CAVIOMORPHS (MAMMALIA, RODENTIA) FROM THE HOLOCENE OF RIO GRANDE DO SUL STATE, BRAZIL: SYSTEMATICS AND PALEOENVIRONMENTAL CONTEXT

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ABSTRACT – The caviomorph rodents are scarcely known from the Quaternary record of Rio Grande do Sul State, Brazil. This work deals with caviomorphs from two sites, with datings including the Early to Late Holocene. The taxa recorded were: *Cavia* sp., *C. aperea*, *C. magna*, *Ctenomys* sp., *Phyllomys* sp., *Myocastor coypus*, *Euryzygomatomys mordax*, *Dicolpomys fossor*, the last two of which are extinct. A new fossil species, *Clyomys riograndensis* sp.nov. is also described. The stratigraphic distribution of these taxa allows us to suggest a slow and gradual climatic change during the Holocene and a mosaic environment with grasslands and gallery forests, which is indicated by the presence of fossorial animals that typify open areas, coexisting with taxa of forested areas.

Key words: Caviidae, Ctenomyidae, Echimyidae, Holocene, palaeoenvironment, Rio Grande do Sul.

RESUMO – Os roedores caviomorfos são pouco conhecidos no registro do Quaternário do Rio Grande do Sul, Brasil. Este trabalho trata dos caviomorfos oriundos de dois sítios, com datações abrangendo do Holoceno inicial ao final. Registou-se os táxons: *Cavia* sp., *C. aperea*, *C. magna*, *Ctenomys* sp., *Phyllomys* sp., *Myocastor coypus*, *Euryzygomatomys mordax*, *Dicolpomys fossor*, sendo os dois últimos extintos. Descreveu-se também uma nova espécie fóssil, *Clyomys riograndensis* sp.nov. A distribuição estratigráfica dos táxons sugere uma mudança climática lenta e gradual durante o Holoceno e um ambiente em mosaico, com campos e florestas de galeria, indicado pela presença de animais fossoriais típicos de áreas abertas coexistindo com táxons de áreas florestadas.

Palavras-chave: Caviidae, Ctenomyidae, Echimyidae, Holocene, paleoambiente, Rio Grande do Sul.

INTRODUCTION

Currently, Rodentia is the largest mammalian Order in number of species among mammals, and the Suborder Hystricomorpha includes more than 160 extinct and living genera distributed in at least 13 South American families (“caviomorphs”; see McKenna & Bell, 1997; Woods & Kilpatrick, 2005). This group is first recorded in South America in the Early Oligocene (Tinguirirican South American Land Mammal Age - SALMA-; Flynn *et al.*, 2003), and by the Late Oligocene (Deseadan SALMA) they had already experienced a wide adaptive radiation (Vucetich *et al.*, 1999).

In the Pleistocene, caviomorphs have a noteworthy record in Argentina and Bolivia (e.g., Hoffstetter, 1963; Frailey *et al.*, 1980; Marshall & Sempere, 1991; Werdelin, 1991; Vucetich *et al.*, 1997; Vucetich & Verzi, 2002; Verzi *et al.*, 2002); however, they are scarcely known in the Brazilian Subregion (Vucetich *et al.*, 1999). For the Quaternary of Brazil, they are known for the states of Minas Gerais (Lund, 1839a,b; 1840a,b; Winge, 1888; Souza-Cunha & Guimarães, 1978; Souza-Cunha & Magalhães, 1986; Emmons & Vucetich, 1998), São Paulo (Ameghino, 1907; Lino *et al.*, 1979; Barros-Barreto *et al.*, 1982; Castro & Langer, 2005), Espírito Santo (Paula-Couto, 1978), Bahia (Cartelle & Lessa, 1989), Rio Grande do Norte (Oliveira

et al., 1985), Piauí (Guérin, 1991), Pará (Toledo *et al.*, 1999 a,b; Moraes-Santos *et al.*, 1999), Goiás (Salles *et al.*, 1999), Mato Grosso do Sul (Salles *et al.*, 2006), and Rio Grande do Sul (e.g., Oliveira, 1992; Rodrigues & Ferigolo, 2004). Most of these Brazilian records are from caves, with little or no dating, and in some cases with only tentative identification. Auler *et al.* (2006) assigned the assemblages of cave deposits in Minas Gerais and Bahia to Middle Pleistocene ($\pm 350,000$ years) to Early Holocene.

During the last years, archaeological excavations in Rio Grande do Sul recovered assemblages of small-sized mammals, with a large number of specimens, excellent stratigraphic control and C^{14} datings (Mentz-Ribeiro & Ribeiro, 1999; Dias & Jacobus, 2003). The caviomorph assemblages from two of these archaeological localities, encompassing a large part of the Holocene, are here reported. The goal of this contribution is increasing the knowledge of the diversity of Quaternary caviomorphs of southern Brazil, and its palaeoenvironmental context.

MATERIAL AND METHODS

The material studied constituted more than 400 skull and mandible fragments found during the excavation, by sieving or after by manual selection with the aid of a binocular magnifier among the sieved sediments. The material from Garivaldino site is deposited in the UNISC, and that from Sangão site is at MARSUL. The excavations at the Garivaldino site were performed at arbitrary levels at 10 cm intervals, comprising twenty-three levels (Dias & Jacobus, 2003), and at the Sangão site at 5 cm intervals for a total of thirteen arbitrary levels (Dias, 2003). At Garivaldino site we had access to material from the grids A/6, B/5, C/6, and D/6; at Sangão site the reported material comes from grids D/13, E/12, E/13, F/8 and F/16, the ones with largest number of specimens (see details in Mentz-Ribeiro *et al.*, 1989; Dias, 2003).

The specimens received compound number (e.g., 1754-4); the first one (in this case, 1754) indicates the level into a grid from where it was excavated, according to the institutional catalogue numeration for levels and grids. The second number (in this case, 4) indicates the specimen itself, and obeys a sequential order into a level of a grid.

The material was compared with recent specimens (see Appendix) from scientific collections. Original samples and illustrations of species from Lagoa Santa (Minas Gerais), deposited in ZMUC, were also examined. Bone nomenclature follows Woods & Howland (1979), and dental structures follow Contreras (1964) and Emmons & Vucetich (1998). Measurements were taken according to Patton & Rogers (1983), Vucetich *et al.* (1997), Leite (2003), and Iack-Ximenes *et al.* (2005). For the taxonomy of families and subfamilies, conservative criteria have been followed (Woods & Kilpatrick, 2005; but see e.g. Galewsky *et al.*, 2005). In the examined material section for each species the catalog number is followed by a brief description of the material; the grid; and the level.

Figure 1. Geomorphologic scheme of Rio Grande do Sul State (Brazil), showing the location of the studied sites.

Institutional abbreviations. MARSUL, Museu Arqueológico do Rio Grande do Sul, Taquara; MCN-M, mastozoologia, Museu de Ciências Naturais da FZBRS, Porto Alegre; MLP, Museo de La Plata, La Plata; MN, Museu Nacional, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UNISC, Centro de Ensino e Pesquisas Arqueológicas da Universidade de Santa Cruz do Sul, Santa Cruz do Sul; ZMUC, Zoological Museum of the University of Copenhagen, Copenhagen.

Anatomical abbreviations. AP, anteroposterior length; AW, anterior width; IFL, incisive foramen length; IFW, incisive foramen width; LDL, lower diastema length; MD, mandible height; n, sample size; PW, posterior width; SD, standard deviation; UDL, upper diastema length; $\bar{x}$, mean average; W, width.

GEOLOGICAL SETTING

The first locality is Garivaldino site (site RS-TQ-58: Afonso Garivaldino Rodrigues), Municipality of Montenegro, on the boundary between the Central Depression and Serra Geral Plateau ($29^{\circ}34'5''$ S and $51^{\circ}38'4''$ W; Figure 1). The second is Sangão site (site RS-S-327: Sangão), Municipality of Santo Antônio da Patrulha, Coastal Plain ($29^{\circ}46'2''$ S and $50^{\circ}33'4''$ W; Figure 1).

Both sites are rock shelters eroded in the sandstone of the Botucatu Formation (Mentz-Ribeiro & Ribeiro, 1999; Dias, 2003). The Garivaldino site is 72 m above sea level, with a

21.40 m opening facing North, is 8.50 m deep and 8.60 m high (Mentz-Ribeiro & Ribeiro, 1999). Sangão site is 52 m above sea level, its opening being 7 m above the Sinos River, with a 25 m opening facing South, and is 10 m deep and 6 m high (Dias, 2003). Both sites and shelter plans are shown in Mentz-Ribeiro & Ribeiro (1999), and Dias (2003).

A taphonomic analysis of the small-mammal fauna from the Garivaldino site suggested that this bone deposit was caused by non-human predators, particularly Strigiforms and/or Falconiforms birds (Queiroz, 2004). For food remains associated to human occupation [including mammals such as *Mazama americana* (Erxleben), *Ozotocerus* sp. Ameghino, *Tapirus terrestris* (Linneau), *Dasypus* sp. (Linneau), *Cabassous* sp. McMurtrie, *Cuniculus paca* (Linneau), and *Myocastor coypus* (Molina)] see Mentz-Ribeiro & Ribeiro (1999), Dias & Jacobus (2003), and Dias (2004), and for archaeological findings (lithic material, pottery, and pieces made with shells, and bones) see Mentz-Ribeiro *et al.* (1989), Mentz-Ribeiro & Ribeiro (1999), and Dias (2003). C14 datings indicate that the sequence integrated for both sites represents the interval Early Holocene (9,400 years BP) – Late Holocene (3,730 years BP; see Table 1).

SYSTEMATICS

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOMORPHA Brandt, 1855
Infraorder HYSTRICOGNATHI Brandt, 1855
Family CAVIIDAE Fischer de Waldheim, 1817
Cavia Pallas, 1766

Material. UNISC 1515-1; fragment of isolated teeth; A/6; 11. UNISC 1689-1; fragment of edentulous left maxilla; C/6; 02. UNISC 1690-6; fragment of right mandible with m2; C/6; 03. UNISC 1691-1; fragment of left mandible with dp4-m3; C/6; 04. UNISC 1691-2; fragment of left mandible with m1-2; C/6; 04. UNISC 1691-3; fragment of edentulous right mandible; C/6; 04. UNISC 1692-1; fragment of left mandible with dp4-m3; C/6; 05. UNISC 1694-1; fragment of edentulous right mandible; C/6; 07. UNISC 1696-6; fragment of edentulous right mandible; C/6; 09. UNISC 1698-1; fragment of edentulous right mandible; C/6; 11. UNISC 1699-1; fragment of edentulous left mandible; C/6; 12. UNISC 1702-2; fragment of left mandible with broken dp4; C/6; 15. UNISC 1702-9; fragment of edentulous right mandible; C/6; 15. UNISC 1703-11; fragment of edentulous right mandible; C/6; 16. UNISC 1704-1; fragment of edentulous left mandible; C/6; 17. UNISC 1704-2; fragment of edentulous right maxilla; C/6; 17. UNISC 1705-2; fragment of edentulous right maxilla; C/6; 18. UNISC 1752-10; fragment of edentulous right mandible; D/6; 02. UNISC 1754-13; fragment of left mandible with dp4-m3; D/6; 04. UNISC 1755-19; fragment of left mandible with m2; D/6; 05. UNISC 1759-9; fragment of edentulous left mandible; D/6; 09. UNISC 1760-3; fragment of right mandible with m1-2; D/6; 10. UNISC 1761-10; palatal fragment with right DP4-M1 and left DP4-M2, respectively; D/6; 11. UNISC 1761-17; fragment of edentulous right mandible; D/6; 11. UNISC 1761-19; fragment of edentulous right mandible; D/6; 11. UNISC 1768-13; fragment of left mandible with dp4-m3; D/6; 18. UNISC 1769-1; fragment of right mandible with dp4-m1; D/6; 19. UNISC 1770-2; fragment of right mandible with m1; D/6; 20. UNISC 1771-

3; fragment of edentulous right mandible; D/6; 21. MARSUL 514-52; isolated left dp4; D/13; 01. MARSUL 515-50; fragment of left mandible with dp4-m3; D/13; 02. MARSUL 515-51; fragment of right mandible with m1-3; D/13; 02. MARSUL 516-51; fragment of left mandible with dp4-m2; D/13; 03. MARSUL 516-52; fragment of right mandible with m2-m3; D/13; 03. MARSUL 517-50; right mandible with dp4-m3; D/13; 04. MARSUL 518-50; fragment of right mandible with dp4-m2; D/13; 05. MARSUL 519-50; fragment of edentulous right mandible; D/13; 06. MARSUL 519-53; fragment of right maxilla with broken DP4; D/13; 06. MARSUL 519-54; isolated right m1?; D/13; 06. MARSUL 520-51; fragment of right maxilla with broken DP4; D/13; 07. MARSUL 523-50; isolated right m1?; D/13; 10. MARSUL 657-50; fragment of left mandible with dp4-m3; E/12; 02. MARSUL 660-51; fragment of edentulous right maxilla; E/12; 05. MARSUL 662-51; fragment of left maxilla with DP4; E/12; 07. MARSUL 664-18; fragment of right mandible with dp4-m2; E/12; 09. MARSUL 667-21; fragment of left mandible with dp4-m3; E/12; 12. MARSUL 669-50; fragment of right mandible with m1-2; E/13; 01. MARSUL 670-16; fragment of left mandible with dp4-m1; E/13; 02. MARSUL 671-50; fragment of edentulous left mandible; E/13; 03. MARSUL 671-51; fragment of edentulous left mandible; E/13; 03. MARSUL 672-50; fragment of edentulous left mandible; E/13; 04. MARSUL 673-25; fragment of right mandible with dp4-m3; E/13; 05. MARSUL 673-50; fragment of right mandible with dp4-m1; E/13; 05. MARSUL 678-6; fragment of left mandible with dp4-m3; E/13; 08. MARSUL 683-16; fragment of right mandible with broken m2; F/8; 02. MARSUL 684-12; fragment of left mandible with m1 and m3; F/8; 03. MARSUL 687-23; fragment of left mandible with m1-3; F/8; 06. MARSUL 697-4; fragment of left mandible with dp4-m3; F/16; 01. MARSUL 697-26; fragment of left mandible with dp4-m3; F/16; 01. MARSUL 698-12; fragment of right mandible with m1-3; F/16; 02. MARSUL 700-50; fragment of right mandible with m2; F/16; 04. MARSUL 701-52; fragment of edentulous right maxilla; F/16; 05. MARSUL 701-54; fragment of edentulous left maxilla; F/16; 05. MARSUL 701-55; fragment of edentulous left maxilla; F/16; 05. MARSUL 702-5; fragment of left mandible with dp4-m3; F/16; 06. MARSUL 703-51; fragment of left mandible with m2; F/16; 07. MARSUL 703-52; fragment of edentulous right mandible; F/16; 07. MARSUL 703-53; fragment of edentulous left mandible; F/16; 07. MARSUL 704-7; fragment of right mandible with dp4-m1; F/16; 08. MARSUL 704-28; fragment of left mandible with dp4-m2; F/16; 08. MARSUL 705-52; isolated right m3?; F/16; 09. MARSUL 707-50; fragment of edentulous right mandible; F/16; 11.

Comments. This genus was already recorded for the Quaternary of São Paulo, Mato Grosso do Sul, Minas Gerais and Rio Grande do Sul states (Souza-Cunha & Guimarães, 1978; Lino *et al.*, 1979; Mentz-Ribeiro *et al.*, 1989; Salles *et al.*, 2006).

Cavia differs from other genera of the family by having the first prism of the upper and lower molars sublamina, i.e. very compressed antero-posteriorly; hypoflexus/hypoflexid with parallel walls and filled with abundant cement; M3 with a short prolongation of the second prism, and no anterior prolongation in p4 (Kraglievich, 1930; Quintana, 1997). In Brazil there are four living species: *Cavia aperea* Erxleben, *C. fulgida* Wagler, *C. magna* Ximenez and *C. intermedia* Cherem, Olimpio & Ximenez (Cherem *et al.*, 1999). The identification of species of this genus through fragmentary remains is difficult, especially through incomplete mandibles. Cherem (1999) described interspecific differences only in the angular process; but this process is not preserved in

specimens of our samples. Thus, in this paper, only undamaged upper teeth could be identified at species level. The remainder of specimens are listed here as *Cavia* sp.

Cavia aperea Erxleben, 1777
(Figure 2A, Table 1)

Material. UNISC 1508-3; isolated left DP4; A/6; 04. UNISC 1690-1; fragment of left maxilla with DP4-M2; C/6; 03. MARSUL 701-56; isolated left M3; F/16; 05. MARSUL 705-51; fragment of left maxilla with M1; F/16; 09.

Comments. These specimens present an external secondary sulcus deeper than in *C. magna*, and in *C. intermedia*, but not as deep as in *C. fulgida*, a rectangular shape of the labial end of hypoflexus, the first prism more antero-posteriorly compressed than in *C. fulgida*, in *C. magna*, and in *C. intermedia*, and a masseteric tuberosity more antero-posteriorly elongated than in *C. magna*.

This taxon was previously recorded for the Quaternary of Minas Gerais (Lund, 1839b; 1840a,b; Winge, 1888).

Living *Cavia aperea* is found in Brazil, Paraguay, Uruguay and northeastern Argentina (Ximenez, 1980), in environments with soils covered by herbaceous vegetation, but also in environments deeply altered by humans (Silva, 1984).

Cavia magna Ximenez, 1980
(Figure 2B, Table 1)

Material. MARSUL 514-50; fragment of right maxilla with DP4-M3; D/13; 01. MARSUL 515-53; fragment of right maxilla with DP4-M1; D/13; 02. MARSUL 521-51; fragment of left maxilla with DP4-M1; D/13; 08. MARSUL 659-5; fragment of left maxilla with DP4-M3; E/12; 04. MARSUL 664-39; palatal fragment with left M1-3 and right DP4-M2; E/12; 09. MARSUL 702-52; fragment of left maxilla with DP4-M3; F/16; 06. MARSUL 704-4; fragment of left maxilla with DP4-M2; F/16; 08.

Comments. These specimens present the first prisms of the

upper molars more slightly compressed antero-posteriorly than in *C. aperea* and in *C. fulgida*, but more compressed than in *C. intermedia*, the external secondary sulcus shallower than in *C. fulgida* and *C. aperea*, but deeper than in *C. intermedia*, a rounded shape of the labial end of the hypoflexus, and a circular masseteric tuberosity (Ximenez, 1980; Cherem, 1999).

This species is in Sangão site. It was mentioned by Queiroz (2004) also for the Garivaldino site; however, we were unable to review the material studied by him and we can not identify this species in this site.

The species is living today throughout Uruguay and in the states of Rio Grande do Sul and Santa Catarina (Ximenez, 1980). It is adapted to a semi-aquatic life, inhabiting preferentially the areas of vegetation behind the dunes in restinga habitats, but can also lives in estuaries and next to lagoons (Ximenez, 1980).

Table 1. Occurrence of the taxa in Sangão and Garivaldino sites.

Site	Level	Age (ybp)	<i>Cavia aperea</i>	<i>Cavia magna</i>	<i>Ctenomys</i> sp.	<i>M. coypus</i>	<i>Phyllomys</i> sp.	<i>E. mordax</i>	<i>C. riograndensis</i>	<i>D. fossor</i>
Sangão	01			X	X	X	X			X
	02			X			X		X	X
	03				X					X
	04	3,730		X	X		X			X
	05	3,970	X		X		X			X
	06	4,160		X	X		X			X
	07						X			X
	08	4,710		X	X	X	X			X
	09		X	X			X		X	
	10	7,390					X			X
	11				X		X			X
	12								X	
	13	8,800								
Garivaldino	01									X
	02						X			X
	03		X				X	X	X	X
	04		X				X	X	X	X
	05						X	X	X	X
	06	7,250					X	X	X	X
	07							X	X	X
	08						X	X	X	X
	09							X	X	X
	10							X	X	X
	11						X	X	X	X
	12						X	X	X	X
	13							X	X	X
	14	8,020							X	X
	15							X	X	X
	16							X	X	X
	17							X	X	X
	18	8,290						X	X	X
	19							X	X	X
	20								X	X
	21	9,430						X		
	22									
	23

Figure 2. Ventral view of fragment of left maxilla with DP4-M2 of: **A**, *Cavia aperea*, UNISC 1690-1; **B**, *Cavia magna*, MARSUL 704-4. Scale bars = 1 mm.

Family CTENOMYIDAE Lesson, 1842
Ctenomys Blainville, 1826

Material. MARSUL 660-50; edentulous left maxilla; E/12; 05. MARSUL 661-52; rostrum without teeth; E/12; 06. MARSUL 673-52; fragment of right maxilla with DP4; E/13; 05. MARSUL 676-47; fragment of edentulous right mandible; E/13; 08. MARSUL 682-35; isolated right lower molar; F/8; 01. MARSUL 684-13; edentulous right mandible; F/8; 03. MARSUL 685-25; isolated lower molars; F/8; 04. MARSUL 686-35; isolated upper molars; F/8; 05. MARSUL 687-24; right mandible with dp4-m2; F/8; 06. MARSUL 689-25; isolated right lower molar; F/8; 08. MARSUL 701-53; palatal edentulous fragment; F/16; 05. MARSUL 707-4; fragment of edentulous right mandible; F/16; 11.

Comments. The genus *Ctenomys* has nearly 85 described species (Woods & Kilpatrick, 2005) in southern South America, from Bolivia, south of Peru, down to Tierra del Fuego (Mares & Ojeda, 1982; Lessa & Cook, 1998; Freitas, 2006). In Rio Grande do Sul, four species are currently recognized: *Ctenomys torquatus* Lichtenstein, which occurs in the southern state portion, in open sandy fields; *C. flamarioni* Travi in the first line of dunes of the Coastal Plain; *C. minutus* Nehring, also at the Coastal Plain but more inland (from Santa Catarina State to São Jose do Norte, Rio Grande do Sul); finally, *C. lami* Freitas in the region of Coxilha das Lombas, extending from Porto Alegre to Lagoa dos Barros (Freitas, 2006; Gonçalves, 2007).

The alpha systematics of *Ctenomys* species is in flux state because of the difficulties for recognizing taxonomical hierarchy in its variability (see e.g., Reig *et al.*, 1990). The fragmentary preservation of the material precludes specific recognition. However, the available remains are enough for reliable generic assignation.

The genus *Ctenomys* is adapted to subterranean life, inhabiting galleries, which they excavate, with controlled environmental conditions (e.g., Busch *et al.*, 2000). In Rio Grande do Sul it inhabits mostly sandy open fields and/or dunes (Freitas, 1995).

The genus is first recorded in the Pliocene of northwestern Argentina (Verzi, 2008). For the Quaternary of Brazil, *Ctenomys* was listed for zooarchaeological localities, including Garivaldino site and for Santa Vitoria do Palmar Municipality, in the Coastal Plain (Mentz-Ribeiro *et al.*, 1989; Buchmann, 2002). However, after the revision of the material (PH, pers. obs.), this genus could not be confirmed for such localities. Therefore, *Ctenomys* is here reported only for the Sangão site.

Family ECHIMYIDAE Gray, 1825
 Subfamily ECHIMYINAE Gray, 1825

Phyllomys Lund, 1839

Phyllomys sp.

(Figure 3, Table 1)

Material. UNISC 1508-2; fragment of right mandible with m1?; A/6; 04. UNISC 1515-2; fragment of left mandible with m1?; A/6; 11. UNISC 1516-2; fragment of right maxilla with DP4; A/6; 12. UNISC 1516-3; fragment of left maxilla with DP4-M1; A/6; 12. UNISC 1689-2; fragment of right maxilla with DP4-M2; C/6; 02. UNISC 1689-3; fragment of left maxilla with M1-2; C/6; 02. UNISC 1689-

4; fragment of left maxilla with M1; C/6; 02. UNISC 1689-7; fragment of right mandible with dp4-m2; C/6; 02. UNISC 1689-8; fragment of left mandible with dp4-m1; C/6; 02. UNISC 1690-2; fragment of right maxilla with DP4; C/6; 03. UNISC 1690-3; fragment of right maxilla with DP4; C/6; 03. UNISC 1690-8; fragment of left mandible with dp4; C/6; 03. UNISC 1690-9; fragment of right mandible with dp4-m2; C/6; 03. UNISC 1690-10; fragment of left mandible with dp4-m2; C/6; 03. UNISC 1690-12; fragment of right mandible with dp4-m1; C/6; 03. UNISC 1691-7; fragment of right maxilla with DP4-M1; C/6; 04. UNISC 1692-2; fragment of right mandible with m1-2; C/6; 05. UNISC 1693-3; fragment of left mandible with m1; C/6; 06. UNISC 1752-11; fragment of left mandible with dp4-m2; D/6; 02. UNISC 1752-12; fragment of left mandible with dp4; D/6; 02. UNISC 1753-24; fragment of left maxilla with DP4-M1; D/6; 03. UNISC 1754-4; fragment of left maxilla with DP4; D/6; 04. UNISC 1754-6; fragment of right mandible with dp4-m1; D/6; 04. UNISC 1754-7; fragment of left mandible with dp4-m1; D/6; 04. UNISC 1754-8; fragment of right mandible with m1; D/6; 04. UNISC 1754-9; fragment of left mandible with dp4; D/6; 04. UNISC 1754-14; fragment of left mandible with dp4; D/6; 04. UNISC 1754-15; fragment of right mandible with dp4; D/6; 04. UNISC 1755-14; fragment of right maxilla with DP4-M1; D/6; 05. UNISC 1755-15; fragment of right maxilla with DP4; D/6; 05. UNISC 1755-18; fragment of left mandible with dp4; D/6; 05. UNISC 1755-20; fragment of right mandible with dp4-m3; D/6; 05. UNISC 1755-22; fragment of left mandible with dp4-m3; D/6; 05. UNISC 1756-10; palatal fragment with both DP4-M3; D/6; 06. UNISC 1756-12; fragment of right maxilla with DP4-M1; D/6; 06. UNISC 1756-13; fragment of right maxilla with DP4-M1; D/6; 06. UNISC 1756-14; fragment of left maxilla with broken DP4; D/6; 06. UNISC 1756-17; fragment of left mandible with m1; D/6; 06. UNISC 1756-22; fragment of right mandible with dp4-m2; D/6; 06. UNISC 1758-11; fragment of left mandible with dp4-m1; D/6; 08. UNISC 1758-12; fragment of left mandible with m1; D/6; 08. MARSUL 514-51; fragment of right mandible with dp4-m1; D/13; 01. MARSUL 515-52; fragment of right maxilla with DP4-M2; D/13; 02. MARSUL 519-51; fragment of left mandible with m1; D/13; 06. MARSUL 519-52; fragment of right mandible with dp4-m2; D/13; 06. MARSUL 520-50; fragment of left mandible with dp4-m1; D/13; 07. MARSUL 522-50; fragment of right maxilla with DP4-M2; D/13; 09. MARSUL 656-50; fragment of right mandible with dp4; E/12; 01. MARSUL 657-51; fragment of right maxilla with DP4-M2; E/12; 02. MARSUL 657-52; fragment of right mandible with dp4; E/12; 02. MARSUL 659-50; fragment of right maxilla with DP4-M1; E/12; 04. MARSUL 661-50; fragment of right mandible with m1-2; E/12; 06. MARSUL 661-51; palatal fragment with right DP4 and left DP4-M2; E/12; 06. MARSUL 662-50; fragment of left mandible with dp4-m1; E/12; 07. MARSUL 663-51; fragment of left maxilla with DP4-M1; E/12; 08. MARSUL 666-50; fragment of right mandible with m1-2; E/12; 11. MARSUL 673-51; fragment of left mandible with m1; E/13; 05. MARSUL 674-50; fragment of right mandible with dp4; E/13; 06. MARSUL 674-51; palatal fragment with right M2 and left M1-2; E/13; 06. MARSUL 678-3; fragment of right mandible with dp4-m2; E/13; 10. MARSUL 682-35; fragment of left mandible with dp4-m1; F/8; 01. MARSUL 682-36; fragment of left mandible with m1; F/8; 01. MARSUL 682-37; fragment of right mandible with dp4-m1; F/8; 01. MARSUL 682-39; palatal fragment with right M1-3 and left M2-3; F/8; 01. MARSUL 683-15; fragment of right mandible with m1; F/8; 02. MARSUL 686-33; fragment of right maxilla with DP4-M1; F/8; 05. MARSUL 688-29; fragment of left mandible with dp4-m1; F/8; 07. MARSUL 688-30; fragment of left mandible with

Figure 3. *Phyllomys* sp. **A**, UNISC 1756-10, palatal fragment with both DP4-M3 in ventral view; **B**, MARSUL 682-39, palatal fragment with right M1-3 and left M2-3 in ventral view; **C**, MARSUL 697-50, fragment of right maxilla with M1-2 in ventral view; **D**, MARSUL 703-54, fragment of right maxilla with DP4-M3 in ventral view; **E**, MARSUL 706-50, fragment of left mandible with dp4-m2 in lateral view; **F-G**, UNISC 1755-22, fragment of left mandible with dp4-m3 in lateral (**F**) and occlusal (**G**) views; **H**, UNISC 1690-10, fragment of left mandible with dp4-m2 in occlusal view. Scale bars = 1 mm.

m1-2; F/8; 07. MARSUL 690-14; fragment of right maxilla with M1; F/8; 09. MARSUL 690-15; fragment of left mandible with dp4-m1; F/8; 09. MARSUL 697-50; fragment of right maxilla with M1-2; F/16; 01. MARSUL 697-51; fragment of right mandible with dp4; F/16; 01. MARSUL 698-50; fragment of right mandible with dp4-m3; F/16; 02. MARSUL 698-52; fragment of left mandible with dp4-m1; F/16; 02. MARSUL 702-51; fragment of left mandible with dp4; F/16; 06. MARSUL 703-50; fragment of right mandible with dp4-m1; F/16; 07. MARSUL 703-54; fragment of right maxilla with DP4-M3; F/16; 07. MARSUL 704-50; fragment of left maxilla with DP4-M2; F/16; 08. MARSUL 706-50; fragment of left mandible with dp4-m2; F/16; 10. MARSUL 706-51; fragment of left mandible with m1-2; F/16; 10. MARSUL 706-52; fragment of right mandible with m1?; F/16; 10. MARSUL 707-52; fragment of left mandible with m1?; F/16; 11.

Comments. *Phyllomys* is one of the most speciose genera of the Echimyidae. Currently the following species have been recognized: *P. brasiliensis* Lund, *P. fossilis* (Lund), *P. blainvilli* (Jourdan), *P. nigrispinus* (Wagner), *P. unicolor*

(Wagner), *P. dasythrix* Hensel, *P. thomasi* (Ihering), *P. medius* (Thomas), *P. lamarum* (Thomas), *P. kerri* (Moojen), *P. pattoni* Emmons, Leite, Kock & Costa, *P. lundi* Leite and *P. mantiqueirensis* Leite (Emmons *et al.*, 2002; Leite, 2003).

The studied material is fragmentary but well preserved, with representation of juvenile and adult individuals. This material was assigned to *Phyllomys* essentially according to the molar morphology. Although *Diplomys* has a similar dental morphology, this genus has parallel and independent lophids whereas in *Phyllomys* a connection between lophids results in a sigmoid occlusal figure (Leite, 2003; Emmons, 2005).

Emmons *et al.* (2002) and Leite (2003) proposed some distinctive features among the species, but these characters proved not to be useful in our sample. Therefore, even though the material of *Phyllomys* is abundant in the studied sample (more than eighty fragments), it was not possible to recognize species. However, it was possible to restrict the universe of probable species to nine of them: *P. brasiliensis*, *P. blainvilli*,

Figure 4. *Euryzygomatomys*. **A-D**, *E. mordax*. **A**, UNISC 1761-8, palatal fragment with right DP4, and M2 and left M1 in ventral view; **B-D**, UNISC 1769-17, palatal fragment with right M1-2 and left M2 in ventral (**B**) and anterolateral (**C**) views; **D**, right M1-2 in occlusal view; **E-G**, *E. spinosus*; **E**, MN 4029, right DP4-M3 in occlusal view; **F**, MCN-M 2364, anterior portion of the skull in ventral view; **G**, MCN-M 2364, skull in anterolateral view; **H-I**, *E. mordax*, UNISC 1768-4, fragment of left rostrum with DP4-M2 in ventral (**H**) and lateral (**I**) views. Scale bars = 1 mm.

P. nigrispinus, *P. dasythrix*, *P. medius*, *P. lamarum*, *P. kerri*, *P. pattoni* and *P. mantiqueirensis*. *P. fossilis* might be recognized through material not comparable with that of our sample, but Emmons *et al.* (2002) considered it as *nomen dubium* and possible synonym of *P. brasiliensis*. *P. unicolor* and *P. thomasi* are two large-sized species, with the length of DP4-M3 greater (> 13 mm) than that of our sample ($\bar{X} = 11.27$ mm; $SD = 0.05$ mm). *P. lundi* shows M3 with only three laminae, while specimens of our sample have four.

Today *Phyllomys* includes arboreal species endemic to the Atlantic Forest, occurring from the State of Ceará to Rio Grande do Sul, of which only *P. dasythrix* and *P. medius* occur in the last one (Leite, 2003). The only fossil records for *Phyllomys* were from the Quaternary of the Minas Gerais State (Lund, 1839a,b; 1840a,b; Souza-Cunha & Guimarães, 1978), and now for Rio Grande do Sul State.

Subfamily EUMYSOPINAE Rusconi, 1935

Euryzygomatomys Goeldi, 1901

Euryzygomatomys mordax (Winge, 1888)

(Figures 4A-D, H-I, 5A-F; Tables 1,2)

Mesomys mordax Winge, 1888:72, pl.8, fig. 7.

Euryzygomatomys mordax (Winge): Paula-Couto, 1946:5.

Type-material. Winge (1888) described this species based on two skulls, skull 1 and 2, belonging to ZMUC (with no catalog numbers), and sketched the most complete one, skull 1 (Winge, 1888:pl.8, fig. 7).

Material. UNISC 1690-5; fragment of right mandible with m1; C/6; 03. UNISC 1691-4; fragment of right mandible with dp4-m2; C/6; 04. UNISC 1693-1; fragment of left mandible with m2; C/6; 06. UNISC 1695-3; fragment of right mandible with m2; C/6; 08. UNISC 1697-1; fragment of right mandible with dp4-m2; C/6; 10. UNISC 1697-5; fragment of left mandible with m1-2; C/6; 10. UNISC

Figure 5. *Euryzygomatomys*. **A-F**, *E. mordax*. **A**, UNISC 1759-3, fragment of right mandible with m1-2 in occlusal view; **B**, UNISC 1703-2, fragment of left mandible with dp4-m3 in occlusal view; **C-D**, UNISC 1755-21, fragment of left mandible with m1-2 in occlusal (**C**) and lateral (**D**) views; **E-F**, UNISC 1691-4, fragment of right mandible with i and dp4-m2 (**E**) and detail of dp4-m2 (**F**) both in occlusal view; **G-H**, *E. spinosus*, MCN-M 2364, left mandible, (**G**) lateral view, **H**, dp4-m3 in occlusal view. Scale bars = 1 mm.

1697-7; fragment of left maxilla with M1-2; C/6; 10. UNISC 1698-9; fragment of right mandible with m1-3; C/6; 11. UNISC 1703-2; fragment of left mandible with dp4-m3; C/6; 16. UNISC 1703-5; fragment of left maxilla with M1-3; C/6; 16. UNISC 1704-3; fragment of right mandible with m1-2; C/6; 17. UNISC 1704-7; fragment of left mandible with m1-3; C/6; 17. UNISC 1754-12; fragment of left mandible with dp4-m2; D/6; 04. UNISC 1755-21; fragment of left mandible with m1-2; D/6; 05. UNISC 1756-15; fragment of right mandible with m1; D/6; 06. UNISC 1756-19; fragment of right mandible with m1-2; D/6; 06. UNISC 1757-7; fragment of left maxilla with broken M1; D/6; 07. UNISC 1759-3; fragment of right mandible with m1-2; D/6; 09. UNISC 1761-8; palatal fragment with right DP4, and M2 and left M1; D/6; 11. UNISC 1761-18; fragment of left mandible with m1-2; D/6; 11. UNISC 1762-4; fragment of left mandible with m1-3; D/6; 12. UNISC 1763-6; fragment of left maxilla with M1-2; D/6; 13. UNISC 1763-11; fragment of left maxilla with M2; D/6; 13. UNISC 1765-6; fragment of left maxilla with M1; D/6; 15. UNISC 1766-4; fragment of right maxilla with M1-2; D/6; 16. UNISC 1766-8; fragment of left mandible with m2-3; D/6; 16. UNISC 1767-3; fragment of right maxilla with DP4-M2; D/6; 17. UNISC 1768-3; fragment of left maxilla with DP4 and M2; D/6; 18. UNISC 1768-4; fragment of left rostrum with DP4-M2; D/6; 18. UNISC 1768-6; fragment of right maxilla with DP4-M1; D/6; 18. UNISC 1769-17; palatal fragment with right M1-2 and left M2; D/6; 19. UNISC 1769-20; fragment of left maxilla with DP4-M1; D/6; 19.

Locality and stratigraphic occurrence. The original material of this extinct species was collected in Lapa da Escrivania Nr. 5, Lagoa Santa, Minas Gerais (Late Pleistocene/Holocene). The new specimens come from Garivaldino site (Holocene).

Revised diagnosis. Fossa for the temporal muscle more developed than in *Euryzygomatomys spinosus* (G. Fischer);

upper incisors stronger and more procumbent than in *E. spinosus*; protuberance formed by the bottom of the alveolar sheath of the upper incisor lateral to DP4 (see Winge, 1888: pl.8, fig.7); lateral flange of the canal for infraorbital nerve absent or poorly developed, and posterior portion of incisive foramen narrower than in *E. spinosus*.

Description. *Euryzygomatomys mordax* is the largest Eumysopinae here studied (Table 2), but it is smaller than the living *Euryzygomatomys spinosus*. The premaxilla-maxilla suture is similar to that of *E. spinosus*. The posterior portion of the incisive foramen is narrower than in *E. spinosus*; in spite of variation of this character in the latter, it is never as narrow as in *E. mordax*. The masseteric tuberosity is well developed, from it projecting a well-defined ridge similar to that in *E. spinosus*, and never so well-defined as in *Clyomys*. In some individuals, the masseteric tuberosity is more anterior to DP4 when compared to *E. spinosus*. The base of the alveolar sheath of the upper incisor forms a marked prominence lateral to the DP4, more posterior than in *E. spinosus* (Winge, 1888). The lateral flange of the canal for infraorbital nerve is absent, or it is scarcely developed (UNISC 1768-6).

The original material of *E. mordax* from Lagoa Santa does not include mandibles (Winge, 1888); but taking into account the cranio-mandibular morphological correlation in the living *E. spinosus*, we were able to recognize the mandibles of *E. mordax* in our samples. The mandibles of *E. mordax* and *E. spinosus* are very similar. The masseteric fossa of some specimens of *E. mordax* is slightly shallower than in *E.*

spinosus. The protuberance formed by the bottom of the lower incisor is less defined than in *E. spinosus*, although this is a variable feature. The mandibular foramen is proximal to the condyle.

The teeth have a quadrangular occlusal outline, especially those with more wear. DP4-M3 are trilophodont. They show reentrant flexi that form elongate fossettes when worn. The deepest part of the hypoflexus turns forward and, in the majority of specimens, it ends anteriorly to the anterior flexus/fossette (para- + mesoflexus/fossette) while in *E. spinosus* it is less extended forward, ending at the level of this fossette. The metafossette is more persistent than that in *Clyomys*; is transverse, or oblique and labially divergent from the anterior fossette. In *E. spinosus* the metafossette is generally inclined in the opposite way, being labially convergent with the anterior fossette. The molars show a mure connecting protocone and hypocone, except for the juvenile UNISC 1697-7.

The lower teeth are similar to those of *E. spinosus*, having a quadrangular occlusal outline, except dp4 which is more rectangular. The hypoflexid is deep and turns posteriorly. The lingual flexids are deep reentrants, forming elongate fossettids. The mesofossettids are turned anteriorly, while the metafossettids are transverse.

Comments. This taxon was described by Winge (1888) as *Mesomys mordax*. Paula-Couto (1946) assigned the species tentatively to the genus *Euryzygomatomys*. He did not justify the assignment. This species can be attributed to *Euryzygomatomys* by the very deep reentrant flexi/flexids, forming elongate fossettes/fossettids and by the anterior fossette and metafossette subequal in size. These two features are different in *Clyomys* (Thomas, 1916; Verzi *et al.*, 1995). Winge (1888) pointed out that *E. mordax* presents more conspicuous fossorial adaptation than *E. spinosus*, such as more procumbent upper incisors and more extended fossae for temporal muscles (see Winge, 1888: pl.7, fig.7).

The living species *E. spinosus* occurs currently in south and southeast Brazil, northeast Argentina and Paraguay (Woods & Kilpatrick, 2005). Until now, *E. mordax* was known only through the materials described by Winge (1888) for the Quaternary of Lagoa Santa. The material here studied is the first record of this species for the Holocene of Rio Grande do Sul, where it was found only in the Garivaldino site.

Dicolpomys Winge, 1888

Dicolpomys fossor Winge, 1888

(Figure 6; Tables 1, 2)

Dicolpomys fossor Winge, 1888:99, pl.8, fig.10.

Type-material. Winge (1888) relied on five mandibles (mandibles 1, 2, 3, 4 and 5) belonging to ZMUC (with no catalog numbers), and sketched (pl.8, fig.10) two of them, mandibles 2 and 3, and the complete molariform series of the mandible 1.

Material. UNISC 1508-1; fragment of left maxilla with M1; A/6; 04. UNISC 1515-3; fragment of right mandible with m2; A/6; 11. UNISC 1562-1; fragment of right mandible with m1-2; B/5; 16.

UNISC 1562-2; fragment of left mandible with m1-2; B/5; 16. UNISC 1688-1; fragment of right mandible with m1-2; C/6; 01. UNISC 1689-5; fragment of right mandible with dp4-m2; C/6; 02. UNISC 1689-6; fragment of left mandible with m1; C/6; 02. UNISC 1690-7; fragment of left mandible with dp4-m3; C/6; 03. UNISC 1690-11; fragment of right mandible with dp4-m1; C/6; 03. UNISC 1690-13; fragment of left mandible with m1-2; C/6; 03. UNISC 1691-5; fragment of right mandible with m1; C/6; 04. UNISC 1691-6; fragment of right mandible with dp4-m3; C/6; 04. UNISC 1695-2; fragment of left mandible with m1-3; C/6; 08. UNISC 1696-2; fragment of right mandible with dp4-m3; C/6; 09. UNISC 1696-3; fragment of left mandible with m1; C/6; 09. UNISC 1696-4; fragment of right mandible with m1; C/6; 09. UNISC 1696-5; fragment of

Table 2. Measurements (in mm) of *Euryzygomatomys mordax*, *Dicolpomys fossor* and *Clyomys riograndensis* sp.nov.

	<i>E. mordax</i>		<i>D. fossor</i>		<i>C. riograndensis</i>		
	($\bar{X} \pm SD$)	n	($\bar{X} \pm SD$)	n	UNISC 1768-7	($\bar{X} \pm SD$)	n
UDL	9.55 ± 0.15	02	9.4 ± 0.2	02	9.0	-	-
IFL	-	-	4.4 ± 0	01	4.0	-	-
IFW	-	-	1.8 ± 0	01	1.8	-	-
DP4-M3	-	-	7.75 ± 0.11	04	7.6	8.21 ± 0.22	08
I1 AP	-	-	-	-	2.1	-	-
I1 W	-	-	-	-	1.8	-	-
DP4 AP	1.96 ± 0.10	07	1.91 ± 0.20	09	2.0	2.12 ± 0.14	26
DP4 AW	2.13 ± 0.12	07	2.18 ± 0.18	09	2.0*	2.07 ± 0.10	26
DP4 PW	1.97 ± 0.05	07	1.88 ± 0.17	09	2.0*	1.92 ± 0.12	27
M1 AP	2.13 ± 0.26	10	1.95 ± 0.20	19	2.1	2.22 ± 0.15	33
M1 AW	2.55 ± 0.17	10	2.22 ± 0.20	19	2.1	2.13 ± 0.17	33
M1 PW	2.17 ± 0.23	10	1.95 ± 0.21	19	2.0	1.85 ± 0.24	33
M2 AP	2.26 ± 0.15	12	2.13 ± 0.18	06	2.2	2.29 ± 0.20	10
M2 AW	2.39 ± 0.25	12	2.32 ± 0.07	06	2.0	2.10 ± 0.16	10
M2 PW	2.03 ± 0.25	12	2.02 ± 0.18	06	1.8	1.69 ± 0.16	10
M3 AP	1.9 ± 0	01	-	-	1.4	1.5 ± 0.1	02
M3 AW	1.9 ± 0	01	-	-	1.4	1.26 ± 0.14	02
M3 PW	1.12 ± 0	01	-	-	0.8	0.83 ± 0.18	02
LDL	5.19 ± 0.53	11	4.31 ± 0.37	27		4.54 ± 0.45	20
MD	7.16 ± 0.35	8	5.10 ± 0.44	31		6.14 ± 0.40	16
Dp4-m3	10.71 ± 0.84	10	8.47 ± 0.49	21		9.19 ± 0.46	14
i1 AP	2.3 ± 0	01	1.71 ± 0.16	07		1.9 ± 0	01
i1 W	2.0 ± 0.1	02	1.78 ± 0.19	06		1.9 ± 0	01
dp4 AP	2.53 ± 0.28	03	2.39 ± 0.16	52		2.41 ± 0.27	16
dp4 AW	1.9 ± 0	02	1.54 ± 0.19	52		1.77 ± 0.16	16
dp4 PW	2.1 ± 0.2	02	1.88 ± 0.13	52		2.13 ± 0.08	17
m1 AP	2.36 ± 0.22	15	2.12 ± 0.15	100		2.19 ± 0.13	30
m1 AW	2.41 ± 0.29	14	2.05 ± 0.19	100		2.25 ± 0.23	30
m1 PW	2.41 ± 0.30	15	2.04 ± 0.17	100		2.26 ± 0.17	30
m2 AP	2.42 ± 0.14	16	2.18 ± 0.19	70		2.24 ± 0.13	16
m2 AW	2.33 ± 0.28	16	2.07 ± 0.33	70		2.26 ± 0.22	16
m2 PW	2.48 ± 0.18	16	1.91 ± 0.33	70		2.18 ± 0.27	16
m3 AP	1.91 ± 0.25	04	1.7 ± 0.2	15		1.76 ± 0.31	08
m3 AW	2.11 ± 0.12	04	1.62 ± 0.38	15		1.77 ± 0.20	07
m3 PW	1.7 ± 0.14	04	0.9 ± 0.40	15		1.3 ± 0.2	08

Figure 6. *Dicolpomys fossor*. **A-B**, MARSUL 699-51, fragment of rostrum with both DP4-M1, **A**, ventral view, **B**, left DP4-M1 in detail; **C-D**, MARSUL 698-53, fragment of right rostrum with DP4-M1 in occlusal (**C**) and lateral (**D**) views; **E**, UNISC 1763-14, fragment of right maxilla with DP4-M1 in occlusal view; **F-H**, UNISC 1699-3, fragment of left mandible with dp4-m3 in occlusal (**F**) and lateral (**G**) views; **H**, dp4-m3 in detail; **I**, UNISC 1702-7, fragment of right mandible with m2-3 in occlusal view; **J**, UNISC 1765-18, fragment of left mandible with m1-2 in occlusal view. Scale bars = 1 mm.

right mandible with m2; C/6; 09. UNISC 1697-2; fragment of right mandible with m1; C/6; 10. UNISC 1697-3; fragment of left mandible with m1; C/6; 10. UNISC 1697-4; fragment of right mandible with m1-3; C/6; 10. UNISC 1697-6; fragment of left mandible with m1-2; C/6; 10. UNISC 1698-2; fragment of left mandible with m1-2; C/6; 11. UNISC 1698-3; fragment of right mandible with m1-2; C/6; 11. UNISC 1698-4; fragment of left mandible with m1-2; C/6; 11. UNISC 1698-5; fragment of left mandible with m2-3; C/6; 11. UNISC 1698-6; fragment of left mandible with m1; C/6; 11. UNISC 1698-11; fragment of left mandible with m2; C/6; 11. UNISC 1699-2; fragment of left mandible with m2; C/6; 12. UNISC 1699-3; fragment of left mandible with dp4-m3; C/6; 12. UNISC 1699-4; fragment of right mandible with dp4-m2; C/6; 12. UNISC 1700-3; fragment of left mandible with m1; C/6; 13. UNISC 1700-4; fragment of left mandible with dp4-m1; C/6; 13. UNISC 1701-4; fragment of right maxilla with M1-2; C/6; 14. UNISC 1701-5; fragment of right mandible with m1; C/6; 14. UNISC 1702-3; fragment of left mandible with dp4-m1; C/6; 15. UNISC 1702-4; fragment of right mandible with m1; C/6; 15. UNISC 1702-7; fragment of right mandible with m2-3; C/6; 15. UNISC 1702-8; fragment of right mandible with m2;

C/6; 15. UNISC 1703-6; fragment of right mandible with m1-3; C/6; 16. UNISC 1703-9; fragment of left mandible with m1-2; C/6; 16. UNISC 1703-10; fragment of left mandible with m1-2; C/6; 16. UNISC 1703-12; fragment of left mandible with dp4-m2; C/6; 16. UNISC 1704-4; fragment of right mandible with dp4-m2; C/6; 17. UNISC 1704-5; fragment of right mandible with dp4-m1; C/6; 17. UNISC 1704-9; fragment of right mandible with dp4-m2; C/6; 17. UNISC 1706-3; fragment of right mandible with m1; C/6; 19. UNISC 1706-4; fragment of left mandible with m1-3; C/6; 19. UNISC 1706-6; fragment of left mandible with m1-2; C/6; 19. UNISC 1706-8; fragment of right mandible with m1; C/6; 19. UNISC 1707-1; fragment of left maxilla with DP4-M2; C/6; 20. UNISC 1754-10; fragment of right mandible with m2?; D/6; 04. UNISC 1754-11; fragment of left mandible with dp4-m1; D/6; 04. UNISC 1755-16; fragment of right mandible with m1-2; D/6; 05. UNISC 1755-17; fragment of left mandible with dp4 and m2; D/6; 05. UNISC 1756-16; fragment of right mandible with dp4-m3; D/6; 06. UNISC 1756-18; fragment of right mandible with m1; D/6; 06. UNISC 1756-20; fragment of right mandible with dp4-m2; D/6; 06. UNISC 1756-23; fragment of right mandible with m1; D/6; 06. UNISC 1757-5;

fragment of right maxilla with M2; D/6; 07. UNISC 1757-6; fragment of left maxilla with M1-2; D/6; 07. UNISC 1757-10; fragment of right mandible with m3?; D/6; 07. UNISC 1757-11; fragment of left mandible with dp4-m1; D/6; 07. UNISC 1757-12; fragment of right mandible with m2?; D/6; 07. UNISC 1757-13; fragment of right mandible with dp4-m1; D/6; 07. UNISC 1757-14; fragment of left mandible with m1; D/6; 07. UNISC 1758-7; fragment of right mandible with m1?; D/6; 08. UNISC 1758-9; fragment of right mandible with dp4-m1; D/6; 08. UNISC 1758-10; fragment of right mandible with dp4-m1; D/6; 08. UNISC 1759-4; fragment of right mandible with dp4-m1; D/6; 09. UNISC 1759-5; fragment of right mandible with dp4-m1; D/6; 09. UNISC 1759-6; fragment of left mandible with broken m1; D/6; 09. UNISC 1759-8; fragment of right mandible with dp4; D/6; 09. UNISC 1761-12; fragment of right mandible with m1-2; D/6; 11. UNISC 1761-13; fragment of right mandible with dp4-m2; D/6; 11. UNISC 1761-14; fragment of left mandible with dp4-m3; D/6; 11. UNISC 1761-16; fragment of right mandible with m1; D/6; 11. UNISC 1761-20; fragment of left mandible with m2; D/6; 11. UNISC 1762-5; fragment of left mandible with dp4-m2; D/6; 12. UNISC 1762-7; fragment of right mandible with dp4-m2; D/6; 12. UNISC 1762-8; fragment of left mandible with m1; D/6; 12. UNISC 1763-7; fragment of right maxilla with DP4; D/6; 13. UNISC 1763-12; fragment of left maxilla with M1-2; D/6; 13. UNISC 1763-13; fragment of right maxilla with M1-2; D/6; 13. UNISC 1763-14; fragment of right maxilla with DP4-M1; D/6; 13. UNISC 1763-15; fragment of right mandible with dp4 and m2; D/6; 13. UNISC 1763-16; fragment of right mandible with m2; D/6; 13. UNISC 1763-17; fragment of right mandible with m2; D/6; 13. UNISC 1763-20; fragment of left mandible with m1; D/6; 13. UNISC 1763-21; fragment of right mandible with dp4-m2; D/6; 13. UNISC 1763-22; fragment of right mandible with m1-2; D/6; 13. UNISC 1764-1; Fragment of left maxilla with M1; D/6; 14. UNISC 1764-2; fragment of right mandible with dp4-m2; D/6; 14. UNISC 1764-3; fragment of right mandible with m1-2; D/6; 14. UNISC 1764-5; fragment of right mandible with dp4-m2; D/6; 14. UNISC 1764-6; fragment of left mandible with dp4-m1; D/6; 14. UNISC 1764-7; fragment of left mandible with m1; D/6; 14. UNISC 1765-2; fragment of left maxilla with M1; D/6; 15. UNISC 1765-11; fragment of right mandible with m1; D/6; 15. UNISC 1765-12; fragment of right mandible with m1; D/6; 15. UNISC 1765-13; fragment of left mandible with dp4; D/6; 15. UNISC 1765-14; fragment of left mandible with m2-3; D/6; 15. UNISC 1765-17; fragment of left mandible with m1; D/6; 15. UNISC 1765-18; fragment of left mandible with m1-2; D/6; 15. UNISC 1766-3; fragment of right maxilla with M1; D/6; 16. UNISC 1766-5; fragment of left mandible with dp4; D/6; 16. UNISC 1766-7; fragment of left mandible with dp4; D/6; 16. UNISC 1767-6; fragment of right mandible with m1; D/6; 17. UNISC 1767-7; fragment of left mandible with dp4; D/6; 17. UNISC 1767-8; fragment of right mandible with dp4-m2; D/6; 17. UNISC 1768-8; fragment of left mandible with dp4-m2; D/6; 18. UNISC 1768-10; fragment of right mandible m1-2; D/6; 18. UNISC 1768-12; fragment of right mandible with m1-3; D/6; 18. UNISC 1768-14; fragment of right mandible with m2; D/6; 18. UNISC 1768-15; fragment of left mandible with m1; D/6; 18. UNISC 1769-4; fragment of left mandible with m1-2; D/6; 19. UNISC 1769-5; fragment of left mandible with dp4; D/6; 19. UNISC 1769-6; fragment of left mandible with dp4-m1; D/6; 19. UNISC 1769-7; fragment of right mandible with dp4-m2; D/6; 19. UNISC 1769-9; fragment of right mandible with dp4-m3; D/6; 19. UNISC 1769-10; fragment of left mandible with dp4-m1; D/6; 19. UNISC 1769-14; fragment of left mandible with m2; D/6; 19. UNISC 1769-15; fragment of left mandible with dp4-m1; D/6; 19. UNISC 1769-22; fragment of right maxilla with DP4-M1; D/6; 19. UNISC 1770-1; fragment of left mandible with m1-2; D/6; 20. UNISC 1770-3; fragment of right mandible with m1; D/6; 20. UNISC 1770-5;

fragment of left maxilla with M1-2; D/6; 20. UNISC 1770-7; fragment of left mandible with m2; D/6; 20. MARSUL 516-50; fragment of right mandible with m1; D/13; 03. MARSUL 520-52; isolated left DP4; D/13; 07. MARSUL 521-50; fragment of left mandible with m2; D/13; 08. MARSUL 656-1; fragment of left mandible with dp4-m1; E/12; 01. MARSUL 656-51; fragment of right mandible with m1-2; E/12; 01. MARSUL 663-50; fragment of left mandible with m2; E/12; 08. MARSUL 665-50; fragment of left mandible with m1; E/12; 10. MARSUL 669-51; fragment of left mandible with m1; E/13; 01. MARSUL 671-52; fragment of right mandible with m1-2; E/13; 03. MARSUL 671-53; fragment of right mandible with m1; E/13; 03. MARSUL 671-54; fragment of right mandible with dp4-m1; E/13; 03. MARSUL 672-51; fragment of right maxilla with DP4; E/13; 04. MARSUL 678-50; fragment of left mandible with dp4-m1; E/13; 08. MARSUL 687-21; fragment of left mandible with dp4-m1; F/8; 06. MARSUL 687-22; fragment of left mandible with dp4-m1; F/8; 06. MARSUL 689-24; fragment of right mandible with dp4-m1; F/8; 08. MARSUL 698-51; fragment of right mandible with m2; F/16; 02. MARSUL 698-53; fragment of right rostrum with DP4-M1; F/16; 02. MARSUL 699-51; fragment of rostrum with both DP4-M1; F/16; 03. MARSUL 699-52; fragment of left maxilla with DP4-M1; F/16; 03. MARSUL 699-53; fragment of right mandible with m1-2; F/16; 03. MARSUL 701-51; fragment of right mandible with m1-2; F/16; 05. MARSUL 702-50; fragment of right mandible with dp4-m1; F/16; 06. MARSUL 707-51; fragment of right mandible with m2-3; F/16; 11.

Locality and stratigraphic occurrence. The original material of this extinct species was collected in Lapa da Escrivania Nr. 5, Lagoa Santa, Minas Gerais (Late Pleistocene/Holocene). The new specimens come from both the Garivaldino and Sangão sites (Holocene).

Revised diagnosis. Upper diastema more rectilinear and more dorsally inclined than in *Euryzygomatomys* and *Clyomys*; premaxilla-maxilla suture, in ventral view, more anterior to the origin of the zygomatic arch than in *Clyomys* and *Euryzygomatomys*; lateral flange for the infraorbital nerve absent; condyloid and coronoid processes lower than in *Clyomys*; masseteric crest less developed than in *Clyomys* and *Euryzygomatomys*; cheek teeth with figure-eight occlusal surface; metafossette and mesofossettid very ephemeral.

Description. In the preserved rostra, the premaxilla-maxilla suture, in ventral view, is more anterior to the zygomatic arch than in *Euryzygomatomys* and *Clyomys*. The upper diastema is more straight and more dorsally inclined than in *Euryzygomatomys* and *Clyomys*. The premaxilla-maxilla suture divides the incisive foramina in two nearly equal portions; these foramina attenuate posteriorly more than in the new species of *Clyomys* described below, but less than in *E. mordax*. The maxillary fossa is well defined. The masseteric tuberosity is poorly developed. The alveolar sheath of the root of the upper incisor forms a protuberance lateral to the DP4; in certain specimens this protuberance is extended more anteromedially. The lateral flange for the infraorbital nerve is absent.

The mandible of *Dicolpomys* is similar to that of *Clyomys*, but more graceful. The masseteric fossa is deep. The masseteric crest is poorly developed when compared to *Clyomys* and *Euryzygomatomys*. The protuberance formed by the alveolus for the root of the lower incisor is well developed. The mandibular foramen is located proximal to the condyle.

Figure 7. *Clyomys* species. **A-E**, *C. riograndensis* sp. nov., **A-C**, UNISC 1768-7, holotype, fragment of skull with both DP4-M3 in ventral (**A**), anterolateral (**B**), and lateral (**C**) views; **D**, UNISC 1702-11, palatal fragment with both DP4-M2 in occlusal view; **E**, UNISC 1700-6, left DP4-M3 in occlusal view; **F-H**, *C. bishopi*, MN 43074; **F**, anterior portion of the skull in ventral view; **G**, skull in anterolateral view; **H**, left DP4-M3 in occlusal view; **I-K**, *C. laticeps*, **I**, MN 31549, anterior portion of the skull in ventral view; **J**, MN 31547, skull in anterolateral view; **K**, MN 31549, left DP4-M3 in occlusal view. Scale bars = 1 mm.

The cheek teeth have an eight-like occlusal figure, with single persistent lingual and labial flexus/ids that define two lobes (Figure 6). Both lobes of DP4-M3, and m1-3 are generally sub-equal. The hypoflexus is a little more reentrant than in the new species of *Clyomys* described below, but less than in *E. mordax*. The hypoflexus is opposite to the anterior flexus (or fossette), and its labial end is anteriorly oriented, especially in M1-2. Likewise, the anterior flexus is transverse or slightly anteriorly oriented (Figure 6B). The metafossette disappears very early ontogenetically, but a small vestige of this fossette can be observed in the DP4 and M1 of the juvenile UNISC 1763-14 (Figure 6E). The dp4 of juveniles has two

lingual flexids and three lophids, but with increasing wear the anterior flexid closes forming an anterior fossettid. In older specimens, all flexids may become fossettids. The m1 shows a vestige of the mesofossettid in some juveniles (Figure 6J; UNISC 1562-2, 1765-18, MARSUL 671-54, 702-50). The shape of the lobes of m1-2 is variable; can be equal in size (Figure 6F), or the anterior lobe can be smaller and thinner (usually in m1), or even the posterior lobe can be smaller and wider (usually in m2, Figure 6I; Table 2). The m3 is clearly smaller than m1-2, and especially its posterior lobe is very reduced. In some individuals (UNISC 1696-2, 1697-4, 1702-7) the m3 has no distinct lobes (Figure 6I).

Comments. *Dicolpomys fossor* shows a very simplified dental morphology, convergent to that of the Octodontidae, which led Winge (1888) to relate this species to extant members of that family. Later, Ameghino (1889) established the affinities of *Dicolpomys* with the Echimyidae (= Echinomyidae) by the presence of well defined and individualized roots. *Dicolpomys fossor* presents upper and lower molars with three roots like in Eumysopinae (Figure 6A, I; Emmons, 2005). Besides the mesoflexid closes earlier than the metaflexid like in the remaining Echimyidae (Verzi *et al.*, 1994). Vucetich & Verzi (1996) proposed that *Dicolpomys* is related to the Late Miocene echimid *Reigechimys* from central Argentina.

Dicolpomys fossor would have had fossorial habits, as suggested especially by the morphology and deep implantation of the incisors (see Winge, 1888:pl. 8, fig.10; Winge, 1941; Verzi & Olivares, 2006).

This is the first record of *D. fossor* for the Holocene of Rio Grande do Sul State.

Clyomys Thomas, 1916

Clyomys riograndensis sp. nov.

(Figures 7A-E, 8A-C; Tables 1, 2)

Holotype. UNISC 1768-7, skull fragment with both DP4-M3.

Hypodigm. UNISC 1511-1; fragment of right maxilla with M1?; A/6; 07. UNISC 1516-1; fragment of left maxilla with DP4-M1; A/6; 12. UNISC 1690-4; fragment of left maxilla with DP4-M1; C/6; 03. UNISC 1692-3; fragment of right maxilla with DP4-M3; C/6; 05. UNISC 1693-2; fragment of right mandible with dp4-m3; C/6;

06. UNISC 1694-3; fragment of left maxilla with M1; C/6; 07. UNISC 1696-1; fragment of left mandible with m1-3; C/6; 09. UNISC 1697-8; fragment of left maxilla with DP4-M1; C/6; 10. UNISC 1698-10; fragment of right maxilla with DP4-M2; C/6; 11. UNISC 1698-13; fragment of left maxilla with DP4-M1; C/6; 11. UNISC 1699-5; fragment of left mandible with dp4-m1; C/6; 12. UNISC 1699-7; fragment of left maxilla with DP4; C/6; 12. UNISC 1700-1; fragment of right mandible with dp4-m3; C/6; 13. UNISC 1700-2; fragment of left mandible with dp4-m2; C/6; 13. UNISC 1700-6; fragment of left maxilla with DP4-M3; C/6; 13. UNISC 1700-7; fragment of right maxilla with DP4-M2; C/6; 13. UNISC 1701-1; fragment of right mandible with m3; C/6; 14. UNISC 1701-2; fragment of right mandible with dp4-m1; C/6; 14. UNISC 1702-1; fragment of right mandible with dp4-m1; C/6; 15. UNISC 1702-6; fragment of right mandible with m1; C/6; 15. UNISC 1702-10; palatal fragment with left M1-2 and right DP4-M1; C/6; 15. UNISC 1702-11; palatal fragment with both DP4-M2; C/6; 15. UNISC 1703-1; fragment of right mandible with dp4-m1; C/6; 16. UNISC 1703-3; fragment of left mandible with dp4-m2; C/6; 16. UNISC 1703-4; fragment of left mandible with dp4-m2; C/6; 16. UNISC 1703-7; fragment of left mandible with dp4; C/6; 16. UNISC 1704-6; fragment of left mandible with dp4-m1; C/6; 17. UNISC 1704-8; fragment of right mandible with m2; C/6; 17. UNISC 1706-1; fragment of left mandible with dp4-m1; C/6; 17. UNISC 1706-5; fragment of right maxilla with DP4; C/6; 19. UNISC 1717-1; fragment of right maxilla with M1; C/6; 19. UNISC 1729-1; fragment of right mandible with dp4-m2; C/6; 19. UNISC 1756-21; fragment of right mandible with m1; D/6; 06. UNISC 1757-4; fragment of left maxilla with DP4-M1; D/6; 07. UNISC 1757-8; fragment of right maxilla with DP4-M1; D/6; 07. UNISC 1758-3; fragment of right maxilla with M1; D/6; 08. UNISC 1758-6; fragment of right maxilla with

Figure 8. *Clyomys* species. A-C, *C. riograndensis* sp. nov., UNISC 1700-1, fragment of right mandible with dp4-m3 in lateral (A), and medial (B) views; C, right dp4-m3 represented as left in occlusal view; D-F, *C. bishopi*, MN 43071, left mandible in lateral (D) and medial (E) views; F, dp4-m3 in occlusal view; G-I, *C. laticeps*, G-H, MN 31548, left mandible in lateral (G), and medial (H) views; I, MN 31547, left dp4-m3 in occlusal view. Scale bars = 1 mm.

DP4-M2; D/6; 08. UNISC 1758-8; fragment of left mandible with dp4; D/6; 08. UNISC 1759-7; fragment of left mandible with m1-2; D/6; 09. UNISC 1760-2; fragment of right maxilla with M1; D/6; 10. UNISC 1761-6; fragment of left maxilla with M2; D/6; 11. UNISC 1762-1; fragment of right maxilla with DP4; D/6; 12. UNISC 1762-3; fragment of right maxilla with DP4-M1; D/6; 12. UNISC 1763-3; fragment of left maxilla with M1; D/6; 13. UNISC 1763-5; fragment of right maxilla with DP4; D/6; 13. UNISC 1763-8; fragment of left maxilla with DP4; D/6; 13. UNISC 1763-9; fragment of right maxilla with DP4; D/6; 13. UNISC 1763-10; fragment of left maxilla with DP4-M1; D/6; 13. UNISC 1763-18; fragment of left mandible with dp4; D/6; 13. UNISC 1763-23; fragment of right mandible with dp4-m3; D/6; 13. UNISC 1764-4; fragment of right mandible with dp4-m2; D/6; 14. UNISC 1765-3; fragment of left maxilla with M1; D/6; 15. UNISC 1765-6; fragment of left maxilla with M1; D/6; 15. UNISC 1765-7; fragment of right maxilla with M1; D/6; 15. UNISC 1765-8; fragment of right maxilla with DP4-M1; D/6; 15. UNISC 1765-9; fragment of right maxilla with DP4-M1; D/6; 15. UNISC 1765-10; fragment of left mandible with dp4-m3; D/6; 15. UNISC 1765-15; fragment of right mandible with m1; D/6; 15. UNISC 1765-16; fragment of right mandible with dp4-m1; D/6; 15. UNISC 1766-6; fragment of left mandible with m1; D/6; 16. UNISC 1767-1; fragment of left maxilla with M1; D/6; 17. UNISC 1767-2; fragment of left maxilla with M1?; D/6; 17. UNISC 1767-4; fragment of left maxilla with DP4-M1; D/6; 17. UNISC 1767-10; fragment of right mandible with m1-3; D/6; 17. UNISC 1768-1; fragment of right maxilla with M1-2; D/6; 18. UNISC 1768-7 (holotype); fragment of skull with both DP4-M3; D/6; 18. UNISC 1768-9; fragment of right mandible with m1-3; D/6; 18. UNISC 1768-11; fragment of left mandible with m1; D/6; 18. UNISC 1769-2; fragment of left mandible with m1-2; D/6; 19. UNISC 1769-3; fragment of right mandible with dp4-m2; D/6; 19. UNISC 1769-8; fragment of right mandible with dp4-m2; D/6; 19. UNISC 1769-11; fragment of left mandible with m1; D/6; 19. UNISC 1769-16; fragment of right maxilla with DP4-M2; D/6; 19. UNISC 1769-19; fragment of left maxilla with DP4-M1; D/6; 19. UNISC 1770-6; fragment of right maxilla with DP4-M2; D/6; 20. UNISC 1770-8; fragment of right maxilla with M1?; D/6; 20. MARSUL 667-38; fragment of right mandible with dp4-m2; E/12; 12. MARSUL 683-14; fragment of left maxilla with DP4-M1; F/8; 02. MARSUL 705-50; fragment of left mandible with dp4-m1; F/16; 09.

Etymology. *riograndensis* in reference to Rio Grande do Sul State, where it was collected.

Locality and stratigraphic occurrence. The holotype comes from the Garivaldino site. It was collected by P. Mentz-Ribeiro during the Project of the Archaeological Survey in the Valleys of the Taquari and Cai rivers (Mentz-Ribeiro *et al.*, 1989). The species is known from the type locality and the Sangão site (Holocene). For details of the provenance of the rest of material see hypodigm.

Diagnosis. It differs from the two living species, *Clyomys laticeps* (Thomas) and *C. bishopi* Ávila-Pires & Wutke, in: shorter diastema; narrower and more elliptical incisive foramina; premaxilla limiting more than half the incisive foramina length; protuberance of the bottom of the upper incisor lateral to DP4; lesser development of the masseteric tuberosity; absence of the lateral flange for the infraorbital nerve; mandibular foramen more proximal to the condyle; greater reduction of M3; and lesser persistence of the metafossette, especially in M2 and M3.

Description. This is the smallest species of *Clyomys* (see Table 2); although there is a partial overlap of the

measurements of *C. riograndensis* sp.nov. and *C. laticeps* from Brasília and Xavantina (see Ávila-Pires & Wutke, 1981), all specimens of the former are smaller than the largest specimens of the latter. The upper diastema is proportionally a little shorter than in *C. laticeps* ($\chi = 10.47$ mm; SD = 0.26 mm) and *C. bishopi* ($\chi = 11.0$ mm; SD = 0.33 mm). The incisive foramina are narrower and they are more elliptical than in *C. laticeps* and *C. bishopi*. The premaxilla limits more than half of the incisive foramina length. The masseteric tuberosity is less developed than in the other species; it begins more proximal to the DP4 than in *Euryzygomatomys*. Different to the living species of *Clyomys*, the protuberance of the bottom of the upper incisor is not antero-lateral to the DP4 but lateral to this tooth, and in some specimens less prominent. The lateral flange for the infraorbital nerve is absent, different from the extant species of the genus. The mandible is slightly less robust than that in *C. laticeps* and *C. bishopi*. The lower diastema has a step anterior to the dp4 much more marked than in the extant species, similar to that of the fossil specimen MLP 91-IV-25-135 (*Clyomys* sp.) from Argentina (Vucetich *et al.*, 1997); the anterior portion of the diastema is more steep than in MLP 91-IV-25-135. The masseteric fossa is less defined than in the extant species, but the difference is very tenuous and a little variable in the fossil sample. The masseteric crest begins at the level of the anterior portion of the m1, as occurs in the extant species, but more anterior than in MLP 91-IV-25-135. The protuberance formed by the bottom of the alveolus for the lower incisor is displaced in the direction of the condyle. The mandibular foramen is more ventral and posterior than in the living species.

The upper molars have less reentrant flexi than in *Euryzygomatomys*. The hypoflexus is a little deeper than in MLP 91-IV-25-135, at least in M1, and it is less turned anteriorly than in the other species of the genus. The anterior fossette persists longer than the metafossette; the latter is less persistent than in the other species of *Clyomys*, especially in M2 and M3. M3 is proportionally smaller than in the extant species. The lower molars also show less reentrant flexids than in *Euryzygomatomys*. Nevertheless, the flexids are more reentrant than those of the recent *Clyomys*, especially the hypoflexid, although this is a variable feature. The hypoflexid is not so turned posteriorly as in the fossil from Argentina (MLP 91-IV-25-135, 91-IV-25-116), although this character showed some variability in the material studied. The mesoflexid closes a little before the metaflexid. The m1 and m2 are sub-equal in size, not showing the difference seen in MLP 91-IV-25-135, in which m2 is larger than m1. The m3 is more reduced than in MLP 91-IV-25-135.

Comments. Thomas (1909) described the species *Echimys laticeps* (= *Clyomys laticeps*), and reported its differences from *Echimys spinosus* (= *Euryzygomatomys spinosus*) based on recent material from the region of Lagoa Santa, Minas Gerais. In 1916, Thomas established the genus *Clyomys* to encompass the species *C. laticeps* (= *Echimys laticeps*), and he characterized this genus through its large foreclaws, hypertrophied auditive bullae and small molars with posterior transverse cleft [metaflexus] of the last upper molar less

persistent than in *Euryzygomatomys*. Ávila-Pires & Wutke (1981) described *C. bishopi*, based on material from São Paulo, and differentiated it from the type species through external characteristics, mainly the color of the fur. Bezerra (2003) did not identify substantial differences between the two species, and suggested that they represent a single taxon.

The material here studied is referred to *Clyomys* on the basis of molar morphology, with little reentrant flexi/flexids and ephemeral metafossette (Thomas, 1916; Verzi *et al.*, 1995).

Clyomys laticeps currently occurs in the Brazilian Cerrado and Paraguayan Chaco, and *C. bishopi* in islands of Cerrado in the State of São Paulo (Bezerra, 2003). These species inhabit open areas and show fossorial habits. The deeper insertion of the lower incisors – as indicated by the position of the mandibular foramen –, suggests that *C. riograndensis* sp. nov. would have used the incisors for digging more than the extant species (see Winge, 1888; Verzi & Olivares, 2006).

Vucetich *et al.* (1997) described Pleistocene specimens of *Clyomys* for central-eastern Argentina, which represent a different species from those distributed in Paraguay and Brazil. Another specimen tentatively referred to this genus was described for the Late Miocene of Argentina central (Montalvo *et al.*, 1998). For the Quaternary of Brazil, *Clyomys* was recorded for the State of Mato Grosso do Sul, in the Serra da Bodoquena (Salles *et al.*, 2006), and *C. laticeps* for the State of Minas Gerais, in Lagoa Santa (Lund, 1839b). The material here studied is the first record of the genus for the Holocene of Rio Grande do Sul.

Family MYOCASTORIDAE Ameghino, 1902

Myocastor coypus (Molina, 1782)

Material. MARSUL 669-52, right M3 isolated; MARSUL 704-15, anterior fragment of right mandible with m1.

Comments. Currently *M. coypus* is the only living species of the genus and occurs in Paraguay, Uruguay, Bolivia, Argentina, Chile, and Southern Brazil (Eisenberg & Redford, 1989).

During the Quaternary *M. coypus* had a much wider distribution in Brazil, extending at least up to Bahia (Cartelle & Lessa, 1989). The material here assigned to this species is very scarce (see Table 1).

DISCUSSION

The assemblages described in this paper are among the best caviomorph samples known for the Quaternary of Brazil. These include a new species of *Clyomys*, and the first record of *Phyllomys* sp., *Euryzygomatomys mordax* and *Dicolpomys fossor* for southern Brazil, allowing to enlarge the knowledge of the temporal and geographic distribution of these species. In addition, the great abundance of materials, including the first mandibles of *E. mordax* and maxillae of *D. fossor*, supports the taxonomic status of these genera and species and allows future morphological variability studies.

Previous records of caviomorphs for the Holocene and the Pleistocene of Rio Grande do Sul are scarce. For the Holocene, *Agouti paca*, *Dasyprocta azarae*, *Myocastor*

coypus, *Hydrochoerus hydrochaeris*, *Cavia* sp., *C. aperea*, *C. magna*, *Ctenomys* sp., and *Echimyus* sp. (e.g., Mentz-Ribeiro *et al.*, 1989; Rosa, 1996, 2006a, b; Dias, 2003; Queiroz, 2004; Schmitz *et al.*, 1997) were recorded, but some of these materials are in need of a taxonomic revision. Pleistocene caviomorphs include *H. hydrochaeris*, *M. coypus*, *Microcavia* sp., Dolichotinae indet., and Echimyidae indet. (Bombin, 1976; Oliveira, 1992; Oliveira & Lavina, 2000; Rodrigues & Ferigolo, 2004; Ubilla *et al.*, 2007). In addition, Buchmann (1994, 2002) listed *Ctenomys* sp. and *Cavia* sp. for Concheiros locality, Santa Vitoria do Palmar Municipality. However, a revision of the material analyzed by Buchmann (PH, pers. obs.) rejects these identifications. Presence of families Hydrochoeridae, Caviidae, Echimyidae, Myocastoridae, and the species *M. coypus* and *H. hydrochaeris* (Rodrigues & Ferigolo, 2004) is confident at least since the Late Pleistocene. These occur at present in Rio Grande do Sul, with a very ample distribution.

In the rest of Brazil, caviomorphs are widely recorded, but these records are punctual and fragmentary except for the faunas from São Paulo and Minas Gerais. The seminal works of Lund (1839a,b; 1840a,b) and Winge (1888) report the most important Quaternary caviomorph assemblages of Brazil, comprising about 22 taxa from the region of Lagoa Santa, Minas Gerais.

The Holocene caviomorph fauna from Rio Grande do Sul, mainly the Echimyidae, shows taxonomic similarities with the Quaternary caviomorph faunas from central Brazil (see e.g., Winge, 1888; Ameghino, 1907; Paula-Couto, 1946). In addition, this fauna presents also “pampean” taxa, like *Ctenomys*, recorded in the Pleistocene of Argentina, Uruguay, Bolivia, and Chile (Mones & Castiglioni, 1979; Marshall *et al.*, 1984; Reig *et al.*, 1990), and *Cavia magna* (Ximenez, 1980). The similarity between the Quaternary mastofauna from southern Brazil and that from Argentina and Uruguay, which has already been suggested (e.g., Bombin, 1975; Cartelle, 1999), became established for the Late Pleistocene through the megafauna and caviomorph rodents like *Microcavia* and Dolichotinae (Tonni, 1981; Ubilla *et al.*, 1999). Consequently, the Rio Grande do Sul fauna was a mixture of “pampean” and brazilian taxa; it is possible that one or other faunal elements were predominant in the composition of the fauna at different times. Nowadays, both influences are evident, and two biogeographic neotropical subregions are represented: Chaco and Parana (Morrone, 2001).

The record of *C. magna* only in Sangão site agrees with its current geographic distribution (see Ximenez, 1980). It is possible that this taxon has kept such a distribution pattern since the Holocene, extending to the North through the littoral of Rio Grande do Sul State, but not occurring in interior localities like Garivaldino site. *C. aperea* is recorded in both sites, although its record is very scarce. Despite this poor record in our sample, *C. aperea* is one of the best represented taxa in other archaeological sites of Rio Grande do Sul, being recorded in central, littoral and southern portion of the state (e.g., Schmitz *et al.*, 1997; Rosa 2006a; Silva & Rosa, 2006).

For the Holocene of Rio Grande do Sul, *Ctenomys* is recorded mainly in sites from the Coastal Plain (e.g., Silva &

Rosa, 2006). The previous record in Garivaldino site (Mentz-Ribeiro *et al.*, 1989) was not confirmed (see above).

The records of *Phyllomys* sp. and *Dicolpomys fossor* in Rio Grande do Sul extend their distribution southward, and chronologically to the Late Holocene, because they were known, until now, only from the Late Pleistocene/Early Holocene in central Brazil (Minas Gerais and São Paulo; Lund, 1839a,b, 1840a,b; Winge, 1888; Ameghino, 1907; Souza-Cunha & Guimarães, 1978; Castro & Langer, 2005). *Phyllomys* shows since the Quaternary the ample geographic distribution that presents nowadays, being recorded in central and southern Brazil. *Euryzygomatomys mordax* has also its geographic occurrence extended southward.

Clyomys riograndensis sp.nov. extends the distribution of the genus to the south in the Holocene (at least until 3,700 years BP). The earliest records of *Clyomys* also show a different geographic distribution than the current one, being distributed in the Early Pleistocene (Ensenadan SALMA) of Argentina (Vucetich *et al.*, 1997). Today, *Clyomys* occurs only in the Brazilian Cerrado, and Paraguayan Chaco (Woods & Kilpatrick, 2005).

The new records support the statement of Vucetich & Verzi (2002) that very recent extinctions of caviomorphs occurred in northern South America. The Holocene Brazilian caviomorph fauna is more diverse than today, since a genus and at least three species became extinct. *Euryzygomatomys mordax* became extinct after 7,200 years BP, and *Clyomys riograndensis* sp.nov. and *D. fossor* after 3,700 years BP (see Table 1). Vucetich & Verzi (1999) had suggested that caviomorph faunas from central Brazil (Cerrado) and central Argentina had different evolutionary characteristics in the Pleistocene, that from Argentina being more stable. Also, in this aspect, the Holocene caviomorph fauna from Rio Grande do Sul was like that from central Brazil, presenting extinctions of genera and species.

The caviomorphs record from Garivaldino and Sangão sites is essentially homogeneous (Table 1), with only scarce breaks in the pattern. This probably reflects an absence of climatic pulses that could have interfered with the distribution of the species. That is, the climate was probably relatively constant, with mild and gradual changes, as can also be interpreted from the stratigraphic distribution of the marsupials in these sites (Hadler *et al.*, in press).

There are differences in faunal composition between the analyzed sites: *C. magna*, *Ctenomys* sp. and *M. coypus* are taxa exclusive of the Sangão site, whereas *E. mordax* is only found at Garivaldino. This could be due to local environmental differences, Sangão being an area more humid, with the Sinos River course just below the rock shelter, permitting the presence of the semi-aquatic *M. coypus* and *C. magna*. Causes for the distinctive distribution of *E. mordax* and *Ctenomys* sp. are not evident.

The occurrence of fossorial taxa of open areas, *E. mordax*, *C. riograndensis* sp.nov., *D. fossor* and *Ctenomys*, at the same levels as that of *Phyllomys*, typical of forested areas, may indicate a mosaic environment with grasslands and gallery forests. Furthermore, the high abundance of

Figure 9. Minimal number of individuals (MNI) of the Echimyidae species in Garivaldino site.

caviomorphs presumably related to grasslands attests to the predominance of these environments (Figure 9). These evidences are comparable with those provided by marsupials for the same areas (Hadler *et al.*, in press) and agree with palynological data. These latter have shown a scenario of grasslands predominating during the Late Pleistocene ($\pm 40,000$ years BP), substituted by forests, which were fully established by the end of Holocene. During the Early and Middle Holocene, climate became warmer, but still dry, grasslands continuing to predominate. General replacement of grasslands by forests occurred around 1,000 years BP, determined by a very humid climate, with no drought seasons (Behling *et al.*, 2001; Grala & Lorscheitter, 2001; Behling, 2002; Bauermann, 2003; Behling *et al.*, 2004, 2005).

Still according to palynological data, forest expansion would have started at different moments in some areas of Rio Grande do Sul. Whereas in the region of Serra Velha (Montenegro County, near Garivaldino site) forest expansion started at about 6,000 years BP, in Barrocas locality (Santo Antônio da Patrulha County, near Sangão site) it occurred around 3,000 years BP (Grala & Lorscheitter, 2001; Bauermann, 2003). This is not consistent with the presence of *Phyllomys* sp. in both sites around 8,000 years BP (Table 1), indicating already in this moment the presence of some forest. A possible explanation is that this rodent might have inhabited gallery forests. In this context, the proximity of Sangão site to Sinos River would have allowed the presence of *Phyllomys* at Early Holocene, even though the expansion of forests seem to have occurred only at 3,000 years BP in Santo Antônio da Patrulha (Bauermann, 2003).

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- Appendix.** Comparative material examined in this study: *Cavia aperea*, MCN-M 038, MCN-M 184, MCN-M 186, MCN-M 188, MCN-M 264, MCN-M 2818, MCN-M 2819; *Cavia fulgida*, MCN-M 386, 387; *Cavia magna*, MCN-M 222, 303, 304; *Clyomys* sp., MLP 91.IV.25.116, MLP 91.IV.25.135, MLP 91.IV.25.171; *Clyomys bishopi*, MN 43071, MN 43074, 68970; *Clyomys laticeps*, MN 31547, MN 31548, MN 31549, MN 31550, MN 31551; MZUSP 25880, MZUSP 25907, MZUSP 26660, MZUSP 26765; *Dicolpomys fossor*, ZMUC mandible 1, 2, 3, 4, 5 (Lund collection in Winge, 1888); *Euryzygomatomys mordax* ZMUC skull 1 (Lund collection in Winge, 1888); *Euryzygomatomys spinosus*, MCN-M 2364; MN 1984, MN 4029, MN 7284, MN 31519; *Kannabateomys amblyonyx*, MCN-M 1320; *Phyllomys blainvillei*, MN 1345, MN 1350, MN 1512, MN 21512; *Phyllomys dasythrix*, MCN-M 044, MCN-M 046, MCN-M 047, MCN-M 048; *Phyllomys lamarum*, MN 11259, MN 21654, MN 21664; *Phyllomys medius*, MCN-M 391; *Thrichomys* sp., MN 29126, MN 29128, MN 29140, MN 42191, MN 42192.

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