



Capybaras (Rodentia: Hystricognathi: Hydrochoeridae) from the late Pleistocene of southern Brazil

Leonardo Kerber and Ana Maria Ribeiro

With 9 figures and 2 tables

KERBER, L. & RIBEIRO, A.M. (2011): Capybaras (Rodentia: Hystricognathi: Hydrochoeridae) from the late Pleistocene of southern Brazil. – N. Jb. Geol. Paläont. Abh., **261**: 1–18; Stuttgart.

Abstract: The Hydrochoeridae are caviomorph rodents of medium to large size. They are euhypsodont and elasmodont, with a peramorphic trend to increase the number of M3 prisms from basal to advanced taxa. The diversity of this family was higher during the Miocene/Pliocene, but today they are represented by a single genus, with two species, *Hydrochoerus hydrochaeris* (LINNAEUS, 1766) and *H. isthmius* GOLDMAN, 1912. In this paper we described fossil remains assigned to *H. hydrochaeris* from Touro Passo Creek (Touro Passo Formation, upper Pleistocene, Lujanian Age) in western Rio Grande do Sul State, southern Brazil. The main characters used to assign these specimens to *H. hydrochaeris* are: M3 with 13 free prisms, upper diastema shorter than the maxillary cheek teeth, rostral area relatively wide, smaller proportions than *Nechoerus* HAY, 1926 and larger than *H. isthmius*. The presence of *H. hydrochaeris* suggests that in late Pleistocene of western Rio Grande do Sul State, probably existed environments with permanent water bodies.

Key words: Caviomorpha; hydrochoerids; *Hydrochoerus hydrochaeris*; Quaternary; Touro Passo Formation; Rio Grande do Sul State.

1. Introduction

The Hydrochoeridae (GRAY, 1825) GILL, 1872 are caviomorphs of medium to large size and, together with the Dinomyidae ALSTON, 1876 and Neopiblemidae KRAGLIEVICH, 1926, they are the largest members of Rodentia (MONES 1991). According to MONES (1984), the hydrochoerids have a long skull, laterally compressed (not including the zygomatic arches), with the paroccipital process and masseteric crest [horizontal crest *sensu* PÉREZ & WALTON 2008] well developed, and the dentary with reduced coronoid process. Capybaras are euhypsodont and elasmodont, with a para-

morphic trend to increase the number of M3 prisms from basal to advanced taxa. The diversity of this family was higher during the Miocene/Pliocene. However, as most of the taxa were described on the basis of few and fragmentary specimens this diversity has been contested. Recent studies analyzing the variation, mainly ontogenetic, have shown that several of the proposed taxa were different ontogenetic stages of a small number of species (VUCETICH et al. 2005; DESCHAMPS et al. 2007). Today, Hydrochoeridae is represented by a single extant genus, *Hydrochoerus* BRISSON, 1762, with two species, *H. hydrochaeris* (LINNAEUS, 1766) and *H. isthmius* GOLDMAN, 1912 (MONES & OJASTI 1986).

The phylogenetic relationships of hydrochoerids with other Caviioidea *s.s.* KRAGLIEVICH, 1930 are not completely elucidated. Some authors suggest that the Hydrochoeridae are derived from the Eocardiidae AMEGHINO, 1891, while other suggest a closer relationship with the caviids Cardiomyiinae KRAGLIEVICH, 1930 (see MONES 1991; VUCETICH *et al.* 2005). Traditionally, the family was composed by four subfamilies: the Cardiatheriinae KRAGLIEVICH, 1930, Protohydrochoerinae KRAGLIEVICH, 1930, Anatochoerinae MONES & VUCETICH (in MONES 1991) and Hydrochoerinae (GRAY, 1825) WEBER, 1928, *sensu* KRAGLIEVICH, 1930. However, in the cladistic analysis of PRADO *et al.* (1998) the Cardiatheriinae appears as paraphyletic, Anatochoerinae as polyphyletic, Protohydrochoerinae and Hydrochoerinae as monophyletic groups. According to VUCETICH *et al.* (2005) the subfamily “Cardiatheriinae” has no phylogenetic meaning and should be abandoned, and the “Anatochoerinae” must be reanalyzed.

Fossil records of Hydrochoerinae have been recognized since the late Pliocene (PASCUAL *et al.* 1966). They have medium to large size, M3 with a variable number of prisms (between 12 and 18) separated in labial face, m2-3 with hpi (primary internal flexid) always open in labial view, m3 with 6 plates and incisor with labiomedial groove, but unstable in some cases of *Nechoerus* HAY, 1926 (MONES 1984). They are the only members of the family dispersed in the three Americas. After the formation of the Isthmus of Panama, they arrived in North America. The earliest fossil records of this continent are from the late Pliocene (AHEARN & LANCE 1980).

The present paper provides a description and comparison of the fossil remains of hydrochoerids from the late Pleistocene of Rio Grande do Sul State, southern Brazil and discusses aspects on their palaeoenvironmental significance.

2. Material and methods

The remains are new specimens, except of MCPU-PV 047 that was previously reported, but not described and compared (KERBER & OLIVEIRA 2008a). The materials here studied are from the collections of Pontifícia Universidade Católica do Rio Grande do Sul, Uruguaiiana (MCPU-PV) and Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN-PV). The cranial remains were compared to *Nechoerus* sp. UNSGH 645, *Nechoerus* cf. *N. aesopi* MHD-P 273 and to 31 extant specimens of *H. hydrochaeris* (Table 1-2). The extant specimens were classified in the age classes ranging from 0 to 4 according to OJASTI (1971) and MONES (1991). The criterion is based on the degree of fusion of the basicranium bones. The femur was compared with specimens of *H. hydrochaeris* (MCN-

M 050, 2679, 2727). The systematics follows MONES (1991); anatomical nomenclatures follow MONES (1991) and PÉREZ & WALTON (2008). The tooth nomenclature is given in Spanish. The measurements were taken with a caliper accurate to 0.05 mm and are expressed in millimeters.

Institutional abbreviations: MCPU-PV, Coleção de Paleovertebrados do Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Uruguaiiana; MCPU-M, Coleção de Mastozoologia do Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Uruguaiiana; MCN-PV, Coleção de Paleovertebrados do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul; MCN-M, Coleção de Mastozoologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul; MHD-P, Museo Histórico Departamental de Artigas; UNSGH, Universidad Nacional del Sur, Geología Histórica.

Anatomical abbreviations: Skull - AL, alisphenoid; lp, lacrimal process; BS, basisphenoid; BO, basioccipital; enc, external nuchal crest; BUL, bullae; SQ, squamosal; mf, masseteric fossa; gf, glenoid fossa; FR, frontal; LA, lacrimal; MX, maxilla; PA, parietal; ip, incisor process of premaxilla; PAL, palatine; PM, premaxilla; pop, postorbital process; zps, zygomatic process of squamosal; dzr, dorsal zygomatic root; vzr, ventral zygomatic root; fps, frontoparietal suture. Dentary - hc, horizontal crest; mfn, mental foramen; mf, masseteric fossa; ap, angular process; ia, incisor alveolus; sy, symphysis. Dentition - P4, fourth upper premolar; M1, first upper molar; M2, second upper molar; M3, third upper molar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar; Pr. I-XIII, prisms of upper cheek teeth; HPE, primary external flexus; HSE, secondary external flexus; HFI, fundamental internal flexus; pr. I-II, prisms of lower molariforms; pr. Ia, anterior plate of pr. I; pr. Ib, posterior plate of pr. I; pr. IIa', posterior plate of pr. IIa; pr. IIa'', anterior plate of pr. IIa; pr. IIb', posterior plate of pr. IIb; pr. IIb'', anterior plate of pr. IIb; hse, secondary external flexid; hfe, fundamental external flexid; hpi, primary internal flexid; hsi, secondary internal flexid; hti, tertiary internal flexid; pr.s.a, anterior secondary prism. Femur: he, head; lt, lesser trochanter, ne, neck.

Measurements: The cranial measurements 1, 2, 3, 4, 7, 9, 17, 18, 19, 20, 21, 22, 23, 24 and of dentary 3, 4, 5, 6, 7, 8, 9, 10 were taken according to MONES (1991) and the cranial 8, 11, 14 according to DESCHAMPS (1998). The other measurements were adapted according to the structures present in the fossil specimens (Fig. 1). The dental measurements were taken in the alveolus, because the teeth are often absent in comparative specimens. Cranial measurements: 1. Total length of the skull; 2. Length of upper diastema, between the mesial face of P4 alveolus and the lingual face of I; 3. Length of the alveolar P4-M3 series; 4. Width of skull between the lacrimal processes; 5. Rostral width, in the anterior area of nasal cavity; 6. Length of frontal, in the sagittal line; 7. Width of the interorbital constriction; 8. Intraorbital length, between the lacrimal (below the lacrimal process) and the squamosal; 9. Width of upper diastema, at the level of premaxillary-maxillary suture; 10. Maximum width of

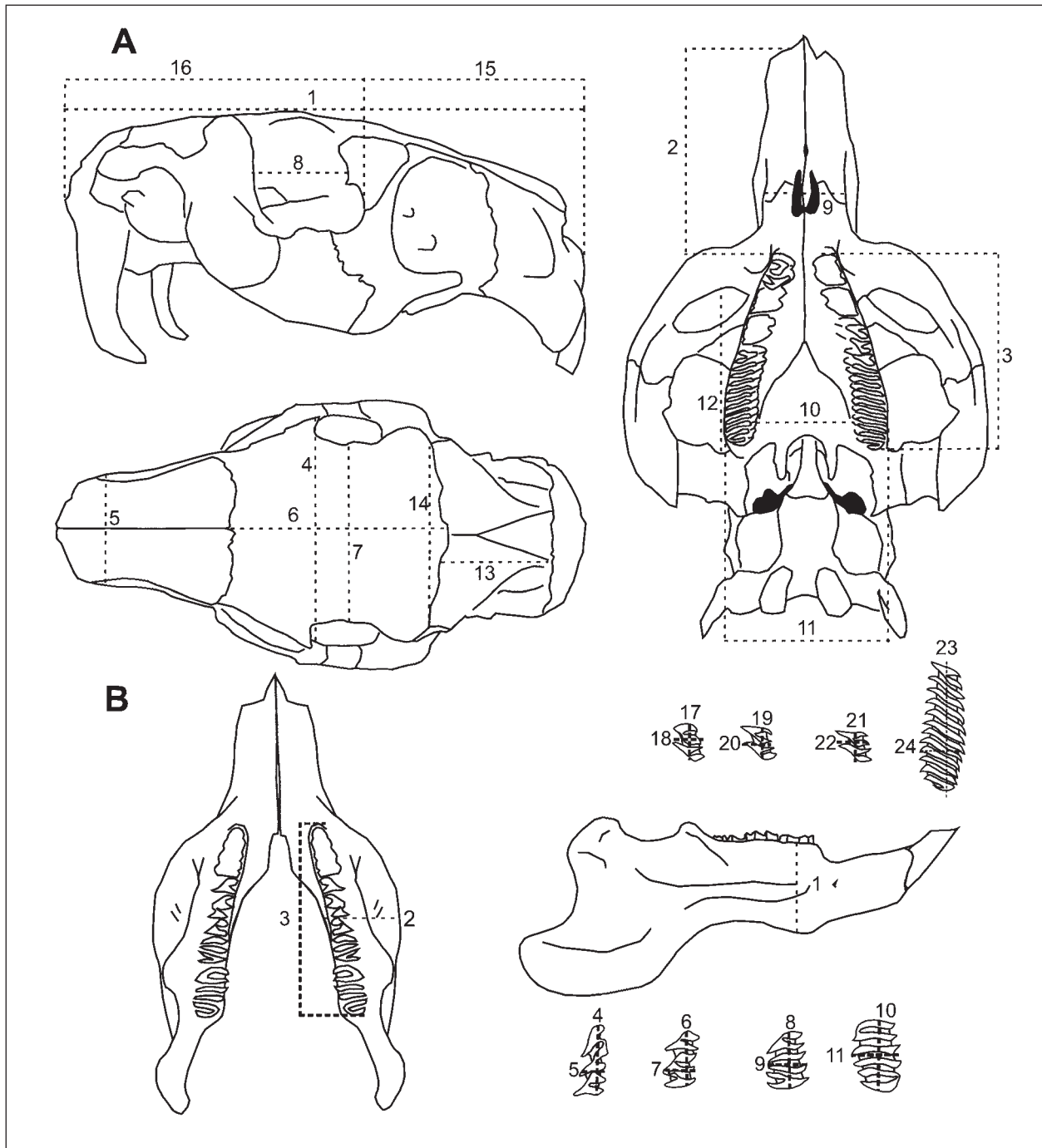


Fig. 1. Measurements used for comparison with living *H. hydrochaeris*. A – Skull and upper cheek teeth; B – dentary and lower cheek teeth.

palatine, at the level of Pr. IX of M3; 11. Maximum width of palatal area, at the level of Pr. XI of M3; 12. Distance between the ventral zygomatic root and zygomatic process of squamosal; 13. Length of parietal, taken in the parasagittal line; 14. Length of frontoparietal suture; 15. Length of rostral area, between the lowest point of the lacrimal and the anterior area of premaxilla; 16. Length of cranial portion,

between the lowest point of the lacrimal and the occipital; 17. Mesiodistal length (MDL) of P4 alveolus; 18. Linguolabial width (LLW) of P4 alveolus; 19. MDL of M1 alveolus; 20. LLW of M1 alveolus; 21. MDL of M2 alveolus; 22. LLW of M2 alveolus; 23. MDL of M3 alveolus; 24. LLW of M3 alveolus. Dentary: 1. Maximum height of the body of dentary, at the level of p.r. s. a.; 2. Width of dentary, taken be-

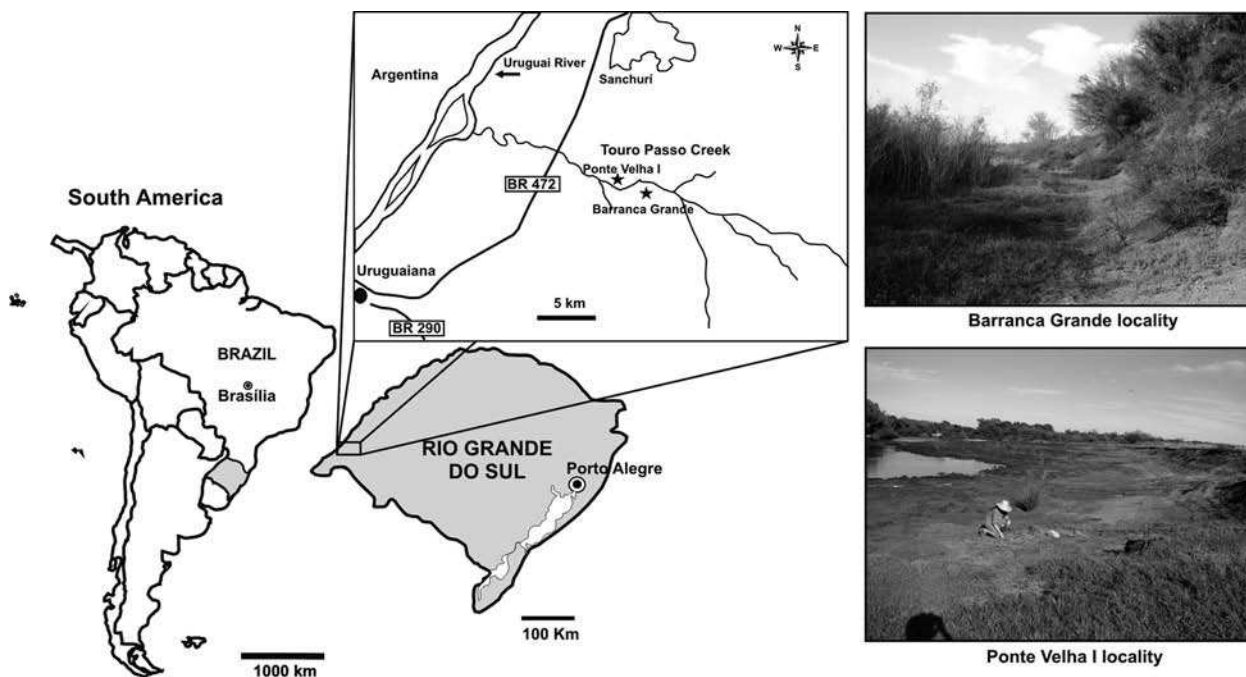


Fig. 2. Location map of Touro Passo Creek and its fossiliferous localities. Photographs of Barranca Grande by L. KERBER and Ponte Velha I by E.V. OLIVEIRA.

tween the medial face of dentary and the masseteric crest, at the level of m1/m2 contact; 3. Length of the alveolar series p4-m3; 4. MDL of p4 alveolus; 5. LLW of p4 alveolus; 6. MDL of m1 alveolus; 7. LLW of m1 alveolus; 8. MDL of m2 alveolus; 9. LLW of m2 alveolus; 10. MDL of m3 alveolus; 11. LLW of m3 alveolus.

3. Location and geological setting

The materials studied here were collected in the Touro Passo Creek, in Uruguaiana municipality, western Rio Grande do Sul State (Fig. 2). BOMBIN (1976) formally proposed the Touro Passo Formation for the upper Pleistocene fossiliferous deposits from western Rio Grande do Sul, based on the type section at the Milton Almeida locality, Touro Passo Creek. In the Touro Passo Creek, there are several fossiliferous deposits assigned to the upper Pleistocene, Lujanian Age (*Equus neogaeus* Biozone, *sensu* CIONE & TONNI 2005) and the most important fossiliferous localities are the Ponte Velha I and II, Milton Almeida, Barranca Grande and Confluência do Pindaí (KERBER & OLIVEIRA 2008a). Radiometric dating by thermoluminescence, AMS and ^{14}C obtained ages between 43 and 11 ka BP (BOMBIN 1976; MILDER 2000; KOTZIAN et al. 2005). The fossil remains

are usually disarticulated, reworked, and exhibiting diagenetic alterations (KERBER 2008). Several Pleistocene vertebrates have been reported for Touro Passo Creek, as the xenarthrans *Glyptodon* spp. OWEN, 1838, *Panochthus* BURMEISTER, 1866, *Glossotherium* (OWEN, 1842), *Pampatherium typum* GERVAIS & AMEGHINO, 1880, *Propraopus* spp. AMEGHINO, 1881, *Holmesina paulacoutoi* CARTELLE & BOHORQUEZ, 1985; the notoungulate *Toxodon* OWEN, 1837 and litoptern *Macrauchenia patachonica* OWEN, 1838; the artiodactyls *Morenelaphus* CARETTE, 1922, *Antifer* AMEGHINO, 1889, *Hemiauchenia paradoxa* GERVAIS & AMEGHINO, 1880, *Lama* spp. CUVIER, 1800, and *Catagonus stenocephalus* LUND in REINHARDT, 1880; the perissodactyls *Equus neogaeus* LUND, 1840, *Hippidion* OWEN, 1869, *Tapirus* sp. BRÜNNICH, 1772 (OLIVEIRA 1992; KERBER & OLIVEIRA 2008a, b; GASPARINI et al. 2009; SCHERER et al. 2009); and turtles, lizard and bird (HSIOU 2007a, b), freshwater mollusks (OLIVEIRA & MILDER 1990), wood and silicophytoliths (BOMBIN 1976).

The fossil assemblages were deposited by a meandering river system in flood plains, represented by silt and sand with carbonate concretions at the top, and point bars represented by basal conglomerates

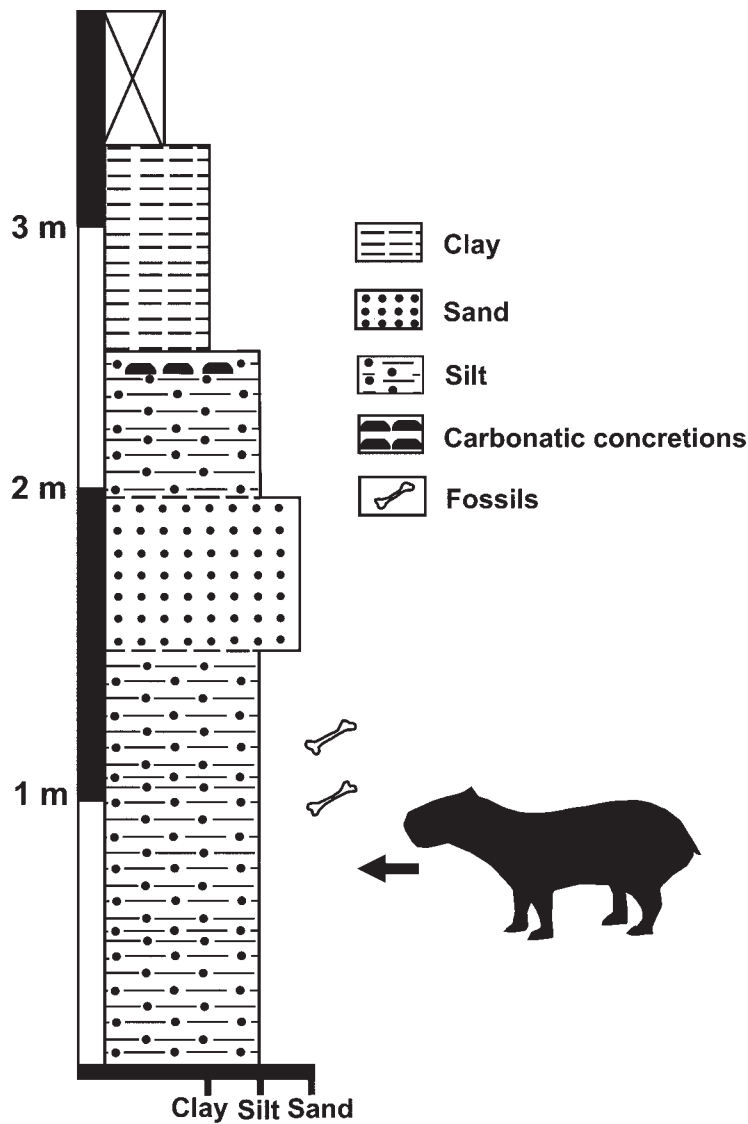


Fig. 3. Stratigraphic profile of Barranca Grande locality.

and sandstone, deposited on the Cretaceous basalts of Serra Geral Formation (BOMBIN 1976; DA-ROSA 2003; OLIVEIRA & KERBER 2009). The Barranca Grande (29°40'31.98" S and 56°51'46.14"W) and Ponte Velha I (29°39'56"S, and 56°52'14"W) are important fossiliferous localities of Touro Passo Creek, and some of the materials here studied are from these localities. In the Barranca Grande locality there are vertebrate remains semi-articulated or disarticulated. The fossil vertebrates were collected in a siltstone level (Fig. 3). The taphonomic aspects of this locality, as polytypic

and polyspecific composition and absence of selection of Voorhies Groups (*sensu* VOORHIES 1969) suggest a deposition in an environment of flood plain. There is evidence of previous transport, but this was not enough to select the remains and to cause physical abrasion (KERBER 2008). At the Ponte Velha I locality the fossils were collected in a level of conglomerates of small-size gravel and sandstone. According to KERBER (2008), the remains of this locality are in the taphonomic Group I of VOORHIES (1969), indicating elements transported.

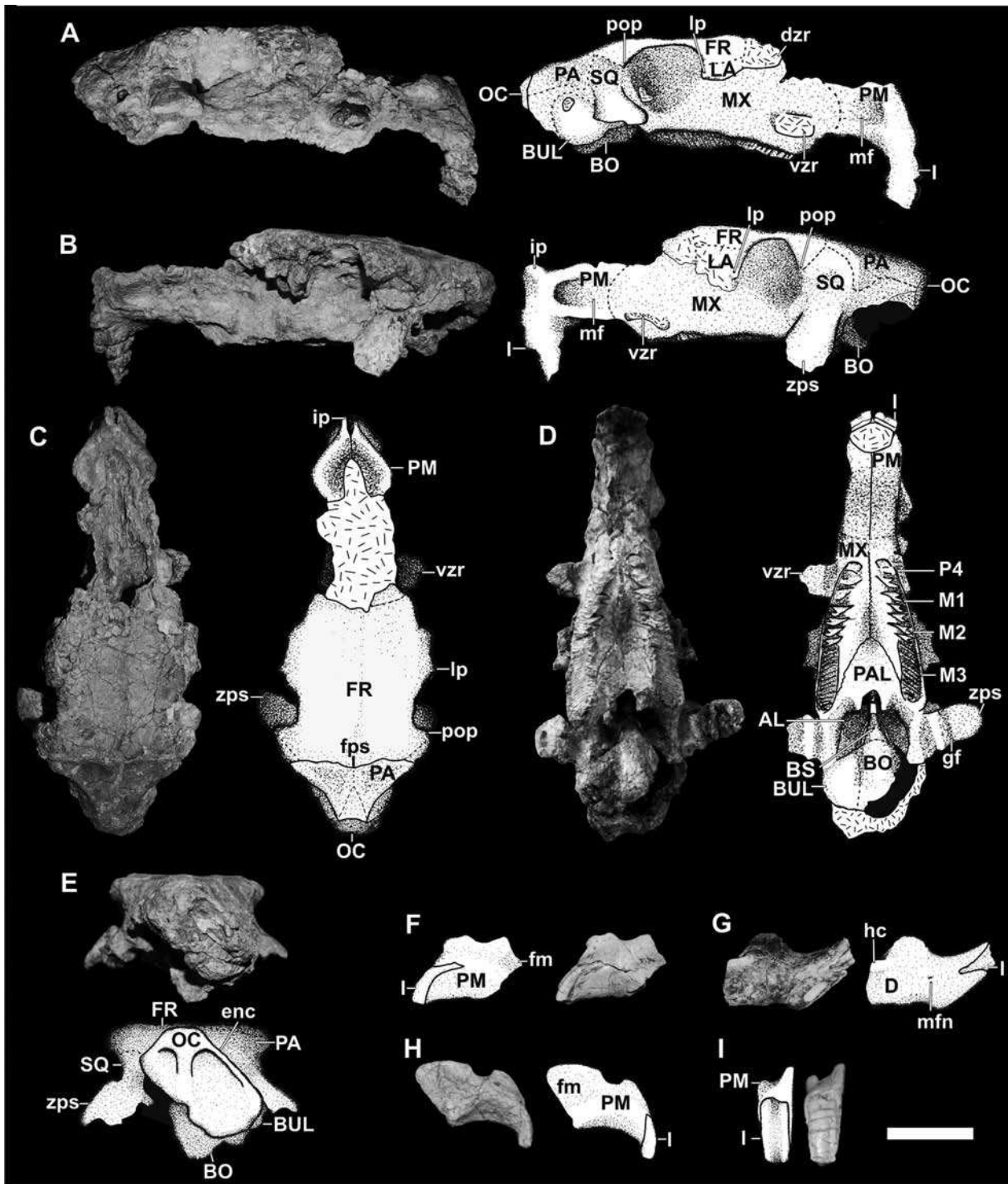


Fig. 4. *Hydrochoerus hydrochaeris* from Touro Passo Creek. **A-E** – Skull MCPU-PV 047, right side in lateral (**A**), left side in lateral (**B**) dorsal (**C**), palatal (**D**) and posterior (**E**) views; **F** – left premaxilla (MCN-PV 2072) in lateral view; **G** – fragment of right dentary (MCN-PV 9572) in lateral view; **H-I** – right premaxilla (MCN-PV 1978) in lateral (**H**) and anterior (**I**) views. Scale-bar = 30 mm.

4. Systematic palaeontology

Rodentia BOWDICH 1821
 Hystricognathi TULLBERG, 1899
 Caviomorpha WOOD & PATTERSON (*in* WOOD, 1955)
 Family Hydrochoeridae (GRAY, 1825) GILL, 1872
 Genus *Hydrochoerus* BRISSON, 1762

Hydrochoerus hydrochaeris (LINNAEUS, 1766)
 Figs. 4-7

Studied material: MCPU-PV 047, nearly complete skull lacking the zygomatic arches and nasals, with the dental series poorly preserved; MCN-PV 9574, portion of the skull lacking the rostral area; MCN-PV 9573, right dentary lacking the posterior portion, with the cheek teeth preserved; MCPU-PV 043, left m1; MCN-PV 1978, right premaxilla; MCN-PV 2072, left premaxilla; MCN-PV 9572, fragment of dentary and MCN-PV 2088, proximal portion of a left femur.

Geographical and stratigraphic provenance: MCPU-PV 047, Barranca Grande locality, Touro Passo Creek; MCPU-PV 043, Ponte Velha I locality, Touro Passo Creek; MCN-PV 1978, MCN-PV 2072, MCN-PV 2088, MCN-PV 9572, MCN-PV 9573, MCN-PV 9574, uncertain localities of Touro Passo Creek, upper Pleistocene.

Description: The specimen MCPU-PV 047 is fragmented, lacking the zygomatic arches, nasals and a portion of the basicranium. The MCN-PV 9574 lacks the rostral and posterior portions and is showing a taphonomic alteration, in which part of the lateroventral region of right maxilla (area of p4, m1 and ventral zygomatic root) is crushed and a fragment of premaxilla and incisor are welded on the right maxilla, near to the infraorbital foramen (see Fig. 5A, D).

The skull MCPU-PV 047 is long, low and narrow (Fig. 4A, C). The rostral area is relatively wide. The incisor alveolus forms a prominence on the lateral face of the premaxilla, which extends almost until the ventral zygomatic root. The rostral masseteric fossa is wide, extending on the maxilla and premaxilla. (Fig. 4A, B, H). The upper diastema is shorter than the length of the upper cheek teeth.

On the maxilla of MCPU-PV 047 (Fig. 4A, B) and left side of MCN-PV 9574 (Fig. 5C) is preserved a small portion of the ventral zygomatic root. It is thin, laterally directed, and located at the level of P4. On the ventral surface of this structure there is a small elliptical fossa (to attachment of *muscle masseter lateralis*) that extends anteriorly to the P4 (Fig. 4D). The dorsal zygomatic root is more posterior than the ventral root (Fig. 4A). The cheek teeth are posteriorly divergent and the palatal region has subtriangular shape (Figs. 4D, 5A). The suture between the palatine process of maxilla and the horizontal plate of palatine is serrated (Figs. 4C, 5A). In the posterior area of the horizontal plate of palatine, the mesopterygoid fossa reaches the level of Pr. X or XI of M3. The central area of the palate shows a concavity not very deep (Figs. 4D, 5A).

The dorsal surface of frontal is flat and it compose one

third of the dorsal face of the skull (Fig. 4C). The frontal is relatively constricted on the interorbital region of MCPU-PV 047, but not so evident in MCN-PV 9574. The frontoparietal suture is slightly undulating. The postorbital process is short and strong. The lacrimals are poorly preserved (MCPU-PV 047, MCN-PV 9574), and the lacrimal process is lateroposteriorly directed. The zygomatic process of squamosal is lateroventrally directed and on its ventral surface is preserved the medial wall of the glenoid fossa (MCPU-PV 047, MCN-PV 9574) being this one long anteroposteriorly and slightly tilted (Figs. 4D, 5A). The parietal crests and the external nuchal crest of supraoccipital portion of occipital of MCPU-PV 047 are poorly developed. The right tympanic bulla of MCPU-PV 047 is fragmented and has globular shape. The pterygoid fossa is deep and it is perforated by a fracture. In MCPU-PV 047 the sutures of basicranium are ossified, suggesting that it is adult (class 4 of OJASTI 1971 and MONES 1991).

Dentary – The dentary (MCN-PV 9573) is fragmented, lacking its posterior area (Fig. 6A). The coronoid process is fragmented and only its origin is preserved, located at the level of the distal region of m2. The symphysis is wide and elliptical (Fig. 6C). The incisor alveolus forms a prominence on the medial face and extends posteriorly almost up to the level of pr. II of m1. The lower diastema is shorter than the lower cheek teeth length. The ventral face of dentary is rather straight. The horizontal crest (*sensu* PÉREZ & WALTON 2008) is well developed and robust, lacking the anterior and posterior portions, and the anterior area of masseteric fossa is situated at the level of the pr. I of m1 (Fig. 6B). The mental foramen is located anteriorly of the p4 (Figs. 4G, 6A).

Dentition – The prisms are constituted of dentin, surrounded by enamel. Between the prisms, and in the flexus/flexids, there is cement. In the upper teeth, the lingual ends are linguomesially oriented. The incisors are preserved in MCN-PV 2072, MCN-PV 1978 and poorly preserved in MCPU-PV 047 (Fig. 4A-B, F, H-I). The specimen MCN-PV 9574 shows the distal portion of an incisor preserved (Fig. 5D). The incisors have a medial groove on the labial face (Fig. 4I). The upper cheek teeth are better preserved in MCN-PV 9574. The P4 is fragmented in the lingual area (Fig. 5F). P4, M1 and M2. These teeth are constituted by two Y-shaped prisms (Pr. I and Pr. II), with a flexus quite developed in the labial area (HPE in the mesial prism and HSE in the distal prism). The prisms are separated by HFI. These teeth are very similar, however the P4 has longest length than M1 and M2. The M3 has some of its prisms fragmented at the ends. The first prism (Pr. I) is Y-shaped, with a flexus in labial face (HPE), that extends up to half of occlusal surface. This one is similar to the prisms of the P4, M1, M2 (Fig. 5F). The Pr. I is followed by 12 laminar prisms with similar morphology, but progressively increasing the width up to Pr. VII, and then diminishing up to Pr. XIII (Fig. 5E-F). The Pr. XII and Pr. XIII differ from the other prisms because they are united labially and Pr. XIII is rudimentary.

The lower cheek teeth are better preserved in MCN-PV 9573. The p4 is poorly preserved and in the m1, the pr. I and the lingual ends of pr. II are fragmented. The pr. II has the hti, hpi and hse well developed (Fig. 6E). The m2 lacks the

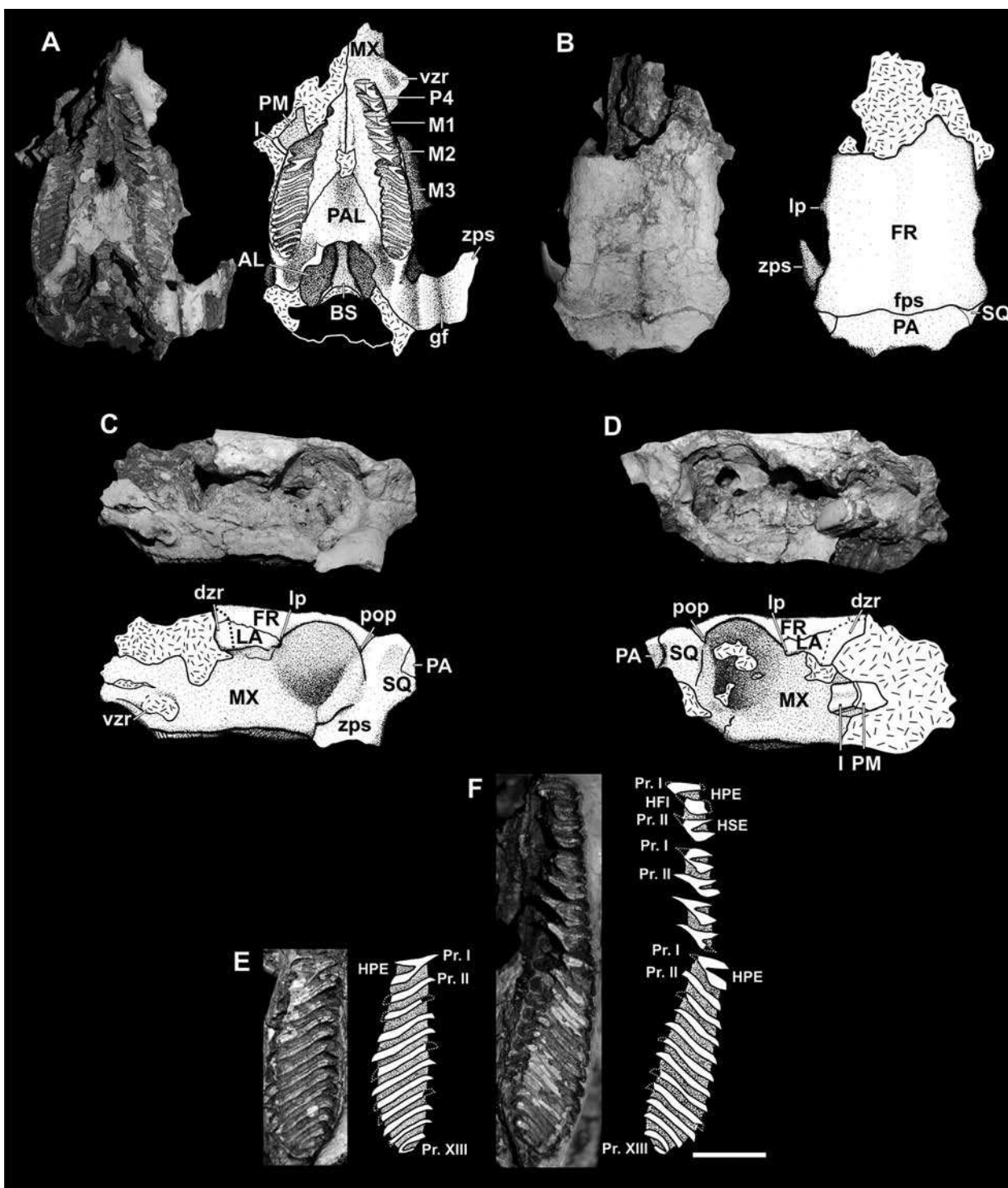


Fig. 5. *Hydrochoerus hydrochaeris* from Touro Passo Creek. **A-D** – Skull MCN-PV 9574 in palatal (**A**), dorsal (**B**), left side in lateral (**C**) right side in lateral (**D**) views; **E-F** – upper dental series of MCN-PV 9574 in occlusal view, right and left respectively. Scale-bar to **A-D** = 30 mm and to **E-F** = 20 mm.

lingual ends of prisms and the pr. IIb' is fragmented. The pr. I is Y-shaped, with a lingual flexid (hsi), and the pr. II is divided in pr. IIa'' and pr. IIa', the pr. IIb'' and pr. IIb' are lingually united and Y-shaped (Fig. 6E). The m3 has five almost complete laminae, lacking the pr. Ia due to fragmentation. The pr. IIa'' and pr. IIa' are separated and the pr. IIb'' and pr. IIb' are lingually united by a thin enamel layer (Fig. 6E). In the specimen MCPU-PV 043 (m1) all the prisms are preserved. The pr. I is Y-shaped with hsi well developed. The pr. I and II are separated by hfe. The hti, hpi and hse are deep and the pr. IIa and pr. IIb are united labially (Fig. 6D).

Femur – The material MCN-PV 2088 is a proximal part of a left femur (Fig. 7). The head of femur is fused to the neck and has globular shape (Fig. 7A). The fovea capitis femoris is positioned posteromedially (Fig. 7A). The neck is slightly flattened anteroposteriorly and has a slope of approximately 45° (Fig. 7B, C). The lesser trochanter is a rounded posteromedial tubercle (Fig. 7B).

5. Discussion

5.1. Morphology and systematics

According to the review of MONES (1991), Hydrochoerinae have two genera: *Nechoerus* and *Hydrochoerus*. However, in the cladistic analysis of PRADO et al. (1998), *Hydrochoeropsis* KRAGLIEVICH, 1930, previously included in Anatochoerinae, is more closely related to Hydrochoerinae. *Nechoerus* and *Hydrochoerus* are morphologically very similar (VUCETICH & VERZI 1999), except by the largest size of *Nechoerus*, almost a third larger than *Hydrochoerus* (PAULA COUTO 1979), and its M3 has about 14 to 18 prisms, while *Hydrochoerus* has between 11 and 14 (MONES 1975; DESCHAMPS 1998). Due to the great morphological similarity between *Nechoerus* and *Hydrochoerus*, some authors questioned the generic independence of these taxa (e.g., ALVAREZ 1971). UBILLA (1996), using the principal components analysis (PCA), with 23 linear measurements, recognized *Nechoerus* and *Hydrochoerus* as independent taxa. For MONES (1991) both genera are independent, and there are five species of *Nechoerus*: *N. aesopi* LEIDY, 1854, *N. tarijensis* AMEGHINO, 1902, *N. sulcidens* (LUND 1839), *N. dichroplax* AHEARN & LANCE, 1980 and *N. fontanai* RUSCONI, 1933, and three of *Hydrochoerus*: *H. hydrochaeris*, *H. isthmius*, and *H. ballesterensis* (RUSCONI 1934). Recently, MACPHEE et al. (2000) proposed the new species *H. gaylori*.

The specimens described in this paper show the rostrum relatively wide, not narrow as in *Chapalmatherium* AMEGHINO, 1908 and not wide as in *Anatochoerus* MONES & VUCETICH (in MONES, 1991). The rostral masseteric fossa extends on the maxilla and premaxilla. This character is shared with *Nechoerus*

and *Hydrochoerus* and differs from *Chapalmatherium*, *Hydrochoeropsis*, *Anatochoerus*, *Kiyutherium* FRANCIS & MONES, 1965 (= *Cardiatherium* AMEGHINO, 1883), in which the fossa is located on the maxilla with only a small area on the premaxilla (MONES 1991; PRADO et al. 1998). The upper diastema is shorter than the maxillary cheek teeth, while *Nechoerus* has the same proportion and in *Chapalmatherium* is longer (PRADO et al. 1998). The ventral zygomatic root (vzr) is located at the level of P4, as in *Nechoerus* and *Hydrochoerus*, and projected laterally, different from “Anatochoerinae”, in which the roots are posteriorly directed (MONES 1991). In the description of *Nechoerus* cf. *N. aesopi* from the Sopas Formation, UBILLA (1996) reports that the zygomatic ventral roots are projected more posteriorly than in *H. hydrochaeris*. The small fossa of the ventral surface of the vzr is extended anteriorly to the P4, as in *Nechoerus* (DESCHAMPS 1998), but proportionally smaller, as in *Hydrochoerus*. The skull roof is flat, differing from *Anatochoerus* which is curved laterolaterally (MONES 1991). The frontoparietal suture is slightly undulating and not rectilinear as observed in *Nechoerus* by UBILLA (1996) and DESCHAMPS (1998). The parietal crests are less developed than the comparative specimens of *Nechoerus*.

In the dentary, the incisor alveolus extends posteriorly up to the level of pr. II of m1, differing of *H. ballesterensis* that extends up to the level of pr. II of m2 (RUSCONI 1934). In comparative specimens of *H. hydrochaeris*, the incisor extends up to the level of pr. II of p4 and pr. I of m1. In *N. sulcidens* the incisor extends up to the level of pr. IIa of m1 and in *N. aesopi* up to the pr. I of the same tooth (MONES 1991). The lower diastema is shorter than the length of the lower cheek teeth. This character is shared with *Nechoerus* and *Hydrochoerus*, different from *Chapalmatherium* in which it is proportional or slightly longer (PRADO et al. 1998). The anterior area of the masseteric fossa of dentary is located at the level of pr. I of m1, as in *H. hydrochaeris* and *Nechoerus*.

As in other Hydrochoeridae, the teeth are euhyposodont and elasmodont, with prisms constituted of dentin surrounded by enamel, and the spaces between the prisms are filled by cement. The incisor shows a labiomedial groove, differing from *Cardiatherium* and *Chapalmatherium*. In the later, the enamel is finely striated longitudinally (KRAGLIEVICH 1941a), and in “Anatochoerinae” this character is not known. In Hydrochoerinae the presence of the labiomedial groove in the incisor appears to be unstable, occurring, or not in *Nechoerus* (MONES 1984). In the upper cheek

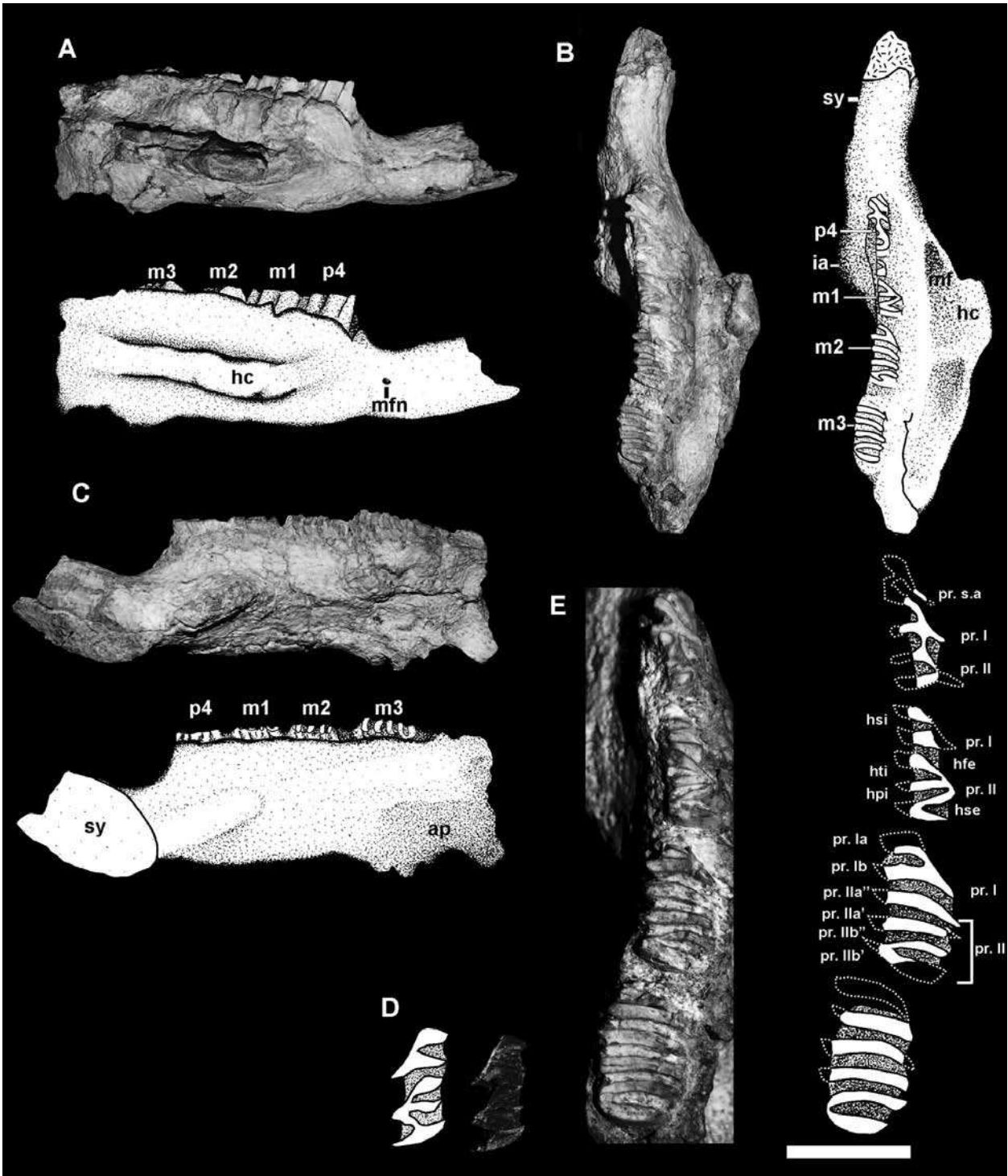


Fig. 6. *Hydrochoerus hydrochaeris* from Touro Passo Creek. **A-C** – Right dentary MCN-PV 9573 in lateral (**A**), occlusal (**B**) and medial (**C**) views; **D** – m1 in occlusal view (MCPV-PV 047); **E** – lower dental series of MCN-PV 9573, in occlusal view. Scale-bars to **A-C** = 35 mm and to **D-E** = 20 mm.

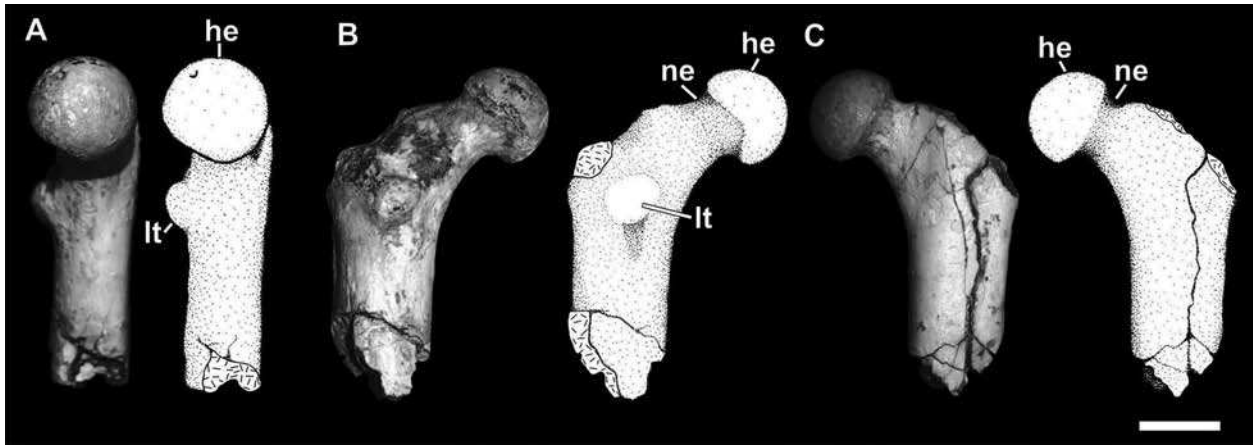


Fig. 7. *Hydrochoerus hydrochaeris* from Touro Passo Creek. **A-C** – Left femur MCN-PV 2088, in medial (**A**), posterior (**B**) and anterior (**C**) views. Scale-bar = 20 mm.

teeth, the HSE is well developed, differing of *Cardiatherium* and *Anatochoerus* in which it is poorly or tenuously developed. The prisms are totally separated by HFI differing from “*Cardiatheriinae*” and *Anatochoerus* that have the prisms united and *H. gaylordi* in which Pr. I and II of M2 are labially united (MACPHEE et al. 2000).

The morphology of M3 has the same pattern and number of prisms that *H. hydrochaeris* (KRAGLIEVICH 1941b; MONES 1975). *Nechoerus* and *Hydrochoeropsis* have the morphology of M3 very similar to *Hydrochoerus*, but they have more prisms, between 14 and 18, and 13 and 15 respectively. *Hydrochoeropsis* shows HEE (external extraordinary flexus), and in *Nechoerus* the HEE appears in some cases (AHEARN & LANCE 1980; DESCHAMPS 1998). The prisms after Pr. I of M3 are laminar and free, differing from those homologous of “*Cardiatheriinae*” and “*Anatochoerinae*” that have the prisms united by a thin enamel layer. Distally, the prisms increase in width until the Pr. VII. After Pr. VII the prisms begin to shorten, as described for *H. hydrochaeris* (KRAGLIEVICH 1941b). The m3 has the same morphology and number of prisms of *Nechoerus* (CARRANZA-CASTAÑEDA & MILLER 1988; UBILLA 1996), but smaller in size, as in *Hydrochoerus*.

The size of MCPV-PV 047 was compared to *H. isthmius*, *H. hydrochaeris* and *Nechoerus* cf. *N. aesopi* (Fig. 8) in an univariant analysis and it was placed within the variation of *H. hydrochaeris*. *H. isthmius* has similar morphology to *H. hydrochaeris*, with little differences of proportions and about half its size (MONES & OJASTI 1986). The measurements of

the fossil specimens are similar to the adults of living *H. hydrochaeris* (Tables 1-2). The morphology of the femur does not differ from *H. hydrochaeris* used for comparison.

The capybaras from the late Pleistocene of southern Brazil are assigned to *H. hydrochaeris*. The main features that allow this assignment are: M3 with Pr. I Y-shaped followed by 12 free prisms, upper diastema shorter than the P4-M3 series, rostral area relatively wide, smaller size than *Nechoerus* and larger than *H. isthmius*; the posterior end of the lower incisor alveolus does not extend as back as that of *H. ballesterensis*; m1 with free pr. I and pr. II, differing from *H. gaylordi*.

5.2. Palaeobiogeography and palaeoenvironmental significance

Today, *H. hydrochaeris* is distributed in most regions of South America, excluding areas where the water and temperature are limiting factors, such as the Andes, Patagonia and Caatinga regions (Fig. 9A) (MONES & OJASTI 1986). The fossil records of *Hydrochoerus* are restricted to South America (Fig. 9B). In the north region of this continent, specimens are recognized from islands, relatively close to coast. HOOIJER (1959) described teeth of *H. hydrochaeris* for the Pleistocene of Curaçao, northwestern Venezuela and MACPHEE et al. (2000) described *H. gaylordi* from the Pliocene/Pleistocene of Grenada. In Colombia, *Hydrochoerus* sp. is mentioned for Santander, Curiti (PORTA 1969). In Bolivia, HOFFSTETTER (1968) reported *Hydrochoerus* sp. for Quebrada de Ñapua and WERDELIN (1991) for

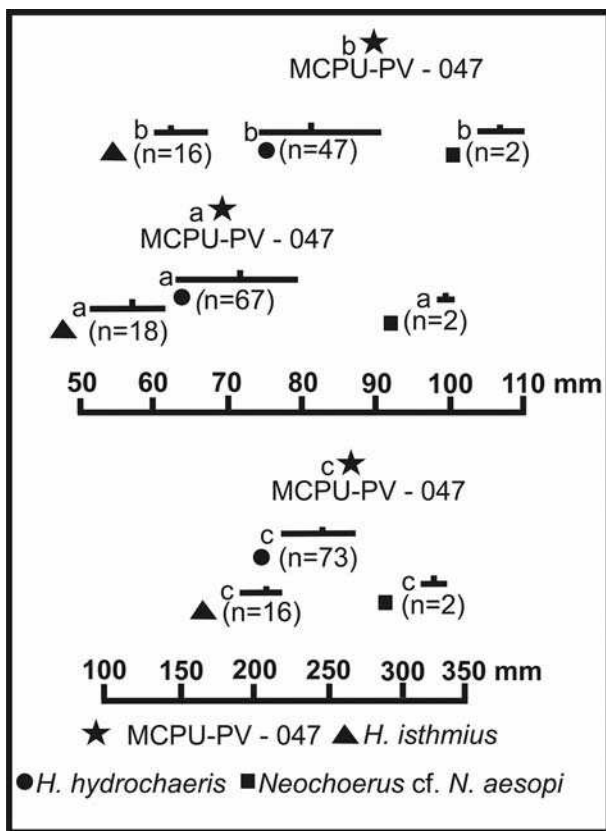


Fig. 8. Univariate diagram comparing measurements of *H. hydrochaeris*, *H. isthmus*, *Nechoerus cf. aesopi* and MCPU-PV 047. **a** – Length of upper diastema; **b** – length of P4-M3 series; **c** – total length of skull. Measurements of *H. hydrochaeris* and *H. isthmus* taken from MONES (1991) and of *Nechoerus cf. aesopi* from UBILLA (1996).

Tarija. In Argentina, *H. ballesterensis* is recognized from late Pliocene of Villa Ballester, Buenos Aires Province (RUSCONI 1934). From the late Pleistocene of Uruguay, UBILLA (1996) described *Hydrochoerus hydrochaeris* from the Sopas Formation. In Brazil there are few confirmed records of the genus. OLIVEIRA et al. (1985) reported *H. hydrochaeris* from the Quaternary of Lageado da Escada, Baraúna, Rio Grande do Norte State. SALLES et al. (2006) mentioned *H. hydrochaeris* for the Quaternary of Serra da Bodoquena, Mato Grosso do Sul State, however, the material is not described or figured. In Minas Gerais State, PETER LUND described fossil remains in 1843 as *H. sulcidens*, however, currently the material is assigned to *N. sulcidens* (MONES & OJASTI, 1986). In the southern Brazil,

the only records are from Rio Grande do Sul State. The first record was made by BOMBIN (1976). However, this author did not describe neither refer material. Subsequently, OLIVEIRA (1992) reported *H. hydrochaeris* from the late Pleistocene of Quaraí River and Touro Passo Formation. *H. cf. hydrochaeris* was reported for the late Pleistocene of Touro Passo Formation by KERBER & OLIVEIRA (2008a) and now we confirmed this assignment and reported new specimens. The distribution of *Hydrochoerus* during the late Pleistocene shows some differences in comparison with the current. The southernmost Pleistocene record of this genus is in northern Uruguay, whereas today its distribution reaches the southern Buenos Aires Province, in Argentina. Besides, there is a Quaternary record in northeastern Brazil in a locality where there are no living representatives.

Fossils of *Nechoerus* were recorded in three Americas. In South America this taxon is mentioned for Bolivia, Uruguay, Argentina, Venezuela, Colombia, Ecuador, Peru and Brazil. In Brazil it is recorded for the late Pleistocene of Lagoa Santa, Minas Gerais State, caves of Bahia State and Rio Madeira Formation, Rondônia State (MONES 1991; UBILLA 1996; DESCHAMPS 1998; COZZUOL et al. 2006; LESSA et al. 2008) (Fig. 9B).

The capybaras are semiaquatic mammals, living in permanent water bodies, as rivers, lakes, ponds, marshes and swamps (OJASTI 1971, 1973). They are herbivorous, feeding mainly grasses and aquatic vegetation. They live in groups, in several environments, such as riparian vegetation, seasonally flooded savannas, some up to 500 meters away from the water (OLIVEIRA & BONVICINO 2006). Thus, the presence of this taxon in the late Pleistocene of western Rio Grande do Sul State suggests, at least in a span of time of 42 and 11 Ka BP, the presence of environments with hydrophilic vegetation and permanent water bodies.

6. Conclusions

The hydrochoerids from Rio Grande do Sul State are assigned to *H. hydrochaeris*. The presence of this taxon suggests the presence of environments with permanent water bodies during the late Pleistocene of Rio Grande do Sul State. Up to now, remains of *Nechoerus* have not been found in southern Brazil. On the other hand, in northern Uruguay, in deposits correlated with the late Pleistocene of Rio Grande do Sul, *Nechoerus* and *Hydrochoerus* were reported.

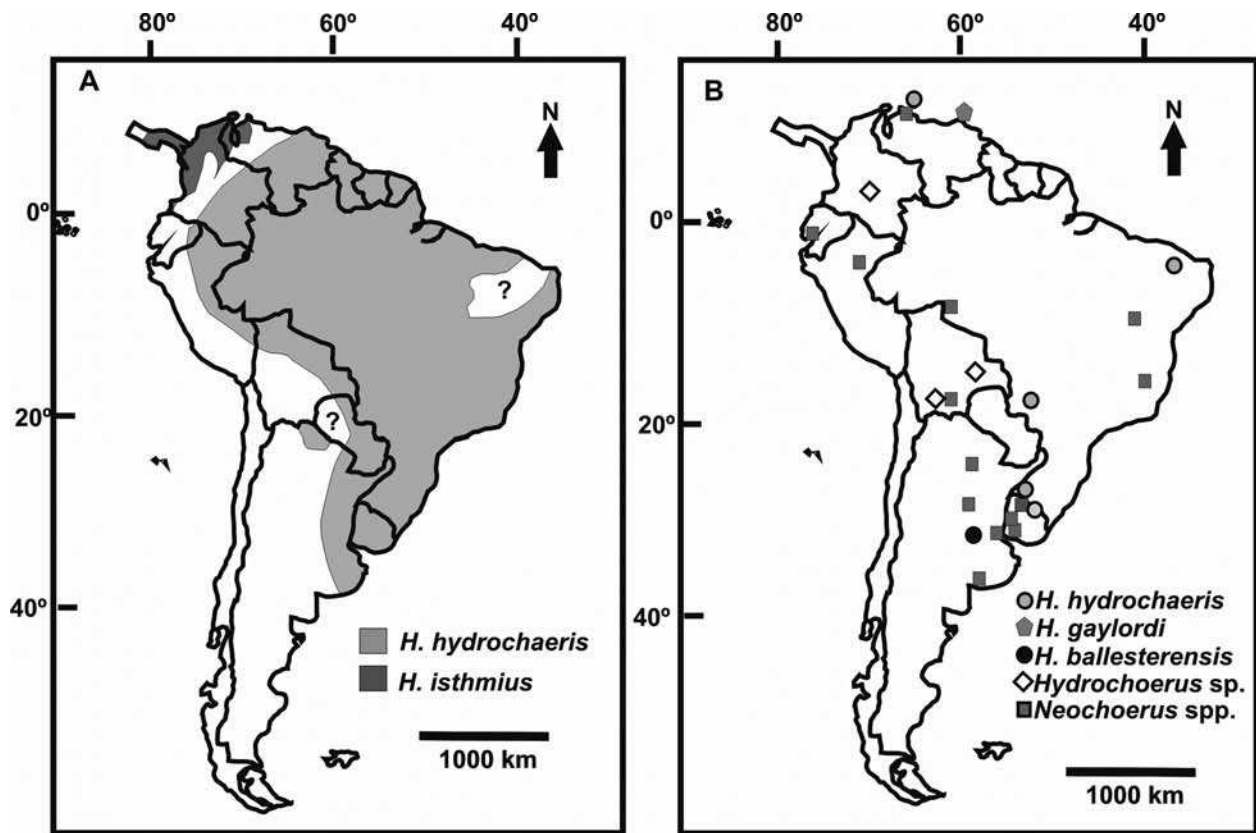


Fig. 9. **A** – Current distribution of the genus *Hydrochoerus*. **B** – Localities with fossil record of *Hydrochoerus* and *Nechoerus* in South America. For references see text.

Acknowledgements

We thank the CNPq (Conselho Nacional de Pesquisa e Tecnologia) for financial support to L.K. in form of fellowship of Programa de Pós-Graduação em Geociências (UFRGS); CNPq for financial support (Universal 474485/2008-0) and PROSUL 490299/2008-3. PUCRS for the loan of the specimens; FZBRS for the infrastructure provided; É.V. Oliveira for the suggestions; A. MONES and C. DESCHAMPS for the bibliographies; J. FERIGOLO (MCN/FZBRS) for the discussions on the anatomy of rodents; A.S. HSIU for reading and commenting the manuscript; E. Holanda for the suggestions; J. SOLOVYI (MHD), M. JARDIM, D. SANFELICE (MCN/FZBRS), M.G. VUCETICH and C. DESCHAMPS (MLP) for access to collection under their care; RICARDO DUARTE and NILZA DORNELLES (Cabanha Touro Passo), for help with fieldwork; J.C. Cisneros (UFRGS) for the suggestions about the illustrations; A.A.S. DA-ROSA for the suggestions about the stratigraphy; M.E. PÉREZ for the unpublished information about the homologies of the mandibular crests in Caviioidea; M.B. SANTOS for improving the English version; the reviewers C. DESCHAMPS and A. RINDERKNECHT for their useful comments that improved the manuscript.

References

- AHEARN, M.E. & LANCE, J.F. (1980): A new species of *Nechoerus* (Rodentia, Hydrochoeridae) from the Blancan (late Pliocene) of North America. – Proceedings of the Biological Society of Washington, **93** (2): 435-442.
- ALVAREZ, T. (1971): Variación de la figura oclusal del pre-molar inferior en carpinchos fósiles (Rodentia: Hydrochoeridae) de Jalisco, México. – Instituto Nacional de Antropología e Historia, Investigaciones, **21**: 1-35.
- BOMBIN, M. (1976): Modelo paleoecológico evolutivo para o Neokuaternário da região da Campanha-Oeste do Rio Grande do Sul (Brasil). A Formação Touro Passo, seu conteúdo fossilífero e a pedogênese pós-deposicional. – Comunicações do Museu de Ciências da PUCRS, **15**: 1-90.
- CARRANZA-CASTAÑEDA, O. & MILLER, W.E. (1988): Roedores caviomorfos de la Mesa Central de México, Blancano Temprano (Plioceno Tardío) de la fauna local Rancho Viejo, Estado de Guanajuato. – Universidad Nacional Autónoma de México, Instituto de Geología Revista, **7**: 182-199.

- CIONE, A.L. & TONNI, E.P. (2005): Bioestratigrafía basada en mamíferos del Cenozoico Superior de la Provincia de Buenos Aires, Argentina. – In: BARRIO, R.E., ETCHÉVERRY, R.O., CABALLÉ, M.F. & LLAMBIAS, E. (Eds.): Geología y recursos Minerales de la Provincia de Buenos Aires Relatorio del XVI Congreso geológico Argentino, 183-200; La Plata.
- COZZUOL, M.A., HOLANDA, E.C., NASCIMENTO, E.R. DO & WEISS, F.L. (2006): Registro do gênero *Nechoerus* (Rodentia, Caviomorpha, Hydrochoeridae) para o Pleistoceno da Amazônia Sul-Occidental. – *Paleontologia em Destaque*, **53**: 43-44.
- DA-ROSA, A.A.S. (2003): Preliminary correlation of fluvial deposits at the extreme west of Rio Grande do Sul State, Southern Brazil. – 3° Latinamerican Congress of Sedimentology, Belém, Abstracts: 243-245.
- DESCHAMPS, C.M. (1998): The presence of *Nechoerus* HAY (Rodentia, Hydrochoeridae) in Pleistocenic sediments of southwestern Buenos Aires Province. – *Quaternary of South America and Antarctic Peninsula*, **11**: 1-14.
- DESCHAMPS, C.M., OLIVARES, A.I., VIEYTES, E.M. & VUCETICH, M.G. (2007): Ontogeny and diversity of the oldest capybaras (Rodentia, Hydrochoeridae; Late Miocene of Argentina). – *Journal of Vertebrate Paleontology*, **27**: 683-692.
- GASPARINI, G.M., KERBER, L. & OLIVEIRA, E.V. (2009): *Catagonus stenocephalus* (LUND in REINHARDT, 1880) (Mammalia, Tayassuidae) in the Touro Passo Formation (Late Pleistocene), Rio Grande do Sul, Brazil. Taxonomic and palaeoenvironmental comments. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **254**: 261-273.
- HOFFSTETTER, R. (1968): Ñapua, un gisement de vertébrés pléistocènes dans le Chaco bolivien. – *Bulletin Du Muséum National d'Histoire Naturelle*, **40**: 823-836.
- HSIOU, A.S. (2007a): A new Teiidae species (Squamata, Scincomorpha) from the Late Pleistocene of Rio Grande do Sul State, Brazil. – *Revista Brasileira de Paleontologia*, **10**: 181-194.
- HSIOU, A.S. (2007b): O estado atual do registro fóssil de répteis e aves no Pleistoceno do Estado do Rio Grande do Sul, Brasil. – 1° Workshop “O Quaternário do Rio Grande do Sul: Integrando Conhecimentos”, Canoas, Resumos: 23-24.
- HOOLIER, D.A. (1959): Fossil rodents from Curaçao and Bonaire. – *Studies on the Fauna of Curaçao and other Caribbean Islands*, **9** (35):1-27.
- KERBER, L. (2008): Paleovertebrados e considerações tafonômicas da Formação Touro Passo (Pleistoceno Superior) oeste do Rio Grande do Sul. – *Revista da graduação PUCRS*, **2**: 1-93.
- KERBER, L. & OLIVEIRA, E. (2008a): Fósseis de vertebrados da Formação Touro Passo (Pleistoceno Superior), Rio Grande do Sul, Brasil: atualização dos dados e novas contribuições. – *Gaea, Journal of Geoscience*, **4**: 49-64.
- KERBER, L. & OLIVEIRA, E. (2008b): Sobre a presença de *Tapirus* (Tapiridae, Perissodactyla) na Formação Touro Passo (Pleistoceno Superior), oeste do Rio Grande do Sul. – *Biodiversidade Pampeana*, **6**: 9-14.
- KOTZIAN, C.B., SIMÕES M.G., DA-ROSA, A.A.S. & MILDER, S.E.S. (2005): AMS Radiocarbon dating of freshwater mollusk shells from the Touro Passo Formation (Pleistocene-Holocene), RS, Brazil. – 19° Congresso Brasileiro de Paleontologia and 6° Congresso Latino-Americano de Paleontologia, Aracaju, Resumos: CD-Rom.
- KRAGLIEVICH, L. (1941a): Monografía del gran carpincho corredor plioceno *Protohydrochoerus* (Rovereto) y formas afines. – In: TORCELLI, A.J. & MORELLI, C.A. (Eds.): *Obras de Geología y Paleontología 3* (Obras completas y trabajos científicos inéditos). 487-556, Buenos Aires; (Ministerio de Obras Públicas de la Provincia de Buenos Aires).
- KRAGLIEVICH, L. (1941b): Morfología normal y morfogénesis de los molares de los carpinchos y caracteres filogenéticos de este grupo de roedores. (La primera parte en colaboración con el Sr. Lorenzo J. Parodi). – In: TORCELLI, A.J. & MORELLI, C.A. (Eds.): *Obras de Geología y Paleontología 3* (Obras completas y trabajos científicos inéditos). 438-484, Buenos Aires; (Ministerio de Obras Públicas de la Provincia de Buenos Aires).
- LESSA, G., CARTELLE, C. & MANDUCA, E.G. (2008): Reevaluation of rodent assemblages from Pleistocene/Holocene of Bahia, Brazil: morphologic and environmental considerations. – In: 3° Congreso Latinoamericano de Paleontología de Vertebrados, Trelew, Resúmenes, 137.
- MACPHEE, R.D.E., SINGER, R. & DIAMOND, M. (2000): Late Cenozoic Land Mammals from Grenada, Lesser Antilles Island-Arc. – *American Museum Novitates*, **3302**: 1-20.
- MILDER, S.E.S. (2000): Arqueologia do Sudeste do Rio Grande do Sul: Uma perspectiva Geoarqueológica. – Unpublished thesis, Universidade de São Paulo. 172 pp.
- MONES, A. (1975): Estudios sobre la Familia Hydrochoeridae (Rodentia), V. Revalidación de sus caracteres morfológicos dentarios con algunas consideraciones sobre la filogenia del grupo. – 1° Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán, Actas, 463-476.
- MONES, A. (1984): Estudios sobre la Familia Hydrochoeridae, XIV. Revisión sistemática (Mammalia, Rodentia). – *Senckenbergiana biológica*, **65**: 1-17.
- MONES, A. (1991): Monografía de la Familia Hydrochoeridae (Mammalia, Rodentia). Sistemática – Paleontología – Bibliografía. – *Courier Forschungs-Institut Senckenberg*, **134**: 1-235.
- MONES, A. & OJASTI, J. (1986): *Hydrochoerus hydrochaeris*. – *Mammalian Species*, **264**: 1-7.
- OJASTI, J. (1971): El chigüire. – *Revista Defensa de la Naturaleza*, **1**: 1-10.
- OJASTI, J. (1973): Estudio biológico del chigüire o capibara. – 275 pp.; Caracas (Fondo Nacional de Investigaciones Agropecuarias).
- OLIVEIRA, E.V. (1992): Mamíferos fósseis do Quaternário do Estado do Rio Grande do Sul, Brasil. – Unpublished Master's thesis, Programa de Pós Graduação em Geociências, Universidade Federal do Rio Grande do Sul. 118 pp.
- OLIVEIRA, E.V. & KERBER, L. (2009): Paleontologia e aspectos geológicos das sucessões do final do Neógeno no sudoeste do Rio Grande do Sul, Brasil. – *Gaea, Journal of Geoscience*, **5**: 21-34.

- OLIVEIRA, E.V. & MILDER, S.E.S. (1990): Considerações preliminares sobre uma nova fauna de moluscos fósseis da Formação Touro Passo (Pleistoceno Superior-Holoceno Inferior). Observações estratigráficas e paleoecológicas. – *Veritas*, **35**: 121-129.
- OLIVEIRA, L.D.D., SOUZA-CUNHA, F.L. & LOCKS, M. (1985): Um Hydrochoeridae (Mammalia, Rodentia) no Pleistoceno do nordeste do Brasil. – In: CAMPOS, D.A., FERREIRA, C.S., BRITO, I.M. & VIANA, C.F. (Eds.): Coletânea de Trabalhos Paleontológicos, 93-97; (DNPM).
- OLIVEIRA, J.A. & BONVICINO, C. (2006): Ordem Rodentia. – In: REIS, N.R., PERACCHI, A.L., PEDRO, W.A. & LIMA, I.P. (Eds.). Mamíferos do Brasil, 347-400; Londrina (Universidade Estadual de Londrina).
- PASCUAL, R., ORTEGA HINOJOSA, E.J., GONDAR, D.G. & TONNI, E.P. (1966): Vertebrata. – In: BORRELLO, A.V. (Ed.): Paleontografía Bonaerense – Vertebrata I. – 202 pp.; Buenos Aires (Comisión de Investigaciones Científicas de la provincia de Buenos Aires).
- PAULA COUTO, C. (1979): Tratado de Paleomastozoologia. – 590 pp.; Rio de Janeiro (Academia Brasileira de Ciências).
- PÉREZ, M.E. & WALTON, A. (2008). Un nuevo caviomorfo (Rodentia, Hystricognathi) del Mioceno Medio del noroeste del Chubut y las homologías mandibulares de *Cavioidea S.S.* – 3° Congreso Latinoamericano de Paleontología de Vertebrados, Trelew, Resúmenes, 193.
- PORTA, J. (1969): Les vertébrés fossiles de Colombie et les problèmes posés par l'isolement du continent sud-américain. – *Paleovertebrata*, **2**: 77-94.
- PRADO, J.L., CERDEÑO, E. & ROIG-JUÑENT, S. (1998): The giant rodent *Chapalmatherium* from the Pliocene of Argentina: new remains and taxonomic remarks on the Family Hydrochoeridae. – *Journal of Vertebrate Paleontology*, **18**: 788-798.
- RUSCONI, C. (1934): Tercera noticia sobre los vertebrados fósiles del Puelchense de Villa Ballester. – *Anales de la Sociedad Científica Argentina*, **117**: 177-186.
- SALLES, L.O., CARTELLE, C., GUEDES, P.G., BOGGIANI, P.C., JANOO, A. & RUSSO, C.A. (2006): Quaternary mammals from Serra da Bonoquena, Mato Grosso do Sul, Brazil. – *Boletim do Museu Nacional, Nova Série Zoologia*, **521**: 1-12.
- SCHERER, C.S., PITANA, V.G. & RIBEIRO, A.M. (2009): Protheriidae and Macrauchenidae (Liptoterna, Mammalia) from the Pleistocene of Rio Grande do Sul State, Brazil. – *Revista Brasileira de Paleontologia*, **12**: 231-246.
- WERDELIN, L. (1991): Pleistocene vertebrates from Tarija, Bolivia in the collections of the Swedish Museum of Natural History. – In: SUAREZ-SORUCO, R. (Ed.): Fósiles y Facies de Bolivia – Vol. I Vertebrados. – *Revista Técnica de YPF*, **12** (3-4): 673-684.
- UBILLA, M. (1996): Paleozoología del Cuaternario continental de la Cuenca Norte del Uruguay: Biogeografía, Cronología y aspectos climático-ambientales. – Unpublished thesis, Universidad de la República, Montevideo. – 232 pp.
- VOORHIES, M.R. (1969): Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. – *Contributions to Geology*, **1**: 69.
- VUCETICH, M.G., DESCHAMPS, C.M., OLIVARES, A.I. & DOZO, M.T. (2005): Capybaras, size, shape, and time: a model kit. – *Acta Palaeontologica Polonica*, **50**: 259-272.
- VUCETICH, M.G. & VERZI, D.H. (1999): Changes in Diversity and Distribution of the Caviomorph Rodents during the Late Cenozoic in South America. – *Quaternary of South America and Antarctic Peninsula*, **12**: 207-223.

Manuscript received: May 31st, 2010.

Revised version accepted: July 8th, 2010.

Address of the authors:

LEONARDO KERBER, ANA MARIA RIBEIRO, Seção de Paleontologia, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Av. Salvador França, 1427, 90690-000, Porto Alegre, RS, Brasil;
E-mail: leonardokerber@gmail.com

Appendix

Table 1. Measurements of the skull of fossil and extant specimens of *H. hydrochaeris*. The specimen highlight in bold is the fossil. AC: Age Classes 0-4 of OJASTI (1971) and MONES (1991), Ind: Indefinite.

Specimen	AC	1	2	3	4	5	6	7	8	9	10	11	12
MCPU-PV 047	4	268.0	75.0	96.0	91.5	49.0	84.0	71.0	47.0	37.0	35.0	71.0	80.0
MCN-PV 9574	Ind.	----	----	89.0	92.0	----	90.0	77.0	51.0	----	35.0	69.0	84.5
MCN-M 3222	4	278.0	76.5	92.0	104.0	51.0	96.0	76.0	55.0	34.0	38.0	70.0	87.0
MCN-M 2652	4	275.5	77.5	93.0	101.0	50.0	88.0	75.0	55.0	34.5	35.5	63.0	84.0
MCN-M 1698	4	270.5	76.0	89.0	95.0	47.0	85.0	65.0	53.5	32.5	36.5	66.0	79.0
MCN-M 3223	4	270.0	81.5	86.0	101.0	50.0	89.0	72.0	55.0	29.0	27.0	63.0	85.0
MCN-M 1098	4	265.0	75.5	89.0	102.0	51.0	90.0	75.0	53.0	37.0	38.5	69.5	80.0
MCN-M 2830	4	262.0	75.0	84.0	95.0	50.0	79.0	71.0	50.5	38.5	37.5	70.0	76.0
MCN-M 2727	4	260.0	74.0	86.0	96.3	54.0	82.0	67.5	55.5	35.0	36.0	69.0	77.5
MCN-M 2721	4	259.0	71.0	87.0	93.0	51.0	77.5	67.0	51.0	34.5	35.0	65.0	77.5
MCN-M 3221	4	255.0	80.0	81.0	98.0	53.0	83.0	68.5	49.0	31.0	37.0	70.0	74.0
MCPU-M 041	4	255.0	71.0	84.5	90.0	48.0	86.5	68.5	47.0	33.0	37.0	70.0	74.0
MCN-M 1696	Ind.	254.0	68.0	86.0	86.0	47.0	80.0	64.5	51.0	34.0	30.0	66.0	78.5
MCN-M 2679	4	246.0	71.0	79.0	91.0	46.0	76.0	62.5	50.0	33.0	33.5	60.0	70.0
MCN-M 1699	4	246.0	70.5	84.0	92.5	48.5	76.0	69.0	51.0	35.0	35.0	65.0	74.0
MCN-M 1691	4	253.0	65.0	88.0	88.0	50.0	82.0	66.5	49.0	36.0	39.0	69.0	75.0
MCPU-M 047	4	245.0	75.0	80.0	90.5	50.0	79.0	67.0	46.0	36.0	37.0	66.5	71.0
MCN-M 3206	3	245.0	68.5	79.0	86.0	44.0	79.0	62.0	45.0	33.0	31.0	58.0	69.0
MCN-M 3205	3	241.0	65.0	80.0	89.0	47.0	81.0	65.0	45.0	32.0	31.0	59.0	72.0
MCN-M 3207	2	237.0	66.0	77.0	83.0	43.5	70.0	60.0	49.0	31.0	34.0	62.5	73.0
MCN-M 3217	Ind.	237.0	67.0	77.0	85.0	45.5	78.0	63.0	45.0	32.0	32.0	58.0	73.0
MCN-M 1639	3	235.0	65.0	78.0	85.0	42.5	77.0	63.0	47.0	30.8	30.0	57.0	68.0
MCN-M 2812	Ind.	232.0	61.0	75.0	81.0	38.0	77.0	62.0	46.0	28.5	31.0	58.0	68.0
MCN-M 3224	2	232.0	61.0	78.0	85.0	42.5	75.0	66.0	47.5	29.0	32.5	57.5	70.0
MCN-D 0350	4	230.0	69.0	78.5	91.0	46.0	72.0	68.5	45.0	31.5	34.5	65.0	70.0
MCN-M 1697	3	226.0	61.0	81.5	82.0	43.5	72.0	54.0	45.5	31.0	33.0	60.0	68.5
MCN-M 3026	Ind.	220.0	61.0	75.0	90.0	35.0	70.0	59.0	45.0	27.5	27.0	52.0	69.0
MCPU-046	2	212.0	56.0	67.0	81.0	38.0	71.0	61.0	41.0	29.0	30.0	56.0	60.0
MCN-M 0502	1	205.0	58.0	65.0	84.0	40.0	71.0	61.0	39.0	31.0	30.0	56.0	68.0
MCN-M 3219	Ind.	188.0	45.0	61.0	66.0	32.0	61.0	51.0	39.0	24.0	35.0	49.0	54.5
MCN-M 3208	Ind.	185.0	45.0	59.5	69.0	33.0	61.0	50.0	38.0	24.0	25.0	46.0	55.0
MCN-M 3239	Ind.	176.5	41.0	55.0	65.0	32.5	66.0	49.0	35.0	23.0	25.0	41.0	51.0
MCN-M 1766	Ind.	146.0	38.5	47.0	54.0	27.5	55.0	40.0	32.0	21.5	22.5	38.5	47.0

Specimen	Age	13	14	15	16	17	18	19	20	21	22	23	24
MCPU-PV 047	4	48.5	71.0	150.0	118.0	19.0	15.0	15.0	15.5	14.8	14.0	47.5	19.0
MCN-PV 9574	Ind.	----	74.5	----	----	18.0	13.0	14.0	13.5	14.0	13.5	47.0	18.0
MCN-M 3222	4	56.0	77.0	147.0	132.0	18.0	15.5	13.0	14.0	14.0	14.5	51.0	19.0
MCN-M 2652	4	51.0	75.0	145.0	131.5	16.0	13.0	13.0	13.0	12.5	13.0	51.0	16.0
MCN-M 1698	4	51.0	66.5	143.0	127.5	15.0	14.0	13.0	14.0	13.0	14.0	48.5	17.0
MCN-M 3223	4	50.0	75.0	145.0	125.5	15.0	14.0	14.0	14.0	13.5	13.5	47.0	17.0
MCN-M 1098	4	48.0	77.0	145.0	120.0	16.0	14.5	13.0	14.0	13.0	14.0	46.0	17.0
MCN-M 2830	4	47.0	73.0	143.0	119.0	15.0	14.0	13.0	14.0	13.0	13.0	47.0	17.0
MCN-M 2727	4	48.0	71.0	135.0	125.0	16.0	15.0	12.5	13.5	12.5	13.5	45.0	17.0
MCN-M 2721	4	46.0	69.0	139.0	120.0	14.0	13.0	13.0	12.0	13.0	12.0	46.0	17.0
MCN-M 3221	4	49.0	73.0	135.0	120.0	15.0	13.0	13.0	13.0	13.0	12.5	43.0	15.0
MCPU-M 041	4	46.5	74.0	133.0	121.5	15.0	13.0	13.0	12.0	13.0	12.0	46.0	16.0
MCN-M 1696	Ind.	47.5	64.5	133.0	121.0	13.5	13.0	11.0	12.0	11.0	13.0	45.0	15.5
MCN-M 2679	4	45.0	65.0	136.0	110.0	14.0	13.0	12.0	11.0	12.0	11.0	42.0	16.0
MCN-M 1699	4	48.0	72.0	130.0	116.0	16.0	14.5	12.0	14.0	12.0	14.0	44.0	16.0
MCN-M 1691	4	42.0	66.5	138.0	115.0	18.5	12.0	13.5	13.0	13.0	13.5	43.5	15.0
MCPU-M 047	4	46.0	71.0	127.0	120.0	14.0	13.5	13.0	13.0	13.0	13.0	41.5	15.5
MCN-M 3206	3	49.0	63.5	131.0	144.0	13.5	12.5	11.5	11.0	11.5	11.0	38.5	19.0
MCN-M 3205	3	46.0	66.5	131.0	110.0	14.5	12.5	12.5	14.0	12.5	12.0	45.0	16.0
MCN-M 3207	2	47.0	66.5	119.0	118.0	13.5	14.0	11.0	13.5	11.0	13.5	43.0	15.5
MCN-M 3217	Ind.	43.0	64.0	127.0	110.0	14.0	12.5	11.0	11.0	11.0	11.0	40.0	14.5
MCN-M 1639	3	45.0	68.0	126.0	109.0	11.5	12.0	12.0	13.0	12.0	13.0	42.0	14.0
MCN-M 2812	Ind.	45.0	66.0	120.0	112.0	14.0	12.5	12.0	12.0	12.0	12.0	38.0	13.0
MCN-M 3224	2	48.0	68.0	120.0	112.0	15.0	12.5	10.5	12.0	12.0	11.5	40.0	13.5
MCN-D 0350	4	45.5	69.0	125.0	110.0	15.0	12.5	13.0	15.0	13.0	15.0	41.0	16.0
MCN-M 1697	3	42.5	62.5	121.0	105.0	14.0	10.0	12.0	12.0	12.0	11.5	45.0	16.0
MCN-M 3026	Ind.	43.0	60.0	118.0	102.0	14.0	12.0	11.5	12.0	11.0	12.0	39.0	13.5
MCPU-046	2	44.0	62.0	107.0	105.0	13.0	10.5	10.5	11.0	11.0	11.0	33.5	13.0
MCN-M 0502	1	44.0	61.0	105.0	100.0	12.0	10.0	10.0	10.0	10.0	10.0	31.0	12.0
MCN-M 3219	Ind.	36.5	58.0	92.0	95.0	11.0	10.0	9.0	10.0	9.0	10.0	31.0	11.5
MCN-M 3208	Ind.	39.0	57.0	93.0	92.0	11.5	10.0	9.0	10.0	9.0	10.0	30.0	11.0
MCN-M 3239	Ind.	38.0	54.0	88.5	88.0	10.0	8.0	9.0	8.0	9.0	8.0	28.5	10.0
MCN-M 1766	Ind.	35.0	50.5	74.5	71.5	8.0	7.0	7.0	6.0	7.0	6.0	23.0	8.0

Table 2. Measurements of the dentary of fossil and extant specimens of *H. hydrochaeris*. The specimens highlight in bold are the fossils. AC: Age Classes 0-4 of OJASTI (1971) and MONES (1991), Ind: Indefinite.

Specimen	AC	1	2	3	4	5	6	7	8	9	10	11
MCN-PV 9573	Ind.	39.5	40.0	86.0	20.5	10.5	18.5	11.5	20.0	13.0	24.5	16.0
MCN-M 2727	4	42.0	37.5	86.0	23.5	12.0	20.0	13.0	20.0	15.0	24.0	16.0
MCN-M 3221	4	41.0	36.0	79.0	21.0	12.0	19.0	12.5	20.0	13.5	24.0	15.5
MCPU-047	4	41.0	33.5	80.5	20.5	11.5	17.5	11.0	20.0	18.5	24.0	15.0
MCN-M 2830	4	39.5	40.0	90.0	23.0	12.0	20.0	12.0	22.0	16.5	23.0	17.5
MCN-M 2652	4	39.5	35.0	89.0	22.0	10.0	18.5	11.0	22.2	15.0	26.5	17.0
MCN-M 2721	4	38.0	32.0	78.0	21.0	10.0	19.0	11.0	20.0	12.0	24.0	15.0
MCN-M 1691	4	38.0	36.0	80.0	20.5	10.0	20.0	11.0	18.0	14.0	22.0	15.0
MCN-M 3222	4	37.5	35.5	90.0	24.0	12.0	21.0	25.0	22.5	16.0	26.0	18.0
MCN-M 2812	Ind.	37.0	29.0	75.0	19.0	10.0	17.0	11.0	18.0	13.0	22.0	14.0
MCPU-041	4	37.0	35.5	84.0	22.0	11.0	20.0	12.0	20.0	15.0	23.0	16.0
MCN-M 1639	3	37.0	29.0	75.9	20.0	12.0	16.5	12.5	17.0	12.5	19.0	14.0
MCN-M 3207	2	36.5	32.0	76.5	19.5	10.0	17.5	11.5	19.0	14.0	24.0	15.5
MCN-M 3217	Ind.	36.0	32.5	76.0	19.0	11.0	16.0	22.0	18.5	22.0	21.0	15.0
MCN-M 2679	4	36.0	32.0	78.0	21.0	10.0	19.0	11.0	20.0	12.0	24.0	15.0
MCN-M 3205	3	35.5	20.5	78.0	21.0	11.0	19.0	12.0	17.0	14.0	23.0	15.0
MCN-D-0350	4	35.0	33.0	80.0	21.0	11.5	18.5	14.0	22.5	20.0	22.0	15.0
MCN-M 3206	3	35.0	32.0	75.0	20.0	10.5	16.0	10.0	17.5	11.0	23.5	15.0
MCN-M 3234	2	35.0	30.5	75.0	20.0	10.5	16.0	10.0	18.0	13.5	23.0	15.0
MCN-M 3223	4	35.0	34.5	84.5	23.0	12.0	20.5	12.5	21.5	15.0	25.0	17.0
MCN-M 3026	Ind.	31.0	30.0	72.0	18.8	11.0	17.0	11.0	18.0	12.5	19.0	19.0
MCN-M 3208	Ind.	29.0	25.5	61.0	15.0	9.0	14.5	10.0	15.0	12.0	17.0	12.0
MCN-M 3219	Ind.	28.5	27.0	61.0	16.0	9.0	13.5	10.0	14.0	12.0	17.0	12.0
MCN-M 2320	Ind.	28.0	27.0	59.8	15.5	8.0	14.0	10.0	14.0	11.0	17.5	11.0
MCN-M 3218	Ind.	25.0	23.5	54.0	15.0	7.5	13.0	90.0	12.0	9.5	16.0	10.0
MCN-M 1766	Ind.	23.0	22.0	48.5	12.0	6.0	10.0	6.0	11.0	7.0	14.0	8.0