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Noteworthy sigmodontine (Rodentia: Cricetidae) diversity in southern Brazil as an indication of environmental change during the Holocene

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ABSTRACT

We describe a new sigmodontine fossil sequence ranging from $8,800 \pm 40$ to $3,730 \pm 60$ years BP retrieved from the archaeological site RS-S-327:Sangão (Rio Grande do Sul, Brazil). The studied material includes 2,683 craniomandibular remains totalizing about 20 sigmodontine species. The assemblage encompasses a variety of taxa associated to both open and forest environments. Among the former, we recorded species today disappeared in southern Brazil such as the rare 'giant' rats *Gyldenstolpia* and *Kunsia*, but also the coney rat *Reithrodon* and the akodontine *Necromys obscurus*. Conversely, an important assemblage of sylvan species, including the genera *Delomys*, *Oecomys*, and *Wilfredomys*, reflects forested environments. Several of the recorded sigmodontines, such as *Deltamys* or *Nectomys*, constitute first mentions for the southern Brazil Quaternary. One of the most remarkable features of the studied sequence is its noteworthy specific richness, probably due to a combination of local environmental heterogeneity in a regional tendency of changing climatic conditions. The evidence of Sangão plus the previously studied samples from Garivaldino and Pilger sites exposes faunal changes during the Holocene in southern Brazil. In this context, the impoverishment of recent sigmodontine assemblages seems a natural result from the progressive disappearance of extensive open environments since Middle Holocene.

ARTICLE HISTORY

Received 21 May 2018
Accepted 13 September 2018

KEYWORDS

Archaeological remains; climate; environment; owl pellets; Rio Grande do Sul

Introduction

Sigmodontine rodents compose the second largest subfamily of the order Rodentia, being a highly diversified clade regarding morphology, habitat and ecology, encompassing about 11 tribes, 86 genera, 432 living species, and several unique lineages (Patton et al. 2015; Pardiñas et al. 2017b). Contrasting with the large volume of information produced in the last decades in order to understand living sigmodontines, past assemblages have been poorly addressed, except for those from middle and high latitudes of South America (e.g. Pardiñas et al. 2002; Teta et al. 2014). Much of the gathered data about fossil sigmodontines came from today arid, semiarid, and temperate regions, such as the Pampas, in southern South America (e.g. Pardiñas et al. 2002; Ortiz et al. 2011; Teta et al. 2014; Tammone et al. 2016). In fact, faunal dynamics of sigmodontine rodents during the Quaternary in tropical and subtropical areas, including the largest forested regions of the subcontinent are, judged against the total surface, almost unknown (e.g. Boroni Martins 2012; Torres et al. 2015; Neves et al. 2017; Pires et al. 2018). Clearly this tackled several aspects of our comprehension about this amazing group of rodents, particularly how and when the recent distributional and compositional pattern was established.

Nonetheless, sigmodontine rodents are very valuable for paleoenvironmental studies due to their great abundance in paleontological and archaeological sites; the facility to compare the Quaternary fossil record to recent species, and, thus, to know the environmental exigences of each species; and, finally, several sigmodontine species are restricted to specific habitats (Pardiñas et al. 2002; Ubilla et al. 2004; Ortiz et al. 2011; Tammone et al. 2016).

The knowledge on Holocene fossil small mammals from the State of Rio Grande do Sul, southern Brazil, has undergone a noticeable improvement in the last years through the detailed study of materials coming from archeological sites. Remarkable examples are Garivaldino, Pilger and Sangão sites (Hadler et al. 2008, 2009, 2010, 2016; Stutz et al. 2017). Such materials are valuable because, unlike those from classical Brazilian caves (e.g. Winge 1887; Lessa et al. 2005), they come from excavations with strict stratigraphic control and radiometric dating.

Chiropterans, marsupials and caviomorph rodents from the three mentioned sites have already been studied (Hadler et al. 2008, 2009, 2010, 2016). Furthermore, the sigmodontine rodents from Garivaldino and Pilger have also been studied, showing an important diversity, with more than 15 taxa registered for the Holocene of northeastern Rio Grande do

Sul (Hadler et al. 2016; Stutz et al. 2017). The studied faunal evidence points to the occurrence of regional extinctions and species replacements in a context of ecosystem changes that happened in Rio Grande do Sul during the Holocene. However, an integrative approach in order to understand how these processes occurred is still under scrutiny.

In Sangão, seven marsupials, seven caviomorph rodents and two chiropteran taxa have been recorded (Hadler et al. 2008, 2009, 2010). This work deals with the taxonomic analysis of the sigmodontine samples retrieved from this archaeological site. The obtained evidence is conclusive in highlight Sangão as the richest sigmodontine sequence in southern Brazil (and also, in South America, surpassing the previously richest assemblages, such as Lapa da Escrivania Nr. 5 or Trafal I Cave, see Winge 1887; and Pearson and Pearson 1993; respectively). In this context, Sangão emerges as a key-site to explore Holocene faunal dynamics in a general tendency of progressive increment of forested environments.

Study area and archaeological sequence

The RS-S-327: Sangão (29°46'2" S and 50°33'4" W, 52 m, Municipality of Santo Antônio da Patrulha, State of Rio Grande do Sul; Figure 1) is a rock shelter eroded in the sandstone of the Botucatu Formation, which was used as a dwelling by people of the Umbu Tradition during the Holocene (Dias 2003). The site is 10 m deep and 6 m high; it has a 25 m opening facing south, 7 m above the Sinos River. Sangão was excavated in the framework of archaeological research during 2000/2001. The excavations took place in a total area of 13 m², at artificial levels of 5 cm (totalizing at most 16 levels) (Dias 2003). Seven radiocarbon dates were performed for Sangão, indicating that the entire sequence cover the Holocene (Table 1). For the purposes of our faunal analysis and taking into account the chrono-stratigraphic data, the

artificial levels were grouped in two temporal units: Unit 1 (Levels #13–10; C¹⁴ age ~ 8800–7390 years BP), and Unit 2 (Levels #9–1; C¹⁴ age ~ 4710–3730 years BP).

The archaeological findings made at Sangão site include lithic and archaeofaunal remains, charcoal and human bones. Among the archaeofaunal remains, gastropods (e.g. *Megalobulimus oblongus* and *Olivancillaria vesica auricularia*), bivalve molluscs (*Iphigenia brasiliana* and *Diplodon* sp.), fishes (e.g. *Charcharinus* sp. and *Pimelodella laticeps*), reptiles (e.g. cf. *Chrysemis* sp. and *Salvator merianae*) and birds (e.g. *Penelope* sp.) were identified, as well as a great amount of medium and large mammals (e.g. *Dasyus septemcinctus*, *Tapirus terrestris*, *Pecari tajacu*, *Mazama americana*, *Leopardus wiedii*) (Dias 2003). As was mentioned above, part of the small mammals, including bats, marsupials and caviomorph rodents were previously studied by Hadler et al. (2008, 2009, 2010).

Material and methods

Remains attributed to sigmodontine rodents are four palatal portions, 1,399 maxillary and 1,280 dentary fragments, coming from grids E12, F8 and G8 excavated in Sangão site. The material is housed at the Museu Arqueológico do Rio Grande do Sul (MARSUL; Taquara, Rio Grande do Sul, Brazil).

The material was cleaned with brushes and histological needle. Afterwards it was numbered and identified by comparison with specialized literature (e.g. Reig 1987; Voss 1993; Pardiñas 1996; Pardiñas et al. 2009) as well as using recent specimens of the following collections: Coleção de Mamíferos do Departamento de Ecologia e Zoologia da Universidade Federal de Santa Catarina (UFSC; Florianópolis, Santa Catarina, Brazil); Coleção do Setor de Mastozoologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN-M; Porto Alegre, Rio Grande do Sul, Brazil); Coleção de Mamíferos do Museu de Ciências

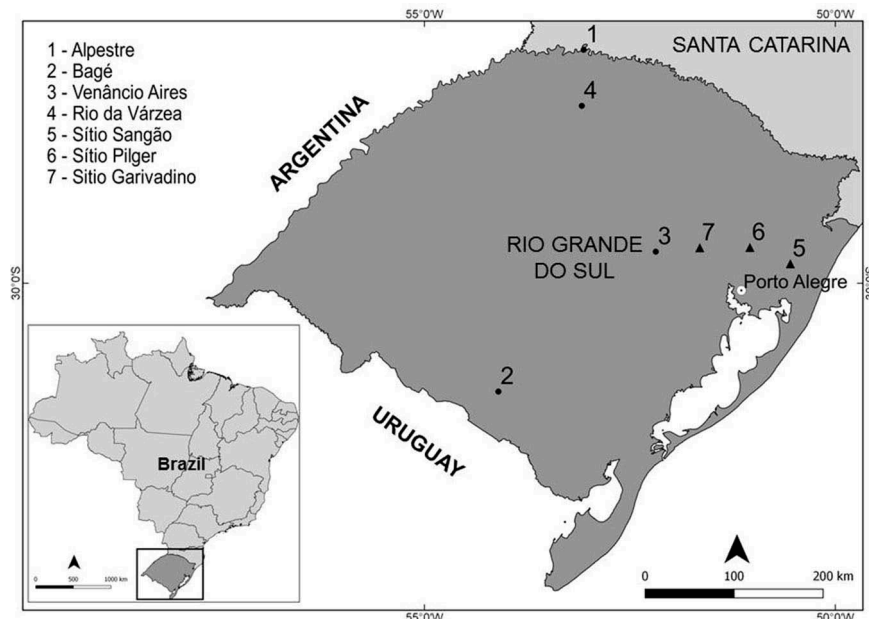


Figure 1. Location of the Sangão, Pilger and Garivadino sites, northeast of the State of Rio Grande do Sul, southern Brazil; and of the modern owl pellets samples from Alpestre (this paper), Bagé (González et al. 1999), Venâncio Aires (Scheibler and Christoff 2004) and Rio da Várzea (Peters et al. 2010).

Table 1. Radiocarbon dates registered for the Sangão site.

Standard age (years)	Calibrated age (years) ¹	Source	Code
3730 + 60 BP	4250 to 3900 BP	F8, level 4 (15 to 20 cm)	Beta Analytics 160846
3940 + 40 BP	4440 to 4260 BP	G9, level 5 (20 to 25 cm)	Beta Analytics 160849
4610 + 140 BP	5610 to 4860 BP	F16, level 6 (25 to 30 cm)	Beta Analytics 160847
4160 + 100 BP	4870 to 4420 BP	D13, level 6 (25 to 30 cm)	Beta Analytics 154351
4710 + 40 BP	5480 to 5310 BP	D13, level (35 to 40 cm)	Beta Analytics 154352
7390 + 40 BP	8330 to 8150 BP	D13, level 10 (45 to 50 cm)	Beta Analytics 154353
8800 + 40 BP	9930 to 9680 BP	E13, level 13 (60 to 65 cm)	Beta Analytics 160845

Notes: ¹Dias (2003).

Naturais da Universidade Luterana do Brasil (MCNU; Canoas, Rio Grande do Sul, Brazil); Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina); Coleção de Mastozoologia do Museu Nacional, Universidade Federal do Rio de Janeiro (MN; Rio de Janeiro, Brazil); Coleção Zoológica da Universidade de Blumenau (CZFURB; Blumenau, Santa Catarina, Brazil); and with fossil specimens housed at Setor de Arqueologia da Universidade Federal do Rio Grande do Sul (UFRGS; Porto Alegre, Rio Grande do Sul, Brazil) and at Centro de Ensino e Pesquisas Arqueológicas da Universidade de Santa Cruz do Sul (UNISC; Santa Cruz do Sul, Rio Grande do Sul, Brazil). The terminology used here for cranial anatomy follows Hershkovitz (1962) and Carleton and Musser (1989); dental structures were named according to Reig (1977) and Hershkovitz (1993). The molar measurements were made with a manual caliper with precision of 0.02 mm or with millimeter ocular lens coupled to a stereo microscope. The rodent systematics employed here follows Patton et al. (2015) and the minimum number of individuals per taxon was calculated according to Beisaw (2013). The molars photographs were made with the Scanning Electron Microscope of the Central Laboratory of Electronic Microscopy of UFSC.

Paleoenvironmental reconstruction was supported on comparisons between both fossil and modern small mammal assemblages derived from owl pellets (e.g. Andrews 1990; Pardiñas 1999; Fernández et al. 2017). Here, as actualistic parameter, we have included four modern pellet samples produced by the common owl *Tyto furcata* (Scopoli, 1769) from Rio Grande do Sul. The studied samples are: 1) Alpestre (27°08'57"S, 53°03'42"W; this paper); 2) Rio da Várzea (28°00'S, 53°02'W/28°19'S, 52°43'W; Peters et al. 2010); 3) Venâncio Aires (29°36'S, 52°11'W; Scheibler and Christoff 2004); 4) Bagé (31°55'36.24"S, 54°06'0081"W; González et al. 1999) (Figure 1). Correspondence analysis was performed in order to explore species and both fossil and modern samples ordination in multivariate space. This exploration was made on a data matrix of relative abundances, using the program PAST (PAleontological STatistics), version 3.12 (Hammer 1999–2018).

Abbreviations: L, length; M1, M2, M3, first, second and third upper molar; m1, m2, m3, first, second and third lower molar; mm, millimeters; MNI, minimum number of individuals; n, sample size; NISP, number of identified specimens;

RSCP, Rio Grande do Sul Coastal Plain; W, width; \bar{x} , arithmetic mean; σ , standard error.

Results

The sigmodontine total assemblage from the Sangão site consists of NISP = 2,683 and MNI = 1,102, distributed in 23 taxa. Akodontini is the tribe with the greatest richness and abundance (11 taxa, MNI = 648), followed by the tribes Oryzomyini (five taxa, MNI = 332), Phyllotini (one taxon, MNI = 44), Wiedomyini (one taxon, MNI = 5) and Reithodontini (one taxon, MNI = 1). Complete lists of the specimens referred to taxa are available as Supplemental Online Material.

Oligoryzomys sp. (\cong 18.5% of the individuals), *Akodon* cf. *A. azarae* (\cong 15% of the individuals), *Necromys lasiurus* (\cong 10% of the individuals) and *Pseudoryzomys simplex* (\cong 9% of the individuals) are the most abundant sigmodontines in Sangão site.

Systematic paleontology

Rodentia Bowdich 1821
Myomorpha Brandt 1855
Muroidea Illiger 1811
Cricetidae Fischer 1817
Sigmodontinae Wagner 1843
Sigmodontinae gen. et sp. indet.

Material

78 maxillary fragments and 38 dentary fragments (Supplemental Online Material).

Description

Most of the studied material is fragmented and the molars, when present, are extremely worn, preventing a solid taxonomical identification beyond subfamilial level. Besides, four maxillary fragments with teeth, corresponding to juveniles, could not be identified.

Sigmodontinae incertae sedis

Delomys Thomas 1917

Delomys sp.

Material

Four palatal portions, five maxillary fragments and four dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A medium-sized sigmodontine with partially lophodont molars. Short palate. Deep dentary, with marked masseteric crest and little developed capsular projection. Upper molars with opposite main cusps and lower molars with alternate main cusps. Upper molars with large mesoloph and three roots; M1 with wide procingulum and deep anteromedian flexus; M1 and M2 with well-developed anteroloph.

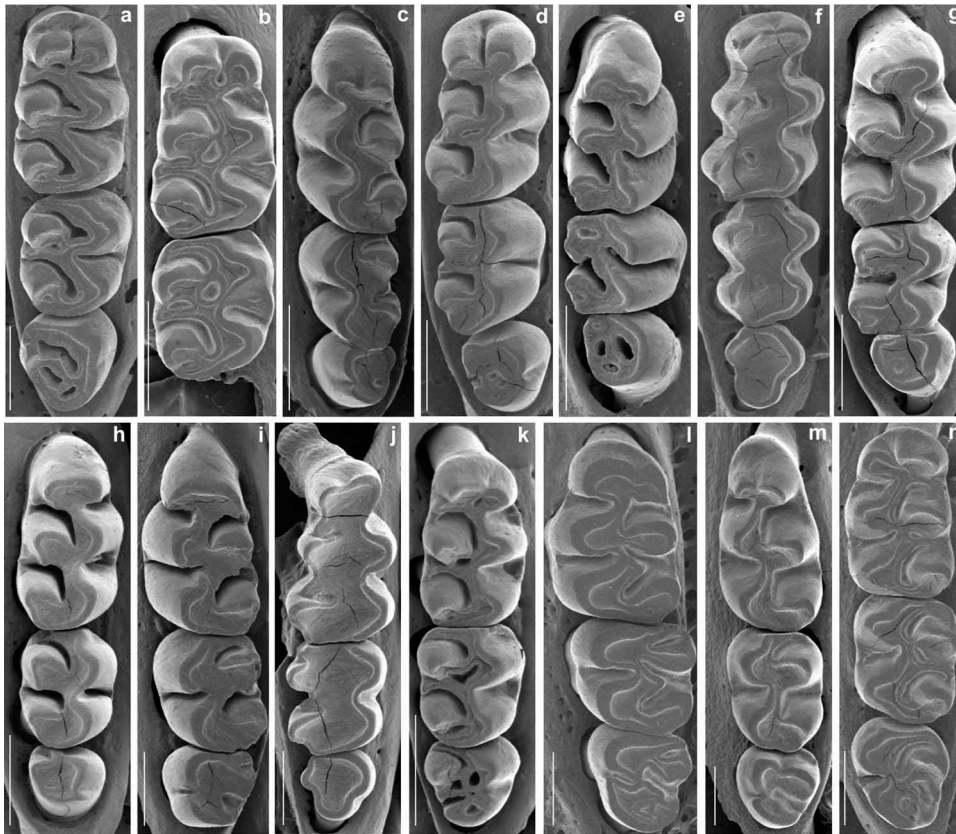


Figure 2. Occlusal view of upper molars of **a**, *Delomys* sp., MARSUL 682-213, right M1–M3; **b**, *Juliomys* sp., MARSUL 684-210, right M1–M2; **c**, *Akodon* cf. *A. azarae*, MARSUL 716-213-15, left M1–M3; **d**, *Akodon* sp., MARSUL 713-208-7, right M1–M3; **e**, *Bibimys* sp., MARSUL 715-208, right M1–M3; **f**, *Brucepattersonius* sp., MARSUL 687-207, right M1–M3; **g**, *Deltamys* sp., MARSUL 713-212-6, right M1–M3; **h**, *Necomys lasiurus*, MARSUL 682-203-7, right M1–M3; **i**, *Necomys obscurus*, MARSUL 685-206-2, left M1–M3; **j**, *Oxymycterus* sp., MARSUL 682-204-3, right M1–M3; **k**, *Oligoryzomys* sp., MARSUL 715-205-15, right M1–M3; **l**, *Pseudoryzomys simplex*, MARSUL 690-200, left M1–M3; **m**, *Calomys* sp., MARSUL 686-205, right M1–M3; **n**, *Wilfredomys oenax*, MARSUL 715-207, left M1–M3. Scale bars a–l and n = 1 mm, m = 500 μ m.

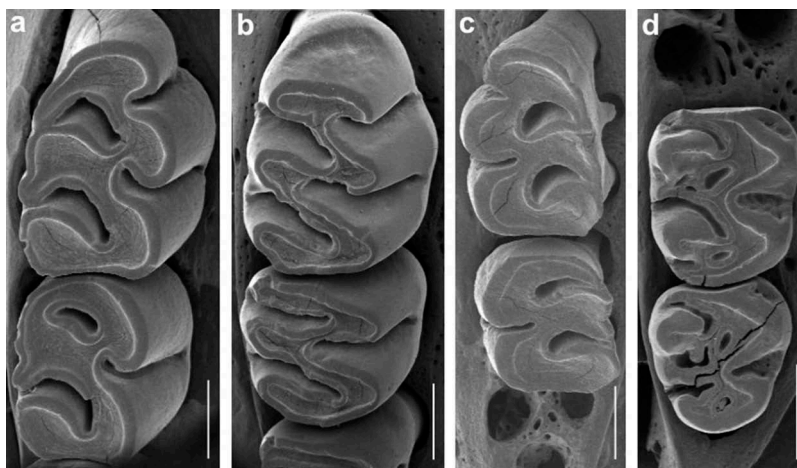


Figure 3. Occlusal view of upper molars of **a**, *Gyldenstolpia* cf. *G. planaltensis*, MARSUL 657-200, right M1–M2; **b**, *Holochilus* sp., MARSUL 715-200, right M1–M2; **c**, *Scapteromys tumidus*, MARSUL 714-215, left M1–M2; **d**, *Sooretamys angouya*, MARSUL 713-210, right M2–M3. Scale bars a–d = 1 mm.

Conspicuous anteromedian flexid and anterolabial cingulum in m1; m1 and m2 with well-marked mesolophids and ectolophids; m3 with only the mesolophid; lower molars with two roots.

Comments

The characteristics cited above, jointly, supported the attribution of the material of the Sangão site to *Delomys* according to Voss (1993). Recent revisions and treatises reported that *Delomys* encompasses three species, mostly differentiated by

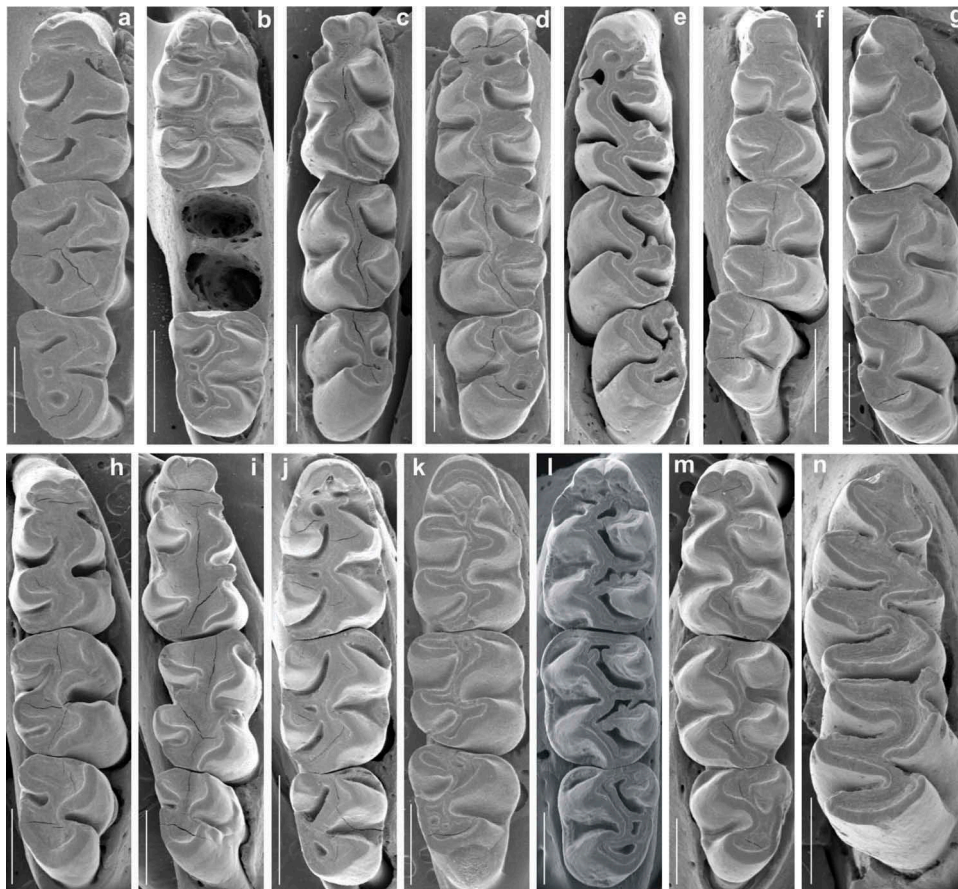


Figure 4. Occlusal view of lower molars of **a**, *Delomys* sp., MARSUL 715-201-1, right m1–m3; **b**, *Juliomys* sp., MARSUL 690-210, right m1 and m3; **c**, *Akodon* cf. *A. azarae*, 684-204-4, left m1–m3; **d**, *Akodon* sp., MARSUL 710-211-3, left m1–m3; **e**, *Bibimys* sp., MARSUL 709-201, left m1–m3; **f**, *Deltamys* sp., MARSUL 681-211-1, right m1–m3; **g**, *Necomys lasiurus*, MARSUL 709-205-1, right m1–m3; **h**, *Necomys obscurus*, MARSUL 715-209-1, right m1–m3; **i**, *Oxymycterus* sp., MARSUL 716-203-1, right m1–m3; **j**, *Oligoryzomys* sp., MARSUL 686-207-4, right m1–m3; **k**, *Pseudoryzomys simplex*, MARSUL 683-200, right m1–m3; **l**, *Sooretamys angouya*, MARSUL 688-203, left m1–m3; **m**, *Calomys* sp., MARSUL 683-205, left m1–m3; **n**, *Reithrodon* cf. *R. typicus*, MARSUL 664-200, right m1–m2. Scale bars a–i and n = 1 mm, m = 500 μ m.

external morphology, karyotypes and molecular markers (Gonçalves and Oliveira 2014; Pardiñas et al. 2017b). The only species of the genus which is recorded today in Rio Grande do Sul is *D. dorsalis* (Hensel 1872) (Gonçalves and Oliveira 2014; Voss 2015a).

Juliomys González 2000

Juliomys sp.

Material

Five maxillary fragments and two dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A small sigmodontine with short incisive foramina and short palate. Dentary with well-marked masseteric crest and conspicuous capsular projection. Upper and lower molars with crested occlusal surface and well developed flexi/flexids. The M1 has deep anteromedian flexus, broad procingulum, well developed anteroloph and protostyle; M1 and M2 with mesoloph and enterostyle. Lower molars with well-developed mesolophids; m1 with deep anteromedian flexid and conspicuous anterolabial cingulum; m1 and m2 with developed ectolophid; m3 with ectostylid.

Comments

The specimens of Sangão site can be attributed to *Juliomys* because they exhibit diagnostic traits such as short palate, well developed mesolophs and presence of anteromedian flexus (González 2000; González et al. 2015a). Nevertheless, the four species of *Juliomys* today recognized are morphologically very similar, being distinguished mainly by cytogenetic and molecular traits (Christoff et al. 2016), which made it impossible to specifically assign the fossil material. *Juliomys pictipes* (Osgood 1933) and the recently described *J. ximenezi* Christoff et al. 2016 are registered in Rio Grande do Sul (González et al. 2015a; Christoff et al. 2016). The latter was proposed as restricted to the Araucaria Forest, while *J. pictipes* is widespread across the Atlantic Interior and Coastal Forest (Pardiñas et al. 2017b).

Tribe Akodontini Vorontsov 1959

Akodon Meyen 1833

Akodon cf. *A. azarae* (J. B. Fischer 1829)

Material

246 maxillary fragments and 215 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A small sigmodontine being within the genus smaller than *Akodon* sp. Low dentary with dorsal mental foramen and moderately developed masseteric crest. Upper molars of *Akodon* cf. *A. azarae* and of *Akodon* sp. morphologically very similar and only differentiated by size. Lower molars narrower than those of *Akodon* sp.; m1 with long and narrow procingulum, which is smaller and narrower than in *Akodon* sp.; deep anteromedian flexid; m1 with anterolabial cingulum less developed than in *Akodon* sp.; m1 and m2 with conspicuous posterolophid; m1 and m2 with meso and ectolophids variable in size and development, being absent in some specimens and, in others, fused with meso and ectostylids; m2 and m3 with well-marked protoflexid; m3 with well-developed hypoflexid.

Comments

The material of the Sangão site was assigned to *Akodon* because it presents the diagnostic characteristics listed by Reig (1987) and Pardiñas et al. (2015d), such as the presence of anteromedian flexid and meso and ectolophids usually present. The molar measurements of the specimens identified as *Akodon* of the Sangão site allowed the distinction of two morphotypes (Table 2; Graphs 1 and 2). One of them, with smaller dimensions, presents CM1–M3 ranging from 3.14 to 3.78 mm ($n = 66$; $\bar{x} = 3.47$ mm; $\sigma = 0.16$) and Cm1–m3 from 3.71 to 4.03 mm ($n = 17$; $\bar{x} = 3.84$ mm; $\sigma = 0.12$), in addition to have a more gracile dentary, more dorsal mental foramen and less developed masseteric crest. These measurements and characteristics match those of the Hershkovitz (1990) *A. boliviensis* group, which includes *Akodon* species of small size. Considering the current valid species of *Akodon* (Pardiñas et al. 2015d) and its geographic ranges, only *A. azarae* occurs currently in Rio Grande do Sul. However, the taxonomy of the *Akodon* species registered in southern Brazil remains unclear and poorly studied (Christoff et al. 2000), making it difficult to come to a more accurate identification of the fossil material.

Akodon sp.

Material

92 maxillary fragments and 86 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

The specimens of *Akodon* sp. are larger than those identified as *Akodon* cf. *A. azarae*. Dentary is relatively deep and robust. Compared to the *Akodon* cf. *A. azarae* specimens, the mental foramen is less dorsal and the masseteric crest is more developed. The m1 has long and wide procingulum; deep anteromedian flexid; conspicuous anterolobial cingulum; m1 and m2 with developed meso and posterolophid, the mesolophid being more marked than in *Akodon* cf. *A. azarae*; m2 and m3 with evident protoflexid, which is shallow, disappearing with wear; narrow m3 with mesolophid and deep hypoflexid.

Table 2. Measurements (in millimeters) of the upper and lower molars of *Akodon* cf. *A. azarae* from the Sangão site.

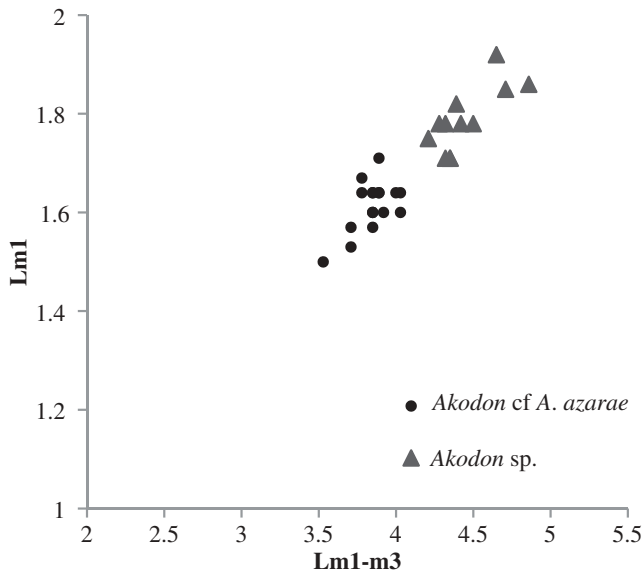
Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 656–200	1.64	3.89		
MARSUL 682–211-6			1.57	3.5
MARSUL 682–211-7			1.71	3.57
MARSUL 682–211-8			1.6	3.35
MARSUL 682–211-9			1.5	3.28
MARSUL 682–211-10			1.6	3.57
MARSUL 682–211-11			1.64	3.35
MARSUL 683–208-1	1.6	3.85		
MARSUL 683–208-3			1.57	3.32
MARSUL 683–208-4			1.6	3.46
MARSUL 683–208-5			1.53	3.28
MARSUL 684–204-1	1.57	3.71		
MARSUL 684–204-8	1.5	3.53		
MARSUL 685–209-2	1.64	3.89		
MARSUL 685–209-3			1.5	3.21
MARSUL 685–209-4			1.57	3.5
MARSUL 685–209-5			1.53	3.14
MARSUL 685–209-6			1.57	3.42
MARSUL 685–209-7			1.42	3.17
MARSUL 686–211-1	1.6	3.85		
MARSUL 686–211-2	1.53	3.71		
MARSUL 686–211-3			1.57	3.57
MARSUL 686–211-4			1.53	3.5
MARSUL 687–209-3			1.75	3.57
MARSUL 687–209-4			1.46	3.42
MARSUL 688–207-2			1.6	3.46
MARSUL 688–207-3			1.53	3.21
MARSUL 688–207-4			1.64	3.42
MARSUL 688–207-5			1.57	3.57
MARSUL 689–211-1	1.57	3.85		
MARSUL 690–209-1			1.75	3.78
MARSUL 709–210-4			1.6	3.39
MARSUL 709–210-5			1.71	3.71
MARSUL 710–208-1	1.64	4.03		
MARSUL 710–208-2			1.67	3.67
MARSUL 710–208-3			1.6	3.42
MARSUL 711–207-2			1.67	3.71
MARSUL 712–210-3			1.67	3.5
MARSUL 712–210-4			1.64	3.57
MARSUL 712–210-5			1.71	3.64
MARSUL 713–209-1	1.64	4		
MARSUL 713–209-4			1.82	3.78
MARSUL 713–209-5			1.64	3.57
MARSUL 713–209-6			1.57	3.42
MARSUL 713–209-7			1.71	3.71
MARSUL 713–209-8			1.64	3.46
MARSUL 713–209-9			1.64	3.35
MARSUL 713–209-10			1.6	3.42
MARSUL 713–209-11			1.71	3.64
MARSUL 713–209-12			1.6	3.39
MARSUL 714–211-1	1.64	3.78		
MARSUL 714–211-2	1.6	4.03		
MARSUL 714–211-4			1.6	3.35
MARSUL 714–211-6			1.64	3.53
MARSUL 714–211-7			1.53	3.25
MARSUL 714–211-8			1.67	3.64
MARSUL 714–211-9			1.53	3.21
MARSUL 714–211-10			1.64	3.46
MARSUL 715–212-1	1.71	3.89		
MARSUL 715–212-5	1.67	3.78		
MARSUL 715–212-6	1.64	3.85		
MARSUL 715–212-9			1.67	3.64
MARSUL 715–212-10			1.6	3.57
MARSUL 715–212-11			1.64	3.42
MARSUL 715–212-12			1.71	3.71
MARSUL 715–212-16			1.67	3.67
MARSUL 715–212-17			1.71	3.64
MARSUL 715–212-18			1.64	3.5
MARSUL 715–212-19			1.71	3.64
MARSUL 716–213-4			1.5	3.35
MARSUL 716–213-5			1.53	3.28
MARSUL 716–213-6			1.6	3.5
MARSUL 716–213-7			1.57	3.32

(Continued)

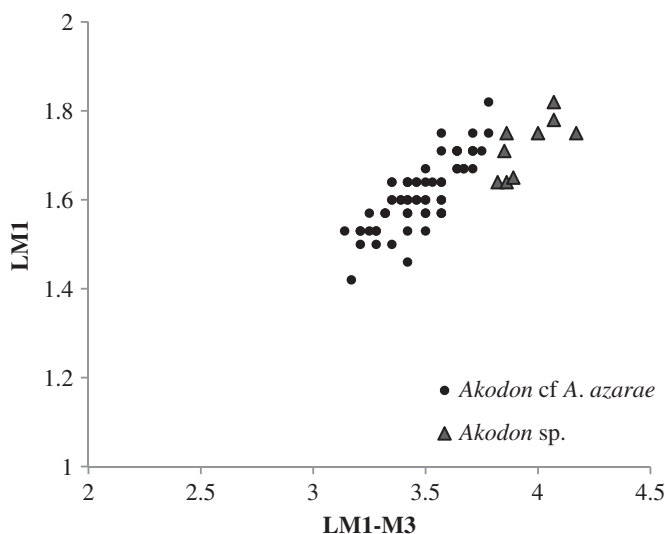
Table 2. (Continued).

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 716–213-8			1.64	3.42
MARSUL 716–213-9			1.57	3.25
MARSUL 716–213-10			1.6	3.5
MARSUL 716–213-11			1.57	3.57
MARSUL 716–213-12			1.53	3.42
MARSUL 716–213-15			1.75	3.71
MARSUL 716–213-16			1.57	3.32
MARSUL 716–213-17			1.71	3.75
MARSUL 716–213-41	1.64	3.85		
MARSUL 716–213-42	1.6	3.92		

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

**Graph 1.** Dispersion graph of the measurements (in millimeters) of Lm1 versus Lm1 – m3 of the specimens of the genus *Akodon* from the Sangão site.

Notes: L, length; m1, m3, first, third lower molars.

**Graph 2.** Dispersion graph of the measurements (in millimeters) of LM1 versus LM1 – M3 of specimens of the genus *Akodon* from the Sangão site.

Notes: L, length; M1, M3, first, third upper molars.

Comments

The molar measurements of specimens identified as *Akodon* sp. demonstrated that this material presents larger size in

Table 3. Measurements (in millimeters) of the upper and lower molars of *Akodon* sp. from the Sangão site.

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 658–201	1.78	4.5		
MARSUL 682–210-1	1.71	4.32		
MARSUL 682–210-2	1.85	4.71		
MARSUL 683–207-5			1.65	3.89
MARSUL 685–208-4			1.75	4.17
MARSUL 685–208-5			1.82	4.07
MARSUL 686–210-1	1.82	4.39		
MARSUL 689–210-1	1.78	4.42		
MARSUL 709–208-1	1.92	4.65		
MARSUL 710–211-3	1.86	4.86		
MARSUL 712–209-3			1.78	4.07
MARSUL 713–208-1	1.75	4.21		
MARSUL 713–208-3	1.71	4.35		
MARSUL 713–208-4	1.78	4.32		
MARSUL 713–208-7			1.75	4
MARSUL 713–208-8			1.64	3.82
MARSUL 713–208-10			1.71	3.85
MARSUL 714–210-7			1.64	3.86
MARSUL 716–212-1	1.71	4.35		
MARSUL 716–212-4	1.78	4.28		
MARSUL 716–212-10			1.75	3.86

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

comparison to the specimens identified as *Akodon* cf. *A. azarae* (Table 3; Graphs 1 and 2). The measurements of CM1–M3 range from 3.82 to 4.07 mm ($n = 9$; $\bar{x} = 3.95$ mm; $\sigma \cong 0.12$) and of Cm1–m3 from 4.21 to 4.86 mm ($n = 12$; $\bar{x} = 4.44$ mm; $\sigma \cong 0.19$). Several large-sized cryptic species of *Akodon* inhabit southern Brazil, such as *A. cursor* (Winge 1887), *A. montensis* Thomas 1913, *A. paranaensis* Christoff et al. 2000, and *A. reigi* González, Langguth and Oliveira 1998 (Gonçalves et al. 2007). Considering the difficulty to recognize these species based only on osteological characters, we identify the material of the larger morphotype of *Akodon* of the Sangão site only at the generic level.

Bibimys Massoia 1979
Bibimys sp.

Material

120 maxillary fragments and 146 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A small sigmodontine characterized by moderately hypsodont molars. Long incisive foramen, reaching the protocone of M1. Short robust dentary, with slightly lateralized mental foramen, marked masseteric crest, little developed capsular projection, and short and backward oriented coronoid process. The complexity of the enamel structures varies considerably according to molar wear. The M1 has short wide procingulum and, when with little wear, incipient anteromedian flexus. With the increasing wear, the anteromedian flexus disappears and the procingulum extends itself labially, through a conspicuous parastyle fused to the paraloph, forming a parafossetus. The M1 with little wear has an evident mesoloph, which, with more wear, fuses itself to the paraloph, forming a labial projection. The M2 with little wear has an elongate and complex

appearance, with conspicuous mesoloph. With the crescent wear, the M2 acquires a squared and bilophodont shape. The M3 is oval in outline and with persistent hypo and parafoesettes. The m1 with little wear has shallow anteromedian flexid, lingually displaced, with the anterolingual conulid smaller than the anterolabial one. With the increasing wear, the anteromedian flexid becomes weakly evident. The m1 with little wear has also conspicuous anterolabial cingulum coalesced with the protostylid; this structure fuses itself to the protoconid with the increasing wear, forming a protofossetid. The m1 with little wear also has conspicuous and independent mesolophid, which, with the crescent wear, becomes less evident and fuses itself to other structures, forming a mesofossetid. The m1 and some m2 have small ectostylid. A well-marked distoflexid (*sensu* Hershkovitz 1993; see Pardiñas 1996) is present in m1 and m2 with little wear; m3 is large, subtriangular and has developed mesolophid and hypoflexid; M1/m1 with four roots and M2/m2 and M3/m3 with three roots.

Comments

The aforementioned characteristics, together, allowed the attribution of the specimens of the Sangão site to *Bibimys* according to Pardiñas (1996). Three species of *Bibimys* are currently recognized, of whom only *B. labiosus* (Winge 1887) was reported in Brazil (Bonvicino et al. 2008; Betat 2012). It is important to emphasize that the taxonomic status of the *Bibimys* species is still uncertain and that the differences in craniodental morphology between them are still poorly addressed (Pardiñas et al. 2015a). In this context we prefer to reference the Sangão material only at generic level.

Brucepattersonius Hershkovitz 1998 *Brucepattersonius* sp.

Material

11 maxillary fragments (Figure 2; Supplemental Online Material).

Description

A small sigmodontine characterized by a skull with pointed rostrum and a low zygomatic plate. Molars smaller and narrower than those identified as *Oxymycterus* sp. (see below). Next to the inferior root of the zygomatic plate, there is a groove on the maxilla and, anterolaterally to it, a bony protuberance. Narrow zygomatic plate; long incisive foramen, reaching the protoflexus of the M1. Molars with narrow cusps and crested occlusal surface. The M1 has long procingulum, incipient anteromedian flexus and anteroloph; M2 with vestigial procingulum; M3 quickly acquires a simple cylinder shape.

Comments

The characteristics mentioned above, jointly, as well as the absence of mesoloph, enabled the attribution of the material of the Sangão site to the genus *Brucepattersonius*, according to Hershkovitz (1998). The genus *Brucepattersonius* presents a problematic alpha taxonomy, with its number of species overestimated (Vilela et al. 2015). The more recent approaches, based on molecular markers, indicate at least

three living species (Dias 2016), being *Brucepattersonius iheringi* (Thomas 1896) widely distributed in southern Brazil and northeastern Argentina (Pardiñas et al. 2017b). In fact, the type locality of *B. iheringi*, the locality of Taquara, is close to Sangão site. However, morphological differences between the species of the genus, particularly those referred to dental features, are still poorly studied, precluding a confident identification of fragmentary material.

Deltamys Thomas 1917 *Deltamys* sp.

Material

56 maxillary fragments and 88 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A small-sized akodontine with minute simplified molars. Delicate maxilla, dentary and molars. Narrow zygomatic plate; long incisive foramen, reaching the procone of M1. Low dentary with dorsal mental foramen, little developed masseteric crest and moderately developed capsular projection. Narrow and simplified molars, quickly losing much of the enamel folding complexity. The M1 has narrow, short and undivided procingulum, only few specimens possess incipient anteromedian flexus; M1 and M2 with small mesoloph and/or mesostyle; M2 with incipient anteroloph, only visible in specimens with little wear; M2 with deep hypo and metaflexi opposite each other; M3 small and circular. Lower molars with deep hypo and mesoflexids opposite each other, turning the median murid very thin; m1 with narrow, short and undivided procingulum; very incipient anteromedian flexid, only visible in some specimens with little wear; m1 with anterolabial cingulum developed and, in some specimens, anterolophid; some m1 and m2 with ecto and/or mesostylids; m2 with protoflexid, which quickly disappears with wear; m3 oval; m1 with three roots, including one accessory labial root, and m2 and m3 with two roots.

Comments

The characteristics cited above, jointly, as well as the molar dimensions (Table 4), allowed the assignment of the material of the Sangão site to the genus *Deltamys*, according to Thomas (1917) and González and Pardiñas (2002). Today, three *Deltamys* lineages are recognized, *D. kempfi* Thomas 1917; *D. araucaria* Quintela et al. 2017; and '*Deltamys* sp. 2n = 40' (Quintela et al. 2017; Pardiñas et al. 2017b). It was not possible to perform morphological comparisons between the material of

Table 4. Measurements (in millimeters) of the upper and lower molars of *Deltamys* sp. from the Sangão site.

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 684–211-1	1.42	3.43		
MARSUL 688–210-1	1.43	3.57		
MARSUL 710–214-4			1.5	3.28
MARSUL 711–213-2			1.57	3.5
MARSUL 713–212-5			1.5	3.35
MARSUL 713–212-6			1.42	3

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

the Sangão site and '*Deltamys* sp. 2n = 40,' since the latter has not yet been formally described and there is no information about its craniodental morphology (cf. Ventura et al. 2011). The material of the Sangão site differs from *D. araucaria* by not having M1 with protoloph and enteroloph and m1 with well-developed ectolophid (Quintela et al. 2017; Pardiñas 2018). With respect to *D. kempfi*, some researchers have reported the existence of considerable genetic and metric variability among its populations (Montes et al. 2008; Ventura et al. 2011; Quintela et al. 2017). The study of recent specimens of *D. kempfi* revealed variation of several molar occlusal structures, including the presence and development of anteromedian flexus/id and mesoloph/id. The material of the Sangão site differs from *D. kempfi* by having a shorter and narrower upper and lower procingulum; more incipient anteromedian flexus and flexid, which are present in only a few specimens; anteroloph and mesolophid absent in most of the specimens; and ectostylid frequently present. In view of the absence of morphological information about '*Deltamys* sp. 2n = 40,' as well as the differences and variability observed in *D. kempfi*, we conservatively identify the material of the Sangão site only at the generic level. However, the hypothesis that the Sangão material represents an undescribed fossil species of *Deltamys* should be examined carefully.

Gyldenstolpia Pardiñas, D'Elía and Teta 2009
Gyldenstolpia cf. *G. planaltensis* (Avila-Pires 1972)

Material

Three maxillary fragments and 11 dentary fragments (Figures 3 and 5; Supplemental Online Material).

Description

A large akodontine characterized by hypsodont molars. Maxilla, dentary and molars large and robust, being only smaller than the fragment identified as *Kunsia tomentosus* (Lichtenstein 1830). Deep dentary with subtle diastema; mental foramen more dorsal than in *K. tomentosus*; relatively little developed masseteric crest; robust coronoid process; and moderately developed capsular projection. Upper and lower molars with alternate and laminate main cusps and planate occlusal surface. Upper molars with small mesoloph in the form of an enamel spur; M1 with undivided procingulum, which extends itself backwards, fusing with the parastyle and touching the paracone, forming a pasafossetus; the paralophule of M1 and M2 with little wear do not touch the metacone, but with the increasing wear it reaches the metacone, forming a metafossetus; M3 rounded, when with little wear it has parafossetus and deep metaflexus, with crescent wear it only has a large central fosse. The m1 has undivided procingulum (except for MARSUL 660–201, which is less worn and presents an evident anteromedian flexid); well-developed protoconulid contiguous to the protoconid; when with little wear the m1 presents oblique mesolophid associated to the entoconid by the entolophulid, forming the median lophid (see Pardiñas et al. 2009); with the crescent wear, the median lophid of the m1 acquires a bifurcated labial tip; m1 with hypoconid with an angular margin, formed by the hypoconulid

coalesced with the ectostylid, which fuse themselves with the hypoconid with the increasing wear; m2 and m3 with conspicuous mesolophid, forming the median lophid; S-shaped m3 with deep meso and hypoflexids.

Comments

The material of the Sangão site can be assigned to *Gyldenstolpia* because it presents the diagnostic characteristics mentioned by Pardiñas et al. (2009), such as the absence of anteromedian flexus and flexid in adult specimens, vestigial mesoloph and developed mesolophid forming a median lophid. The genus *Gyldenstolpia* is little known, with just few specimens deposited in scientific collections (Pardiñas and Bezerra 2015). Currently, two species of *Gyldenstolpia* are recognized, *G. fronto* (Winge 1887) and *G. planaltensis*, and the limits between them are tenuous. Taking into consideration that *G. fronto* is slightly larger than *G. planaltensis*, we tentatively assigned the Sangão material to the latter species.

Kunsia Hershkovitz 1966
Kunsia tomentosus (Lichtenstein 1830)

Material

One dentary fragment (Figure 5; Supplemental Online Material).

Description

The largest of living sigmodontines. Large and robust dentary with abrupt diastema, lateralized mental foramen and masseteric crest proportionally little developed. The m1 has anteromedian flexid; anterofossetid; well-developed anterolophid coalesced with the metastylid; anterolabial conulid projected backwards, fused with the conspicuous anterolabial cingulum, almost reaching the protoconid; median lophid (see Pardiñas et al. 2009) formed by a short mesolophid fused with the mesostylid and the entolophulid; hypoconulid coalesced with the ectostylid, forming a conspicuous structure.

Comments

The aforementioned characteristics, together, allowed the attribution of the material of the Sangão site to *Kunsia tomentosus* according to Pardiñas et al. (2009). *Kunsia* is a monotypic genus, representing the largest living sigmodontine, mostly associated to Cerrado biome (Bezerra 2015; Bezerra and Pardiñas 2016). Although the species is currently absent in Rio Grande do Sul (cf. Bezerra and Pardiñas 2016), it is interesting to remark that the holotype was probably taken in the territory of that state, according to the reconstruction of the trip made by the collector, F. Selow (see Cerqueira 1975; Garbino and Nogueira 2017).

Necomys Ameghino 1889
Necomys lasiurus (Lund 1840)

Material

155 maxillary fragments and 131 dentary fragments (Figures 2 and 4; Supplemental Online Material).

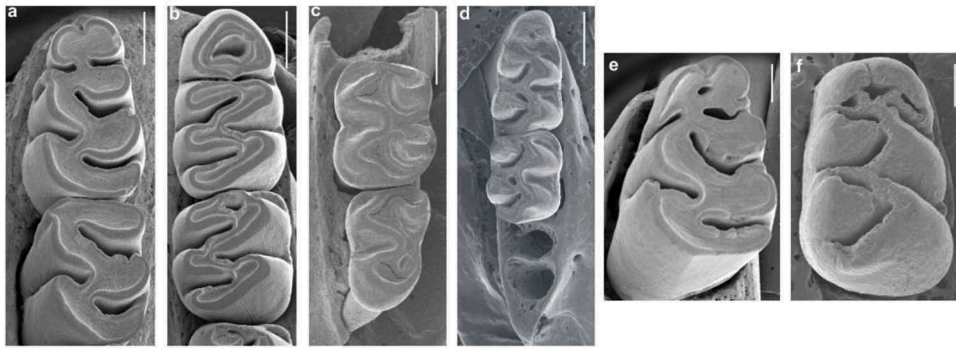


Figure 5. Occlusal view of lower molars of **a**, *Gyldenstolpia* cf. *G. planaltensis*, MARSUL 660-200, left m1–m2; **b**, *Holochilus* sp., MARSUL 716-201, right m1–m2; **c**, *Wilfredomys oenax*, MARSUL 716-205, left m2–m3; **d**, *Oecomys catherinae*, MARSUL 713-213, right m1–m2; **e**, *Kunsia tomentosus*, MARSUL 666-201, left m1; **f**, *Necomys squamipes*, MARSUL 683-213, right m1. Scale bars a–e = 1 mm, f = 500 μ m

Description

Two morphotypes of *Necomys* were identified in the Sangão site. Large animals were referred to *Necomys obscurus* (see below) while those medium-sized are identified as the widespread species *N. lasiurus*. The fragments attributed to the latter possess long incisive foramen, which reaches the protocone of M1; broad and robust zygomatic plate, with anterior margin slightly concave, as in *N. obscurus*; dentary relatively robust, but shorter and more delicate than the one of *N. obscurus*; developed capsular projection and masseteric crest, but less so than in *N. obscurus*; developed and slightly oriented backwards coronoid process. Upper and lower molars narrower than the ones of *N. obscurus* and with alternate main cusps. The M1 has broad undivided procingulum, only few specimens with little wear have incipient anteromedian flexus; antero and mesostyles in varying degrees of development, some specimens have antero and mesoloph; some M2 with mesostyle; M3 quickly acquires a bilophodont shape, with shallow meso and hypoflexi opposite each other. The m1 has broad procingulum, usually undivided, only few specimens with little wear have incipient anteromedian flexid; well-developed anterolabial cingulum; some m1 with ectostylid; m1 and m2 with oblique posterolophid; simplified m3 soon getting a bilophodont shape, with meso and hypoflexids opposite each other.

Comments

According to Reig (1972) and Anderson and Olds (1989), the aforementioned characteristics, jointly, allowed the assignment of the material of the Sangão site to *Necomys lasiurus*. The specimens identified as *N. lasiurus* showed great variability of CM1 and Cm1, as well as of CM1–M3 and Cm1–m3 (Table 5). The measurements of CM1 ranged from 1.7 to 2.1 mm ($n = 13$; $\bar{x} = 1.87$ mm; $\sigma \cong 0.13$) and of CM1–M3 from 3.6 to 4.28 mm ($n = 13$; $\bar{x} = 4.02$; $\sigma \cong 0.14$). As to Cm1, it ranged from 1.7 to 2 mm ($n = 12$; $\bar{x} = 1.88$ mm; $\sigma \cong 0.08$) and Cm1–m3 from 4.2 to 4.7 mm ($n = 12$; $\bar{x} = 4.49$ mm; $\sigma \cong 0.16$). These measures are similar to those reported by Libardi (2013) for *N. lasiurus*. *Necomys lasiurus* is the only species of *Necomys* reported currently in Rio Grande do Sul, with most of the recording localities

concentrated on the northern portion of the state (Betat 2012; Pardiñas et al. 2015c).

Necomys obscurus (Waterhouse 1837)

Material

35 maxillary fragments and 52 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

Broad zygomatic plate, with anterior margin slightly concave, as in *N. lasiurus*, being only larger than the latter; long incisive foramina, reaching the protocone of M1; dentary higher and more robust than the one of *N. lasiurus*, with masseteric crest more developed; capsular projection very well-developed, partially covering the sigmoid notch, and positioned more towards the condyloid process; short and robust coronoid process backwardly curved. Molars wider and more robust than the ones of *N. lasiurus*. The M1 has wide, short undivided procingulum, which is fan-shaped; with the increasing wear, the procingulum extends itself backwards, fusing itself with a well-developed anteroloph; M1 with mesostyle, which, in some specimens is coalesced with a small mesoloph; M2 with marked protoflexus and conspicuous anteroloph; M3 rounded, with deep para and metaflexi. The m1 has broad undivided procingulum, except for some specimens with little wear, which present incipient anteromedian flexid; procingulum projected backwards, through the connection with a well-developed anterolabial cingulum; some m1 with meso and ectostylids; m1 and m2 with long and slightly oblique posterolophid; elongated m3 with a bilophodont aspect.

Comments

The characteristics listed above, together, allowed the assignment of the material of the Sangão site to *N. obscurus*, according to Reig (1972) and Galliari and Pardiñas (2000). The specimens of *N. obscurus* present CM1 ranging from 1.69 to 2.14 mm ($n = 5$; $\bar{x} = 2.02$ mm; $\sigma \cong 0.06$), CM1–M3 from 4.2 to 4.7 mm ($n = 5$; $\bar{x} = 4.46$ mm; $\sigma \cong 0.19$), Cm1 from 2.07 to 2.28 mm ($n = 4$; $\bar{x} = 2.18$ mm; $\sigma \cong 0.09$) and Cm1–m3 ranging from 5.07 to 5.42 mm ($n = 4$; $\bar{x} = 5.21$ mm; $\sigma \cong 0.15$) (Table 6). These measurements coincide with

those reported by Pardiñas (1999) and Galliari and Pardiñas (2000) for *N. obscurus*. The measurements of CM1 and CM1–M3 of *N. lasiurus* (CM1 \cong 2 mm and CM1–M3 \cong 4.2 mm) have a minor overlapping with those of *N. obscurus* (CM1 \cong 2 mm and CM1–M3 \cong 4.3 mm). The analysis of the specimens according to the molar wear and their classification into the age classes defined by Libardi (2013) led to the observation that the specimens of *N. lasiurus* with the highest values of CM1 and CM1–M3 belong to old individuals (age classes 4 and 5). On the other hand, the specimens of *N. obscurus* with the smallest values of CM1 and CM1–M3 are young individuals (age classes 2 and 3). *Necromys obscurus* is the largest living species of the genus and shows today a disjunct distribution, with populations in southern Uruguay and southeastern the Province of Buenos Aires (Argentina), having no current records in Rio Grande do Sul (Betat 2012; Pardiñas et al. 2015c). However, a wider distribution in the recent past has already been suggested for this taxon, which would connect the two present isolated ranges (Galliari and Pardiñas 2000).

Oxymycterus Waterhouse 1837
Oxymycterus sp.

Material

51 maxillary fragments and 90 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

Narrow zygomatic plate; long incisive foramen, reaching the protocone of the M1. Slender dentary, with very little developed masseteric crest and capsular projection, and short triangular coronoid process. Narrow upper and lower molars, quickly losing the enamel occlusal structures. The M1 has long and narrow procingulum; incipient anteromedian flexus; small anteroloph; M1 and M2 with small mesoloph fused to the paralophule; M3 small and circular. The m1 has long narrow procingulum, shallow anteromedian flexid and anterolophid; m1 and m2 with small mesolophid connected to the mesotyloid; some m2 with ectostyloid.

Comments

This material was assigned to *Oxymycterus* because it presents the diagnostic characteristics reported by Hinojosa et al. (1987), Hershkovitz (1994) and Oliveira and Gonçalves (2015), such as long incisive foramen, slender dentary and narrow molars. The genus *Oxymycterus* has wide geographic occurrence, with at least 15 current recognized species. In Rio Grande do Sul, three species are reported: *O. nasutus* (Waterhouse 1837), *O. quaestor* Thomas 1903, and *O. rufus* (Fischer 1814) (Betat 2012; Oliveira and Gonçalves 2015). The *Oxymycterus* species are distinguished by size, external morphology and molecular markers (Oliveira and Gonçalves 2015), making it impossible to specifically attribute the fossil material. *Oxymycterus cosmodus* Winge 1887 is a large fossil form from Quaternary deposits in Lagoa Santa (Voss and Myers 1991; Oliveira and Gonçalves 2015); it was never revised after its original description.

Scapteromys Waterhouse 1837
Scapteromys tumidus (Waterhouse 1837)

Material

Two maxillary fragments (Figure 3; Supplemental Online Material).

Description

A moderately large akodontine. The M1 has wide and proportionally short procingulum, which extends itself labially, fusing with the anteroloph; conspicuous mesoloph, which forms a complex structure named median loph (see Hershkovitz 1966; Reig 1977), since it is coalesced with the paracone and the paralophule and has a bifurcated labial tip (Pardiñas et al. 2009); very conspicuous paralophule, which projects itself and reaches the metacone in the specimen with greater wear (MARSUL 714–215); M2 ‘E-shaped’ with mesoloph fused with the paralophule and the paracone, but the paralophule does not reach the metacone and the metaflexus is still present; the lingual side of M2 only with developed hypoflexus, the protoflexus is not visible; M3 rounded and simplified, with a broad internal enamel ring.

Comments

The aforementioned characteristics, jointly, as well as the dimensions of the fragments, enabled the attribution of the material of the Sangão site to *Scapteromys* according to Massoia (1981a), Pardiñas et al. (2009) and D’Elía and Pardiñas (2015). Currently, three living species of *Scapteromys* are recognized: *S. aquaticus* Thomas 1920; *S. meridionalis* Quintela et al. 2014; and *S. tumidus*. Although all of them have been reported in Rio Grande do Sul (Quintela et al. 2014b; D’Elía and Pardiñas 2015; Pardiñas et al. 2017b), it is clear that *S. aquaticus* is a marginal species limited to the Uruguay river (Bonvicino et al. 2013), while *S. meridionalis* is strongly associated to the *Araucaria* forest (Pardiñas et al. 2017b). When compared to recent specimens of *Scapteromys*, the material of the Sangão site coincides in size and morphology to *S. tumidus*. The anteromedian flexus, although usually present in the M1 of the *Scapteromys* species, is not visible in the material of the Sangão site, which can be due to the significant molar wear.

Tribe Oryzomyini Vorontsov 1959

Holochilus Brandt 1835
Holochilus sp.

Material

Seven maxillary fragments and 11 dentary fragments (Figures 3 and 5; Supplemental Online Material).

Description

A large oryzomyine characterized by lophated molars. Maxilla, dentary and molars large and robust. Deep dentary with well-marked masseteric crest; very developed capsular projection; and

Table 5. Measurements (in millimeters) of the upper and lower molars of *Nectomys lasiurus* from the Sangão site.

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 663–202	1.93	4.64		
MARSUL 682–203-3	2	4.64		
MARSUL 682–203-7			1.71	3.85
MARSUL 683–203-1	1.92	4.57		
MARSUL 683–203-4	1.86	4.46		
MARSUL 684–207-2			1.71	4.14
MARSUL 686–209-6	1.78	4.21		
MARSUL 686–209-12			2.21	4.28
MARSUL 687–205-4	1.86	4.58		
MARSUL 709–205-2	1.92	4.67		
MARSUL 712–204-1	1.85	4.21		
MARSUL 712–204-11			1.89	3.96
MARSUL 712–204-12			1.85	4.03
MARSUL 712–204-19	1.96	4.6		
MARSUL 714–204-4	1.85	4.5		
MARSUL 714–204-13			2.03	4.14
MARSUL 715–210-2	1.71	4.32		
MARSUL 715–210-5			1.75	3.75
MARSUL 715–210-6			1.92	4
MARSUL 715–210-9			1.92	4.1
MARSUL 715–210-10			1.93	4.14
MARSUL 716–210-1	1.93	4.57		
MARSUL 716–210-8			1.75	3.85
MARSUL 716–210-11			1.85	4
MARSUL 716–210-12			1.82	4.07

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

high, large and robust coronoid process. Upper and lower molars with planate occlusal surface and laminate main cusps, which are almost opposite and have rounded margins. The M1 has undivided, broad and short procingulum; M1 and M2 with mesoloph absent or in the form of an enamel spur on the median mure; M1 and M2 with deep hypoflexus; M2 without protoflexus; large M3 with conspicuous mesoloph and deep hypo and paraflexi opposite each other. The m1 has long undivided procingulum, connected to the median murid by a thin anterior murid, and large anterofossetid; m1 and m2 with mesolophid in the form of a small enamel spur on the median murid; m2 and m3 with well-marked protoflexid; m3 sigmoid.

Comments

The aforementioned characteristics, together, enabled to attribute the material of the Sangão site to *Holochilus* and also to the group of species of *H. brasiliensis*, according to Hershkovitz (1955), Massoia (1981b), Carleton and Olson (1999), Pardiñas and Gallari (1998) and Gonçalves et al. (2015). Currently, six living species of *Holochilus* are recognized (Gonçalves et al. 2015), of whom only *H. brasiliensis* (Desmarest 1819) and *H. vulpinus* (Brants 1827) are registered in Rio Grande do Sul, both belonging to the *H. brasiliensis* group (Pardiñas et al. 2013). Dental differences between both species are poorly studied, precluding the confident assignation of fossil material.

Nectomys Peters 1861

Nectomys squamipes Brants 1827

Material

One dentary fragment (Figure 5; Supplemental Online Material).

Table 6. Measurements (in millimeters) of the upper and lower molars of *Nectomys obscurus* from the Sangão site.

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 684–201-1	2.28	5.42		
MARSUL 685–206-2			2.07	4.64
MARSUL 687–204-1	2.07	5.14		
MARSUL 689–208-1			2.1	4.71
MARSUL 714–203-2			1.96	4.28
MARSUL 715–209-1	2.14	5.07		
MARSUL 716–209-2	2.25	5.21		
MARSUL 716–209-3			1.97	4.35
MARSUL 716–209-5			2	4.32

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

Description

Large and robust dentary and molar. Moderately high-crowned m1 with complex procingulum with a very incipient anteromedian flexid, not individualizing two distinct conulids; large anterofossetid, separated by thin enamel bridges of two other contiguous fossetids; anterolophid; conspicuous mesolophid connected to the mesostylid, the latter connected to the entoconid; ectostylid; developed posterolophid; and four roots.

Comments

The characteristics mentioned above, together, as well as the absence of ectolophid, allowed the assignment of the material of the Sangão site to *Nectomys*, according to Hershkovitz (1944) and Bonvicino and Weksler (2015). Moreover, when compared to recent specimens of *Nectomys*, the material of the Sangão site showed great similarity of size and morphology with *N. squamipes*, besides this being the only species of the genus registered today in Rio Grande do Sul (Bonvicino and Weksler 2015).

Oecomys Thomas 1906

Oecomys catherinae Thomas 1909

Material

Two dentary fragments (Figure 5, Supplemental Online Material).

Description

A medium-sized oryzomyine. Lower molars with opposite main cusps; m1 with long procingulum, incipient anteromedian flexid, small anterofossetid, well-developed anterolabial cingulum, anterolophid and small ectolophid; m1 and m2 with ectostylid, well-developed mesolophid connected to the mesostylid, evident entolophid connecting the mesolophid to the entoconid and conspicuous posterolophid; long m2 with well-marked protoflexid; m1 and m2 with two roots.

Comments

The aforementioned features allowed the assignment of the material of the Sangão site to the genus *Oecomys* according to Hershkovitz (1960) and Carleton and Musser (2015). Currently, 17 species of *Oecomys* are recognized, of whom 12 occur in Brazil (Suárez-Villota et al. 2017). The genus

Oecomys is currently under revision and the researches have exposed a greater diversity of species than what is today recognized, with probably new species to be described (Flores 2010; Suárez-Villota et al. 2017). Nevertheless, there are no current records of *Oecomys* in Rio Grande do Sul (Betat 2012). The *Oecomys* species with distribution nearest to the Sangão site is *O. catherinae*, a mostly Atlantic Forest taxon reported in north of the State of Santa Catarina (Asfora et al. 2011; Carleton and Musser 2015), where in fact its type locality is located. Besides, morphological comparisons between the specimens from the Sangão site and recent specimens of *O. catherinae* revealed great similarity of size and morphology between them.

Oligoryzomys Bangs 1900
Oligoryzomys sp.

Material

355 maxillary fragments and 220 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A small oryzomyine with minute molars. Proportionally high dentary with moderately marked masseteric crest and well-developed capsular projection. Upper molars with conspicuous mesoloph fused with the mesostyle; M1/m1 with anteromedian flexus/flexid, which becomes less visible with the increasing wear; M1 with developed anteroloph; M1 and M2 with broad hypoflexus and, in some specimens, enterostyle; M2 with protoflexus; m1 with well-developed anterolabial cingulum; m1 and m2 with conspicuous mesolophid coalesced with the mesostylid; m1 and m2 with long hypoflexid, ectostylid and developed posterolophid; m2 and m3 with evident protoflexid.

Comments

The material of the Sangão site could be assigned to the genus *Oligoryzomys* because it presents the diagnostic characteristics reported by Weksler and Bonvicino (2015), such as conspicuous capsular projection, M1 with developed anteroloph and presence of mesoloph and mesolophid. Furthermore, features such as high dentary; conspicuous mesoloph and mesolophid; M1 with anteromedian flexus and developed anteroloph; and m1 with anteromedian flexid and anterolophid are typically found in *O. flavescens* (Waterhouse 1837) and *O. nigripes* (Olfers 1818), according to Machado et al. (2011). Currently, 23 species of *Oligoryzomys* are recognized, of whom only *O. flavescens* and *O. nigripes* are registered in Rio Grande do Sul (Weksler and Bonvicino 2015). Nonetheless, the differentiation of these two species, as well as of all the *Oligoryzomys* species, is quite complex, due to an unclear alpha taxonomy and the great morphological similarity between the species (Machado et al. 2011). It has been reported by several authors (e.g. Langguth 1963; Weksler and Bonvicino 2005; Machado et al. 2011) that *O. nigripes* has larger and more robust skull and incisive foramen not exceeding the anterior margin of the M1, whereas *O. flavescens* is smaller and has incisive foramen exceeding the anterior

margin of the M1, in addition to other craniodental and external distinctive features. However, the cranial measurements of the two species overlap (Machado et al. 2011). The incisive foramen is not always preserved in the fossil material and, when preserved, it is variable. The molar measurements of the specimens recorded in Sangão site (Table 7) revealed a continuous size sequence, which does not allow distinguishing two distinct morphotypes. Moreover, morphological characteristics enabling the separation of two morphotypes were not observed in the studied material. Therefore, an open taxonomy was chosen.

Pseudoryzomys Hershkovitz 1962
Pseudoryzomys simplex (Winge 1887)

Material

132 maxillary fragments and 121 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

A medium-sized oryzomyine with robust and simplified molars. Broad and oblique zygomatic plate; short and deep dentary with very well-developed masseteric crest and capsular projection. Upper molars with opposite cusps and small posteroloph, which quickly become indistinct with the crescent wear; M1 with short, wide and undivided procingulum; M1 and M2 with incipient mesoloph in the form of a small salience on the median mure, not reaching the mesostyle; M2 and M3 with developed anteroloph. Lower molars with alternate cusps and deep flexids; m1 with long and undivided procingulum and large anterofossetid; m1 and m2 with developed posterolophid; M1/m1 with four roots and M2/m2 and M3/m3 with three roots.

Comments

The aforementioned characteristics, together, allowed the assignment of the material of the Sangão site to *Pseudoryzomys simplex*, according to Voss and Myers (1991). *Pseudoryzomys* is a monotypic genus with no current records in Rio Grande do Sul (Betat 2012; Voss 2015b).

Sooretamys Weksler, Percequillo and Voss 2006
Sooretamys angouya (Fischer 1814)

Material

One maxillary fragment and 13 dentary fragments (Figures 3 and 4; Supplemental Online Material).

Description

Large and robust maxilla, dentary and molars. Incisive foramina reaching the anterior alveolus of M1. Little developed masseteric crest, mental foramen very lateralized and conspicuous capsular projection. The M2 has parafosestus, formed by the direct medial connection between the paracone and the protocone (not through the median mure); metacone connected to the hypocone by a medial metalophule; posterior metalophule

connecting the metacone to the posteroloph; M2 and M3 with conspicuous mesoloph, fused with the mesostyle, and enterostyle; M2 and M3 with well-developed posteroloph and three roots. Long lower molars with opposite cusps, conspicuous mesolophid connected to the mesostylid and ectostylid; m1 with complex procingulum, which is visible in molars with little wear, formed by a shallow anteromedian flexid, metastylid, protolophid coalesced with the protostylid, and anterior metalophid connecting the metacone to the anterolingual conulid; m1 and m2 with one or more entolophulids connecting the mesolophid to the entoconid; m1 with three or four roots (with one or two accessory roots) and m2 and m3 with three roots.

Comments

The characteristics mentioned above, together, permitted the attribution of the material of the Sangão site to *Sooretamys angouya*, according to Chiquito et al. (2014). *Sooretamys* is a monotypic genus, which occurs today in Rio Grande do Sul (Percequillo 2015).

Tribe Phyllotini Vorontsov 1959

Calomys Waterhouse 1837
Calomys sp.

Material

40 maxillary fragments and 45 dentary fragments (Figures 2 and 4; Supplemental Online Material).

Description

Small and delicate maxilla, dentary and molars. Dentary proportionally deep, with little developed capsular projection located below the coronoid process. Upper and lower molars with crested occlusal surface and alternate main cusps; M1 with evident anteromedian flexus, which delineates an anterolingual conule smaller than the anterolabial one; squared M2; rounded M3; M1 with four roots and M2 and M3 with three roots; m1 with little wear with incipient anteromedian flexid; m1 and m2 with short and well-developed posterolophid; m1 with four roots and m2 and m3 with three roots.

Comments

The characteristics listed above, as well as the absence of mesoloph and mesolophid, allowed the assignment of the material of the Sangão site to the genus *Calomys*, according to Hershkovitz (1962) and Salazar-Bravo (2015). Today, 13 species of the genus *Calomys* are registered, of whom only two occur in Rio Grande do Sul: *C. laucha* (G. Fischer 1814) and *C. tener* (Winge 1887) (Salazar-Bravo 2015). The species of *Calomys* are morphologically very similar, being more reliably differentiated by molecular characters (González-Ittig et al. 2014; Quintela et al. 2014a), making it impossible to specifically assign the fossil material.

Tribe Reithrodontini Vorontsov 1959

Reithrodon Waterhouse 1837
Reithrodon cf. *R. typicus* Waterhouse 1837

Material

One dentary fragment (Figure 4; Supplemental Online Material).

Description

High and robust dentary with well-marked masseteric crest. High-crowned molars with laminate alternate cusps; elongated m1 with triangular procingulum, with three conulids; m2 with reduced protoflexid and developed protolophid.

Comments

The aforementioned characteristics, as well as the absence of meso and ectolophids and meso and ectostylids, allowed attributing the material of the Sangão site to the genus *Reithrodon*, according to Pardiñas et al. (2015b). Currently, three species of the genus *Reithrodon* are recognized: *R. auritus* (G. Fischer 1814), *R. caurinus* Thomas 1920, and *R. typicus* Waterhouse 1837 (Pardiñas and Galliari 2001; Pardiñas et al. 2017b). The alpha taxonomy of the genus remains unclear and the species are distinguished mainly by chromosomal and molecular characteristics (Pardiñas et al. 2015b). We follow here parsimony criteria taking into account that *R. typicus* is the only species registered in Uruguay and southernmost Brazil (Pardiñas et al. 2017b).

Tribe Wiedomyini Reig 1980

Wilfredomys Avila-Pires 1960
Wilfredomys oenax (Thomas 1928)

Material

Five maxillary fragments and two dentary fragments (Figures 2 and 5; Supplemental Online Material).

Description

Brachyodont upper molars with well-developed mesoloph; M1 with broad procingulum; deep oblique anteromedian flexus, which distinguishes an anterolingual conule smaller than the anterolabial one; M1 with conspicuous anteroloph; m2 and m3 with well-developed mesolophid, ectostylid and deep and broad hypoflexid; m3 large when compared to the m2.

Comments

The characteristics listed above, jointly, as well as the absence of ectolophid, allowed to assign the material of the Sangão site to *Wilfredomys oenax*, according to Percequillo et al. (2004) and González et al. (2015b). *Wilfredomys* is a monotypic genus, which occurs in Paraná, Rio Grande do Sul, São Paulo, and northern Uruguay, with scarce information about its natural history and few specimens deposited in scientific collections (González et al. 2015b).

Table 7. Measurements (in millimeters) of the upper and lower molars of *Oligoryzomys* sp. from the Sangão site.

Specimen	Lm1	Lm1–m3	LM1	LM1–M3
MARSUL 682–209-11			1.4	3.2
MARSUL 709–202-1	1.3	3.35		
MARSUL 709–202-5	1.4	3.7		
MARSUL 709–202-9			1.4	3.2
MARSUL 709–202-13			1.3	3.25
MARSUL 711–205-1			1.4	3.4
MARSUL 711–205-3			1.4	3.5
MARSUL 711–205-4			1.45	3.35
MARSUL 712–207-1	1.4	3.65		
MARSUL 712–207-7			1.35	3.2
MARSUL 712–207-8			1.8	4.1
MARSUL 712–207-9			1.45	3.35
MARSUL 712–207-10			1.25	3.1
MARSUL 713–204-1	1.45	3.6		
MARSUL 713–204-5			1.4	3.2
MARSUL 713–204-17	1.65	3.9		
MARSUL 714–207-1	1.25	3.1		
MARSUL 714–207-3			1.15	2.95
MARSUL 714–207-7			1.45	3.05
MARSUL 714–207-8			1.35	3.25
MARSUL 714–207-9			1.3	3.2
MARSUL 714–207-15			1.4	3.3
MARSUL 714–207-16			1.4	3.32
MARSUL 714–207-17			1.45	3.35
MARSUL 715–205-18			1.4	3.35
MARSUL 715–205-19			1.5	3.5
MARSUL 715–205-20			1.8	4.05
MARSUL 715–205-24			1.4	3.52
MARSUL 715–205-25			1.5	3.6
MARSUL 716–207-4			1.2	3
MARSUL 716–207-5			1.2	3.05
MARSUL 716–207-9	1.25	3.2		
MARSUL 716–207-10	1.22	3.25		
MARSUL 716–207-18			1.4	3.4
MARSUL 716–207-26			1.4	3.45
MARSUL 716–207-27			1.5	3.5
MARSUL 682–209-3	1.3	3.2		
MARSUL 682–209-4			1.7	3.9
MARSUL 682–209-5			1.45	3.4
MARSUL 682–209-6			1.4	3.6
MARSUL 682–209-7			1.4	3.25
MARSUL 682–209-10			1.52	3.22
MARSUL 682–209-17	1.25	3.1		
MARSUL 683–206-5			1.4	3.35
MARSUL 683–206-8			1.5	3.5
MARSUL 683–206-9			1.4	3.45
MARSUL 683–206-10			1.4	3.3
MARSUL 683–206-11			1.37	3.32
MARSUL 684–206-5			1.3	3.2
MARSUL 684–206-6			1.25	2.97
MARSUL 684–206-8			1.47	3.4
MARSUL 685–205-4			1.27	3.15
MARSUL 685–205-6	1.3	3.2		
MARSUL 685–205-11	1.32	3.22		
MARSUL 685–205-12			1.4	3.3
MARSUL 686–207-4	1.55	3.25		
MARSUL 686–207-5	1.35	3.35		
MARSUL 686–207-15			1.5	3.35
MARSUL 686–207-16			1.47	3.4
MARSUL 686–207-17			1.3	3.2
MARSUL 687–207-3	1.42	3.52		
MARSUL 687–207-6			1.3	3.05
MARSUL 687–207-8			1.47	3.3
MARSUL 688–208-1	1.25	3.12		
MARSUL 689–207-4	1.4	3.1		
MARSUL 689–207-6			1.35	3.05
MARSUL 689–207-7			1.4	3.35
MARSUL 690–205-4			1.45	3.2
MARSUL 691–205-4			1.4	3.4

Notes: L, length; M1, M3, first, third upper molars; m1, m3, first, third lower molars.

Discussion

Sigmodontine rodent taxonomy and Holocene assemblages in southern Brazil

The data presented in this work complement those published by Hadler et al. (2008, 2009, 2010, 2016) and Stutz et al. (2017) regarding the small mammal remains from three archaeological sites on northeastern Rio Grande do Sul (Garivaldino, Pilger and Sangão sites). Despite the sigmodontine material recovered in Sangão site being fragmented and incomplete, a reliable generic assignment is possible through the comparison with recent specimens. The major impediment in order to reach the specific level is not only the poorly resolved taxonomy of recent sigmodontine rodents, but several cases where alpha-taxonomy rests mostly on molecular markers. Detailed craniodental assessments on living taxa are needed to improve our capacity in the specific assignment of the material retrieved from archaeological and paleontological sites.

In overall, the Sangão record shows a predominance of the tribe Akodontini; the same was detected in Garivaldino (Stutz et al. 2017). By the contrary, Pilger assemblage was characterized by a predominance of Oryzomyini (Hadler et al. 2016). Today, tropical and subtropical environments in the eastern portion of South America are typified by the diversity of oryzomyines, being the akodontines the second group in abundance (Prado et al. 2014; Maestri and Patterson 2016; Pardiñas et al. 2017b).

A noteworthy feature of Sangão assemblage is that it embraces the greater richness, with 23 sigmodontines, whereas Garivaldino site has 17, and Pilger Site, 15 taxa (Hadler et al. 2016; Stutz et al. 2017). Interestingly, almost all taxa registered in Garivaldino and Pilger are also common to Sangão site, with the sole exception of the sylvan semifossorial akodontine *Thaptomys nigrita* (Lichtenstein 1829), until now restricted to Garivaldino site (Stutz et al. 2017).

Among the taxa found exclusively in Sangão site, *Brucepattersonius* sp., *Deltamys* sp., *Nectomys squamipes*, *Oecomys catherinae* and *Reithrodon* cf. *R. typicus* represent the first records for the Holocene of Rio Grande do Sul. *Scapteromys tumidus* had already been listed for the Holocene of Rio Grande do Sul in a zooarchaeology study (Queiroz 2004).

The genus *Brucepattersonius* is endemic of the Atlantic Forest biome, especially of forest environments, but there is scarce information about the natural history of its species (Hershkovitz 1998; Pardiñas et al. 2017b). *Brucepattersonius iheringi* is the only species that occurs today in Rio Grande do Sul, being registered in locations near Sangão site, such as Osório, Taquara (Vilela et al. 2015), São Francisco de Paula and Viamão (Christoff et al. 2013). The specimens from Sangão site represent the second fossil record of *Brucepattersonius*. Previously, a species coined by Lund in 1839 based on material recovered in Lagoa Santa caves, State of Minas Gerais, *Mus talpinus*, was allocated in *Brucepattersonius* (Pardiñas and Teta 2013).

Until recently, the genus *Deltamys* was considered monotypic and with distribution limited to the Pampa

biome, occurring in low humid grasslands, gallery forests and marshes of Argentina, Uruguay and southernmost Brazil (Pardiñas and Teta 2015). New findings, early based on cytogenetics and molecular work, have shown the existence of two novelty *Deltamys* lineages coming from the Ombrophilous Mixed Forest of northern Rio Grande do Sul, a region characterized by higher altitudes (reaching 1,000 m above the sea level) known as the Meridional Plateau. One of them was recently described as *D. araucaria* (see Quintela et al. 2017; Pardiñas 2018); the other remains unnamed until now (*Deltamys* sp. 2n = 40' according to Ventura et al. 2011). Both taxa enlarge the genus range and ecosystem distribution. Genetic and craniometric analysis of *D. kempfi* (Montes et al. 2008; Ventura et al. 2011; Quintela et al. 2017) have revealed the presence of two distinct groups inside this taxon, one corresponding to the populations from north and centre of the Rio Grande do Sul Coastal Plain (RSCP) and the other to the southern populations of RSCP, with both probably overlapping in the west of Patos Lagoon. This break inside *D. kempfi* seems to be related to marine transgressive-regressive events that occurred in the RSCP during the Quaternary, which have formed the Barrier-Lagoon systems (Tomazelli et al. 2000). These systems originated several lagoons on the RSCP (including the Patos lagoon) that may have acted as geographical barriers, causing the differentiation of the distinct groups of *D. kempfi* (Quintela et al. 2017). This differentiation pattern was also observed for the sympatric *Scapteromys tumidus* (Quintela et al. 2015). However, Quintela et al. (2017) considered the differences inside *D. kempfi* not consistent with its taxonomic division, the taxon would still be passing through a differentiation process and its groups should be considered as independent Evolutionary Significant Units. Thus, it is possible to notice that *Deltamys* has a complex biogeographic history, with one lineage dispersing across the Meridional Plateau highlands and differentiating into two forms (*D. araucaria* and *Deltamys* sp. 2n = 40') and another lineage spreading through the coastal plain (*D. kempfi*) (Quintela et al. 2017). The specimens from the Sangão site constitute the first fossil record for *Deltamys* (Pardiñas and Teta 2015). Regrettably, its specific assignation is hampered by the poorly-resolved alpha-taxonomy of the genus.

Scapteromys tumidus is a medium-sized akodontine species closely related to fresh water bodies, living in lowlands and marshes (Massoia and Fornes 1964; Hershkovitz 1966). It occurs today in Rio Grande do Sul in the RSCP (Christoff et al. 2013; Quintela et al. 2014b). Although the genus was cited with fossils in Argentina dated as Late Pliocene (*S. herskovitzi* Reig 1994), this generic placement was disputed (Pardiñas et al. 2009). Confident records for the genus in the Province of Buenos Aires, Argentina, are about one million of years ago (see Voglino and Pardiñas 2005). In Brazil, *S. tumidus* was listed for the Quaternary of Serra da Bodoquena, State of Mato Grosso do Sul (Salles et al. 2006), and for the Holocene of Rio Grande do Sul (Queiroz 2004). However, these materials are in need of revision, since they

were presented before the description of *S. meridionalis* (Quintela et al. 2014b), besides they have not been described or figured.

Nectomys are large semiaquatic oryzomyine rodents devoted to fresh waters in tropical and subtropical South American lowlands (Hershkovitz 1944; Bonvicino and Weksler 2015). The genus is now under revision (see Chiquito 2015), and it probably encompasses a living diversity of about seven species (Pardiñas et al. 2017b). *Nectomys squamipes* is the southernmost living species of the genus, widespread in Rio Grande do Sul, being recorded in localities near Sangão site, such as Sapiranga and Taquara (Christoff et al. 2013). In addition to the specimen from Sangão site here presented, the only reliable fossil record of *Nectomys* is one from Lagoa Santa region, Minas Gerais (Winge 1887; Pardiñas and Barbière 2017).

Oecomys is a speciose oryzomyine genus, mainly associated to tropical lowland forests, especially in northern South America. *Oecomys catherinae* is a sylvan species widely distributed in eastern Brazil, with records in the Atlantic coast forest from the states of Santa Catarina to Paraíba, but also in gallery forests of the Cerrado biome and in forested zones in south of the Amazon river (Flores 2010; Asfora et al. 2011; Carleton and Musser 2015). The fragments from the Sangão site represent the first record of *Oecomys* from the Holocene of Rio Grande do Sul. Otherwise, the fossil record of *Oecomys* in Brazil includes materials from the Quaternary of Serra da Mesa, State of Goiás (Salles et al. 1999) and for the Quaternary of the State of Tocantins (Pires et al. 2018).

Reithrodon is a genus typically recorded in open lands of South America southern cone (Pardiñas et al. 2015b). *Reithrodon typicus* is registered in southernmost Rio Grande do Sul, and extensively in Uruguay and neighboring Argentinean territory (Barlow 1969; Freitas et al. 1983; González et al. 1999; Pardiñas et al. 2015b). *Reithrodon* has one of the widest temporal ranges inside the sigmodontine radiation. Its oldest fossil record has a controversial age of 4–5 millions of years ago (Pardiñas et al. 2017a), being putatively assigned to Monte Hermoso Formation in southern Province of Buenos Aires, Argentina (Pardiñas et al. 2015b). In Late Pleistocene Uruguayan deposits, the genus is widespread (see Ubilla et al. 2004). For the Pleistocene of Rio Grande do Sul, previous records are restricted to isolated dental material from the municipality of Uruguaiana (Oliveira 1992) and from the RSCP (Hadler and Ferigolo 2004).

Sangão small mammals as paleoenvironmental indicators

As well as the sigmodontine samples of Garivaldino and Pilger sites, the Sangão site assemblage can also be typified as non-analogous, i.e., the sympatric occurrence of species that today are allopatric or vice-versa (Barnosky 1993). 'Allopatric-pairs' of sigmodontine rodents detected in Sangão assemblage are numerous, including *Kunsia-Reithrodon*, *Gyldenstolpia-Reithrodon*, *Necromys obscurus-*

Kunsia, *Wilfredomys-Gyldenstolpia*, among many others. In addition, Sangão record is plenty of extralimital taxa; *Gyldenstolpia* cf. *G. planaltensis*, *Kunsia tomentosus*, *Necomys obscurus*, *Oecomys catherinae* and *Pseudoryzomys simplex* do not occur today in Rio Grande do Sul, being, therefore, regionally extinct. Almost the same is the case of *R. typicus*, since this sigmodontine has only two records on the Brazilian-Uruguayan border (Freitas et al. 1983; González et al. 1999). Among these taxa, both *N. obscurus* and *R. typicus* are typical Pampean species, occurring in territories further south than the Sangão site, namely Argentina and Uruguay (Pardiñas et al. 2015c). In contrast, the genera *Gyldenstolpia*, *Kunsia* and *Pseudoryzomys* currently occur further north and west than the Sangão site, in open lands of the Cerrado and Chaco biomes (Bezerra 2015; Pardiñas and, 2015; Voss 2015b), while *O. catherinae* occur further north than the Sangão site in the Atlantic Forest and Cerrado biomes (Asfora et al. 2011). The records of *K. tomentosus* from the Garivaldino, Pilger and Sangão sites, as well as the record of *O. catherinae* from the Sangão site, constitute the southernmost localities for these taxa (Pardiñas et al. 2009; Bezerra 2015; Carleton and Musser 2015), whereas the records of *N. obscurus* from Garivaldino, Pilger and Sangão sites are the northernmost occurrences of this species (Pardiñas et al. 2015c).

However, beyond the typification of Sangão small mammal assemblage, the main point to address is the paleoenvironmental meaning, if any, of the noteworthy richness recorded in this archaeological locality. An accurate reconstruction of past environmental conditions based on a small mammal sample depends on three main factors (Terry 2010; Fernández et al. 2016): (1) well-supported taxonomy; (b) resolved taphonomy and chronology; and (3) adequate knowledge about the environmental requirements of the species recorded.

Although the integral taphonomic analysis of the material from Garivaldino, Pilger and Sangão sites is still in progress, it is clear that these samples have been accumulated by different agents. In overall, while medium and large caviomorphs and also largest sigmodontines (i.e. *Kunsia tomentosus*, *Gyldenstolpia* cf. *G. planaltensis*) seem to be introduced into archaeological sites by humans, most of the sigmodontines are apparently related to the predation by owls with the lowest levels of modification, possibly *Tyto furcata*. The main evidence for the latter is the little corrosion observed on the bone and dental material caused by stomach acids of the predator, consistent with the one produced by this species (Andrews 1990; Fernández et al. 2017). This owl can live in caves and is an opportunistic predator, feeding on the most abundant small mammal species in the area, which makes the owl pellets suitable samples in order to infer the local environment (Faria and Passamani 2013).

The marked discrepancy among the studied grids of the Sangão site involving small mammal remains sample sizes can be explained by taphonomy. The grid E12 has a much lower sample size ($n = 32$) when compared to the grids F8 ($n = 1,015$) and G8 ($n = 1,636$). Besides, the grid E12 contains mainly large-sized sigmodontine rodents (e. g. *Gyldenstolpia* cf. *G. planaltensis*, *K. tomentosus*, *Holochilus* sp.). Dias (2003),

when detailing the Sangão site excavation, reported that the largest amount of small mammal remains was found in those grids located beneath a flap in the roof of the shelter, capable to serve as owls nesting or roosting site. In fact, this is the spatial location of both grids F8 and G8, and can be connected with the high abundance of small and medium-sized sigmodontines recorded there. Conversely, the grid E12 is located far from this roof flap, but it records plenty of archaeological material (Dias 2003).

One of the noteworthy features of Sangão assemblage is its greater diversity. Can the variety and number of sigmodontine species recorded in this site be related to local environmental conditions? Sangão differs from Garivaldino and Pilger sites by presenting a larger number of taxa strictly associated to wetlands, such as *Deltamys* sp., *Scapteromys tumidus*, *Holochilus* sp. and *Nectomys squamipes*. Semi-aquatic taxa of caviomorphs, like *Myocastor coypus* and *Cavia magna*, were also registered exclusively in Sangão site (Hadler et al. 2008). These data suggest a more humid local environment around the Sangão when compared to Garivaldino and Pilger sites. Actually, the Sangão site is a cave located close to the Sinos river, characterizing the area as inside or next to a riparian zone. The riparian zones are complex ecosystems well known for its special ecological mechanisms and patterns (Naiman and Décamps 1997). Natural riparian zones exhibit high animal wildlife diversity since it can be used as a habitat by riparian species (obligate and generalists), species seeking edge habitat, species associated with early successional plant communities, exotic species, among others (Naiman et al. 2000). Several authors have considered that riparian zones have greater richness when compared to adjacent uplands (e.g. Woinarski et al. 2000; Catterall et al. 2001). Other authors proposed that riparian zones have greater richness because they harbor different species pools altogether and not because they have a higher number of species (Sabo et al. 2005). Thus, in the case of the Sangão site, the proximity to the Sinos river and its respective riparian zone could have an important role in determining the composition and richness of the fauna observed in the site. Concerning the other two studied sites on northeastern Rio Grande do Sul, the Pilger site is also located close to a river (Caí river) and possess great sigmodontine richness, 15 taxa, despite having a small number of fragments (only 232 sigmodontine craniodental remains) (Hadler et al. 2016). On the other hand, the Garivaldino site is situated farther from a river (Taquari river) than Pilger and Sangão sites (Stutz et al. 2017), thus it could suffer less influence of the river and its corresponding ecosystems on its assemblage.

Comparisons with modern samples

There are still few studies about the modern *Tyto furcata* pellets from Rio Grande do Sul, which makes it difficult to compare these assemblages to the fossil ones. González et al. (1999) worked in Bagé, southern Rio Grande do Sul, in the Pampa biome. Scheibler and Christoff (2004) analyzed owl pellets from an agrosystem area of Venâncio Aires, centre of Rio Grande do Sul. Peters et al. (2010) gathered samples in the region of Rio da Várzea Hydrographic Basin, which encompasses remnants of

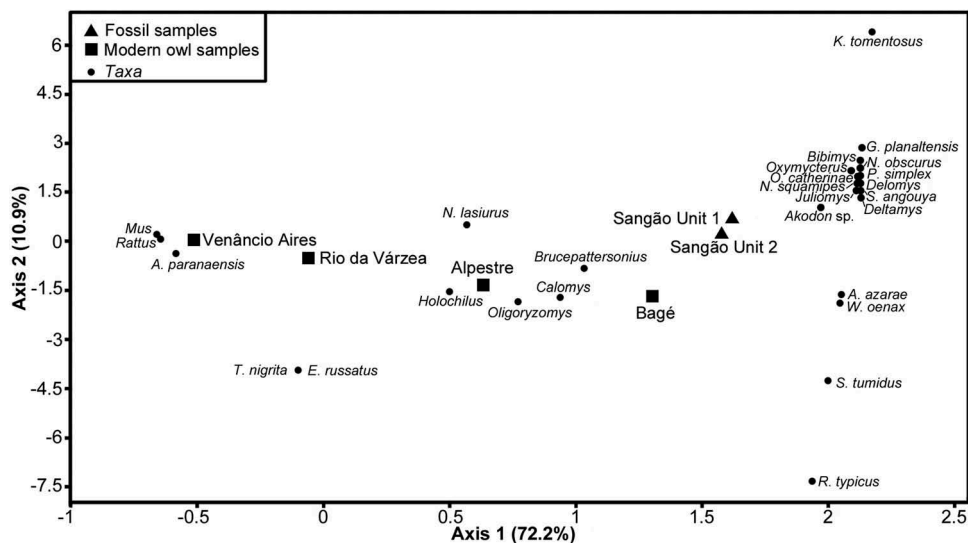


Figure 6. Correspondence analysis of small mammal fossil assemblages from Sangão site (Units 1 and 2) and modern owl pellet samples from Rio Grande do Sul. Percentages of both axes show the variance.

Ombrophilous Mixed Forest, Deciduous Seasonal Forest and steppes. J. J. Cherem (this paper) collected samples in Alpestre, northwestern Rio Grande do Sul, region of Semideciduous Forest occurrence. All of these sampled areas show some disturbance by anthropic action. Numerically, only the Venâncio Aires sample is comparable to the amount of sigmodontine fragments from the Sangão site, with 3,509 maxillary fragments. Despite this great abundance of fragments, the richness observed in Venâncio Aires owl pellets (10 taxa) is lower than the one observed in Sangão site (23 taxa). Moreover, important changes in the faunal composition can be noted between the modern owl pellets records and those from the Holocene.

Taxa like *Akodon* spp., *Oligoryzomys* spp. and *Calomys* spp. are present in all modern and Holocene samples. *Oligoryzomys* spp. stands out as a taxon with great abundance in Bagé ($\cong 42.6\%$ of the individuals) and in Alpestre ($\cong 55\%$ of the individuals) samples. In contrast, in the Sangão site, *Oligoryzomys* sp., despite being the taxon with the highest abundance, represents only 18% of the individuals, suggesting a smaller importance of this taxon in the Holocene community. In Rio da Várzea and Venâncio Aires assemblages, *Oligoryzomys* spp. does not have great abundance, since these localities registered a significant predominance of *Mus musculus*. *Mus musculus* and *Rattus* spp. are exotic murids which are present in Alpestre, Rio da Várzea and Venâncio Aires samples, the first being also recorded in Bagé.

Correspondence analysis result (Figures 6) shows both temporal archaeological units samples grouped, but modern owl samples did not, considering the main factor (Axis 1, 72.2% of the total variance). This suggests that the main structure of sigmodontine rodent communities has remained stable during the Early and Middle Holocene in Sangão area, whereas the deepest change apparently occurs towards the Late Holocene and recent times. The main factor grouped to the right side of the taxa only recorded in Sangão. For example, the Cerrado and Chaco taxa (*Gyldenstolpia* cf. *G. planaltensis*, *Kunsia tomentosus*, *Pseudoryzomys simplex*), the

Pampean species (*Necomys obscurus*), and forest taxa (*Delomys* sp., *Juliomys* sp., *Oecomys catherinae*, *Sooretamys angouya*) are restricted to Holocene, but do not appear in modern assemblages, except for *Brucepattersonius iheringi* in Venâncio Aires, *Brucepattersonius* sp. in Alpestre and *Euryoryzomys russatus* in Rio da Várzea. However, there are also some taxa, such as *Bibimys* sp., *Nectomys squamipes*, which occur today in Rio Grande do Sul, but that are absent in recent owl pellets. Correspondence analysis also shows that Bagé is the modern sample closest to the fossil ones. Some species allied to open areas such as the Pampean species *Reithrodon typicus* and *Akodon azarae*, species associated to forest (*Wilfredomys oenax*) and taxa that inhabit low flooded grass areas and marshes (such as *Scapteromys tumidus*, *Deltamys*) were recorded only in Sangão and Bagé. Conversely, Venâncio Aires is the modern sample the farthest to the fossil ones, possibly due to its peri-urban location, with high abundance of the exotic and sinantropic murids (*Mus* and *Rattus*). The anthropic action can be related to the appearance and proliferation of exotic species and, possibly, to an apparent loss of sigmodontine diversity, mainly of forest species.

Sangão small mammals and the Holocene environmental evolution in southern Brazil

During the Quaternary, the climate and landscape of Rio Grande do Sul were greatly influenced by the glacio-eustatic processes of fluctuations in sea level. Marine transgressive-regressive cycles are responsible for the formation of four barrier-lagoon depositional systems, a process that spent at least the last 400,000 years BP, and are related to the last peaks of the oxygen isotopic curve. These events shaped the shoreline and adjacent lands of the state (and also the adjacent Uruguayan shoreline; cf. Rodríguez 2011), forming the current RSCP and several lagoons (Tomazelli et al. 2000; Wildner and Lopes 2010).

Palynological studies carried out in Santo Antônio da Patrulha, same locality of the Sangão site, and in other locations

in Rio Grande do Sul (Bauermann 2003; Behling et al. 2004; Oliveira et al. 2005; Macedo et al. 2010), suggested a dominance of grasslands in the region in Early Holocene, along with the prevalence of a cold dry climate. At the end of Middle Holocene, with increasing temperatures and humidity, there would have been the expansion of the Atlantic Forest in the region, with its full establishment around 4,000–3,000 years BP.

As to the marsupials and caviomorph rodents from the Sangão site, but also from the Garivaldino and Pilger sites, their assemblages are composed by open land (e.g. *Ctenomys* sp., *Euryzygomatomys mordax*) and forest species (e.g. *G. microtarsus*, *Phyllomys* sp.). According to this data, it has been proposed for northeastern Rio Grande do Sul a mosaic environment, with open lands and forests since Early Holocene. Moreover, the small mammal assemblages suggest that climate was probably constant, with no significant climatic pulses, and the changes, when they have occurred, were slow and gradual (Hadler et al. 2008, 2009). The expansion of the forests in the region would have resulted in the regional extinction of open land taxa, such as *Euryzygomatomys mordax*, *Dicolpomys fossor* and *Clyomys riograndensis* (Hadler et al. 2008, 2009).

The Sangão sigmodontine assemblage composition supports these previous hypotheses. Forest taxa such as *Delomys* sp., *Juliomys* sp., *Oecomys catherinae* and *Sooretamys angouya*, are present in Sangão site since Middle Holocene. On the other hand, open land taxa (e.g. *Gyldenstolpia* cf. *G. planaltensis*, *Necomys* spp., *Calomys* sp.) also largely occur throughout all levels of Sangão site, including the superior ones. Regional extinctions (e.g. *Gyldenstolpia* cf. *G. planaltensis*, *K. tomentosus*, *N. obscurus*, *O. catherinae* and *P. simplex*) have also been revealed.

Thus, the Sangão small mammal fossil assemblage suggests that faunal changes, such as extinctions and regional extinctions, happened during the Holocene in northeastern Rio Grande do Sul. The causes of these changes must be studied in detail. However, it seems clear that these changes led to an impoverishment of the small mammal diversity in Rio Grande do Sul, and the current assemblage represents a depauperate subset.

Further studies dedicated to paleoenvironment and taphonomic issues are in course and shall provide a more robust and comprehensive view of the small mammal faunal dynamics during the Holocene in southern Brazil.

Acknowledgments

We thank A. Dias and the MARSUL for the material loan, P.C. Simões-Lopes and M.E. Graipel for the access of the UFSC collection, A. Christoff for the access of the MCNU collection, T. Trigo for the access of the MCN-M collection, A. Dias for the access of the UFRGS collection, S. Klant for the access of the UNISC collection, S. Althoff for the access of the CZFURB collection and J.A. Oliveira for the access of the specimens of *Wilfredomys oenax* of the MN collection. We also want to thank the Central Laboratory of Electronic Microscopy of UFSC for the MEV photos, JP. Saldanha for the preparation of Figure 1; P. Teta, E. González and Historical Biology editors for their useful suggestions; and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), the Agencia Nacional de Promoción Científica y Tecnológica and the Consejo Superior de Investigaciones Científicas de Cooperación Internacional for the financial support.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was financially supported by the CNPq under Grant 133086/2017-8 (NS) and Grant 444508/2014-7 (PH), Agencia Nacional de Promoción Científica y Tecnológica under Grant PICT 2014-1039 (UFJP); and Consejo Superior de Investigaciones Científicas de Cooperación Internacional under Grant i-COOPB-20287 (FJF).

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