

# On the presence of *Holochilus brasiliensis* (Desmarest, 1819) (Rodentia: Cricetidae: Sigmodontinae) in the late Pleistocene of southern Brazil

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### ABSTRACT

Fossil remains of the sigmodontine rodent *Holochilus brasiliensis* (Desmarest, 1819) from two geographic areas from the state of Rio Grande do Sul, southern Brazil are reviewed and described here. The specimens came from two localities: Quaraí River in the western region, which has yielded a dentary with an incisor and molars, and Chuí Creek in the eastern region, where a fragmented right dentary and a maxillary fragment with molars were collected. The presence of this taxon in the late Pleistocene of meridional Brazil suggests the existence of perennial water bodies.

**Keywords:** mammals, rodents, late Pleistocene, paleoenvironment, Rio Grande do Sul.

### RESUMO

SOBRE A PRESENÇA DE *HOLOCHILUS BRASILIENSIS* (DESMAREST, 1819) (RODENTIA: CRICETIDAE: SIGMODONTINAE) NO PLEISTOCENO FINAL DO SUL DO BRASIL. Fósseis do roedor sigmodontíneo *Holochilus brasiliensis* (Desmarest, 1819), identificados em duas áreas geograficamente distintas do Estado do Rio Grande do Sul, sul do Brasil, são aqui revisados e descritos. Os espécimes analisados provêm de duas localidades: o Rio Quaraí, no extremo oeste, onde foi identificado um dentário, com um incisivo e molares, e o Arroio Chuí, na porção leste, onde foram coletados um dentário direito fragmentado e um fragmento de maxilar com molares. A presença deste táxon no Pleistoceno final do Brasil meridional sugere a presença de corpos de água perenes.

**Palavras-chave:** mamíferos, roedores, Pleistoceno final, paleoambiente, Rio Grande do Sul.

## INTRODUCTION

The marsh rats of the genus *Holochilus* Brandt, 1835 (Cricetidae: Sigmodontinae) comprise three extant and one extinct species (Pardiñas and Teta, 2011). This taxon shows a wide geographic distribution, covering almost all regions of South America, except the Andes and southern Patagonia. The living species include *H. sciureus* Wagner, 1842, found in Venezuela, Guyana, Colombia, Ecuador, Bolivia, Peru, and northern Brazil; *H. chacarius* Thomas, 1906 found in Paraguay (Chaco), Brazil (State of Mato Grosso do Sul) and northern Argentina; and *H. brasiliensis*, distributed through eastern Paraguay, southern, southeastern and some areas of northeastern Brazil, Uruguay and Argentina (Hershkovitz, 1955; Marques, 1988; Eisenberg and Redford, 1989; Barreto and García-Rangel, 2005; Oliveira and Bonvicino, 2006; Weksler *et al.*, 2008; Pardiñas and Teta, 2011). Hershkovitz (1955) recognized several subspecies of *H. brasiliensis*.

The only recognized extinct species of the genus is *H. primigenus* Steppan, 1996 from the middle Pleistocene of Bolivia. However, this taxon shares several dental features with *Lundomys* Voss and Carleton, 1993 and its generic position must be re-evaluated (Pardiñas and Teta, 2011). Although a major review of *Holochilus* is needed (see Pardiñas and Teta, 2011), these recognized species are distinguished by several cranial and dental features.

The stratigraphic distribution of *Holochilus* ranges from the early Pleistocene to the Recent. Fossils of *H. brasiliensis* have been reported from the Ensenadan (early Pleistocene) to Platan (Holocene) of Argentina (Mazzanti and Quintana, 1997; Pardiñas, 1999; Quintana, 2004; Teta *et al.*, 2004, 2005; Pardiñas and Teta, 2011; Fernández *et al.*, 2011) and late Pleistocene to Holocene of Brazil (Winge, 1887; Voss and Myers, 1991; Oliveira, 1992; Salles *et al.*, 1999, 2006; Rosa and Jacobus, 2009 and references therein). *H. chacarius* was reported from the Holocene of Bolivia and Argentina (Pardiñas and Galliari, 1998; Pardiñas

and Teta, 2011). *H. sciureus* was reported for the late Pleistocene of Venezuela (Rincón, 2006). The only record of *H. primigenus* is from the middle Pleistocene Tarija beds of Bolivia (Steppan, 1996). More information on the fossil record of the marsh rats can be seen in the extensive review of Pardiñas and Teta (2011).

The knowledge about the Pleistocene sigmodontines in southern Brazil is scarce (Pardiñas, 1999). The only records in the literature consist of a dentary assigned to *Holochilus brasiliensis* (Desmarest, 1819) from the upper Pleistocene deposits of the Quaraí River (Oliveira, 1992); a molar of a Cricetidae aff. *Reithrodon* from the Touro Passo Formation (Oliveira *et al.*, 1999); and an m1 of *Reithrodon auritus* (Fisher, 1814) from the continental shelf (Rodrigues and Ferigolo, 2004), all from the State of Rio Grande do Sul. The material from the Touro Passo Formation referred by Oliveira *et al.* (1999) is currently lost and its taxonomic status cannot be confirmed. According to Pardiñas (1999)

the material reported by Oliveira (1992) could possibly be attributed to *Lundomys molitor* (Winge, 1887) – “the murid record is restricted to *Holochilus brasiliensis* (may be *Lundomys molitor*?)” (Pardiñas, 1999, p. 246).

In this paper, we review the presence of the marsh rat *Holochilus brasiliensis* in the upper Pleistocene beds of the State of Rio Grande do Sul, contributing to the knowledge of the southern Brazilian fossil rodents.

## MATERIAL AND METHODS

The fossils described here were collected in the banks of Quaraí River, located in westernmost Rio Grande do Sul State, and in the banks of Chuí Creek, in the coastal plain of the state (Figure 1). The specimens are housed at the paleovertebrate collections of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre) and Museu Coronel Tancredo Fernandes de Melo (Santa

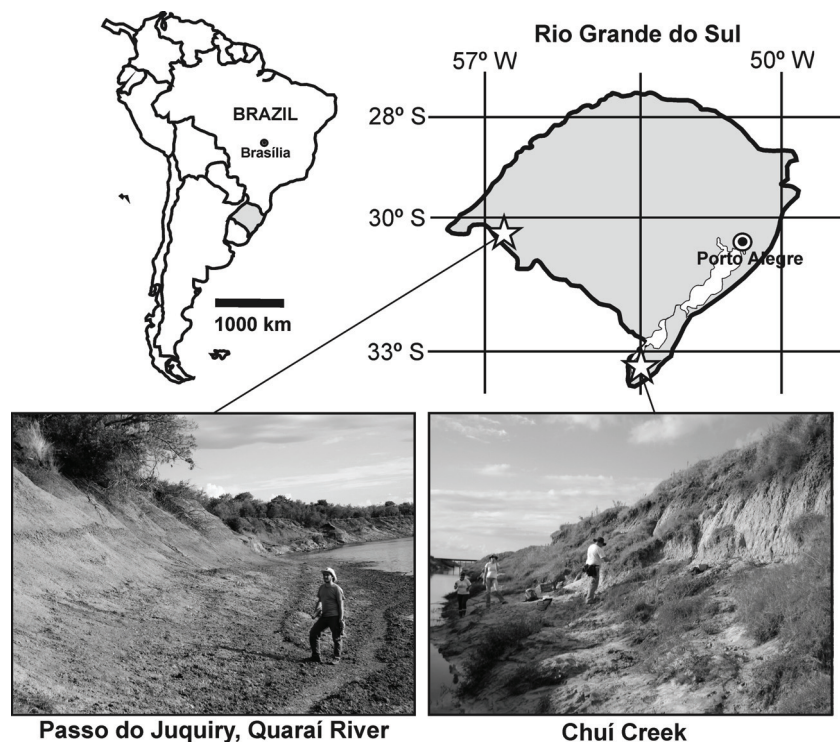


Figure 1. Location and expositions from the Passo do Juquiry (Quaraí River) and Chuí Creek outcrops.

Vitória do Palmar). The material from Quaraí River is the specimen mentioned preliminarily by Oliveira (1992) and the specimens from the Chuí Creek were recently collected. These fossil remains were compared with recent specimens of *Holochilus brasiliensis* (MCN-M 661, MCN-M 326, MCN-M 668, MCN-M 651, MCN-M 1722, MCN-M 666, MCN-M 594) and anatomic descriptions in the literature (see the description and comparison). The dental nomenclature follows Reig (1977). The measurements (expressed in millimeters) were taken with a digital caliper accurate to 0.01 mm and a stereomicroscope.

**Institutional Abbreviations.**

MCN-M: mammals collection of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre. MCN-PV: paleovertebrates collection of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre. MCTFM: paleovertebrates collection of Museu Coronel Tancredo Fernandes de Melo, Santa Vitória do Palmar.

**Geological and biostratigraphic remarks**

Quaraí River is located in Brazilian-Uruguayan border; the fossiliferous beds in the Brazilian side of the border have not been formally named, but are correlated to the Sopas Formation of Uruguay (Ubilla *et al.*, 2004). The beds exposed along its banks are composed of brownish muddy sandstones, with paleosols that exhibit carbonatic rhizonecretions levels (Da-Rosa, 2003). On the Brazilian side there are four well-studied localities: Lagoa da Música, Passo da Cruz, Cerro da Tapera and Passo do Juquiry; the material described here was collected in the latter.

Available absolute ages (<sup>14</sup>C and thermoluminescence) for the fossil and sediments from the Brazilian banks give an interval between 33 and 10 ka BP (Miller, 1987; Ribeiro *et al.*, 2008), but some older ages were obtained from the deposits of Uruguay (Ubilla *et al.*, 2004). The presence of *Equus* (*Amerhippus*)

*neogus* Lund, 1840 in the Quaraí River (Ubilla *et al.* 2004; Kerber and Oliveira, 2008) suggests a Lujanian Age/Stage for these deposits, according to the biostratigraphic scheme of Cione and Tonni (1999). However, according to Ubilla *et al.* (2004), some taxa found in the Sopas Formation were originally described from the Ensenadan and Bonaerian beds from Argentina, such as *Neuryurus rudis* (Gervais, 1878), *Lestodon armatus* (Owen, 1842), *Neolicaphrium recens* Frenguelli, 1921, *Antifer ultra* (Ameghino, 1888) and *Morenelaphus brachyceros* (Gervais and Ameghino, 1880). The previous knowledge about the Passo do Juquiry local fauna indicates the presence of: *Hydrochoerus hydrochaeris* (Linnaeus, 1766), *Ho-*

*lochilus brasiliensis* (material here revised), Glyptodontidae indet., Tremarctinae indet., *Antifer* Ameghino, 1889, *Equus* (*A.*) *neogus* and *Notiomastodon platensis* (Ameghino, 1888) (= *Stegomastodon waringi* Holland, 1920) (Oliveira, 1992; 1996; Ribeiro *et al.*, 2003; Kerber and Oliveira, 2008; Marcon, 2008).

Chuí Creek is located on the southernmost portion of the coastal plain (Figure 1) and the fossils are found mostly in the lower portion of a ~1 meter-thick muddy sand layer overlying shallow marine sediments with *Ophiomorpha nodosa* and *Rosselia* sp. ichnofossils and other bioturbations (Figure 2). In several places along the banks, 30 to 40 centimeter-thick lenses of organic

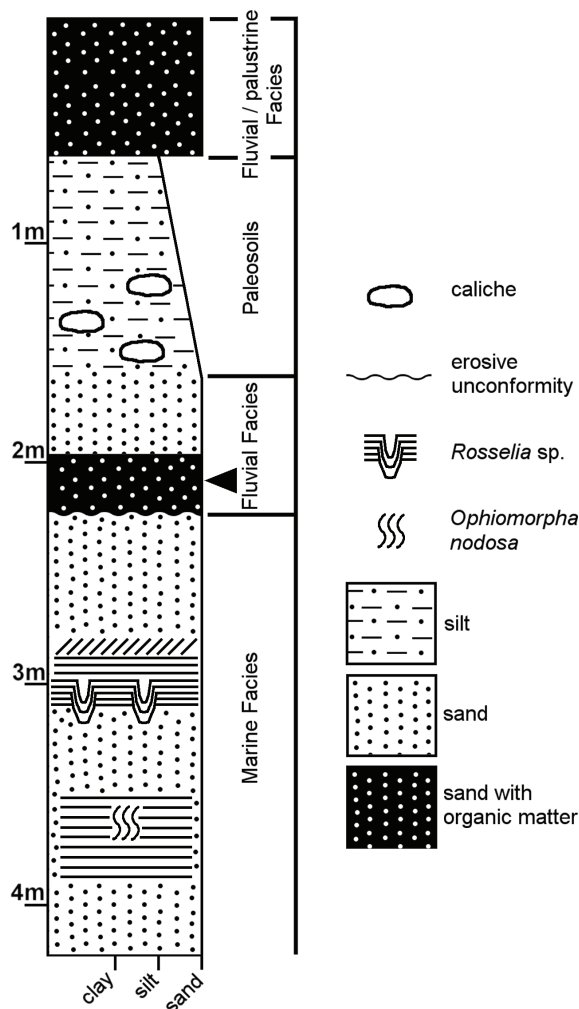


Figure 2. Stratigraphic section at Chuí Creek.

matter-rich brown sand deposited by fluvial systems are found in the interface between the underlying marine facies and the upper continental beds. These lenses are considered to represent small water bodies (oxbow lakes) and besides mammals have also yielded fish remains (Lopes *et al.*, 2005; Lopes and Pereira, 2011). Other fossil-bearing sand-muddy lenses with very low organic matter content, located at the same stratigraphic level as the dark lenses, also suggest fluvial deposition, but under different environmental conditions.

The mammalian remains are found either articulated or isolated, mostly fragmented, but also including complete and well-preserved specimens, probably deposited and reworked in meandering fluvial systems (Lopes *et al.*, 2001, 2005). Lopes *et al.* (2010) dated teeth of megamammals from the fossiliferous level using Electron Spin Resonance obtaining ages between 226 and 33 ka BP. The most common taxa are large-bodied herbivores, but some carnivores and rodents have also been found (Oliveira *et al.*, 2005; Kerber *et al.*, 2011a; Pereira *et al.*, 2011; 2012; Lopes *et al.*, 2011; Lopes, 2013).

## SYSTEMATIC PALEONTOLOGY

Rodentia Bowdich, 1821

Muroidea Miller & Gidley, 1918

Cricetidae Fisher, 1817

Sigmodontinae Wagner, 1843

Oryzomyini Vorontsov, 1959

*Holochilus* Brandt, 1835

*Holochilus brasiliensis* (Desmarest, 1819)

(Figures 3-4; Table 1)

**Material.** MCN-PV 1457, a left dentary with the m1–m3 series; MCTFM-PV 0916, a fragment of right dentary with the complete m1–m3 series; MCTFM-PV 870, a right maxillary fragment with M1–M2.

**Geographic and stratigraphic provenance.** MCN-PV 1457 – Passo do Juquiry locality - Quaraí River, upper Pleistocene. MCTFM-PV 870, MCTFM-PV 0916 – Lower portion of the fossiliferous horizon, Chuí Creek, upper Pleistocene. MCTFM-PV0916 was collected from a dark sand lens at the same stratigraphic position as MCTFM-PV0870, but some 2 km to the south. This sand lens has also yielded several fragments of other taxa such as *Toxodon* and *Lestodon*. MCTFM-PV870 was collected from a muddy sand lens of the fluvial facies located at the marine-continental transition; this lens has also yielded an isolated tooth of *Myocastor* (Pereira *et al.*, 2012).

**Description and comparison.** Dentary (MCN-PV 1457) – The body of the dentary is deep and robust. The chin is well developed, as described for *Holochilus*, differing from *Lundomys*, in which it is reduced (Pardiñas and Deschamps, 1996). The superior and inferior masseteric crests are convergent at the level of the m1/m2 contact, below the mental foramen, forming a single crest that extends anteriorly up to the anterior area of the m1 (Figure 3A), this character being described for *H. brasiliensis* (Voss and Carleton, 1993). In *H. chacarius*, the convergence of these crests occurs more anteriorly (at the level of the mesial area

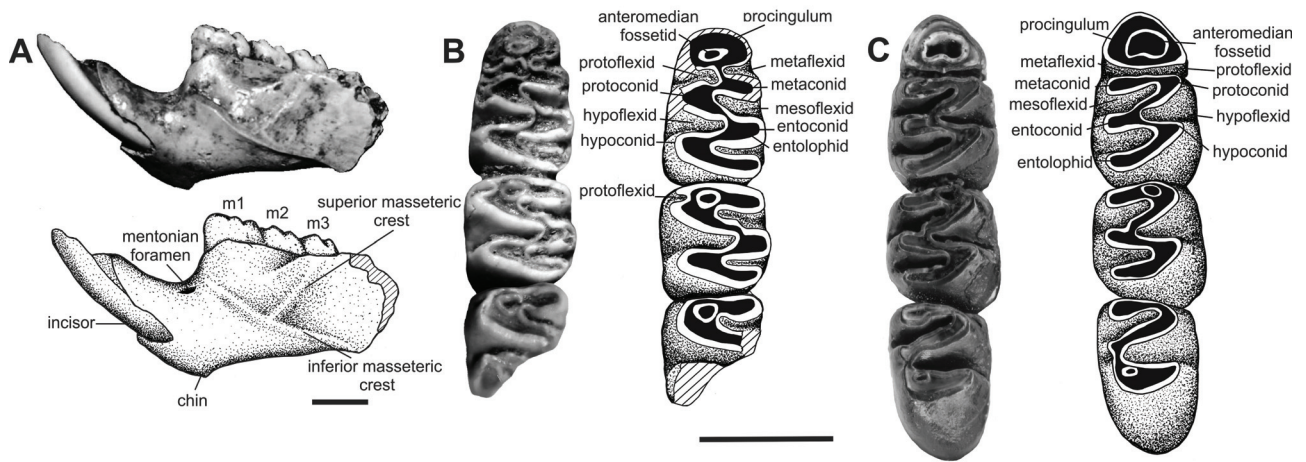
of m1) than in *H. brasiliensis*, and it is at the level of the mental foramen (Vogolino *et al.*, 2004). In *Lundomys* the contact between both crests forms a chevron and not a single crest as in *Holochilus* (Voss and Carleton, 1993).

Lower teeth (MCN-PV 1457 and MCTFM-PV 0916) – The labial surface of the lower incisor is convex mesiodistally. The m1 has a subelliptical outline (Figure 3B-C). The lophids are not as compressed as in *H. chacarius* and *H. sciureus* (Pardiñas and Teta, 2011). The enamel layer that mesially surrounds the procingulum of MCN-PV 1457 is rounded and it is fractured. In the middle of the procingulum there is a transversely elongated anteromedian fossetid, larger in MCTFM-PV 0916 (Figure 3C) than in MCN-PV 1457. In *H. chacarius* and *H. sciureus* this fossetid is located more labially (Pardiñas and Galliari, 1998; Vogolino *et al.*, 2004) and in *Lundomys* it is rounded (Pardiñas and Lezcano, 1995). The metaflexid is transversely oriented, penetrating up to the midline of the tooth in MCN-PV 1457, while in MCTFM-PV 0916 it is in connection with the protoflexid (Figure 3C). In *H. chacarius* and *H. sciureus*, the metaflexid is poorly developed (Pardiñas and Galliari, 1998). The mesoflexid is slightly oblique, differing from *H. chacarius* and *H. sciureus*, in which the mesoflexid is transversely oriented (Pardiñas and Teta, 2011). The protoflexid and hypoflexid are transversely oriented and the lingual end of the latter is opposite the entolophid (Figure 3B).

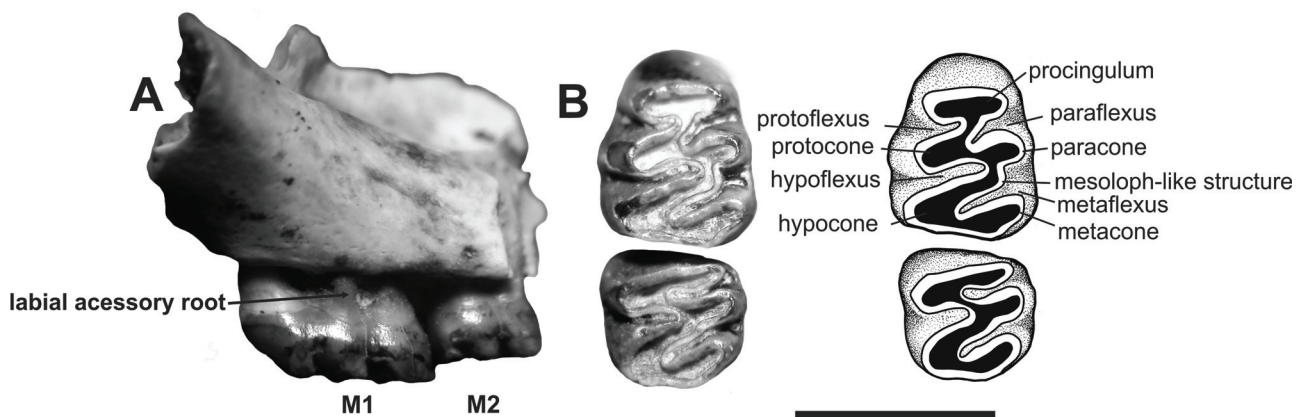
The m2 has a subquadrangular outline and it retains a vestigial metalophid. This

**Table 1.** Measurements (in mm) of *H. brasiliensis* from the late Pleistocene of southern Brazil and living *H. brasiliensis* from the State of Rio Grande do Sul. 1. Mesiodistal length (MDL) of m1. 2. Linguolabial width (LLW) of m1. 3. MDL of m2. 4. LLW of m2. 5. MDL of m2. 6. LLW of m2. 7. Height of the dentary body, at the level of m1. 8. MDL of M1. 9. LLW of M1. 10. MDL of M2. 11. LLW of M2. Specimens in bold are the fossils.

Specimens	1	2	3	4	5	6	7	8	9	10	11
<b>MCN-PV 1457</b>	3.32	2.22	2.38	2.27			6.98	-----	-----	-----	-----
<b>MCTFM-PV 0916</b>	3.20	2.21	2.37	2.15	2.39	2.16	-----	-----	-----	-----	-----
<b>MCTFM-PV 870</b>	-----	-----	-----	-----	-----	-----	-----	3.39	2.82	2.58	2.55
MCN-M 661	3.48	2.13	2.29	2.25	2.58	2.03	7.73	3.36	2.60	2.35	2.40
MCN-M 326	3.30	2.14	2.49	2.24	2.62	2.09	8.07	3.09	2.42	2.23	2.30
MCN-M 668	3.36	2.29	2.52	2.25	2.48	2.05	7.07	3.20	2.46	2.29	2.35
MCN-M 651	3.31	2.34	2.30	2.15	2.65	2.10	7.48	3.42	2.46	2.40	2.39
MCN-M 1722	2.99	2.12	2.09	2.13	2.40	2.15	2.17	3.06	2.27	2.36	2.19
MCN-M 666	3.12	2.28	2.38	2.10	-----	-----	6.94	3.27	2.57	2.21	2.20
MCN-M 594	3.27	2.20	2.10	2.25	2.35	2.09	6.35	3.06	2.27	2.19	2.02



**Figure 3.** Left dentary and lower cheek teeth of *H. brasiliensis* from southern Brazil. **A.** lateral view of the left dentary and **B.** occlusal view of lower cheek teeth of the specimen MCN-PV 1457 from the Quarai River. **C.** occlusal view of the right lower cheek teeth of the specimen MCTFM-PV 0916 from Chuí Creek. The striped area in the schematic drawings indicates fragmented areas. Scale-bars: 3 mm.



**Figure 4.** Fragment of left maxilla and upper cheek teeth of *H. brasiliensis* (MCTFM-PV870) from Chuí Creek. **A.** lateral view of a fragment of left maxilla and **B.** occlusal view of M1 - M2. Scale-bar: 4 mm.

tooth has a poorly developed protoflexid (MCN-PV 1457) plus a small and rounded fossetid located lingually to this flexid. In MCTFM-PV 0916 the protoflexid is absent. The mesoflexid and the entoflexid extend up to the midline of the tooth, with the first penetrating more deeply; the hypoflexid surpasses the midline of the occlusal surface and is opposite the entolophid. In *H. chacarius* and *H. sciureus* the hypoflexid does not reach the midline

(Pardiñas and Galliari, 1998). The m3 of MCN-PV 1457 is very fragmented, lacking its distal portion. On the first lophid there is a small fossetid located as in the m2. In MCTFM-PV 0916 there is a very small fossetid in the lingual area of the the posteroloph (Figure 3C). The hypoflexid is well developed, covering almost the full width of the tooth.

Upper teeth (MCTFM-PV870) – The M1 exhibits in labial view an

accessory labial root, corresponding to the fourth one (Figure 4A). This character differentiates this genus from *Lundomys*, which has only three (Voss and Carleton, 1993; Pardiñas, 2008). The M1 and M2 are subelliptical and subquadrangular, respectively. In both teeth, the margins of the labial and lingual cusps are rounded. The procingulum of the M1 is narrow and transversely oriented (Figure 4B),

without an anteromedian flexid, which is present in other oryzomyines, such as *Pseudoryzomys* Hershkovitz, 1959 and *Carletonomys* Pardiñas, 2008. The lingual end of the paraflexus and metaflexus are distally oriented, more evident in the first. There is a small mesoloph-like structure (*sensu* Pardiñas, 2008). According to Pardiñas (2008), *Lundomys*, *Carletonomys*, *Pseudoryzomys* and *Noronhomys* Carleton & Olson, 1999 share a true minute mesoloph, which arises from the median mure, while *Holochilus brasiliensis* has a poorly developed structure, similar to the mesoloph, but that arises from the coalescence between the most anterior point of the median mure with a parolophule. In *H. sciureus* and *H. chacarius* this structure is absent (Massoia, 1971; Voss and Carleton, 1993; Voglino *et al.*, 2004; Pardiñas, 2008). In the comparative specimens (Table 1), this structure is quite variable, from almost absent or poorly developed (MCN-M 661; MCN-M 666) to well developed, reaching the labial margin (MCN-M 651). The labial end of the hypoflexus surpasses the midline, differing from *Lundomys* and *H. sciureus*, in which it is poorly developed (Voss and Carleton, 1993). The metacone is mesially oriented. In the M2, the hypoflexus extends up to the midline of the tooth (Fig. 4B). The mesoloph-like structure is almost absent.

In both upper (MCTFM-PV 870) and lower (MCTFM-PV 0916; MCN-PV 1457) cheek teeth the occlusal surfaces are planar (*sensu* Hershkovitz, 1955). Their cusps are slightly alternating (less evident in the M1), more alternated than in *Lundomys* and *H. primigenus*, but not so alternated as in *H. sciureus* and *H. chacarius* (Steppan, 1996; Pardiñas and Teta, 2011). Regarding the cusp arrangement, *H. brasiliensis* shows an intermediate morphology between *Lundomys* and *H. sciureus* and *H. chacarius* (Voss and Carleton, 1993; Pardiñas and Teta, 2011). With respect to the size, the specimens here reported are within the variation of *H. brasiliensis* (Table 1). The specimen MCTFM-PV 0916 shows less wear than MCN-PV 1457, being probably younger.

## Final remarks

The specimen MCN-PV 1457 was previously reported by Oliveira (1992) and assigned to *H. brasiliensis*, but without pointing out its diagnostic traits. Here, we maintained this specific assignment and assigned new material to this taxon. The taxonomic assignment is based on the combination of the following characters: (i) presence of a mesoloph-like structure in the M1; (ii) masseteric crests confluent at the level of the m1/m2 contact, forming a single crest; (iii) presence of well-developed hypoflexus/id; (iv) slightly alternating cusps; (v) presence of an accessory labial root in the M1; (vi) oblique mesoflexid; (vii) anteromedian fossetid of m1 transversely elongated and centralized (Hershkovitz, 1955; Massoia, 1971; Voss and Carleton, 1993; Steppan, 1996; Pardiñas and Galliari, 1998; Voglino *et al.*, 2004; Pardiñas and Teta, 2011).

The living representatives of *Holochilus* have semi-aquatic habits, and today live in diverse geographic areas, that include the Amazon Forest, Caatinga, Cerrado, Pantanal, Atlantic Forest, Chaco, Pampean lowlands and northern Patagonian region (Moojen, 1952; Hershkovitz, 1955; Marques, 1988; Barreto and García-Rangel, 2005; Oliveira and Bonvicino, 2006; Formoso *et al.*, 2010). In the State of Rio Grande do Sul, *Holochilus* is found today in almost all regions always associated with marshes and water bodies (Marques, 1988). By analogy its presence in the fossil record in South Brazil allows to infer the existence of perennial water bodies during the late Pleistocene in this area. This inference is supported also by the presence of other aquatic vertebrates such as *Myocastor*, *Hydrochoerus hydrochaeris*, chelonians and fishes (Oliveira, 1992; Hsiou, 2009; Kerber and Ribeiro, 2011; Lopes and Pereira, 2011; Pereira *et al.*, 2012). Its presence in Chuí Creek also reinforces the correlation of the dark sand lenses to perennial, lentic water bodies of fluvial origin proposed by Lopes *et al.* (2005). Nonetheless, other rodents found in Chuí Creek, such as *Microcavia*, *Lagostomus* and Dolichotinae also indicate some intervals

of drier conditions (Ubilla *et al.*, 2008; Kerber *et al.*, 2011a).

Pleistocene sigmodontines from Rio Grande do Sul are poorly known, being restricted to the material herein described, plus that reported by Rodrigues and Ferigolo (2004). Holocene materials from *H. brasiliensis* pointed by Rosa and Jacobus (2009) were not described or figured and need revision and description.

Remains of the marsh rat *Lundomys molitor* have not been found in Quaternary beds of Rio Grande do Sul but there are records of this taxon in the Uruguayan banks of the Quaraí River (Pardiñas and Teta, 2011).

Taking into account the scarcity of data it is impossible to infer if the sigmodontine diversity was distinct in the late Pleistocene when compared to the Holocene, as it is observed among the caviomorphs. The biogeographic patterns of some of the late Pleistocene caviomorphs from Rio Grande do Sul indicate a distinct pattern when compared with the extant ones (Kerber *et al.*, 2011a, 2011b, 2012), but additional specimens with good stratigraphic control are required in order to evaluate this aspect.

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