered from the Paraná Formation represent the first stages of the radiation of these rodents at the latitude of Entre Ríos Province in the context of the whole South American subcontinent. The genesis of the fossiliferous level corresponds to a storm deposit in a littoral marine environment. Capybaras and flamingos suggest the presence of water bodies, saline lagoons, mudflats, or shallow brackish coastal or inland lakes, in accordance with the geological data of the Paraná Formation.

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## 1. Introduction

The “Paranense Sea” is recognized as one of the most widespread Atlantic marine transgressions that covered southern South America during the Middle and Late Miocene (Uliana and Biddle, 1988; Räsänen et al., 1995; Webb, 1995; Aceñolaza, 2000, 2004; Hernandez et al., 2005). It spread over most of the Chaco-Paraná Basin and eastern Patagonia, the northern portion of the Sierras Subandinas and the northwestern Sierras Pampeanas in Argentina, reaching as far north as Bolivia, Paraguay, western Uruguay, and southern Brazil (e.g., Uliana and Biddle, 1988; Alonso, 2000; Hernandez et al., 2005; Fig. 1(1)). The presence of the “Paranense Sea” is widely recognized at Entre Ríos Province in the Mesopotamia area (Argentina), where it corresponds stratigraphically to the outcrops of the Paraná Formation (known also as “Entrerriense”, “Entrerriense-Rionegrense marino”, Entre Ríos Formation, and Entrerriana Formation; Frenguelli, 1920; Aceñolaza, 1976; Cione et al., 2000). Fossil vertebrates come from several continental Neogene units that span the entire Late Miocene-Late Pleistocene of this region (Cione et al., 2000; Candela et al., 2007; Ferrero and Noriega, 2009; Noriega and Agnolin, 2008; Brandoni, 2011). They are particularly well represented in the “Conglom-

erado osífero” (= “Mesopotamiense” *sensu* Frenguelli, 1920; base of the Ituzaingó Formation, late Miocene, Huayquerian age; Cione et al., 2000), where 122 genera were identified (Cione et al., 2000; Candela, 2005; Cozzuol, 2006; Brandoni, 2011). Taxonomical richness, biogeographical relationships, and paleobiological attributes identified in the Late Miocene-Pleistocene continental vertebrates of Entre Ríos Province reveal a complex paleogeographical and paleoenvironmental evolution of Mesopotamia (Candela and Morrone, 2003; Candela, 2004, 2005; Candela and Nasif, 2006; Cozzuol, 2006; Brandoni, 2011).

In this contribution, the first and oldest Miocene continental vertebrates from the Paraná Formation, recorded on the newly emergent oriental border of the “Paranense Sea” at Entre Ríos Province, are described. These vertebrates are evaluated from chronological, paleobiogeographical, and paleoenvironmental perspectives. Based on these studies and further evidence from paleogeographical and geological data, we aim to reconstruct the history of vertebrates that lived during the Paranense transgressive-regressive marine cycle in southern South America, and to evaluate the biogeographical effects of this significant event.

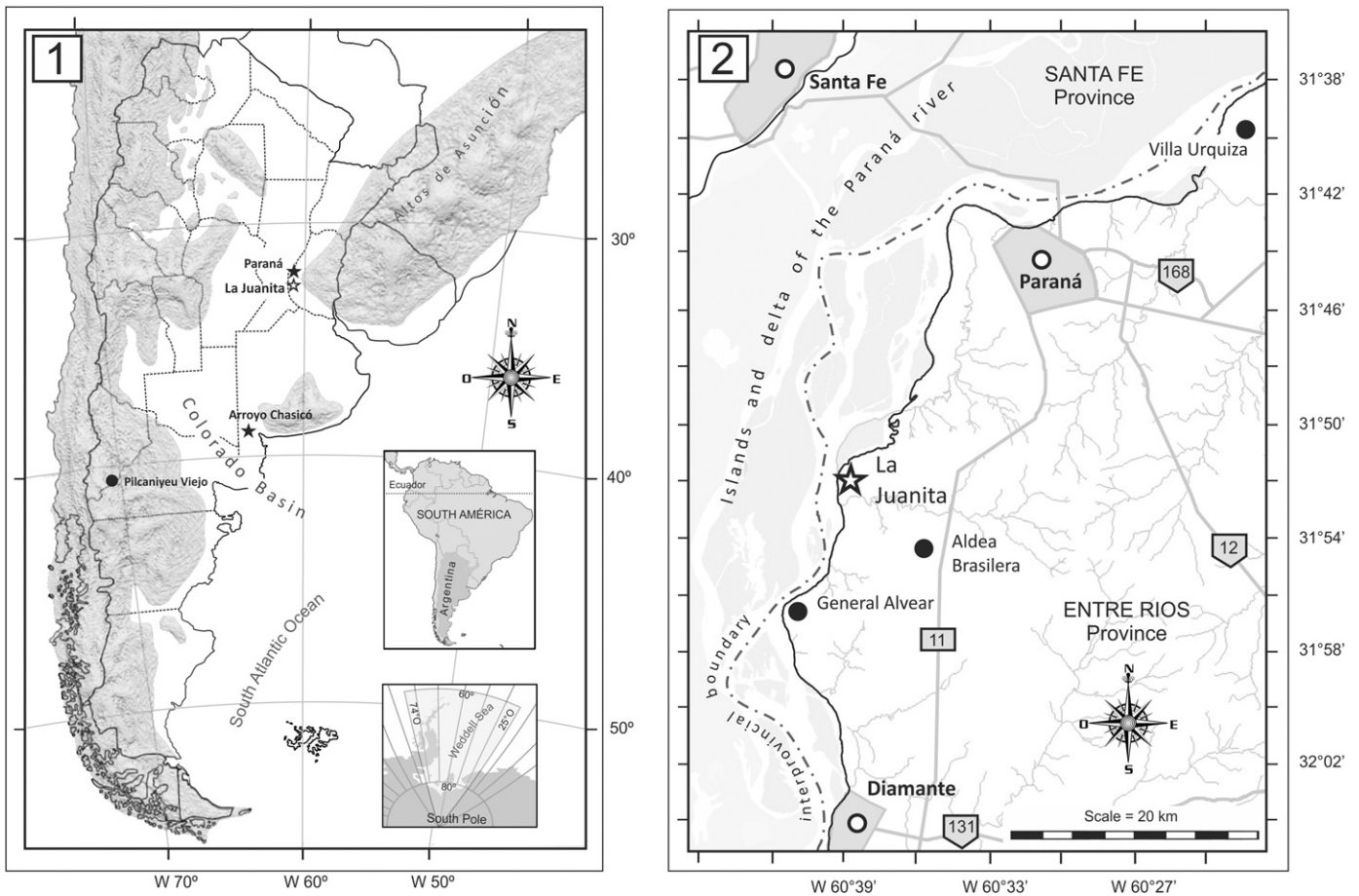
## 2. Geological setting

The materials described herein were collected from upper levels of the Paraná Formation (Fig. 2(2)), outcropping along the cliffs of the Paraná river at La Juanita locality (31° 52' 46" S; 60° 38'

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**Fig. 1.** 1. Paleogeography of south of South America showing the inferred extent of the “Paranense Sea” in white (modified from Aceñolaza, 2000; Alonso, 2000; Hernandez et al., 2005). Circle indicates the location of exposures of the Middle Miocene Collón-Curá Formation (Pilcaniyeu Viejo locality, Río Negro Province). White star indicates the location of exposures of the marine Miocene Paraná Formation (La Juanita locality, Entre Río Province); black stars indicate the location of the continental Late Miocene “conglomerado osífero” (Paraná, Entre Ríos Province), and Arroyo Chasicó Formation (Arroyo Chasicó, Buenos Aires Province) exposures deposited after withdrawal of the “Paranense Sea”. 2. Location map of the Paraná Formation exposures at La Juanita locality, Entre Ríos Province, Argentina. Localities mentioned in the text are also indicated.

59' W), near Aldea Brasilera village, Diamante County, Entre Ríos Province, Argentina (Fig. 1(2)). The fossil-bearing horizon is interpreted as late Miocene (“pre-Huayquerian”) in age (see below, Section 5.1). A diverse fauna of fishes and invertebrates coming from the same level was recently described by Cione et al. (2008) and Pérez et al. (2010). A detailed description of the exposure was reported by Pérez et al. (2010). These authors indicated that the outcropping section comprises a sedimentary succession of about 8 m which begins with whitish to yellowish sandy levels, alternating with greenish clays, strongly bioturbated by *Ophiomorpha nodosa* (Cione et al., 2008; Pérez et al., 2010; Fig. 2(2)). Upward the sequence shows an abrupt increase of the energy indicated by a lenticular bed with erosional base of approximately 150 m of horizontal extent for 50 cm of maximum thickness. This level is interpreted as a storm deposit (see below, Section 5.3) and includes several grain sizes from sabulitic to samitic matrix showing normal gradation. The samitic matrix is strongly cemented by carbonates at the middle part, forming a coquina with vertebrate and invertebrate remains, which would have behaved like bioclasts (Cione et al., 2008; Pérez et al., 2010). The uppermost levels are covered by vegetation.

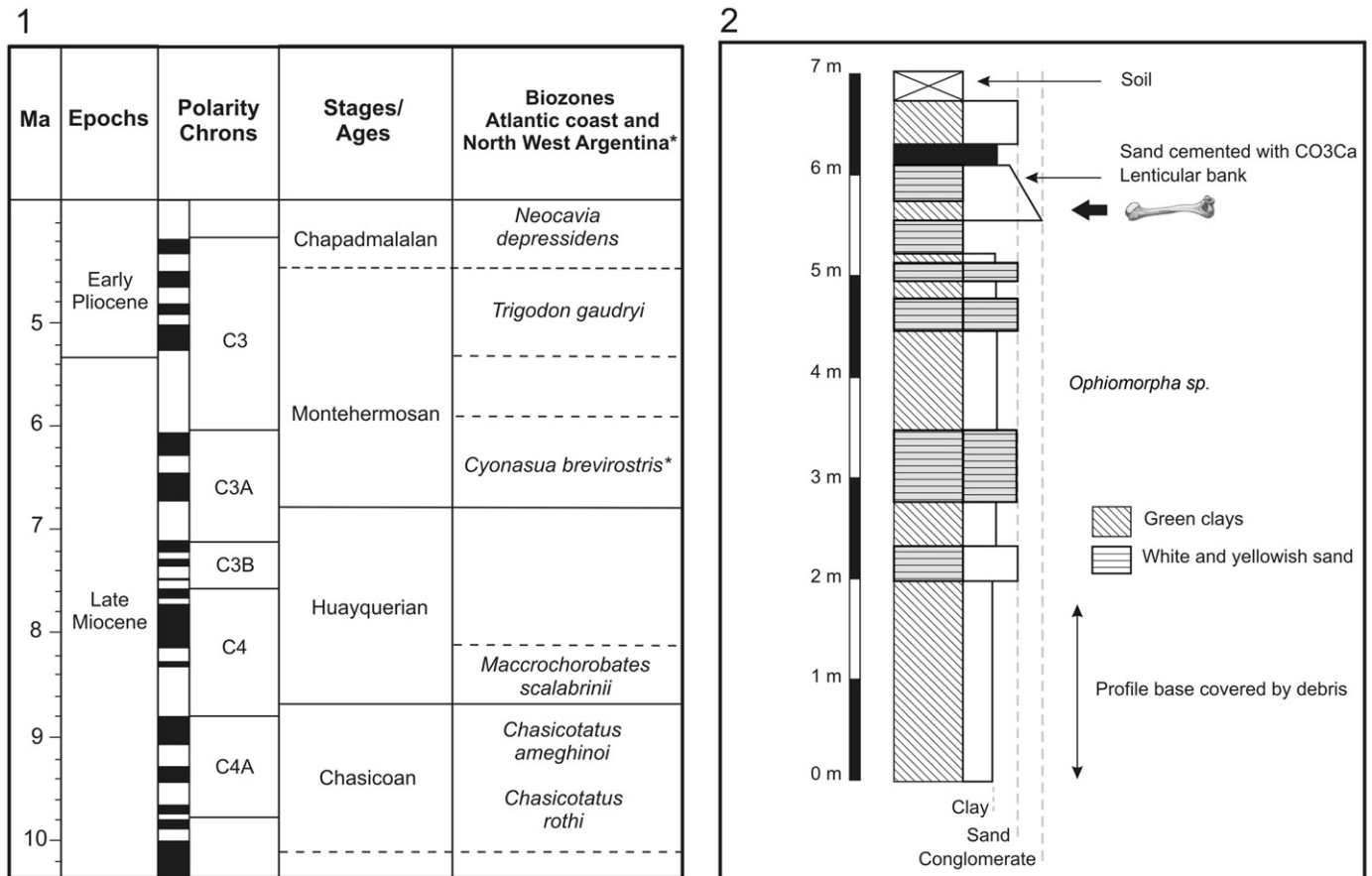
### 3. Material and methods

The new specimens are housed in the collections of the Centro de Investigaciones Científicas y Transferencia de Tecnología a la

Producción (CICYTTP-CONICET), Diamante, Entre Ríos Province, Argentina. They were collected during the 2008 to 2009 joint fieldwork between CICYTTP and Museo de La Plata (MLP). Systematic search for fossil remains was performed by sieving and washing sediments (by means of a water pump) from the lenticular bed exposed at the riverside cliffs.

Stages/ages of the Late Miocene–Late Pliocene of South America (Fig. 2(1)) are based on the information provided by Cione and Tonni (2005) and Reguero and Candela (2011). Limit of Chasicooan stage/age is inferred on the data provided by Zárate et al. (2007).

For anatomical comparisons and systematic identification of collected materials, we examined specimens belonging to different groups of caviomorph rodents, Pampatheriidae, and Aves, housed in the collections of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Museo de La Plata (MLP), and CICYTTP. In the case of the octodontoid *Plesiacaechimys*, all known specimens of the type species *P. koenigswaldi* Vucetich and Vieytes, 2006, deposited at Museo de La Plata were analyzed. Specimen MLP 91-V-1-19 was especially selected for illustration and comparison because it is particularly well-preserved, showing a tooth wear comparable with that of the specimen from the Paraná Formation here described. Among the Miocene hydrochoerids, several specimens described and figured by Vucetich et al. (2005) and Deschamps et al. (2007, 2009) were used for comparisons, most of them being also available for direct examination. Type specimens and several specimens of the extinct caviid *Orthomyctera* Ameghino, 1889, such



**Fig. 2.** 1. Chronostratigraphical chart of the Late Miocene-Early Pliocene of South America (modified from Cione and Tonni, 2005; Reguero and Candela, 2011). 2. Schematic profile exposed at La Juanita locality, showing the vertebrate-bearing level (modified from Pérez, 2010).

as *O. andina* (Rovereto, 1914) and *O. rigens* (Ameghino, 1888), and *Prodolichotis Kraglievich, 1932*, were examined. *Prodolichotis pridi-ana* Fields, 1957, was studied from casts housed at MLP and from bibliographical information (Fields, 1957; Walton, 1997).

Crown structure nomenclature follows Candela (2002) and Candela and Rasia (2012) for the Octodontoidea, and Vucetich et al. (2005) for Hydrochoeridae. The avian osteological nomenclature follows Howard (1929) and Baumel and Witmer (1993). The line drawings were executed with a camera lucida and the digital photographs were taken using a stereomicroscope.

**Institutional Abbreviations:** CICYTTP: Centro de Investigaciones Científicas y de Transferencia Tecnológica a la Producción, Diamante, Argentina; IMUNSJ: Instituto y Museo de la Universidad Nacional de San Juan, San Juan (PVSJ), colección de Paleontología Vertebrados, Argentina; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP: Museo de La Plata, La Plata, Argentina; MMH: Museo Municipal de Monte-Hermoso, Buenos Aires, Argentina; MMP: Museo Municipal de Ciencias Naturales de Mar del Plata, Buenos Aires, Argentina; MPEF: Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

#### 4. Systematic paleontology

Order RODENTIA Bowdich, 1821

Superfamily OCTODONTOIDEA Waterhouse, 1839

Genus *Plesiacarechimys* Vucetich and Vieytes, 2006

**Type species:** *Plesiacarechimys koenigswaldi* Vucetich and Vieytes, 2006.

**Temporal and geographical distribution:** Collón-Curá Formation, middle Miocene; Pilcaniyeu Viejo locality, Río Negro Province, northwestern Patagonia (Vucetich and Vieytes, 2006), and Paraná Formation, late Miocene; La Juanita locality, Entre Ríos Province, Argentina (see below, Section 5.1).

*Plesiacarechimys* nov. sp.?

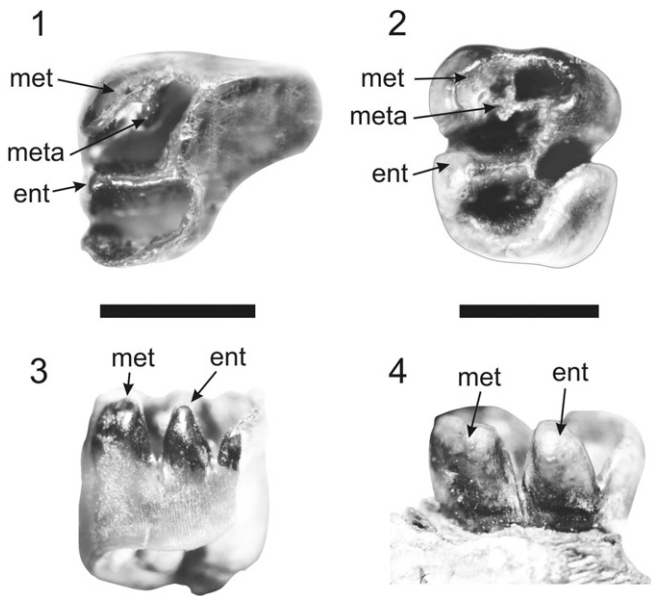
Fig. 3(1, 3)

**Referred material:** CICYTTP-PV-M-1-145, right lower molar, without completely preserved posterior wall.

**Measurements (in mm):** Length, 2.77; width, 3.24.

**Description:** The molar is scarcely worn, indicative of its recent eruption (Fig. 3(1, 3)). It is comparable in size to those of *P. koenigswaldi* (Vucetich and Vieytes, 2006: table 1; Fig. 3(2, 4)), but rather wider. The molar shows unilateral hypsodonty and it has a crown higher than that of *P. koenigswaldi*; the relatively wide fossetids are deeper than those of the latter species. The meta- and entoconid are evident and higher than the rest of occlusal surface like *P. koenigswaldi*, but both cusps are less developed than in the latter. The metaconid is anterolabial-posterolingually elongated and it is separated from the entoconid in a similar degree than that seen in *P. koenigswaldi* (Fig. 3). In the protoconid area, there is a tubercle that seems to correspond to the apex of this cusp. A similar structure present in m3 (specimen MLP 91-V-1-22) of *P. koenigswaldi* would probably merge with the protoconid area with progressive wear. The protoconid is more markedly extended labially than in *P. koenigswaldi*. The anterolophid (= metalophid I) merges with the metaconid and the hypolophid with the entoconid. The posterolophid extends lingually behind the entoconid, delimiting the posterior border of the metaflexid,





**Fig. 3.** 1, 3. *Plasiacarechimys* nov. sp.?, CICYTTP-PV-M-1-145, right lower molar; 1, occlusal; 3, lingual views. 2, 4. *Plasiacarechimys koenigswaldi* MLP 91-V-1-19, left m1 (reversed); 2, occlusal; 4, lingual views. Abbreviations: En: entoconid; Met: metaconid; Meta: metalophulid II. Scale bars: 2 mm.

which is somewhat shallower than the mesoflexid (a feature more clearly seen in lingual view). Thus, as in octodontids, the metaflexid would close before the mesoflexid at a more advanced degree of wear (unlike Echimyidae, where the metaflexid is more persistent than the mesoflexid; Verzi, 1999). A small spur, lower than the other lophids, represents a reduced metalophulid II (see Candela and Rasia, 2012). It arises from the posterior border of the anterolophid at the level of metaconid, and extends by a short distance towards the centre of the anterofossetid.

**Remarks:** CICYTTP-PV-M-1-145 specimen shares with *Plasiacarechimys* the presence of unique combination of features that are diagnostic of this genus (Vucetich and Vieytes, 2006: 83): medium-sized molar, about 50% larger than the largest species of *Acarechimys* Patterson (in Patterson and Wood, 1982), *A. constans* (Ameghino, 1887); lophodont but with well-differentiated cusps in young individuals; metalophulid II (although reduced in CICYTTP-PV-M-1-145) lower than other lophids; with the entoconid and metaconid higher than the rest of tooth. CICYTTP-PV-M-1-145 has the crown higher than in *P. koenigswaldi*; lophids delimited by deeper fossetids; metaconid and entoconid evident but in a lesser degree than in *P. koenigswaldi*; protoconid more labially extended; and metalophulid II more reduced. These features suggest that the

specimen could represent a new species of *Plasiacarechimys*, but it is insufficient at the present time to serve as the basis for a new taxon.

Some features of *Plasiacarechimys*, such as well-developed cusps, presence of metalophulid II, molars with relatively convex walls, and wide and shallow fossetids can be found in other octodontoids as *Acarechimys* (Vucetich and Vieytes, 2006). Note that, according to Vucetich and Vieytes (2006), similarities of *Plasiacarechimys* are great with *Acarechimys*. The latter genus groups very small species (Patterson and Wood, 1982) recorded from the Colhuehuapian up to Laventan (Vucetich et al., 1993; Walton, 1997). Resembling *Plasiacarechimys*, *Acarechimys* shows slight unilateral hypsodonty, convex walls, and well-defined cusps in juveniles (Vucetich and Vieytes, 2006). In *A. minutissimus* (Ameghino, 1887), the smallest species of the genus, the metalophulid II is reduced as in CICYTTP-PV-M-1-145. This specimen resembles in the reduction of the metalophulid II to the m2 of the Colhuehuapian *Acarechimys pulchellus* (Vucetich et al., 2010). However, *Acarechimys pulchellus* is a smaller species, among other features, which allows its differentiation from *Plasiacarechimys*. Again, we consider that the combination of characters observed in the La Juanita specimen allows its attribution to *Plasiacarechimys*, ruling out any other possibility in the context of the present state of knowledge of fossil octodontoids.

History of these rodents was very complex in Patagonia; since their earliest records, during the Oligocene up to the middle Miocene, many genera and species are recognized (Vucetich et al., 2010). Although the understanding of *Plasiacarechimys* affinities are pending integrative phylogenetic analyses, the set of features of this genus indicates closer relationships with Miocene Patagonian octodontoid lineages than with late Miocene “Eumysopinae” with simplified molars (Vucetich and Verzi, 1995). Thus, the new specimen of *Plasiacarechimys* from Paraná represents the most recent record of an indubitable octodontoid related to Patagonian species in Argentina.

#### Family HYDROCHOERIDAE Gill, 1872

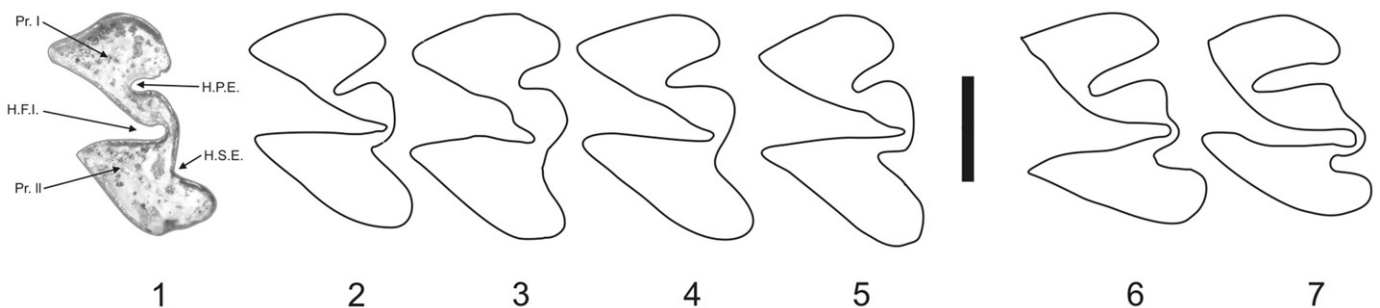
#### Genus *Cardiatherium* Ameghino, 1883

cf. *Cardiatherium* sp. indet.

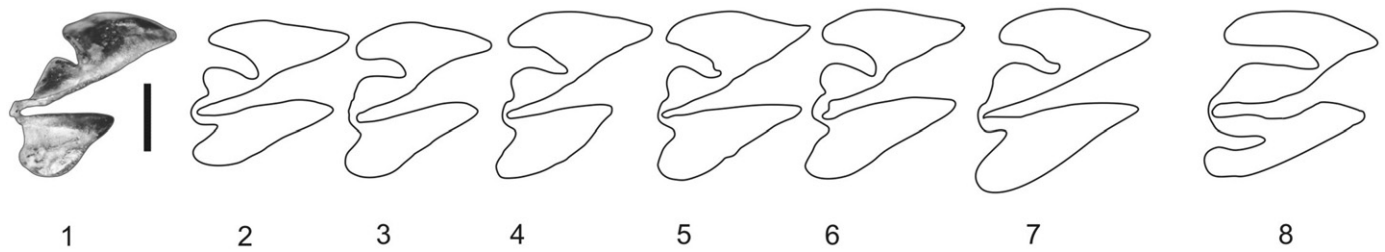
Figs. 4(1) and 5(1)

**Referred materials:** CICYTTP-PV-M-1-147, a left isolated cheek tooth (P4?), and CICYTTP-PV-M-1-148, a right upper cheek tooth (M1-2).

**Description:** CICYTTP-PV-M-1-147 is tentatively identified as a P4 based on the curved anterior side of the prism I and the presence of lobes wider than those of M1-2, especially the anterior of prism I (Pr. I) (Deschamps et al., 2007, 2009). Like *Cardiatherium chasicense* (Pascual and Bondesio, 1968), the primary external flexus (H.P.E.) is relatively shallower than in the Huayquerian



**Fig. 4.** Occlusal views of upper left P4 (or right reversed) of Miocene hydrochoerids: 1. cf. *Cardiatherium* sp. indet., CICYTTP-PV-M-1-147, upper left P4? 2–5. *Cardiatherium chasicense* (modified from Deschamps et al., 2007: fig. 6A–D). 6. *C. orientalis* (modified from Deschamps et al., 2007: fig. 6 E). 7. *C. patagonicum* (modified from Deschamps et al., 2007: fig. 6 F). Abbreviations: H.F.I.: fundamental internal flexus; H.P.E.: primary external flexus; H.S.E.: secondary external flexus; pr.I: prism I; pr.II: prism II. Scale bar: 2 mm.



**Fig. 5.** Occlusal views of right (or left reversed) upper M1-2 of Miocene hydrochoerids: **1.** cf. *Cardiatherium* sp. indet. CICYTTP-PV-M-1-148. **2–7.** *C. chasicoense* (modified from Deschamps et al., 2007: fig. 6 G–L). **8.** *C. patagonicum* (modified from Deschamps et al., 2007: fig. 6 M). Scale bar: 2 mm.

species *Cardiatherium patagonicum* Vucetich, Deschamps, Olivares and Dozo, 2005, *Cardiatherium paranense* (Ameghino, 1883) and *Cardiatherium orientalis* (Francis and Mones, 1965) (Fig. 4(2–7)). As in *C. chasicoense*, the H.P.E. penetrates less than 50% of the total width of Pr. I in CICYTTP-PV-M-1-147, whereas in *C. orientalis* it is up to 55%, and in *C. patagonicum* it is about 60% (Deschamps et al., 2007, 2009). Accordingly, in CICYTTP-PV-M-1-147, as in *C. chasicoense*, the posterior lobule of prism I is relatively smaller than the anterior one and than those of *C. paranense* and *C. patagonicum*. The secondary external flexus (H.S.E.) is shallower than the H.P.E., and the fundamental internal flexus (H.F.I.) is very deep and posterolabially orientated. The prism II (Pr. II) is anteroposteriorly thicker than in *C. patagonicum* and *C. paranense* (which have a more anteroposteriorly compressed Pr. II; Deschamps et al., 2007, 2009), and the posterior lobule behind the H.S.E. is somewhat more labially and posteriorly projected, as in *C. chasicoense*. The small size of CICYTTP-PV-M-1-147 (Table 1) indicates that it likely belongs to a young capybara. This specimen is much smaller than upper cheek teeth of *C. paranense*, *C. patagonicum*, and *C. chasicoense*, being even smaller than known upper cheek teeth of younger (juvenile) specimens of these species (Table 1).

The occlusal pattern of CICYTTP-PV-M-1-148 is similar to that of the species of *Cardiatherium* (Deschamps, 2005; Deschamps

et al., 2007; Fig. 5(2–8)). H.P.E. penetrates into Pr. I less than 50% of the width, a condition similar to that of *C. chasicoense* (Deschamps et al., 2007). H.S.E. is superficial; it is shallower than H.P.E., which is deep and posterolabially orientated. CICYTTP-PV-M-1-148 lacks the cement and it is smaller than adult specimens of *C. chasicoense*, *C. paranense*, and *C. patagonicum* (Vucetich et al., 2005; Deschamps et al., 2007, 2009). Their occlusal apex is smaller than base, which indicates that it is a juvenile specimen.

**Remarks:** In the context of Miocene capybaras, the occlusal design of CICYTTP-PV-M-1-147 is more similar to that of *Cardiatherium* (recorded from the Chasicoan up to Huayquerian ages), especially to that of *C. chasicoense* (Chasicoan age, late Miocene), which is considered the most primitive species of the genus (Deschamps et al., 2007). Thus, for example, the primary external flexus (H.P.E.) in this specimen is shallower, and prism II is thicker and more anteroposteriorly elongated than those of the Huayquerian capybaras *C. patagonicum*, *C. orientalis*, and *C. paranense*. CICYTTP-PV-M-1-147 is also smaller than the known upper cheek teeth of these three species of *Cardiatherium*. Being even smaller than the P4 of PVSJ 537, a young specimen and the smallest known of *C. chasicoense* (Deschamps et al., 2009: table 1; Table 1). Comparing the size of CICYTTP-PV-M-1-147 with the lower cheek teeth size of young *Cardiatherium* specimens, it is even

**Table 1**

Dental measurements (in mm) of upper cheek teeth of Miocene Hydrochoeridae: cf. *Cardiatherium* sp. indet. CICYTTP-PV-M-1-147, CICYTTP-PV-M-1-147, *Cardiatherium chasicoense*, and *C. patagonicum* (data from Vucetich et al., 2005; Deschamps et al., 2007, 2009).

	P4			M1-2		
	APD	AW	PW	APD	AW	PW
cf. <i>Cardiatherium</i> sp. indet. CICYTTP-PV-M-1-147	3.80	2.19	2.26			
cf. <i>Cardiatherium</i> sp. indet. CICYTTP-PV-M-1-148				4.20	2.70	2.90
<i>Cardiatherium chasicoense</i>						
MPEF-PV 740/14	6.88	4.80	6.08			
MPEF-PV 740/22	7.20	4.80	6.24			
MPEF-PV 740/28	9.28	6.56	8.00			
MMP 319-M	8.00	7.20	7.68			
MMP 305-cM	8.64	7.20	7.52			
PVSJ 537	5.91	4.28	6.22			
MMH-CH 88-6-92f	9.28	6.02	7.85			
MMH-CH 88-6-39	9.69	6.32	7.75			
MMH-CH 88-9-71f	9.79	6.12	7.54			
MPEF-PV 740/17				9.92	7.04	8.48
MPEF-PV 740/23				8.00	6.88	7.68
MMP 319-cM				8.16	7.68	8.32
MMP 305 b-M				8.48	6.72	7.68
MMP 305 a-M				9.28	7.20	8.00
PVSJ 537 M1				5.91	4.38	6.12
MMH-CH 87-7-104b				7.85	7.14	7.65
MLP 76-VI-12-98c				8.46	7.14	7.75
MMP 305a-M				9.18	7.55	8.16
<i>Cardiatherium patagonicum</i>						
MPEF-PV 740/8	5.66	5.60	5.84			
MPEF-PV 740/13	5.28	5.44	6.08			
MPEF-PV 740/15	5.12	4.64	5.28			
MPEF-PV 740/16	4.48	3.84	4.32			

APD: anteroposterior diameter; AW: anterior width; PW: posterior width.

smaller than the holotype and the only known specimen (a mandibular fragment with p4–m3) of “*Anchimys marshi*” (Ameghino, 1885). It was recently suggested that the holotype of this species might be a young specimen (newborn?) of *C. paraneense* (Vucetich et al., 2005: 268, table 1). CICYTTP-PV-M-1-147 is comparable in size to the lower m1 of the young specimen MPEF-PV 740/21 (a mandibular fragment with p4–m1), the smallest specimen of *C. patagonicum* (Vucetich et al., 2005). According to these authors, MPEF-PV 740/21 is an unborn specimen because its preserved teeth are only slightly worn (Kraglievich, 1941).

In sum, two features are remarkable in the CICYTTP-PV-M-1-147 specimen: its relatively small size, and its relatively simpler occlusal pattern (expressed especially in a shallower H.P.E.) than those of the Huayquerian species of the genus.

Considering that the number and depth of some flexi display changes associated with the increase of tooth size in capybaras (Vucetich et al., 2005), both size and occlusal pattern of CICYTTP-PV-M-1-147 may be attributed to its juvenile state. Thus, CICYTTP-PV-M-1-147 could be assignable to a young specimen of some species of *Cardiatherium*. However, CICYTTP-PV-M-1-147 shows a worn occlusal surface. This condition suggests that this very small specimen is not a newborn specimen, which would be only slightly worn. In addition, the depth of H.P.I in CICYTTP-PV-M-1-147 is less than 50% of the total tooth width, a diagnostic feature of young and adult specimens of *C. chasicoense* (Deschamps et al., 2009: fig. 5, 20–23).

In this context, it should not be discarded that CICYTTP-PV-M-1-147 represents a new species of *Cardiatherium*, probably closer to *C. chasicoense*, and more primitive and smaller than all known Miocene hydrochoerids. The relatively small size and occlusal pattern as in *Cardiatherium* permit to assign the specimen CICYTTP-PV-M-1-148 tentatively to this genus. As demonstrated by Vucetich et al. (2005) and Deschamps et al. (2007), the occlusal pattern of the species of *Cardiatherium* changes during teeth growing, becoming more complex as the age increases. These studies indicate that the identification of a taxon of fossil capybara based on a single specimen is risky. In this context, it is very difficult to assign the new specimens from Paraná Formation to any previously recognized species of *Cardiatherium*, and it is not possible to determine if the two specimens represent the same or different, new species. In any case, new specimens are potentially very important in understanding dental evolutionary changes and/or ontogenetic processes in the oldest members of this family.

#### Family CAVIIDAE Fischer Von Waldheim, 1817

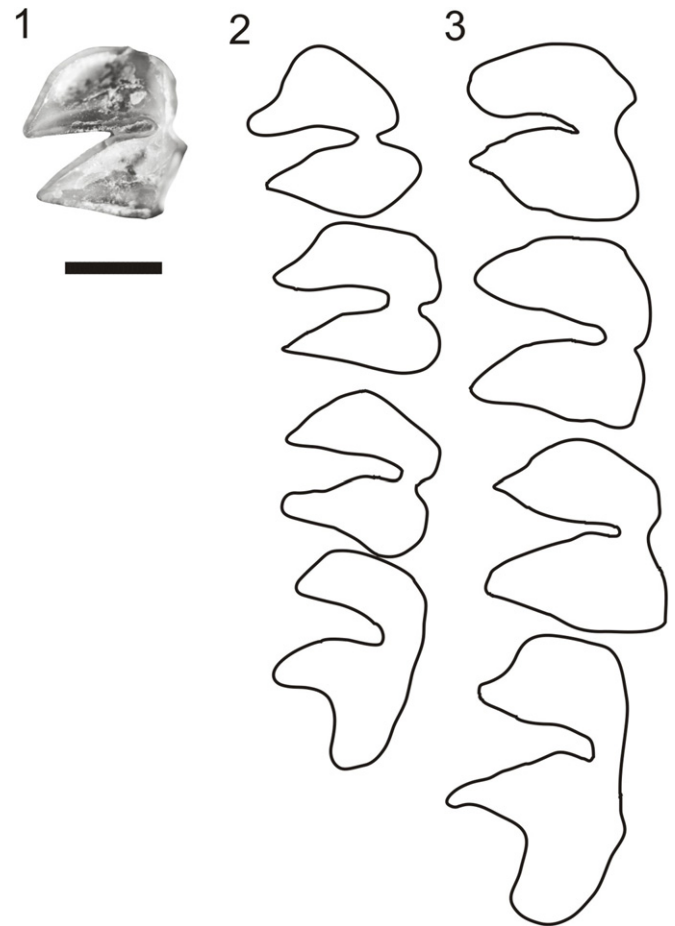
Caviidae gen. and sp. indet.

Fig. 6(1)

**Referred material:** CICYTTP-PV-M-2-267, a left upper M1-2.

**Measurements (in mm):** Length, 3.62; width, 3.30.

**Description:** The molar is similar in size and shape to those of the extinct caviids *Prodolichotis pridiana* Fields, 1957, *Orthomyctera andina* (Rovereto, 1914), and *Orthomyctera rigens* (Ameghino, 1888) (Fig. 6(2, 3)). The anterior prism shows a convex anterior border, and a less curved posterior border; the posterior prism, which is partially broken at the posterolabial portion, displays a posterior border more or less straight and slightly obliquely oriented with respect to the anteroposterior axis of the tooth. Both prisms are separated by a deep lingual flexus (= hypoflexus), which does not reach the labial border of the tooth. A very superficial labial flexus is located more or less opposite to the lingual flexus on the tooth midline, with both prisms connected by a relatively short and wide isthmus. Note that unlike *Guimys unica* and other “eocardiids” (Pérez, 2010), prisms in CICYTTP-PV-M-2-267 have a transverse crest of dentine among other characters shared with caviids.



**Fig. 6.** Occlusal views of upper cheek teeth of extinct caviids: **1.** Caviidae gen. et sp. indet., CICYTTP-PV-M-2-267, left M1 or M2. **2.** *Orthomyctera andina*, type specimen, MACN 8350, P4–M3 series. **3.** *Orthomyctera rigens*, MACN 7319, P4–M3 series. Scale bar: 2 mm.

**Remarks:** CICYTTP-PV-M-2-267 is similar in size and occlusal pattern to those of the smaller Miocene-Early Pliocene previously recognized species of *Orthomyctera* and *Prodolichotis*, such as *O. andina*, *O. rigens*, and *P. pridiana*, but somewhat larger than the two first species and smaller than *P. prisca*. It is smaller than later Pliocene species of either genus *Orthomyctera* and *Prodolichotis*.

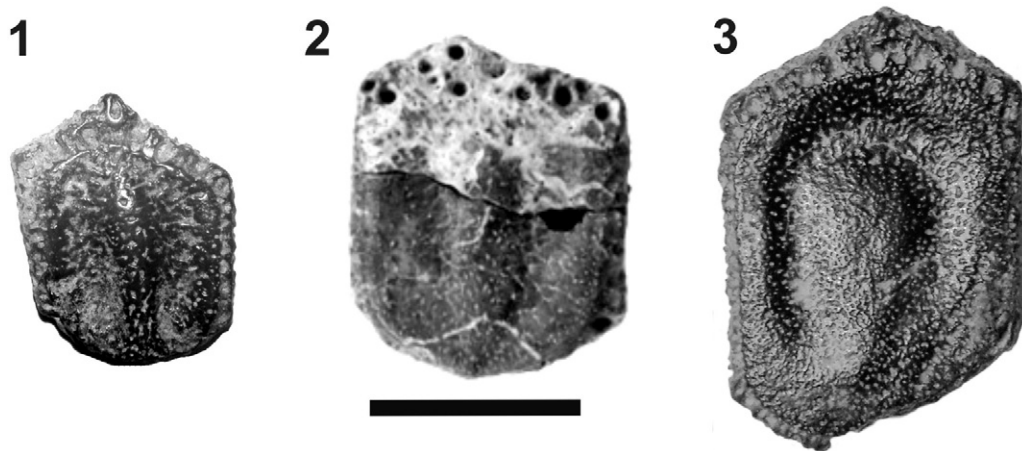
Beyond size, the morphology of this M1 or M2 does not bring diagnostic features in the cited taxa. Indeed, upper dental characters that distinguish *Orthomyctera* and *Prodolichotis* correspond principally to those of the M3 (Kraglievich, 1932). In addition, a great variability is recognized among the Miocene and Pliocene species included in both genera, requiring taxonomical review. This fact prevents assigning an isolated M1-2 to previously recognized genera. Note that the monophyly of Dolichotinae needs to be tested, and *Prodolichotis* has been proposed to belong to Caviinae instead of Dolichotinae. Contrarily, *Orthomyctera* has been excluded from Dolichotinae and included into Caviinae (Quintana, 1997, 1998; Ubilla and Rinderknecht, 2003). In this context, the composition of the traditionally recognized Dolichotinae and Caviinae must be revised. Consequently, a taxonomical revision of these rodents and more complete material are necessary before establishing the generic and subfamily status of the specimen CICYTTP-PV-M-2-267.

Order XENARTHRA Cope, 1889

Family PAMPATHERIIDAE Paula Couto, 1954

Genus **Scirrotherium** Edmund and Theodor, 1997





**Fig. 7.** Fixed osteoderms of pampatheriids: 1. *Scirrotherium* sp. indet., CICYTTP-PV-M-1-144. 2. *Scirrotherium* sp., MEPF-PV 2529 (from Dozo et al., 2010). 3. *Kraglievichia* sp., MLP 69-IX-8-13. Scale bar: 20 mm.

**Type species:** *Scirrotherium hondaensis* Edmund and Theodor, 1997

*Scirrotherium* sp. indet.

Fig. 7(1)

**Referred material:** CICYTTP-PV-M-1-144, a fixed osteoderm.

**Description:** CICYTTP-PV-M-1-144 is a fixed osteoderm sub-hexagonal in outline, comparable in size to *Scirrotherium*. As in the latter, it presents a simple anterior row of foramina forming a posteriorly concave arch; the central figure (= axial elevation) is relatively narrow, elongated, and delimited by shallow grooves (Edmund and Theodor, 1997; Góis and Scillato-Yané, 2010); the sub-marginal bands are well developed and separated anteriorly from the central figure. In contrast, the axial elevation is wider in *Kraglievichia* and limited by deeper grooves.

**Remarks:** The Miocene pampatheres (Fig. 7(2, 3)) are relatively well represented during the “Mesopotamian” (= “Conglomerado osífero”, base of Ituzaingó Formation, late Miocene) by *Kraglievichia paranensis* (Fig. 7(3)), a relatively common species in this unit. Recently, Góis and Scillato-Yané (2010) identified a new species of *Scirrotherium* from the “Mesopotamian”, which was mentioned previously by Cione et al. (2000). *Scirrotherium hondaensis*, the type species, was recorded at the middle Miocene Honda Group from La Venta, Colombia (Edmund and Theodor, 1997). *Scirrotherium* sp. was also identified in Huayquerian sediments from upper levels of Puerto Madryn Formation (Península Valdés, Chubut; Dozo et al., 2010; Fig. 7(2)). Features described above and identified in the CICYTTP-PV-M-1-144 specimen justify its assignment to *Scirrotherium* (Góis and Scillato-Yané, 2010), but the scarce available material does not indicate its specific status.

Class AVES Linnaeus, 1758

Family PHOENICOPTERIDAE Bonaparte, 1831

Genus **Phoenicopterus** Linnaeus, 1758

cf. *Phoenicopterus* sp. indet.

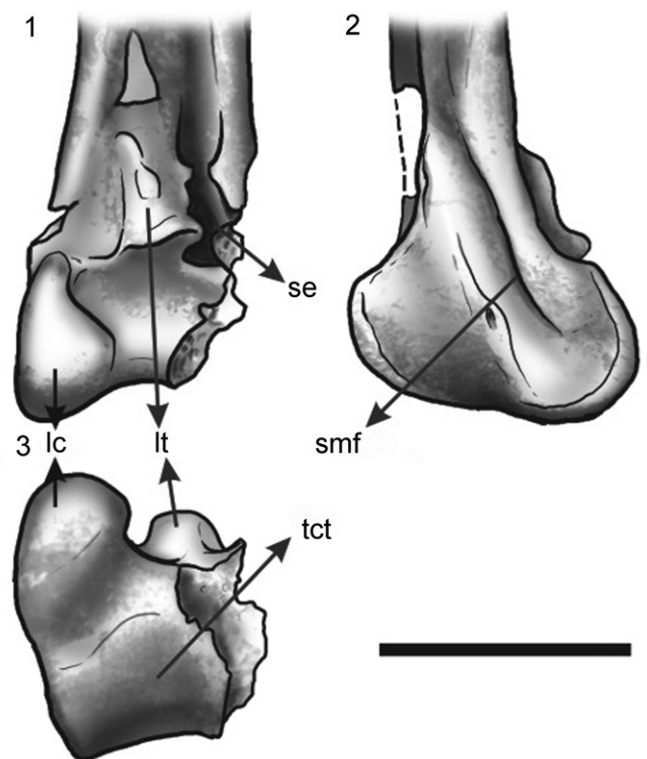
Fig. 8

**Referred material:** CICYTTP-PV-A-1-12, fragment of shaft with distal end of left tibiotarsus.

**Measurements (in mm):** Preserved length (from distal end of crista fibularis to condyles), 280; width of midshaft, 14.85; depth of midshaft, 9.15; distal width (estimated), ca. 19; depth of lateral condyle, 20.85.

**Description:** The overall morphology of this partial tibiotarsus resembles those of the species of modern flamingos, *Phoenicopterus chilensis* Molina, 1782 and *Phoeniconaias minor* (Geoffroy Saint Hillaire, 1798), but it is very much larger. Shaft is longer and

proportionally wider along its preserved extent, making the bone more robust. The condylus lateralis is less directed laterally with respect to the border of shaft than in *P. chilensis*. The morphology of the epicondylus lateralis and the sulcus m. fibularis, as well as that of the tuberculum retinaculi m. fibularis, is similar to *P. chilensis*. The depressio epicondylaris lateralis is somewhat larger and shallower than in *P. chilensis*. The distal depression located between the external margin of the trochlea cartilaginis tibialis and the proximal end of the posterior border of the condylus lateralis is large and oval, whereas it is a more reduced surface in *P. chilensis*, being more elliptical and transversally placed. Although both borders of the trochlea cartilaginis tibialis are eroded, it is evident that the trochlear surface is much less concave than in



**Fig. 8.** cf. *Phoenicopterus* sp., CICYTTP-PV-A-1-12, fragment of shaft with distal end of left tibiotarsus: 1. Anterior; 2. Lateral; 3. Distal views. Abbreviations: lc: lateral condyle; lt: tubercle lateral to pons supratendineus; se: sulcus extensorius; smf: sulcus m. fibularis; tct: trochlea cartilaginis tibialis. Scale bar: 5 mm.

*P. chilensis*. The tubercle lateral to pons supratendineus is prominent and similar to that of *P. chilensis*. The sulcus extensorius is deeper than in *P. chilensis*. The shaft margins, limiting the facies cranialis, which contains the anterior tibiotarsal groove, are well marked. The crista fibularis is not present at the level where the shaft is broken. The posterior tibiotarsal groove is slightly insinuated from the distal half of the shaft onwards, as in *P. chilensis*, making its medial border rather more prominent caudally than the lateral one.

**Remarks:** The isolated, fragmentary, and eroded state of this tibiotarsus rules out its accurate systematic assignment beyond the generic level. It can be referred to the family Phoenicopteridae, which includes modern flamingos, and excluded from Palaeodidae, a plesiomorphic taxon of Tertiary flamingo-like birds, by the following characters: tubercle lateral to pons supratendineus prominent, trochlea cartilaginosa tibialis without a median crest, and distal fossoids behind condyles not deeply excavated (Alvarenga, 1990). Although the distal end of this bone lacks important diagnostic information, its size is within the range of the largest living species included in *Phoenicopterus* (*P. ruber* Linnaeus, 1758), and very much larger and robust than those of other genera, e.g., *Phoeniconaias* Gray, 1869 and *Phoenicoparrus* (Bonaparte, 1856).

Tertiary records of phoenicopterids from South America are restricted to the Late Miocene–Pliocene of Argentina and Uruguay (Ubilla et al., 1990) and Late Oligocene of Brazil (Alvarenga, 1990). All these fossil specimens belong to the genus *Phoenicopterus* or were referred to indeterminate Phoenicopteridae. Thus, the tentative assignment of the tibiotarsus from Paraná Formation to cf. *Phoenicopterus* seems to be the best-supported hypothesis.

## 5. Discussion

### 5.1. Chronology

The outcrops of the Paraná Formation are the lithostratigraphical expression, in the Chaco-Paraná Basin, of the so-called “Paranense Sea” (Aceñolaza and Aceñolaza, 2000; Hernandez et al., 2005). The first contributions to the geology and paleontology of the Paraná Formation date back to the Nineteenth Century when D’Orbigny (1842), Darwin (1846), and Bravard (1858), among others, referred this unit to the Tertiary *sensu lato*. Later, Burmeister (1876) assigned the age of the Paraná Formation to the Upper Tertiary, whereas Döering (1882) and Ameghino (1889, 1891, 1906) correlated it to the Oligocene. Von Ihering (1907) and Rovereto (1914) considered the Paraná Formation as Miocene in age. Frenguelli (1920) referred the basal levels of this formation to the Upper Miocene and the upper levels to the Pliocene. Since then, age attributions have ranged mainly between Middle (e.g., Aceñolaza, 2000; Aceñolaza and Aceñolaza, 2000; Del Río, 2000) and Late Miocene (e.g., Frenguelli, 1920; Camacho, 1967; Aceñolaza, 1976; Zabert, 1978; Cione et al., 2000).

The Paraná Formation, along the lower part of the Paraná River at the southern Paraná Basin, is overlain by fluvial sediments of the Ituzaingó Formation (Cione et al., 2000). So, the deposition of the latter began after the withdrawal of the “Paranense Sea” in the Mesopotamian area. The age of the vertebrate assemblage found in the “Conglomerado osífero” or “Mesopotamiense”, exposed at the base of the Ituzaingó Formation, was assigned to the Huayquerian stage/age (Late Miocene; Cione et al., 2000; Cozzuol, 2006). The Huayquerian is presently placed approximately between < 7 my (ca. 6.8 my) and 8.7 my (Fig. 2(1)). Consequently, continental vertebrates from upper levels of the Paraná Formation at La Juanita locality, coeval with at least the final phases of the regression of the “Paranense Sea”, are older than those from the “Conglomerado osífero”. They would be “pre-Huayquerian” in age, i.e., older than 8.7 Ma.

In the context of the late Miocene continental units, the “Mesopotamiense” mastofauna postdates the mammal assemblage coming from the Arroyo Chasicó Formation (defining the Chasicóan stage/age; Fig. 2(1)) that is exposed south in the Pampean region (Buenos Aires Province; Zárate et al., 2007). In the Mesopotamian area there are no deposits corresponding to the Chasicóan stage/age. At least in some localities, such as Vivero Von Humboldt (Zárate et al., 2007), deposits of the Arroyo Chasicó Formation overlie the Miocene marine sediments of Barranca Final Formation (Malumián, 1978). This fact agrees with the hypothesis that the start of Chasicóan sedimentation is placed after the general withdrawal of the Miocene Atlantic transgression (Pascual et al., 1996). In turn, Chasicóan sediments were interpreted as overlain by Huayquerian fauna-bearing deposits (Cione et al., 2000). Consequently, the continental vertebrate assemblage from the Arroyo Chasicó Formation is the oldest from the southern of the Pampean region in central Argentina (Zárate et al., 2007). Based on radiometric, stratigraphical, and magnetostratigraphical data, Zárate et al. (2007) interpreted that the Chasicóan would range approximately between ca. 8.7 my and probably > 10 my.

It is possible that the continental vertebrates from the Paraná Formation can be correlated to those reported in sediments of the Arroyo Chasicó Formation. If vertebrates from upper levels of the Paraná Formation were coeval with the “Paranense Sea”, and the Chasicóan sediments were deposited once the sea withdrew, a “pre-Chasicóan” age for these vertebrates should not be rejected. Future geochronological data from the Paraná Formation and new fossil collections from the Arroyo Chasicó Formation with accurate stratigraphy (Zárate et al., 2007) are necessary to test these hypotheses of correlation.

The “pre-Huayquerian” age attributed herein to the vertebrate-bearing sediments of the Paraná Formation at La Juanita agrees with the biochrons of the continental mammal taxa recovered from that locality. The pampatheriid *Scirrotherium* is reported in the Middle Miocene of La Venta (Honda Group, Colombia), in the “Conglomerado osífero” of the Ituzaingó Formation, and in the upper levels of the Puerto Madryn Formation. Hydrochoerids are firstly recorded at the Chasicóan stage/age, and caviids have their oldest records in the Middle Miocene of La Venta (Walton, 1997) and Bolivia (Croft et al., 2011), and in Argentina in the Chasicóan stage/age.

Regarding other Miocene marine units, the Paraná Formation was correlated with the Puerto Madryn Formation (Northeastern Patagonia, Chubut Province, Argentina; Aceñolaza, 2000). Recently, continental vertebrate-bearing sediments were reported at Península Valdés (Chubut Province) from upper levels of the Puerto Madryn Formation; on the basis of their fossil mammal content, they were attributed to the Huayquerian age (Dozo et al., 2010). If the temporal assignment suggested above for the Paraná Formation upper levels at La Juanita is confirmed, the latter may be older than the upper levels of the Puerto Madryn Formation at Península Valdés.

Others units in Argentina were recognized as representatives of the Paranense transgression, such as Barranca Final Formation at Colorado basin (de Visconti et al., 2003) and the Salí, Anta, and Palo Pintado formations at Andean and adjacent sites (Aceñolaza, 2000; Hernandez et al., 2005). Accessible data are not sufficient to correlate accurately these units or to show if they correspond to different floodings during the Middle-Late Miocene times (Hernandez et al., 2005; Latrubesse et al., 2010).

### 5.2. Paleogeographical context and biogeography

The “Paranense Sea” corresponds to one of the most significant Atlantic marine transgressions across a great part of southern South America during the Neogene (Uliana and Biddle, 1988;



Räsänen et al., 1995; Webb, 1995; Aceñolaza, 2000, 2004; Hernandez et al., 2005). In Argentina, this transgression spread over most of the Chaco-Paraná Basin from Mesopotamia to the Andes foothills, covering the northeastern Patagonia (Alonso, 2000; Aceñolaza, 2000, 2004). To the east, the “Paranense Sea” was limited by the Altos de Asunción (Asunción High; Fernandez Garrasino and Vrba, 1999), which extends from Paraguay southward along the Argentinian provinces of Misiones, Corrientes, and Entre Ríos (Fig. 1(1)). Consequently, most of the Middle-Late Miocene terrestrial vertebrates lived under the influence of this extensive transgression, but its effect on the geographical distribution patterns and evolution has not been intensively explored. Therefore, the new specimens reported from the Paraná Formation, which are the first records of continental vertebrates on the oriental emergent border of the “Paranense Sea”, become significant in this matter.

The “Paranense Sea” completely separated lands of northeastern Argentina (Mesopotamia) from those of northwestern Patagonia (e.g., Colloncuran fauna; Fig. 1(1)). Continental biota of these areas would have diverged and evolved under different climatic conditions, in accordance with their latitudinal locations (Pascual et al., 1996). In Patagonia, several taxa of octodontoid rodents are identified during the Oligocene-Middle Miocene (Vucetich and Kramarz, 2003; Vucetich et al., 2010). Octodontoids such as *Acarechimys*, *Plesiacharechimys*, and *Acaremyidae*, together with other groups, are members of the first great radiation of caviomorphs in South America (*sensu* Vucetich et al., 1999). Records of *P. koenigswaldi* (Colloncuran, Patagonia) and *Plesiacharechimys* nov. sp.? from Paraná may express the vicariant event of the marine transgression that promoted the splitting of the geographical range of ancestral *Plesiacharechimys*. *Plesiacharechimys* nov. sp.? represents the last survivor, at least at southern South America latitudes, of the Oligocene-Middle Miocene radiation of octodontoid rodents. There are no records of this radiation during the Chasicuan stage/age. Contrarily, during Chasicuan and Huayquerian times, “modern” octodontoids, as Octodontidae and Eumysopinae (Echimyidae) are firstly recorded (Vucetich et al., 1999).

Besides the “modern” octodontoids, new lineages of rodents are registered for the first time in Argentina from sediments of Chasicuan and Huayquerian units (e.g., Arroyo Chasicó, Andalhuala, Ituzaingó formations; Cione et al., 2000; Candela, 2005), including Hydrochoeridae “Cardiatheriinae” and Cardiomyinae, Caviidae, Abrocomidae, giant Neoepiblemidae, and Dinomyidae Eumegamylinae; they constitute the second radiation of caviomorphs (*sensu* Vucetich et al., 1999). This radiation expresses the emergence of new morphological occlusal patterns, which are already clearly identified in the cavioids recorded from the Paraná Formation. Capybaras and caviids from this unit, together with those from the Chasicuan, represent the first stages of the radiation of these rodents at the latitude of the Entre Ríos Province in the context of the whole South American subcontinent. Mesopotamian area during the late Miocene could be the center of the evolution of hydrochoerids (at present associated with water bodies in humid and warm conditions; see next Section). Since the withdrawal of the sea, Hydrochoeridae and Caviidae developed an important taxonomical richness in central and northern Argentina during the Late Cenozoic, being well represented in the “Conglomerado osífero” (Candela, 2005). Development of new environments seems to be necessary to understand the beginning of the second Caviomorph radiation at these latitudes, and the compositional and distributional changes evidenced in diverse mammalian lineages (Pascual et al., 1996; Candela, 2004, 2005; Candela and Morrone, 2003).

Final regressive stages of the “Paranense Sea” were linked to the formation of the pre-Paraná river, which drained into this sea, or into marginal lagoons or marshes (Aceñolaza, 2004). Remarkable

physical changes with establishment of the pre-Paraná river surely affected aquatic, semi-aquatic, and terrestrial communities that inhabited close to the fluvial system. During the development of this fluvial system, the northern ecosystem advanced southward and eventually reached the Mesopotamian area (Cozzuol, 2006: 193). The shared species of aquatic vertebrates between the Mesopotamian (“Conglomerado osífero”) and Acre (Solimões Formation; Late Miocene) regions support the existence of a continuous aquatic connection that allowed faunal interchanges between them during the Late Miocene (Cozzuol, 2006).

Such environmental changes and migration events could promote processes of speciation and extinction. Rapid change and removal of habitats, favored by immigrant species, granted increasing propensities of extinction in caviomorphs of the first radiation. Likewise, fragmentation of habitats could result in new opportunities for speciation by geographical isolation of populations. The relatively high diversity of vertebrates identified from the “Conglomerado osífero” (Cione et al., 2000; Candela, 2005; Cozzuol, 2006) is consistent with important speciation events in such varying types of habitats. Since the retraction of the “Paranense Sea”, various local environmental factors seem superimposed on the general cooling trend and extension of plains inferred as predominant during the late Miocene in southern South America (Pascual et al., 1996). Continental vertebrates from the Paraná Formation, although poorly known, reflect this dynamic history of Mesopotamia during the late Miocene. Future findings turn out to be promising to achieve a better comprehension of this complex evolutionary and biogeographical scenario.

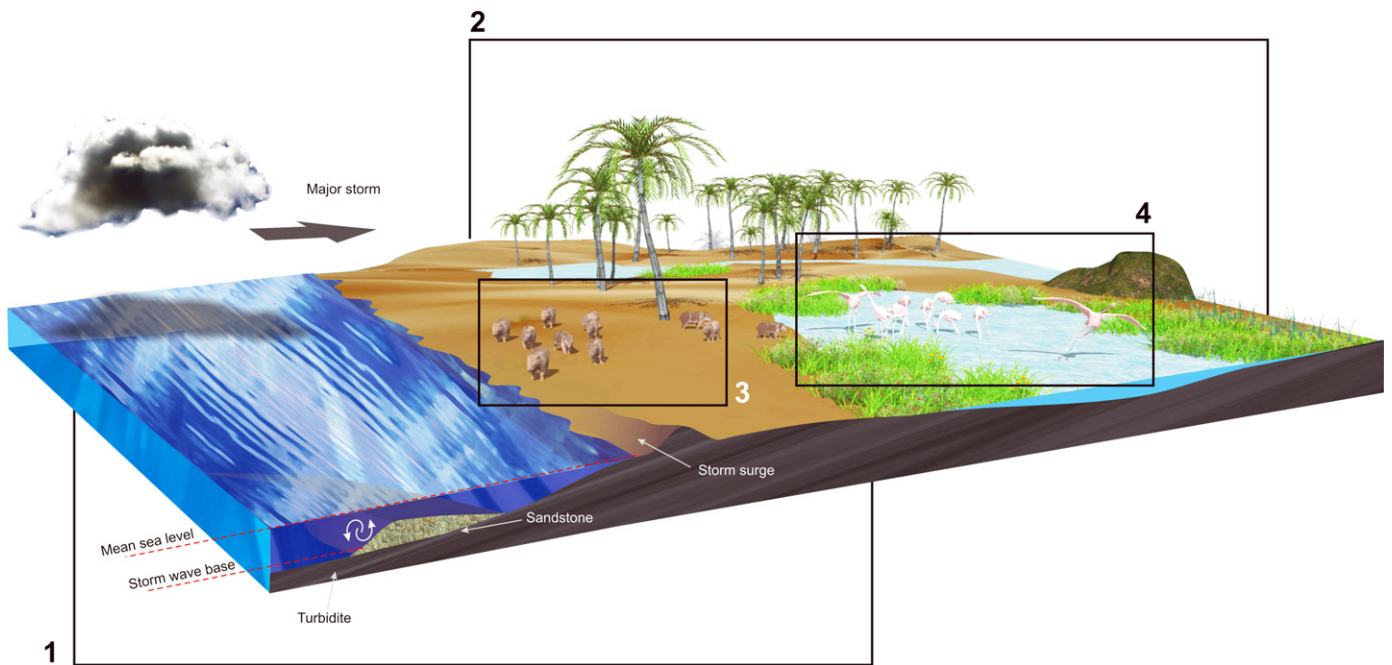
### 5.3. Paleoenvironments

Different studies concluded that the upper levels of the Paraná Formation correspond to marine shallow environments developed near the coast, with influence of continental drainage deposited under tropical to subtropical-temperate conditions (e.g., Aceñolaza, 1976; Herbst and Zabert, 1987; Marengo, 2000; Aceñolaza, 2000, 2004). The ichnofauna recovered at Cantera Cristamine (Aldea Brasileira locality), which is located approximately 3 km east from La Juanita site, suggests an intermareal environment (Aceñolaza and Aceñolaza, 2000). A phytolith association found in marine sediments exposed at Puerto General Alvear locality (approximately 15 km south from La Juanita), is indicative of a depositional environment characterized by an alluvial plain where terrestrial and fluvial communities coexisted, alternating with cyclical marine incursions (Zucol and Brea, 2000).

From the sedimentological information obtained at Arroyo Antónico profile, approximately 20 km north of La Juanita locality, a calm depositional environment with little transport and placed near the coast is inferred (Iriando, 1973). The profile of Villa Urquiza is similar to the latter, but alternating sedimentation in suspension with carrying currents of sands, being the energetic variations of the depositional agent influenced by marine currents (Iriando, 1973).

Particularly, the genesis of the fossiliferous level at La Juanita locality can be attributed to a storm event (Cione et al., 2008; Pérez, 2010). Taphonomy of collected specimens, including preservation of the extremely fragile tibiotarsus of flamingo, shells of mollusks without significant transport and with ligament conjoining both valves (Pérez, 2010), and conservation of delicate lamella (Cione et al., 2008), indicate that they did not suffer transport for long distances and were probably deposited during short episodes of high energy. Likewise, the preservation rules out the possibility that specimens were eroded out and redeposited, and the faunistic association was probably contemporary (Cione et al., 2008).

In sum, the available information indicates that the upper levels of the Paraná Formation at La Juanita correspond to a littoral



**Fig. 9.** 1. Sedimentary dynamics of the storm deposits that formed the fossiliferous levels of the Paraná Formation at La Juanita locality. 2. Paleoenvironmental reconstruction based on paleobotanical (Zucol and Brea, 2000) and geological data (Iriondo, 1973; Aceñolaza, 2004). 3. Hydrochoerids. 4. Flamingos.

marine environment (Fig. 9) containing a storm deposit with mixture of marine and continental fauna (as sharks, whales, continental and amphibiotic fishes, and mollusks typical of the marine littoral). Terrestrial vertebrates are the contribution of streams or rivers to the marine environment from the backshore or nearby inlands.

The depicted scenario is consistent with inferred environmental preferences of some vertebrates here studied. Assuming similar metabolic and ecological requirements, the extinct capybaras, like living species, possibly habited areas close to water bodies developed under warm and humid conditions (Deschamps et al., 2007). The preferred habitats of living flamingos are saline lagoons, mudflats, and shallow brackish coastal or inland lakes. The first two environments, i.e., shallow salt or brackish water bodies separated from the deeper sea by a barrier beach or sandbank, or a coastal wetland formed by deposition of mud by tides or rivers, are in accordance with the geologic data of the Paraná Formation at La Juanita and its nearby localities (e.g., Cantera Cristamine, Puerto General Alvear).

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