

PROTOCYON TROGLODYTES (LUND) (MAMMALIA, CARNIVORA) IN THE LATE PLEISTOCENE OF RIO GRANDE DO SUL AND THEIR PALEOECOLOGICAL SIGNIFICANCE

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ABSTRACT – An incomplete maxilla with P4 and M1, from the late Pleistocene lacustrine sands of the System Barrier III (Santa Vitória Formation), is the first record of *Protocyon troglodytes* (Lund) for the State of Rio Grande do Sul, Brazil. This material differs from *Theriodictis*, a closely related genus, in characters of the P4 (protocone more reduced) and M1 (hypocone more reduced, and the inner half mesiodistally narrower and straighter). Differently of southern Brazil living canids such as *Chrysocyon brachyurus*, *Cerdocyon thous* and *Dusicyon gymnocercus*, *P. troglodytes* developed dental adaptations associated to hypercarnivory in having large paracone on M1, strong reduction of protocone on P4 and reduction and simplification of talonids. In the latest Pleistocene, the climate was colder and grassland landscapes were predominant in southern Brazil, where several potential large and medium-sized ungulate preys were present. *Protocyon troglodytes* probably preyed on medium-sized grazers or browsers but not on the megafauna, or only on young individuals of this size class.

Key words: Canidae, *Protocyon troglodytes*, Arroio Chuí, Pleistocene, Brazil.

RESUMO – Um maxilar incompleto com P4 e M1, coletado em sedimentitos lacustres do Pleistoceno Tardio do Sistema-Barreira III (Formação Santa Vitória), constitui o primeiro registro de *Protocyon troglodytes* (Lund) para o Rio Grande do Sul. Este material difere de *Theriodictis*, gênero intimamente relacionado a *Protocyon*, em caracteres do P4 (protocone reduzido) e do M1 (hipocone mais reduzido e apresentando sua porção lingual comprimida e retilínea). Diferentemente de canídeos sul-brasileiros atuais como *Chrysocyon brachyurus*, *Cerdocyon thous* e *Dusicyon gymnocercus*, *P. troglodytes* desenvolveu adaptações dentárias relacionadas à hipercarnivoria, em tendo um grande paracone no M1, forte redução do protocone no P4 e redução e simplificação de talonidos. No final do Pleistoceno o clima foi mais frio e mais seco no sul do Brasil, prevalecendo áreas abertas, onde várias presas potenciais compostas de ungulados de tamanho grande e médio estiveram presentes. *Protocyon troglodytes*, provavelmente, não predava megamíferos e sim herbívoros de tamanho médio ou apenas indivíduos jovens da megafauna.

Palavras-chave: Canidae, *Protocyon troglodytes*, Arroio Chuí, Pleistoceno, Brasil.

INTRODUCTION

The fossil record of the canids in South America begins during the Pliocene, about 3.0 Ma (Mercerat, 1891), being the oldest recorded taxon represented by *Dusicyon cultridens* (Ameghino) (Berman, 1994). There are records dated as Pleistocene of large extinct taxa that illustrate a diversification of wolf-like and dhole-like forms (Berta, 1981), such as *Canis*

Linnaeus, *Protocyon* Giebel, *Theriodictis* Mercerat, *Chrysocyon* Hamilton Smith, and *Speothos* Lund.

In Brazil, the record includes several remains of *Protocyon troglodytes* (Lund) and *Cerdocyon thous* (Wied) from Lagoa Santa (State of Minas Gerais) and limestone caves of the States of Bahia and Rio Grande do Norte (Lessa *et al.*, 1998; Cartelle & Langguth, 1999; Porpino *et al.* 2004). *Protocyon troglodytes* has been reported in other late Pleistocene

deposits of the states of Piauí, Ceará, Paraíba and Paraná (Born & Sedor, 2001; see Prevosti *et al.*, 2005). *Dusicyon gymnocercus* (Fischer) and *D. vetulus* (Lund) are present at the caves of Minas Gerais (Winge, 1895; Cartelle, 1999).

The record of canids in the southern Brazil late Cenozoic deposits is very scarce including only two isolated teeth described as *Dusicyon avus* and cf. *Theriodictis* (Rodrigues *et al.*, 2004). However, these records does not have precise stratigraphic position because they come from reworked sands ranging from Pliocene to the Holocene (see below).

The discovery of an incomplete maxilla with P4 and M1, from late Pleistocene Arroio Chuí locality, Santa Vitória do Palmar (Figure 1), is the first record of *Protocyon troglodytes* for Rio Grande do Sul. This paper describes this material and discusses its biostratigraphic context and paleoecological significance.

Abbreviations

Institutional. **CI**, Daniel Ibáñez Collection, Mar del Plata; **Ctes-PZ**, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes; **EPN**, Escuela Politecnica Nacional, Quito; **IGC**, Instituto de Geociências da Universidade Federal de Minas Gerais, Minas Gerais; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MCN-PV**, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul; **MCPU-PV**, Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Uruguaiana; **MG**, Museum d’Histoire Naturelle, Geneva; **MLP**, Museo de La Plata, Departamento Científico Paleontología Vertebrados; **MMP**, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Mar del Plata; **MNHN**, Museum National d’Histoire Naturelle, Paris; **MNPA**, Museo Nacional de Paleontología Arqueología, Tarija; **MPS**, Museo

Paleontológico de San Pedro, San Pedro; **MNRJ**, Museu Nacional do Rio de Janeiro, Rio de Janeiro; **UZM L**, Zoologiske Museum, Kopenhagen.

Anatomical. **A**, width; **L**, length; **LLA**, labial length; **LLI**, lingual length; **P4**, upper fourth premolar, **M1**, first upper molar; **fo**, infraorbital foramen.

GEOLOGICAL SETTING AND ASSOCIATED FAUNA

Upper Cenozoic deposits of the coastal plain lagoon sequences from Pelotas Basin are very rich in fossil vertebrates and their geological history has been studied in some detail (Villwock & Tomazelli, 1995; Tomazelli *et al.*, 2000). This vertebrate-bearing deposit has been traditionally located in the “Santa Vitória Member of the Chuí Formation”, which is correlated with the Dolores Formation from Uruguay and “Canañéia transgression” from southeast Brazil (Villwock & Tomazelli, 1995).

The mammal-bearing coastal plain depositional system is the Barrier III (Santa Vitória Formation), which occurs from North to South along the coastal plain. The vertical facies represents a regressive event, including sandy beach facies covered by eolian deposits. Lagoonal facies are represented by cream colored, poorly selected, silt-clayey sands, either massive or with parallel lamination (Figure 2), and bears calcareous and ferruginous pedogenetic concretions (Tomazelli *et al.*, 2000; Buchmann, 2002). Late Quaternary vertebrates recovered from Arroio Chuí, including mammals, are from massive mudstones and sandstones (Figure 2).

A late Pleistocene (Lujanian SALMA age) is suggested by correlation with late Cenozoic Argentinian biostratigraphy (Oliveira, 1999, see below). A mammalian faunal list is presented in Appendix 1.

SYSTEMATICS

CARNIVORA Bowdich, 1821
 CANIDAE Fischer, 1817
Protocyon Giebel, 1855
Protocyon troglodytes (Lund, 1838)
 (Figures 3, 4; Table 1)

Referred material. MCPU-PV 148, incomplete right maxilla with P4 and M1 and distal edge of P3 alveolus.

Locality and age. Arroio Chuí, Santa Vitória do Palmar, Rio Grande do Sul State, Brazil (Figure 1); Santa Vitória Formation (System Barrier III), late Pleistocene.

Description

Measurements of MCPU-PV 148 are given in the Table 1. The infraorbital foramen open mesial to the P4 and the facial tubercle is well developed (Figure 3). The dentition is moderately worn and the paracone of the P4 is broken. This premolar is long but has a very reduced and rounded protocone, which is placed mesiolingually. The

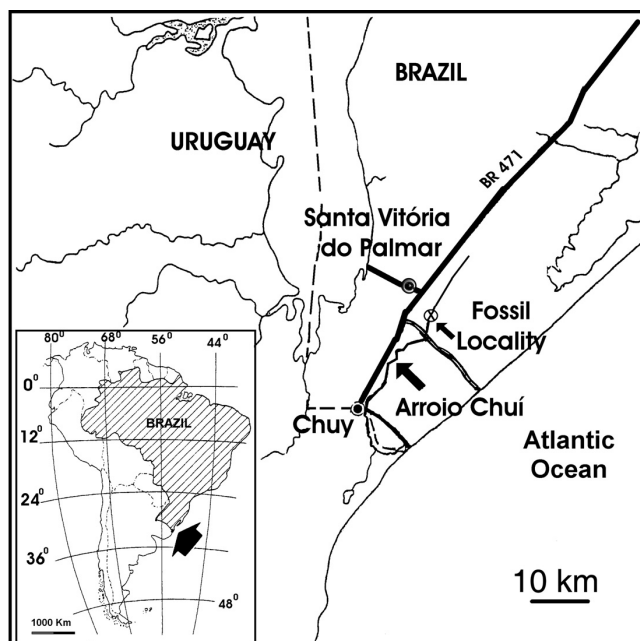


Figure 1. Location map of the Arroio Chuí, at the municipality of Santa Vitória do Palmar.

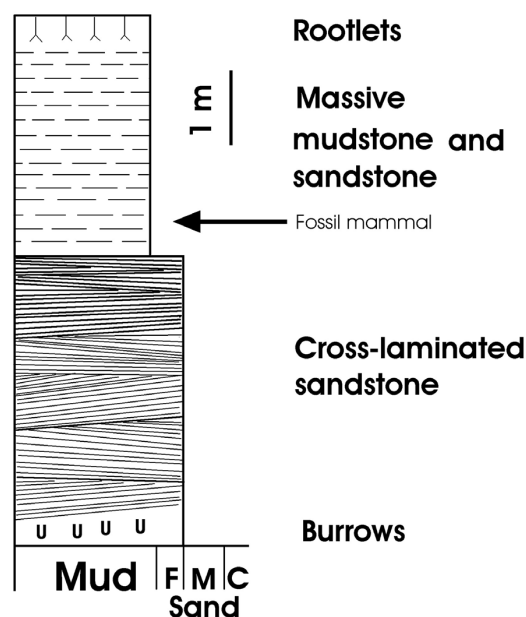


Figure 2. Stratigraphic section of System Barrier III at Arroio Chuí locality showing location of horizon that yielded MCPU-PV 148.

lingual cingulum is weakly developed too. The M1 also shows reduction of structures because the hypocone is small, but is expanded mesially around the protocone, and the labial cingulum is practically absent. Principal cusps of the M1 are sharp and uninflated. In overall occlusal view, the M1 is subtriangular in outline with the paracone much higher and stronger than the metacone. The labial side of paracone is rounded and the ectoflexus is relatively shallow. In lingual view the protocone is extremely low in comparison to the paracone and the metacone. The hypocone is prolonged mesially around the protocone as a thin cingulum and contact the mesial cingulum. Lingually oriented wear facets are present from the base of the paracone and from the metacone to the protocone. The lingual half of the M1 is mesiodistally compressed and the talon deeply excavated.

DISCUSSION

Comparisons

Procyon includes three fossil species: *P. troglodytes* from Brazil, Bolivia, Ecuador and northern Argentina; *P. scagliarum* Kraglievich from Argentina and *P. orcesi* Hoffstetter from Ecuador (see Prevosti *et al.*, 2005). *Procyon scagliarum* can be differentiated from *P. orcesi* and *P. troglodytes* in having p4 with an anterior cusplet and lower premolars widely spaced (Berta, 1981). Cartelle & Langguth (1999) believe that the more notable differences between *P. scagliarum* and *P. troglodytes* are in the P4 by the presence in the former of an anterior cusplet coupled with a more reduced protocone. *Procyon orcesi* differs from *P. troglodytes* by the loss of m3 and in having m2 with a transversely narrow talonid (Berta, 1981, 1988).

The size and dental reductions of the MCPU-PV 148 allied

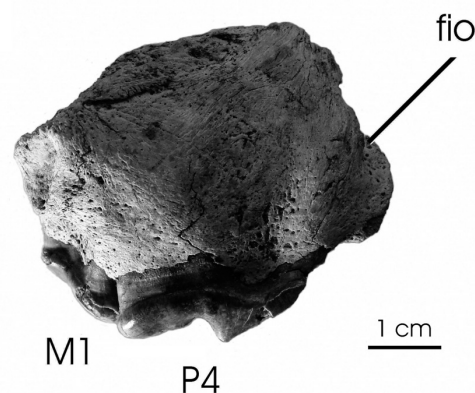


Figure 3. *Procyon troglodytes*, MCPU-PV 148, lateral view of right maxilla with P4 and M1.

it to the hypercarnivore South American genera *Theriodictis* and *Procyon*. The dental size of the MCPU-PV 148 is in the range of *Theriodictis* and is greater than in *Procyon*, but several features separate it from the first genus: the protocone of the P4 is more reduced and positioned more mesially; the hypocone of the M1 is more reduced and the inner half is mesiodistally narrower and straighter, and allow to assign it to *Procyon*. The protocone of the MCPU-PV 148 is similar to the holotype of *P. scagliarum* (MMP 164) and to the specimen assigned to *P. troglodytes* UZML 228. However, in other specimens of *P. troglodytes* (e.g. UZML 5697-98 and cf. *P. troglodytes* Ctes-PZ 7278) this structure is more reduced, mesiodistally narrower and displaced distally. The M1 of *Procyon scagliarum* and *P. orcesi* presents a more developed hypocone and a mesiodistally wider inner half that is more curved in distal direction. The morphology of the M1 is very similar to some specimens of *P. troglodytes*, especially to cf. *P. troglodytes* Ctes-PZ 7278. The morphological evidence suggests that the MCPU-PV 148 belongs to *P. troglodytes*. The size differences could be interpreted as intraspecific variation, upon the variability observed in recent species.

The specimen here described represents the first canid from the state of Rio Grande do Sul with precise stratigraphic location, and the first record of *P. troglodytes* for this state, southernmost Brazil.

Taphonomy and Biostratigraphy

Only the vertebrate assemblages from Arroio Chuí have precise stratigraphic location in the context of the coastal plain Pleistocene sedimentary deposits. Taphonomic observations suggest that vertebrates (mainly mammals) occurring below the present sea level are a mixture of Neogene and Holocene taxa without stratigraphic control (Oliveira,

Table 1. Dental measurements (mm) of *Protocyon* spp. and *Theriodictis* spp. AP4, width of the P4 at the protocone; APP4, width of the P4 taken at the carnassials notch. Asterisks indicate approximate measures; 1 indicates measurements from Cartelle & Langguth, 1999.

TAXA	LP4	AP4	APP4	LLAM1	LLIM1	AM1
<i>P. troglodytes</i> (MCPU-PV148)	29.33*	12.11	9.07	16.08	10.27	18.46
<i>P. troglodytes</i> (MNRJ 3231)				14.56	10.19	17.15
<i>P. troglodytes</i> (UZM L5697/98)	25.90	12.20	9.50	14.25	10.45	16.50
<i>P. troglodytes</i> (UZM L228)	27.75	12.95	10.80			
<i>P. troglodytes</i> (IGC 1) ¹	25.10	11.60		14.40		16.40
<i>P. troglodytes</i> (UZM L5699) ¹	26.30	12.40				
<i>P. troglodytes</i> (UZML2145/46) ¹	28.00	13.50				
<i>P. troglodytes</i> (UZM L643) ¹	26.00*	12.70*				
<i>P. troglodytes</i> (UZM L187) ¹				16.50		18.60
<i>P. troglodytes</i> (UZM-L251) ¹	27.60					
<i>Cf. P. troglodytes</i> (Ctes-PZ 7278)	24.55	12.10	9.30	14.50	9.55	16.15
<i>P. scagliarum</i> (MMP S164)	25.15	11.15	9.25	14.70	9.95	16.10
<i>P. orcesi</i> (EPN V 2877)				13.65	9.50	15.70
<i>Protocyon</i> sp. (CI S/N°)	27.30	12.35	10.40	13.85	10.95	16.10
<i>Protocyon</i> sp. (MNPA V294G)				15.90	9.75	17.70
<i>T. tarijensis</i> (MACN Pv1452)	27.20	12.05	9.20	15.45	10.05	16.20
<i>T. tarijensis</i> (MNHN Tar657)	27.50	12.10	9.60			
<i>T. platensis</i> (MLP 10-51)	25.80	12.6	9.98	14.60	12.55	15.8
<i>T. platensis</i> (MLP96-IX-1-1)	30.20	13.85	11.45	17.40	11.45	18.00
<i>T. platensis</i> (MMP 2700)	29.80	14.5	12.50	19.10	12.7	22.3
<i>T. platensis</i> (MG 634/14)	27.70	11.05*	9.30	15.90	11.4	
<i>T. platensis</i> (MLP S/N°)	26.95	13.05*	9.70	16.50	11.20	18.15
<i>T. platensis</i> (MPS 2)	30.05	14.80	11.2	16.8	11.55	17.50
<i>Theriodictis</i> sp. (MNHNTar662)				16.10	10.60	17.80
<i>Theriodictis</i> sp. (MCN-PV 3639)				16.85	12.95	21.25

1992, 1999). Is very probable that transgressive and regressive late Cenozoic events recorded for Rio Grande do Sul (Villwock & Tomazelli, 1995) produced a time-averaging of several thousands of years. Variations on the sea level and associated distal and proximal storm events, probably reworked deposits of the Taim (Holocene), Santa Vitória (late Pleistocene) and Graxaim (Plio-Pleistocene) formations. In this context, Souza Cunha (1959) and Oliveira (1992) reported for seashore sediments at Santa Vitória do Palmar remains of Toxodontidae related to older or different taxa than the late Pleistocene *Toxodon*.

The vertebrates recovered from lacustrine deposits of Arroio Chuí are associated to “barrier-lagoon system III”, which is interpreted to be formed during the isotopic stage 5e: ± 120 ka, being their fossil mammals thus correlated to the early Lujanian age (Cione & Tonni, 1999). In this local fauna occurs the glyptodont *Doedicurus clavicaudatus*, an exclusive taxon of the Lujanian age. Furthermore, the more important biostratigraphic taxon reported for Arroio Chuí is *Equus neogeus* (Souza Cunha, 1959), which represents a guide fossil possibilizing the chronocorrelation to the *Equus neogeus* Biozone (Cione & Tonni, 1999), that covers the late Pleistocene interval ($\pm 130.000-7.300$ years). However, the absolute age of the Arroio Chuí local fauna is still unknown. The correlation between the Santa Vitória and the Dolores Formation (10.480-11.650 yB.P.) from Uruguay, as supposed by Ubilla *et al.* (1994), not have been confirmed in recent studies (Ubilla, 1999).

Paleoecology

The studies about the late Pleistocene (Lujanian) synecology suggest that during this time existed relatively few carnivores in relation to the number of herbivorous species (Fariña & Vizcaíno, 1999). In the Luján local fauna were considered as predators the canid *Dusicyon avus* Burmeister, the felid *Panthera onca* (Linnaeus), the saber toothed *Smilodon* Lund and the ursid *Arctotherium* Burmeister (Fariña & Viscaíno, 1999). But, *Puma concolor* (Linnaeus) is also identified in this fauna (see Soibelzon, 2002). Of these, *Dusicyon avus*, with an estimated body mass of 15 kg, was interpreted as a moderate carnivorous canid, similar to modern jackals. Fariña (1996) interpreted that the Luján local fauna is ecological “unbalanced” because the low estimated biomass (and densities) and species richness, but the available evidence does not support this reconstruction (Prevosti, personal observation).

The extinct canid here reported offers a different scenario of that of the Luján local fauna. *Protocyon troglodytes* was an important predator in Santa Vitória fauna as well as, in other late Pleistocene mammalian communities, not only by their dental adaptation to the hypercarnivory (see below), but also by their larger size.

In carnivorous mammals such as canids, the upper premolar and lower molar form carnassials, specialized sectorial teeth that slice against each other like scissors to cut sinew and muscle (Biknevičius & Van Valkenburgh, 1996). Among living canids, four out of thirty-six species are hypercarnivorous (i. e. vertebrate meat constitutes more than 70% of their diet). These include the Eurasian and North American gray wolf (*Canis lupus*), the African wild dog, the Indian dhole (*Cuon alpinus*), and the South American bush dog (*Speothos venaticus*) (Van Valkenburgh, 1991). Trenchant heel lower m1, size reduction of m2, complete loss of m3, reduction of the m1 metaconid and the M1 hypocone are dental adaptations in hypercarnivorous canids (Palmqvist *et al.*, 1999).

In *Protocyon*, *Theriodictis* and living omnivorous canids of southern Brazil such as *Cerdocyon thous*, *Chrysocyon*

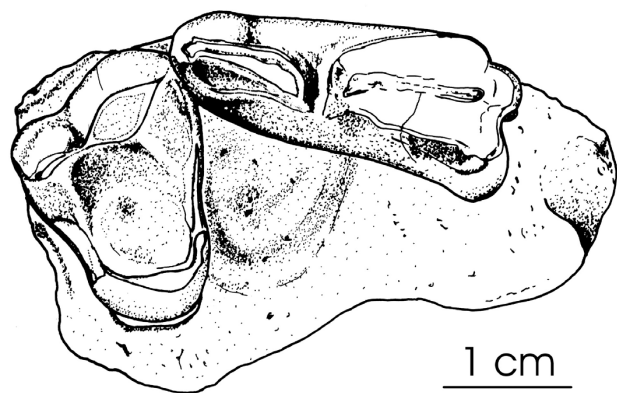


Figure 4. *Protocyon troglodytes*, MCPU-PV 148, occlusal view of right maxilla with P4 and M1 and distal edge of P3 alveolus.

brachyurus (Illiger) and *Dusicyon gymnocercus*, the P4 (carnassial tooth) has a general similar teeth design, i.e. large paracone, reduced protocone and laminated metacone. However, the M1 of the living species (e. g. *Dusicyon gymnocercus*) bears two subequal cusps (paracone and metacone), with the paracone only slightly more developed than the metacone, and the protocone is very wide, with the hypocone well developed (Figure 5). Differently of living canids, the MCPU-PV 148 presents the dental hypercarnivore features described for the genus *Protocyon* like larger paracone than metacone on M1, reduced hypocone, and strong reduction of the protocone on P4. The larger dental size of this specimen, in comparison to other of the genus, suggests that its weight could be greater than the 16-25 kg estimated by Van Valkenburgh (1991) but lower than the 37 kg estimated for a large specimen of *T. platensis* (Prevosti & Palmqvist, 2001).

Living canids in southernmost Brazil are distributed in grassland and campos-forest border areas, including high altitude forests, deciduous forest, campos and gallery forest landscapes (Oliveira, 1999; Indrusiak & Eizirik, 2003). In the latest Pleistocene the climate was colder and grassland landscapes were predominant, where several potential ungulate preys such as the medium sized cervids, tayassuids, camelids, equids and megaherbivores were present. However, as suggested by Cartelle & Langguth (1999), *P. troglodytes* probably preyed on medium sized grazers or browsers but not on the megafauna, or only on young individuals of this size class. The inferred size and the actualistic evidence support this hypothesis.

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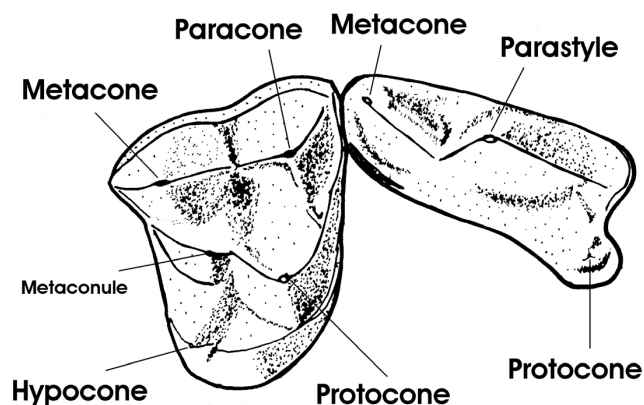


Figure 5. Dental terminology of P4 and M1 in *Dusicyon gymnocercus*.

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Appendix 1. Taxonomic list for the late Cenozoic mammals from the Arroio Chuí locality, State of Rio Grande do Sul, Brazil.

- XENARTHRA
 Dasypodidae
Propraopus cf. *P. grandis*
 Pamphathiidae
Pamphathium sp.
Holmesina paulacoutoi
 Glyptodontidae
Doedicurus clavicaudatus
Glyptodon clavipes
Glyptodon cf. *reticulatus*
Panochthus sp.
 Mylodontidae
Glossotherium robustum
Lestodon sp.
Mylodon darwini
Catonyx sp.
 Megatheriidae
Megatherium americanum
- NOTOUNGULATA
 Toxodontidae
Toxodon sp.
 Toxodontinae indet.
 Haplodontheriinae indet.
- LITOPTERNA
 Macraucheniidae
Macrauchenia patachonica
- RODENTIA
 Hydrochoeriidae
Hydrochoerus hydrochaeris
- PROBOSCIDEA
 Gomphotheriidae
Stegomastodon waringi
- PERISSODACTYLA
 Equidae
Hippidion principale
Equus neogeus
 Tapiridae
Tapirus terrestris
- ARTIODACTYLA
 Cervidae
Antifer sp.
Morenelaphus sp.
Ozotoceros bezoarticus
 Camelidae
Hemiauchenia paradoxa
Lama guanicoe
 Tayassuidae
Brasiliochoerus stenocephalus
Tayassu sp.
- CARNIVORA
 Felidae
Smilodon populator
 Canidae
Procyon troglodytes