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SIGMODONTINE RODENTS (RODENTIA, CRICETIDAE) FROM QUATERNARY CAVE DEPOSITS OF SERRA DA CAPIVARA, NORTHEASTERN BRAZIL

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ABSTRACT – SIGMODONTINE RODENTS (RODENTIA, CRICETIDAE) FROM QUATERNARY CAVE DEPOSITS OF SERRA DA CAPIVARA, NORTHEASTERN BRAZIL. The Serra da Capivara National Park, State of Piauí, Brazil, and surrounding areas preserves a rich archeological and paleontological record of South American mammals. It includes a great amount of sigmodontine rodent remains recovered from limestone caves and rock shelters. We studied sigmodontine material from three caves, named Toca do Gordo do Garrincho, Toca do Barrigudo, and Toca do Serrote das Moendas, and identified the following taxa: *Bibimys* sp., *Necromys lasiurus*, *Pseudoryzomys simplex*, *Holochilus sciureus*, *Cerradomys* sp., *Calomys* sp., and *Wiedomys* sp. This is the first record of *Bibimys* for the Quaternary of northeast Brazil, which suggests that the paleobiogeographic distribution of this genus was different from its currently known range. Thus, we contribute to the knowledge of Quaternary sigmodontine rodents through these new taxonomic records and highlight the great potential of Serra da Capivara paleontological deposits for clarifying the biogeographic dynamics of this group during this period.

Key words: *Bibimys*, Pleistocene, Holocene, caves, mammals, paleobiogeography.

RESUMO – Na região do Parque Nacional Serra da Capivara, Estado do Piauí, Brasil, conhecida pelas descobertas arqueológicas e paleontológicas, numerosos restos de roedores Sigmodontinae foram recuperados de grutas e abrigos calcários. O material aqui estudado provém de três cavernas da região: Toca do Gordo do Garrincho, Toca do Barrigudo e Toca do Serrote das Moendas. Foram identificados os táxons *Bibimys* sp., *Necromys lasiurus*, *Pseudoryzomys simplex, Holochilus sciureus*, *Cerradomys* sp., *Calomys* sp. e *Wiedomys* sp., sendo o registro de *Bibimys* inédito para o Quaternário do nordeste brasileiro, sugerindo uma distribuição paleobiogeográfica diferente da atualmente conhecida para este táxon. Assim, contribuímos para o conhecimento dos sigmodontíneos do Quaternário do Brasil com novos registros do grupo para a Serra da Capivara, mostrando que os materiais recuperados na região apresentam grande potencial para fornecer esclarecimentos sobre a dinâmica biogeográfica destes roedores ao longo do Quaternário.

Palavras-chave: *Bibimys*, Pleistoceno, Holoceno, cavernas, mamíferos, paleobiogeografia.

INTRODUCTION

The sigmodontine rodents (Cricetidae) are the most diverse group of South American mammals (Patton *et al.*, 2015). The great number of species and their wide geographical distribution across different habitats has been used to reconstruct past environments and climates around the world (*e.g.* Simonetti & Saavedra, 1997; Aguilar *et al.*, 1999; Winkler, 2002; Ortiz *et al.*, 2012; Tammone *et al.*, 2014; Hadler *et al.*, 2016). South American sigmodontine fossils are recorded from the upper Miocene–Pliocene onwards (see Barbiere *et al.*, 2016 and references therein), and, in Brazil, several remains have been collected from Quaternary deposits, such as those recovered from Lagoa Santa caves, Minas Gerais, by the Danish naturalist Peter W. Lund during the 19th century (Lund, 1950).

The Serra da Capivara region, in northeastern Brazil, is another promising area for Quaternary records of sigmodontine rodents. This region has preserved many sites of paleontological and archeological interest, including discoveries relating to human settlement in the New World (Guidon *et al.*, 1994; Almeida & Neves, 2009; Peyre *et al.*, 2009).

In addition, there are records of many vertebrates that have been studied mainly to provide taxonomic lists and describe the extinct fauna (*e.g.* Curvello & Guérin, 1993; Faure *et al.*, 1999; Guérin & Faure, 1999, 2004a,b). However, there is little information available about the small mammals recovered from caves and rock shelters in the Serra da Capivara region. Caviomorph rodents were listed by Guérin (1991) and Guérin *et al.* (1996), and were recently described by Kerber *et al.* (2016). Regarding Sigmodontinae, Guérin *et al.* (1996) and Guérin & Faure (2008) listed species recovered from Quaternary deposits of two cave sites in the region (Toca de Cima dos Pilão and Toca da Barra da Janela do Antonião). However, these authors did not describe the specimens or make taxonomic identifications, which hampers the development of accurate taxonomic and biogeographic studies. In order to contribute to the knowledge of small mammals from the Serra da Capivara region, the present study identifies the sigmodontine rodents recovered from three cave sites located in the Serra da Capivara region, named Toca do Serrote das Moendas, Toca do Barrigudo, and Toca do Gordo do Garrincho. We identified seven sigmodontine taxa to generic and specific levels, including new records for the region, which pinpoints the great potential of such material to unveil the biogeography of this group during the Quaternary.

STUDY AREA

Located in the southeast area of State of Piauí (Figure 1A), the Serra da Capivara region is a semiarid zone, with Caatinga vegetation, and some patches of Cerrado, especially in wet areas, for example, inside canyons (Bartorelli, 2012; Pellerin, 2014) (Figures 1B–C). The area encompasses the Parnaíba Basin (NW) and the Peripheral Depression of São Francisco (SE). The latter includes limestone caves and rock shelters (Rodet, 1997; Pellerin, 2014) where Quaternary fossiliferous deposits preserve several small vertebrates, including sigmodontine rodents (Table 1). The material studied comes from three karstic caves described below. Each site has only sparse chronological data available, with dates ranging from late Pleistocene to Holocene.

Toca do Serrote das Moendas. This locality is a limestone cave in the municipality of Coronel José Dias and was excavated in 2006. Different materials and methods were utilized to obtain chronological data. All ages are related to the late Pleistocene period, such as radiocarbon dating on mollusk shells (24,210 ± 150 years BP and 26,970 ± 140 years BP), optically stimulated luminescence (**OSL**) (13,000 ± 3,000 years BP), and electron spin resonance on *Blastocerus* teeth (22,000 ± 2,000 years BP and 23,000 ± 2,000 years BP) (Guidon *et al.*, 2009b).

Toca do Barrigudo. This cave is located in the municipality of Coronel José Dias and was excavated in 2002. The fauna recovered has been considered as late Pleistocene to early Holocene in age (Guérin & Faure, 2004a). However, dental bioapatite samples of small mammals were recently dated by radiocarbon dating. The results revealed Holocene ages: *Kerodon rupestris* (1,680 ± 25 years BP), *Thrichomys* sp.

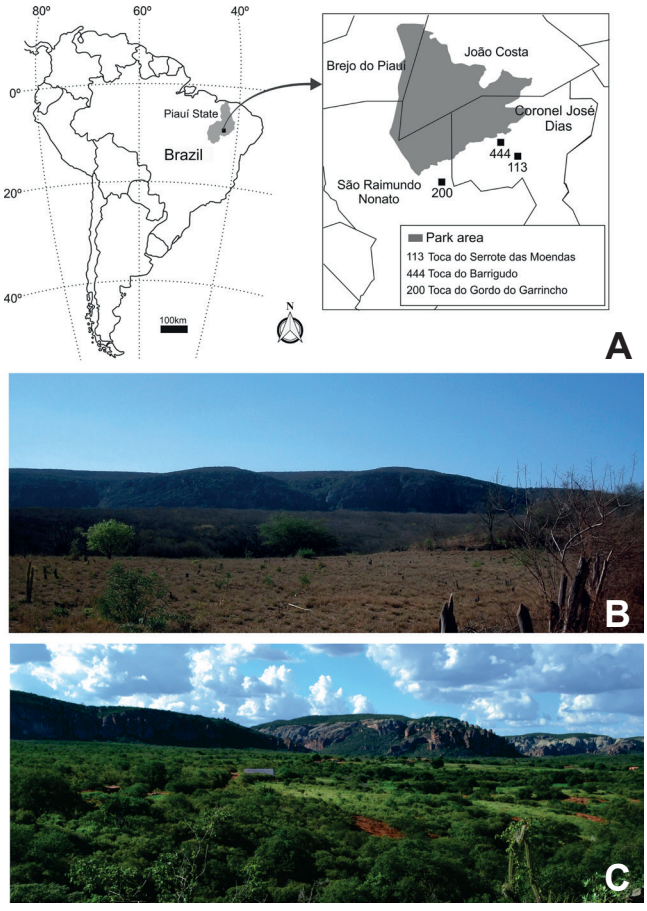

Figure 1. Location of the region of the Serra da Capivara National Park, Piauí, Brazil. **A**, map showing the location of the studied caves; **B–C**, the pictures show the contrast in vegetation between dry (**B**) and wet (**C**) seasons.

(1,670 ± 25 years BP, 3,940 ± 25 years BP, and 4,340 ± 25 years BP) and didelphid marsupials (3,870 ± 30 years BP, 3,900 ± 30 years BP, 4,370 ± 35 years BP, and 5,550 ± 40 years BP) (Ribeiro *et al.*, 2016). As the sigmodontine rodents were associated with dated materials (except *Kerodon*), they were considered to have been deposited during the same chronological range (Ribeiro *et al.*, 2016).

Toca do Gordo do Garrincho. This is a cave located in the municipality of São Raimundo Nonato and was excavated from 1990 to 1992. The deposits unveiled human remains, which contributed to the investigation of the peopling of South America (Peyre *et al.*, 1998; Guidon *et al.*, 2009a), as well as extinct and extant mastofauna (Guérin & Faure, 2008). Charcoal and human teeth samples were dated by radiocarbon (**AMS**) dating, giving results of 10,020 ± 290 years BP and 12,170 ± 40 years BP, respectively (Guidon *et al.*, 2000; Peyre *et al.*, 2009).

MATERIAL AND METHODS

The specimens were collected during the excavations of a Franco-Brazilian expedition in Piauí and are deposited in the paleontological collection of Fundação Museu do

Table 1. Identified rodents from Serra da Capivara caves and surrounds. Compiled from Guérin (1991), Guérin *et al.* (1996), Guérin & Faure (2008) (dark gray), Kerber *et al*. (2016), Mayer *et al.* (2016) (gray) and Neves *et al.* (2014) (white). **Abbreviations: Ant**, Toca da Barra da Janela do Antonião; **Pi**, Toca de Cima dos Pilão; **Ar**, Toca do Serrote do Artur; **Mo**, Toca do Serrote das Moendas; **Ga**, Toca do Gordo do Garrincho; **Ba**, Toca do Barrigudo.

Taxa	Localities					
	Ant	Pi	Ar	Mo	Ga	Ba
Myomorpha						
Muroidea						
Cricetidae						
Sigmodontinae						
Akodon cf. *A. cursor* (Winge, 1887)	x	x				
Calomys callosus (Rengger, 1830)	x	x				
Calomys sp.						x
Holochilus brasiliensis Brandt, 1835	x	x				
Oryzomys sp.	x	x				
Oryzomys cf. *O. subflavus* (= *Cerradomys subflavus* (Wagner, 1842))	x	x				
Pseudoryzomys simplex (Winge, 1887)	x	x				
Caviomorpha						
Cavioidea						
Caviidae						
Caviinae						
Galea sp.			x		x	x
Galea spixii (Wagler, 1831)	x	x				
Hydrochoerinae						
Kerodon rupestris (Wied-Neuwied, 1820)	x	x		x	x	x
Hydrochoerinae gen. et sp. indet.				x		
Cuniculidae						
Cuniculus paca (Linnaeus, 1766)	x	x	x			
Cuniculus rugiceps (Lund, 1837)		x				
Dasyproctidae						
Dasyprocta sp.			x	x	x	
Erethizontidae						
Coendou magnus Lund, 1839				x		
Octodontoidea						
Echimyidae						
Echimyidae cf. *Myocastor*				x		
Thrichomys apereoides (Lund, 1839)	x	x				
Thrichomys sp.			x	x	x	x
Phyllomys sp.			x			
Chinchilloidea						
Niedemys piauiensis Kerber *et al.,* 2016				x		

Homem Americano (**FUMDHAM**). A total of 326 specimens representing skulls, dentaries and isolated teeth were analyzed (Appendix 1) from three localities recorded with the collection numbers 113 (Toca do Serrote das Moendas), 444 (Toca do Barrigudo), and 200 (Toca do Gordo do Garrincho). The rodent material was sorted from among other small vertebrate remains and cleaned under optical stereomicroscope. The best-preserved specimens were photographed using a Nikon AZ100M NIS-Elements AR v.4.3 electronic stereomicroscope and images of the teeth were recorded by a JEOL JSM 6060 Scanning Electron Microscope. The measurements were made by ocular stereomicroscope with a SMZ/K-WF10x14mm/0.1mm micrometric lens.

For taxonomic identification, the specimens were compared to modern specimens housed in the collection of the Universidade Federal de Pernambuco (**UFPE**), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (**MCN-M**), and Departamento de Ecologia e Zoologia da Universidade Federal

de Santa Catarina (**UFSC**) (Appendix 2), and fossil specimens from the Coleção de Arqueologia da Universidade Federal do Rio Grande do Sul (**UFRGS**) studied by Hadler *et al.*(2016), as well as published data (*e.g.* Voss & Myers, 1991; Gonçalves *et al.*, 2005a,b; Weksler *et al.*, 2006; Percequillo *et al.*, 2008; Pardiñas & Teta, 2011). To describe the molars we followed the nomenclature utilized by Reig (1977) and Hershkovitz (1993). The systematic classification follows Patton *et al.* (2015) and the minimum number of individuals was calculated in agreement with Beisaw (2013). **Abbreviations: M/m**, upper and lower molars, respectively; **L**, length; **W**, width; **BP**, before present; **mm**, millimeters; †, extinct species.

SYSTEMATIC

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Suborder MYOMORPHA Brandt, 1855
Superfamily MUROIDEA Illiger, 1811
Family CRICETIDAE G. Fischer, 1817
Subfamily SIGMODONTINAE Wagner, 1843

Sigmodontinae gen. et sp. indet.

Material. One premaxilla, two maxillae, 38 dentaries, 19 isolated incisors, and four isolated m2 (Appendix 1).
Description. The lack of diagnostic features precludes the identification of this material, mainly due to fragmentation and advanced tooth wear.

Tribe AKODONTINI Vorontsov, 1959

Bibimys Massoia, 1979

Type species. *Bibimys torresi* Massoia, 1979.

Bibimys sp. (Winge, 1887)
(Figures 2A–B; 4A)

Material. Four dentaries (Appendix 1).
Description. The inferior ridge of the masseteric crest is well marked. The molars are moderately hypsodont and the main cusps of the molars are alternately arranged. The anteromedian flexid is conspicuous and lingually displaced. The anterolabial conulid reaches the protostylid. The metalophulid is present on m1 in the early stage of wear. The distoflexid is present on m1 and m2 (see Pardiñas, 1996), and the mesolophid is small and fused with the entolophid.
Comments. The material was attributed to the genus *Bibimys* based on the above features and on the measurements in Table 2 (Pardiñas, 1996; Gonçalves *et al.*, 2005b; Pardiñas *et al.*, 2015). As pointed out by Pardiñas (1996), the craniodental features of *Bibimys* species are not clearly defined. Currently, only *B. labiosus* has been found living in south and southeast Brazil (Pardiñas *et al.*, 2015), both regions located at least 1,200 km away from the study area. Taking into consideration the poor morphological and geographical information available for this genus, the specimens from Serra da Capivara were assigned to *Bibimys* sp.

Necromys Ameghino, 1889

Type species. †*Necromys conifer* Ameghino, 1889.

Necromys lasiurus (Lund, 1840)
(Figures 2C–D; 3A; 4B)

Material. One maxilla, 25 dentaries, and four isolated m1 (Appendix 1).
Description. The molars are tetralophodont with a transversal flexus and lophs. The anteromedian flexus is absent on M1. The anteroloph is present on M1 and the paraloph on M1 and M2. The protostylid and ectostylid are present in m1 and m2. The anteromedian flexid is absent in most specimens, except FUMDHAM 444-78429-6B, which shows an incipient structure.
Comments. The material was attributed to the genus *Necromys* based on the characters listed above, mainly due to the absence of the anteromedian flexus/id (see Reig, 1972 and Anderson & Olds, 1989). The lower molar measurements are presented in Table 3 and the upper molar measurements (FUMDHAM 444-78429-6E) in mm are: LM1 = 2.30; WM1 = 1.40; LM2 = 1.30; WM2 = 1.15. The material studied is very similar to modern specimens of *N. lasiurus* (UFSC 3876, UFSC 4815, UFPE 2994). Based on these features allied to the geographical distribution we assign the specimens to *N. lasiurus*.

Tribe ORYZOMYINI Vorontsov, 1959

Cerradomys Weksler, Percequillo & Voss, 2006

Type species. *Hesperomys subflavus* Wagner, 1842.

Table 2. Measurements (mm) of the lower molars of *Bibimys* sp.

Specimens	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm1-m3
FUMDHAM 113-137847-2D	1.75	1.00	1.20	1.05	-	-	-
FUMDHAM 113-137857-2C	1.75	1.05	1.20	1.05	-	-	-
FUMDHAM 113-137882-2C	1.55	1.05	1.10	1.00	0.20	0.75	3.75
FUMDHAM 113-137884-2C	1.65	1.00	1.25	1.00	-	-	-
Average	1.68	1.03	1.19	1.03	0.20	0.75	3.75

Cerradomys sp.
(Figures 2E–F; 4C)

Material. Nine dentaries (Appendix 1).

Description. The dentaries are robust due to the expanded capsular process of the incisive teeth. The inferior ridge of the masseteric crest is conspicuous. The molars are pentalophodont and low crowned, and their measurements are presented in

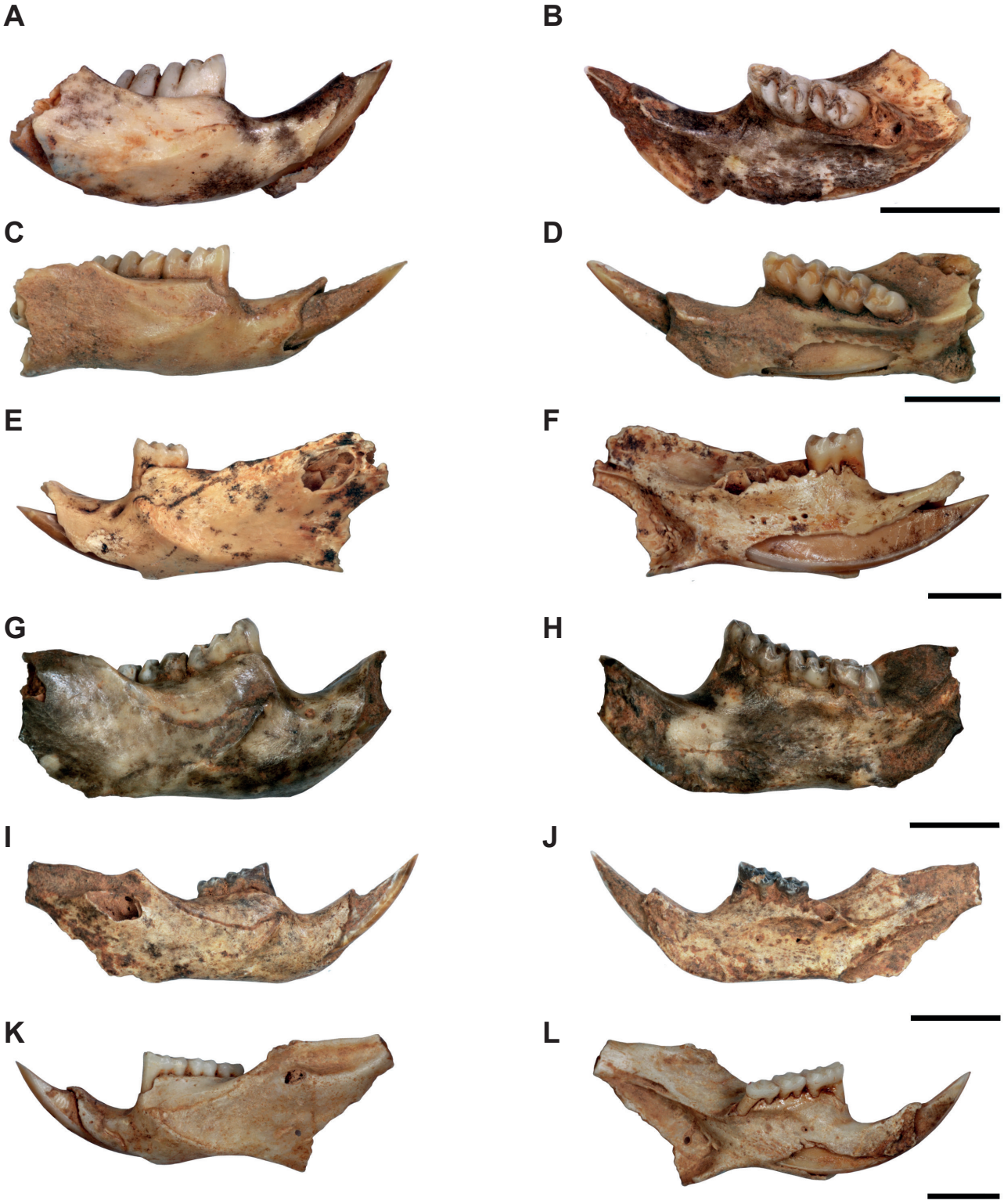

Figure 2. Dentaries of sigmodontines from Serra da Capivara in lateral (left) and mesial (right) view: **A–B**, FUMDHAM 113-137884-2C right dentary of *Bibimys* sp. **C–D**, FUMDHAM 444-78429-6B right dentary of *Necromys lasiurus*. **E–F**, FUMDHAM 444-78438-6B, left dentary of *Cerradomys* sp. **G–H**, FUMDHAM 444-76164-1C, right dentary of *Pseudoryzomys simplex*. **I–J**, FUMDHAM 444-77715-3A, right dentary of *Calomys* sp. **K–L**, FUMDHAM 444-78424-4B left dentary of *Wiedomys* sp. Scale bars = 3 mm.

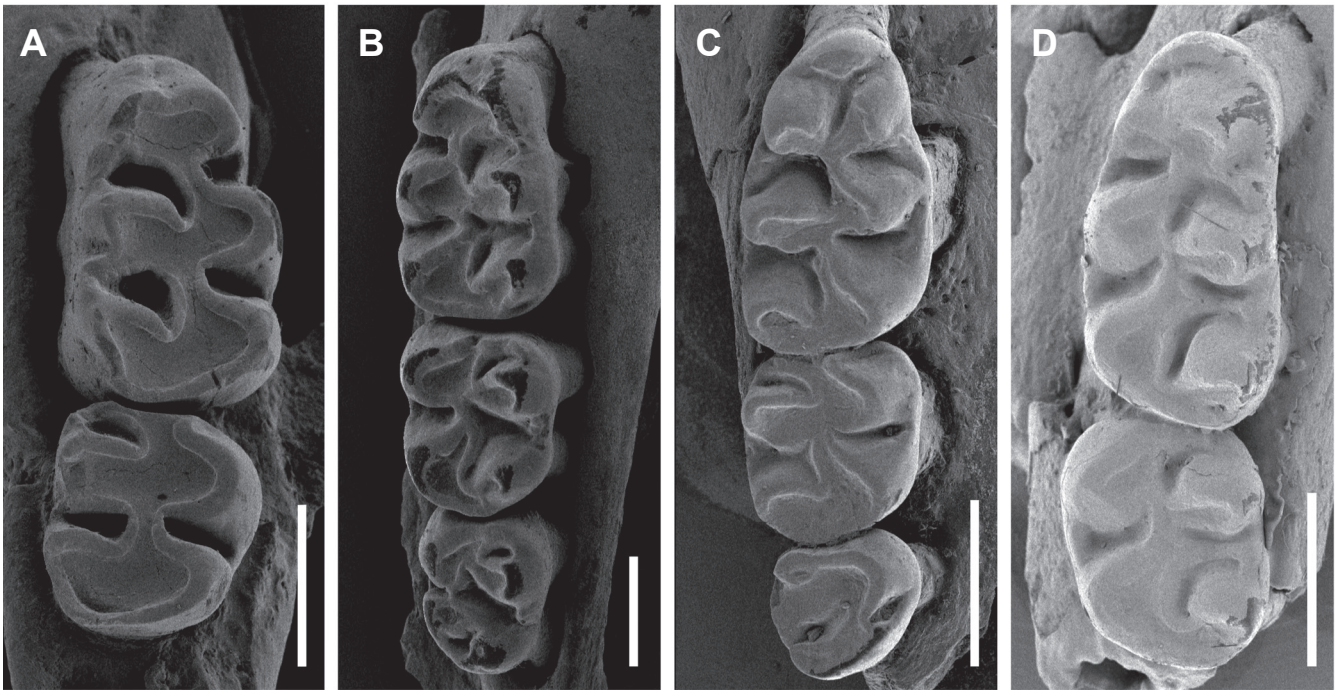

Figure 3. Occlusal view of upper molars of **A**, *Necromys lasiurus* FUMDHAM 444-78429-6E, left M1–M2. **B**, *Pseudoryzomys simplex*, FUMDHAM 113-143300-2, left M1–M3. **C**, *Calomys* sp., FUMDHAM 444-78424-4A, right M1–M3. **D**, *Wiedomys* sp., FUMDHAM 113-137887-2A, left M1–M3. Scale bars = 1 mm.

Table 3. Measurements (mm) of the lower molars of *Necromys lasiurus*.

Specimens		Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm1-m3
FUMDHAM 113-137855-2		2.00	1.10	-	-	-	-	-
FUMDHAM 113-137866-2		1.95	1.05	-	-	-	-	
FUMDHAM 113-137942		1.75	1.05	-	-	-	-	-
FUMDHAM 444-76164-1B	spm. 1	1.90	1.20	-	-	-	-	-
	spm. 2	1.50	1.05	-	-	-	-	-
FUMDHAM 444-76185-1B	spm. 1	1.60	1.05	1.05	1.05	-	-	-
	spm. 2	-	-	1.40	1.15	-	-	-
FUMDHAM 444-78424-4C		1.95	1.10	1.50	1.05	-	-	-
FUMDHAM 444-78429-6B		1.90	1.05	1.30	1.00	0.85	0.70	4.05
FUMDHAM 444-78435-2B		1.85	1.05	1.35	1.00	1.05	0.95	4.30
FUMDHAM 444-78660-3A		1.90	1.05	1.45	1.20	-	-	-
FUMDHAM 444-79089-1B		1.95	1.15	1.45	1.25	-	-	-
FUMDHAM 444-79156-4B	spm. 1	1.85	1.20	-	-	-	-	-
	spm. 2	2.00	1.25	-	-	-	-	-
FUMDHAM 444-78903-1A	spm. 1	1.85	1.20	1.55	1.00	-	-	-
	spm. 2	-	-	-	2.00	1.05	-	-
Average		1.85	1.11	1.38	1.19	0.98	0.83	4.18

Table 4. The anteroconid is undivided and an anterior fossetid is present. The anterolabial cingulid is well developed. The anterolophid is present on m1. The mesolophid is long and narrow on m1 and m2, and they lack an ectolophid. There are two roots and two accessory rootlets on m1 and two roots on m2.

Comments. The material was identified as *Cerradomys* based on the features mentioned above, as well as comments in Weksler *et al.* (2006), Percequillo *et al.* (2008), and Weksler & Percequillo (2011). Species within *Cerradomys* can be distinguished by cranial features not preserved in the studied materials, which hampers their assignation to the specific level. Nevertheless, the presence of a long and narrow mesolophid allows ruling out their attribution to *C. scotti* and *C. maracajuensis* (Percequillo *et al*., 2008).

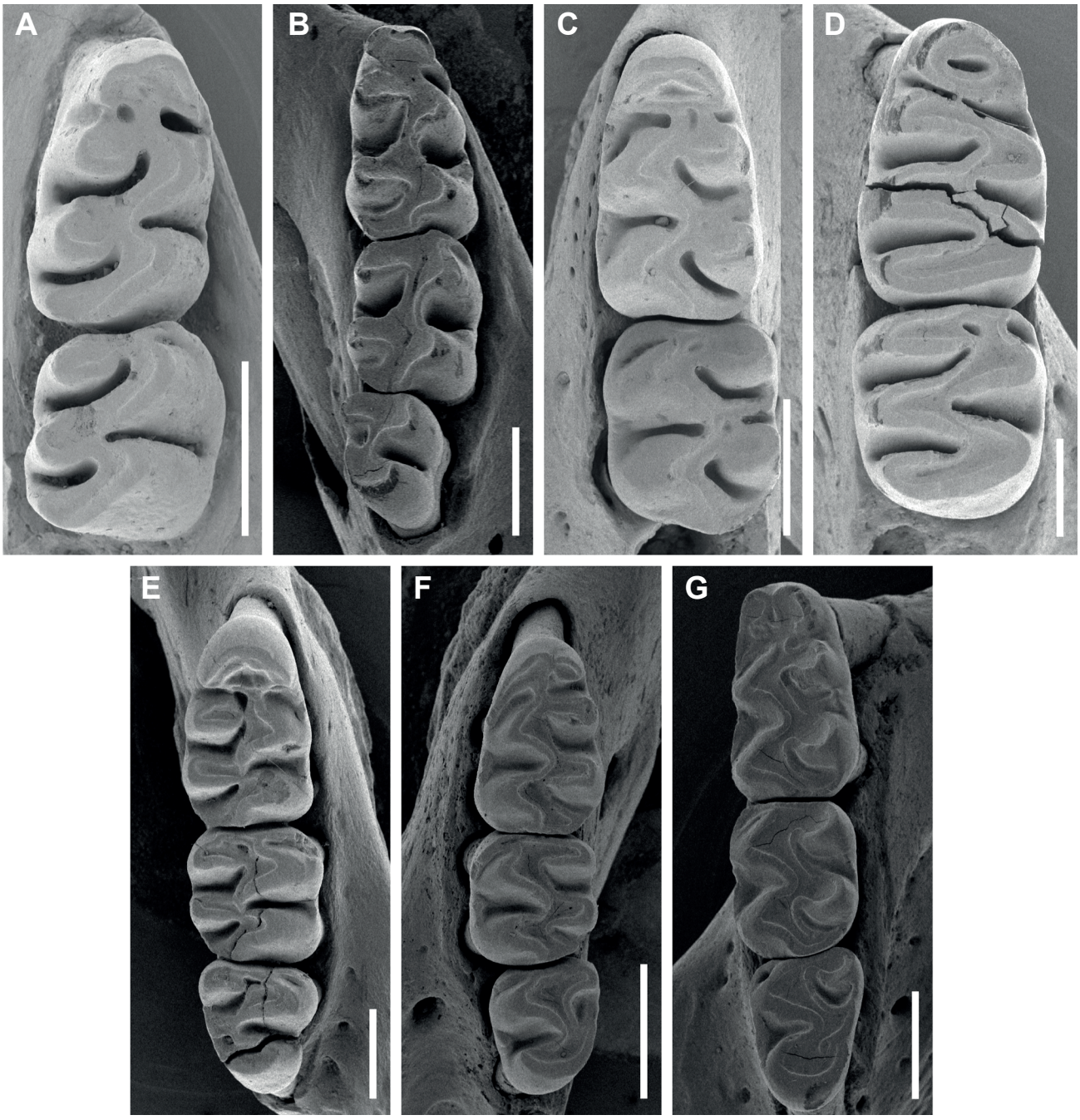

Figure 4. Occlusal view of lower molars of **A**, *Bibimys* sp., FUMDHAM 137884-2C, right m1–m2. **B**, *Necromys lasiurus*, FUMDHAM 444-78429-6B, right m1–m3. **C**, *Cerradomys* sp., FUMDHAM 444-76185-1C, left m1–m2. **D**, *Holochilus sciureus*, FUMDHAM 79089-1E, right m1–m2. **E**, *Pseudoryzomys simplex*, FUMDHAM 444-76164-1C, right m1–m3. **F**, *Calomys* sp., FUMDHAM 444-77715-3B, left m1–m3. **G**, *Wiedomys* sp., FUMDHAM 444-78424-4B, left m1–m3. Scale bars = 1 mm.

Table 4. Measurements (mm) of the lower molars of *Cerradomys* sp.

Specimens	Lm1	Wm1	Lm2	Wm2
FUMDHAM 444-76185-1C	2.15	1.25	3.2	1.20
FUMDHAM 444-78438-6B	2.25	1.04	-	-
FUMDHAM 444-79089-1C	2.05	1.05	1.6	1.25
Average	2.15	1.11	2.40	1.23

Holochilus Brandt, 1855

Type species. *Holochilus sciureus* Wagner, 1842.

Holochilus sciureus Wagner, 1842
(Figure 4D)

Material. One dentary (Appendix 1).
Description. The occlusal surface of the molars is flat and the main cusps are alternately placed. The flexids are

compressed with prismatic outer margins, and a transverse mesoflexid and posteroflexid. The metaflexid is well developed, and is in a diagonal position, almost connected with the protoflexid. The anteromedian murid is centralized and narrow. There is a small and transversally elongated anteromedian fossetid, and the anteromedian flexid and mesolophid are lacking. The molar measurements in mm are: Lm1 = 2.75; Wm1 = 1.85; Lm2 = 2.2; Wm2 = 1.85.
Comments. The material was assigned to *Holochilus sciureus* based on the features described above, as well as those reported by Pardiñas & Teta (2011).

Pseudoryzomys Hershkovitz, 1962

Type species. *Oryzomys wavrini* Thomas, 1921 (= *Hesperomys simplex* Winge, 1887).

Pseudoryzomys simplex (Winge, 1887)
(Figures 2G–H; 3B; 4E)

Material. Seven maxillae, 39 dentaries, two isolated m1, and one isolated m2 (Appendix 1).
Description. The dentaries are robust and short, and the inferior ridge of the masseteric crest is well developed. The upper cheek-teeth rows are parallel. The upper molars are bunodont and their main cusps are placed in opposite pairs. The anterocone of M1 is undivided, and there are small mesolophs on M1 and M2. The M3 is rounded and presents a deep hypoflexus. The mesolophids are absent in the lower molars, the flexids are deep, and the main cusps are alternately placed. The anteromedian fossetid is present and the m1 lacks the anteromedian flexid. The posterolophid is present in m1 and m2. There are two roots and two accessory rootlets on m1 and three roots on m2 and m3.
Comments. The material was attributed to *Pseudoryzomys simplex* based on the features mentioned above, as remarked on by Voss & Myers (1991). The upper molar measurements (Table 5) are similar to those published by Voss & Myers (1991). On the other hand, the dimensions measured in the lower molars (Table 6) are smaller than those reported by Hadler *et al.* (2016) and Pardiñas (1999) for south Brazil and Argentina.

Tribe PHYLLOTINI Vorontsov, 1959

Calomys Waterhouse, 1837

Type species. *Mus bimaculatus* Waterhouse, 1837 (= *Mus laucha* G. Fischer, 1814).

Calomys sp.
(Figures 2I–J; 3C; 4F)

Material. Twelve maxillae, 123 dentaries (Appendix 1).
Description. The dentaries are small but relatively high, and the ridges of the masseteric crest overlap at the level of m1. The molars are tetralophodont and bunodont. The main cusps are parallel on the upper molars, and the flexi are deep. The anteromedian flexus splits the anterocone of M1. The M2 is square shaped and smaller than M1. The M3 is more roundly shaped than M2. The main cusps of the lower molars are slightly alternately placed. The anteromedian flexid splits the anterolabial and anterolingual conulids, which could be difficult to observe in specimens with an advanced stage of tooth wear. There is a labial root on m1 and three roots on m2 and m3. The molar measurements are presented in Tables 7 and 8.
Comments. The material was assigned to the genus *Calomys* based on the features described, in accordance with Salazar-Bravo (2015). The length of the upper molar row (Table 7) (LM1–M3) in FUMDHAM 113-137864-2A and FUMDHAM 444-78424-4A (spm.1), both presenting the complete

Table 5. Measurements (mm) of the upper molars of *Pseudoryzomys simplex*.

Specimens	LM1	WM1	LM2	WM2	LM3	WM3	LM1-M3
FUMDHAM 113-137847-2C	2.30	1.60	1.45	1.50	1.25	1.30	4.90
FUMDHAM 113-137882-2A	2.25	1.50	1.50	1.45	-	-	-
FUMDHAM 113-143300-2	2.10	1.60	1.50	1.50	1.30	1.20	5.00
FUMDHAM 444-76185-1E	2.45	1.50	1.40	1.45	1.25	1.20	4.00
Average	2.28	1.55	1.46	1.48	1.27	1.23	4.63

Table 6. Measurements (mm) of the lower molars of *Pseudoryzomys simplex*.

Specimens		Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm1-m3
	spm.1	2.15	1.25	1.45	1.30	1.50	1.25	5.15
FUMDHAM 113-137813-2B	spm.2	2.00	1.25	-	-	-	-	-
	spm.3	2.25	1.25	1.50	1.40	-	-	-
FUMDHAM 113-137855-2A		2.25	1.30	1.50	1.30	1.50	1.15	5.20
FUMDHAM 113-137857-2B		2.25	1.30	1.55	1.40	-	-	-
FUMDHAM 113-137884-2A		2.10	1.40	1.50	1.40	1.50	1.20	5.20
FUMDHAM 113-123253-2B		1.90	1.10	1.50	1.30	1.30	1.20	4.70
FUMDHAM 444-76164-1C		2.30	1.35	1.50	1.50	1.20	1.25	5.00
Average		2.15	1.28	1.50	1.37	1.40	1.21	5.05

Table 7. Measurements (mm) of the upper molars of *Calomys* sp.

Specimens		LM1	WM1	LM2	WM2	LM3	WM3	LM1-M3
FUMDHAM 113-123253-2A		2.10	1.12	1.15	1.05	-	-	-
FUMDHAM 113-137852-2A		2.05	1.07	1.05	1.05	-	-	-
FUMDHAM 113-137855-2B		2.15	1.29	1.20	1.23	-	-	-
FUMDHAM 113-137864-2A		2.05	1.00	1.15	0.98	0.60	0.90	3.80
FUMDHAM 113-137884-2B		2.20	1.13	-	-	-	-	-
FUMDHAM 444-78424-4A	spm.1	2.05	1.10	1.05	1.00	0.70	0.83	3.85
	spm.2	2.20	1.03	1.25	0.96	-	-	-
FUMDHAM 444-78429-6A		2.05	1.00	-	-	-	-	-
Average		2.11	1.09	1.14	1.05	0.65	0.87	3.83

Table 8. Measurements (mm) of the lower molars of *Calomys* sp.

Specimens		Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm1-m3
FUMDHAM 113-137813-2C	spm.1	1.52	1.03	1.02	1.05	1.02	0.88	3.50
	spm.2	1.60	1.05	1.13	1.00	1.00	0.88	3.73
FUMDHAM 113-137846-2	spm.1	1.64	1.09	1.13	1.06	1.04	0.84	3.81
	spm.2	1.57	1.00	1.17	0.96	-	-	-
FUMDHAM 113-137847-2B	spm.1	1.52	1.05	0.86	4.10	0.85	3.70	3.77
	spm.2	1.55	1.03	1.05	1.08	0.88	0.88	3.70
	spm.3	1.62	1.10	1.12	1.12	1.05	0.97	3.00
	spm.4	1.52	1.10	1.12	1.12	0.90	1.00	2.75
FUMDHAM 113-137855-2B		1.47	0.98	1.05	1.05	-	-	-
FUMDHAM 113-137857-2A	spm.1	1.52	1.05	1.15	-	-	-	-
	spm.2	1.55	1.05	1.15	1.05	1.05	0.75	-
FUMDHAM 113-137864-2A		1.75	1.10	1.10	1.02	0.80	0.80	3.70
FUMDHAM 113-137867-2A		1.52	1.03	1.02	1.00	-	-	-
FUMDHAM 113-137884-2B		1.55	1.03	1.15	1.05	-	-	-
FUMDHAM 113-137887-2B	spm.1	1.63	1.03	1.18	1.00	-	-	-
	spm.2	1.60	1.03	-	-	-	-	-
	spm.3	-	-	1.18	1.15	-	-	-
FUMDHAM 444-76164-1A	spm.1	1.50	1.00	1.13	1.03	-	-	-
	spm.2	1.53	0.98	-	-	-	-	-
FUMDHAM 444-76185-1A	spm.1	1.77	0.77	1.18	0.72	0.80	0.65	3.73
	spm.2	1.65	1.07	1.20	1.02	0.95	0.82	3.70
	spm.3	1.50	1.02	1.10	1.00	0.90	0.80	3.60
FUMDHAM 444-77715-3A	spm.1	1.36	0.86	1.55	-	-	-	-
	spm.2	1.43	0.96	1.00	0.93	1.00	0.73	3.43
FUMDHAM 444-78438-6A		1.50	0.97	-	-	-	-	-
FUMDHAM 444-78903-3B		1.55	1.02	1.13	1.00	-	-	-
FUMDHAM 444-78983-2		1.50	1.02	-	-	-	-	-
FUMDHAM 444-79014-2		1.60	1.02	1.07	1.02	0.98	0.97	3.63
FUMDHAM 444-79089-1A		1.55	1.13	1.02	0.98	-	-	-
FUMDHAM 444-79156-2A		1.55	1.00	1.02	1.00	-	-	-
FUMDHAM 444-79156-4A		1.25	0.72	-	-	-	-	-
FUMDHAM 200-22304-2		-	-	1.25	1.00	-	-	-
FUMDHAM 200-22304-3		1.53	1.00	1.06	1.00	0.96	0.83	3.50
FUMDHAM 200-22304-5		1.30	0.95	-	-	-	-	-
Average		1.55	1.01	1.10	1.15	0.95	1.06	3.55

preservation of all upper molars, is larger than in *C. tener* (LM1–M3 = 3.1–3.4 mm). On the other hand, the length of the upper molar row (LM1–M3) in FUMDHAM 113-137864-2A and FUMDHAM 444-78424-4A (spm.1) is similar to the measurements of *C. expulsus* (LM1–M3 = 3.8–4.2 mm) and *C. callosus* (LM1–M3 = 3.8–4.4 mm), and both species currently inhabit the study area (Bonvicino *et al*., 2010). Taking into account the overlapping of the measurements and geographic distribution in addition to the fragmentary material, we maintain the assignation at the generic level.

Tribe WIEDOMYINI Reig, 1980

Wiedomys Hershkovitz, 1959

Type species. *Mus pyrrhorhinos* Wied-Neuwied, 1821.

Wiedomys sp.
(Figures 2K–L; 3D; 4G)

Material. One maxilla, 33 dentaries (Appendix 1).
Description. The dentaries are small and high, and the inferior ridge of the masseteric crest is well developed. The upper molars are pentalophodont, brachydont, and main cusps are slightly alternately placed. The anterocone is large and unequally splits by anteromedian flexus. Anteroloph present on M1 and mesoloph present on M1 and M2. The anteromedian flexid on m1 is deep and splits completely the anterolabial and the anterolingual cingulid, which always remains distinguishable even with intense tooth wear and in some cases generating a small anterior fossetid. The mesolophid is absent on m1 and m2, and the mesostylid is present on m1. There are three roots on m1 and two roots on m2 and m3.
Comments. The material was assigned to *Wiedomys* based on the features presented and in accordance with Bonvicino (2015). The fragmentary nature of the material precludes the comparison of measurements with published data, such as that presented by Gonçalves *et al.* (2005a), as well as the assignation to species level. The lower molar measurements are presented in Table 9.

CONCLUDING REMARKS

A total of 326 specimens were analyzed and 262 were identified to generic or specific level, that is, around 80% of the sample. The reported material represents new records for the three limestone caves in the Serra da Capivara region, except for a single preliminary record of *Calomys* sp. from Toca do Barrigudo (Neves *et al.*, 2014). The majority of the craniodental remains were recovered from Toca do Barrigudo (233 specimens), followed by Toca do Serrote das Moendas, (89 specimens), and Toca do Gordo do Garrincho (four specimens; see Table 10). Guérin *et al.* (1996) and Guérin & Faure (2008) listed six sigmodontine taxa from another two localities in the Serra da Capivara region, Toca de Cima dos Pilão and Toca da Barra da Janela do Antonião (see Table 1). However, we report here for the first time the presence of *Bibimys* sp., *Necromys lasiurus*, *Holochilus sciureus*, *Cerradomys* sp., and *Wiedomys* sp. for the Quaternary of the Serra da Capivara. The genus *Oligoryzomys* and *Akodon* were preliminary reported from Toca do Barrigudo by Neves *et al.* (2015), however this records was not confirmed herein.

According to Barbosa-Souza & Olmos (1994*),* current data about sigmodontine rodents from the Serra da Capivara are scarce and only *Calomys callosus, Cerradomys subflavus,* and *Oligoryzomys nigripes* were recorded in this region. Based on the modern sigmodontine geographical distribution (Patton *et al.*, 2015) and the mastofauna recorded from Caatinga and Cerrado biomes (*e.g.* Carmignotto *et al.*, 2012; Gutiérrez & Marinho-Filho, 2017), the majority of the identified taxa could be expected for the Serra da Capivara region, with the exception of *Bibimys.* According to Pardiñas *et al.* (2015), three species are known for this genus: *B. chacoensis*, which occurs from eastern Argentina

Table 9. Measurements (mm) of the lower molars of *Wiedomys* sp.

Specimens		Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm1-m3
FUMDHAM 113-137864-2D		-	-	1.50	1.10	-	-	-
FUMDHAM 113-145351-4		1.70	1.00	-	-	-	-	-
FUMDHAM 444-78424-4B	spm.1	1.95	1.25	1.30	1.20	1.30	1.05	4.55
	spm.2	1.75	1.05	1.35	1.15	-	-	-
	spm.3	1.85	1.10	-	-	-	-	-
	spm.4	1.80	1.15	-	-	-	-	-
FUMDHAM 444-78429-6C	spm.1	1.75	1.05	1.25	1.00	-	-	-
	spm.2	1.80	1.05	-	-	-	-	-
	spm.3	-	-	1.35	1.10	1.30	1.00	-
	spm.4	-	-	1.35	1.15	1.35	1.05	-
FUMDHAM 444-78435-2A		1.85	1.15	-	-	-	-	-
FUMDHAM 444-79156-4C	spm.1	1.85	1.05	1.60	1.05	-	-	-
	spm.2	1.80	1.05	-	-	-	-	-
	spm.3	1.60	1.10	-	-	-	-	-
Average		1.79	1.09	1.37	1.11	1.32	1.03	4.55

Table 10. Minimum number of individuals identified in each locality. **Abbreviations: Mo**, Toca do Serrote das Moendas; **Ga,** Toca do Gordo do Garrincho; **Ba**, Toca do Barrigudo.

Taxon	Localities			Total
	Mo	Ba	Ga	
Sigmodontinae gen. et sp. indet.	6	16	0	22
Akodontini				
Bibimys sp.	2	0	0	2
Necromys lasiurus	2	12	1	15
Oryzomyini				
Cerradomys sp.	0	5	0	5
Holochilus sciureus	0	1	0	1
Pseudoryzomys simplex	18	9	0	27
Phyllotini				
Calomys sp.	16	46	2	64
Wiedomyini				
Wiedomys sp.	1	18	0	19

to eastern Paraguay; *B. torresi*, restricted to the northern Buenos Aires and southernmost Entre Ríos provinces of Argentina; and *B. labiosus*, distributed from northern Rio Grande do Sul to northeast Minas Gerais and Rio de Janeiro states, Brazil. The fossil record of *Bibimys* is known from Quaternary deposits from Lagoa Santa, Minas Gerais, through the materials collected by Peter Lund and described by Winge (1887) (= *Scapteromys labiosus*); from Holocene deposits from Rio Grande do Sul (Hadler *et al.*, 2016); and from Holocene deposits from Argentina (see Pardiñas *et al.*, 2015 and references therein; *B. torresi*). Therefore, *Bibimys* records from the Quaternary of the Serra da Capivara suggest that the geographic range of this genus should be extended up to northeastern Brazil. This implies a different paleobiogeographic distribution for this genus, as similarly indicated by Holocene records of *B. torresi* in Argentina (Pardiñas, 1996; Teta *et al.*, 2013; Pardiñas *et al.*, 2015).

The sigmodontine fauna reported herein resembles that reported from limestone caves in Bahia, Brazil (Gomes, 2015; Castro *et al.*, 2014). However, currently there are no records of taxa associated with forested habitats (*e.g. Rhipidomys*) among the Serra da Capivara sigmodontine fauna. Some taxa reported here (*i.e. Bibimys*, *Necromys lasiurus*, *Pseudoryzomys simplex*, and *Calomys* sp.) were recorded in other Brazilian regions, such as Lagoa Santa, Minas Gerais (Winge, 1887), as well as in archeological deposits from Rio Grande do Sul (Hadler *et al.*, 2016). There is also little resemblance with sigmodontine records from the Serra da Bodoquena cave deposits, Mato Grosso do Sul (Salles *et al.*, 2006), and from the Serra da Mesa deposits, Goiás (Salles *et al*., 1999), both in Brazil. However, it is important to emphasize that the comparison of sigmodontine assemblages from different regions in Brazil should be made with caution. Firstly, due to the continental dimensions of this country, each locality presents its own geographic peculiarities, such as geomorphology and climate. Secondly, there is poor data available about site formation processes that encompass the genesis and chronology of Brazilian fossiliferous cave deposits. The complexity of bone emplacement mechanisms acting in caves could result in selective accumulations in relation to the original community compositions, as well as the time spans represented by the bone assemblages, as demonstrated by Auler *et al.* (2006) for fossiliferous cave deposits from Bahia and Minas Gerais.

The majority of the Sigmodontinae taxa reported here have been found living in open environments of Caatinga and Cerrado, according to Patton *et al.* (2015) and Carmignotto *et al.* (2012), such as *Calomys* sp., *Necromys lasiurus*, *Pseudoryzomys simplex*, and *Holochilus sciureus*, the last two associated with flooded areas, such as riverbanks or wetlands (Voss & Myers, 1991; Voss, 2015; Brandão & Nascimento, 2015). However, despite the proposition of paleoenvironmental inferences based on extinct and extant vertebrate fauna from the Serra da Capivara region (Guérin *et al.*, 1996; Guérin & Faure, 2008), in the absence of detailed taphonomic and chronological data, the assemblages potentially represent taxa from different habitats, which were not necessarily part of the same landscape during the Quaternary. Even in fossiliferous cave sites closely situated in the landscape, presumably under the same environmental conditions, bone assemblages could present different chronologies and taphonomic histories, which interferes with interpretations (Andrews, 1990; Auler *et al.,* 2006; Bartorelli, 2012). Moreover, material recovered from the study sites reinforces the idea of chronological contrasts, as revealed by ages ranging from 23,000 ± 2,000 years BP (*Blastocerus* tooth*;* Toca do Serrote das Moendas) to 1,670 ± 25 years BP (*Thrichomys* sp. tooth; Toca do Barrigudo). Thus, despite paleoclimatic studies based on palynology and speleothems suggesting climatic oscillations with changes in the landscape during the Quaternary in the northeast of Brazil (Behling *et al.,* 2000; Cruz *et al.*, 2009), it is difficult to correlate this data with that of the vertebrate fauna from the Serra da Capivara.

Finally, we conclude that this study contributes to knowledge about the taxonomy and biogeography of sigmodontine rodents from the Quaternary of northeast Brazil, by reporting new taxa from three cave sites in the Serra da Capivara. The new record of *Bibimys* for this region indicates a broad distribution of this genus. These findings show the great potential of the Serra da Capivara fossiliferous deposits to clarify the taxonomic composition of the sigmodontine community as well as the biogeographic history of this group during the Quaternary.

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Appendix 1. List of the studied material.

Sigmodontinae indet. Toca do Barrigudo. FUMDHAM 444-76164-1, two isolated incisors, and one fragment of dentary; FUMDHAM 444-76185-1, nine isolated incisors, three isolated m2, two left dentaries, six right dentaries without molars, and two left dentaries with worn m1–m2; FUMDHAM 444-77715-3 and FUMDHAM 444-79089-1, one left and one right dentary without molars; FUMDHAM 444-78424-4, one left dentary without molars, one right dentary with m1; FUMDHAM 444-78429-6, six isolated incisors, nine left dentaries, and three right dentaries without molars; FUMDHAM 444-78438-6, one left dentary without molars; FUMDHAM 444-78911-2, one right dentary without molars; FUMDHAM 444-79156-4, one fragment of right dentary without molars, one fragment of left dentary with m2 and m3, one isolated m2 and two isolated incisors. **Toca do Serrote das Moendas.** FUMDHAM 113-137813-2, one left dentary without molars; FUMDHAM 113-137847-2, one left dentary and one right dentary without molars; FUMDHAM 113-137847-2A, one left dentary without m1–m2; FUMDHAM 113-137852-2, FUMDHAM 113-137864-2, one left maxilla without molars; FUMDHAM 113-137867-2, one right dentary with m1 and m2; FUMDHAM 113-137882-2B, one left dentary with m1–m2, one right dentary with m1; FUMDHAM 113-137884-2 and FUMDHAM 113-123253-2, one right dentary without molars; FUMDHAM 113-137887-2, one right premaxilla with incisor and one right dentary without molars. ***Bibimys* sp. Toca do Serrote das Moendas.** FUMDHAM 113-137847-2D and FUMDHAM 113-137857-2C, one left dentary with m1–m2; FUMDHAM 113-137882-2C, one right dentary with m1–m3; FUMDHAM 113-137884-2C, one right dentary with m1–m2. ***Calomys* sp. Toca do Gordo do Garrincho.** FUMDHAM 200-22304-2, one left dentary with m2; FUMDHAM 200-22304-5, one right dentary with m1; FUMDHAM 200-22304-3, one left dentary with m1–m3. **Toca do Barrigudo.** FUMDHAM 444-76164-1A, one left dentary with m1 and two left dentaries with m1–m2; FUMDHAM 444-76185-1A, one left m2 and one left m1, one right maxilla with M1–M3, two fragments of right dentaries with m1, and one left fragment of dentary with m1, one left dentary and one right dentary with m1, five left dentaries with m1–m2, two left dentaries m1–m3; FUMDHAM 444-77709-2B, one right dentary without molars; FUMDHAM 444-77715-3A, one right and one left dentary with m1–m2, one fragment of left dentary with m1–m3, two left dentaries without molars; FUMDHAM 444-78424-4A, one right maxilla with M1–M3, one left maxilla with M1–M2, left and right dentaries with m1, two left dentaries with m2, two right dentaries with m2, one right dentary and two left dentaries all with m1–m3, four right dentaries without molars; FUMDHAM 444-78429-6A, one left maxilla with M1, two right and four left dentaries with m, three right and three left dentaries with m1–m2, one left and one right dentary with m1–m3, one left dentary with m2, nine left dentaries and five right dentaries without molars; FUMDHAM 444-78438-6A, one right dentary with m1 and one left dentary without molars; FUMDHAM 444-78903-3B, one right dentary with m1–m2; FUMDHAM 444-78911-2A, one left dentary without molars; FUMDHAM 444-78983-2, one right dentary with m1–m2; FUMDHAM 444-79014-2, one right dentary with m1–m3; FUMDHAM 444-79089-1A, one right dentary with m1–m2 and one right dentary without molars; FUMDHAM 444-79156-2A, one right maxilla with M1–M2 and one right dentary with m1–m2; FUMDHAM 444-79156-4A, one right dentary and three left dentaries with m1, three right dentaries and one left dentary with m1–m2, one left dentary with m2, one left dentary with m2–m3, four right dentaries, and one left dentary without molars. **Toca do Serrote das Moendas.** FUMDHAM 113-123253-2A, one right maxilla with M1–M3, two left and one right dentary without molars; FUMDHAM 113-137813-2C, two right dentaries with m1–m3 and one right dentary without molars; FUMDHAM 113-137846-2, one right dentary with m1–m3, one left dentary with m1–m2; FUMDHAM 113-137847-2B, one right dentary with m1–m3, one right and one left dentary with m1–m2; FUMDHAM 113-137852-2A, one left maxilla with M1–M2, one right and one left maxilla without molars, one right and one left dentary without molars; FUMDHAM 113-137855-2B, one right dentary with m1–m2, one right maxilla with M1–M2; FUMDHAM 113-137857-2A, two right and two left dentaries with m1–m3; FUMDHAM 113-137864-2A, one isolated m1, one right maxilla with M1–M3, two right dentaries with m1, one left dentary with m2, one right dentary with m1–m2, one left dentary with m1–m3, one left dentary without molars; FUMDHAM 113-137867-2A, one left dentary with m1–m2, one right dentary with m1–m3; FUMDHAM 113-137884-2B, one right maxilla with M1 and two left dentaries with m1–m2; FUMDHAM 113-137887-2B, one left dentary with m1–m2; one right dentary with m1 and one right dentary with m2; FUMDHAM 113-143298-2A, one left dentary with m1. ***Cerradomys* sp. Toca do Barrigudo.** FUMDHAM 444-76164-1D, one right dentary without molars; FUMDHAM 444-76184-2A, one left dentary with m1–m3; FUMDHAM 444-76185-1C, one left dentary with m1–m2; FUMDHAM 444-77709-2C, one left dentary without molars; FUMDHAM 444-78438-6B, one left dentary with m1; FUMDHAM 444-79089-1C, one right dentary with m1–m2 and one right dentary with m1; FUMDHAM 444-79156-4E, two right dentaries without molars. ***Holochilus sciureus*. Toca do Barrigudo.** FUMDHAM 444-79089-1E, one fragment of left dentary with m1–m2. ***Necromys lasiurus*. Toca do Gordo do Garrincho.** FUMDHAM 200-22304-4, one right dentary without molars. **Toca do Barrigudo.** FUMDHAM 444-76164-1B and FUMDHAM 444-76185-1B, one fragment of right dentary with m1–m2 and one right dentary with m2; FUMDHAM 444-78424-4C, one right dentary with m1–m2; FUMDHAM 444-78429-6B, one right maxilla with M1–M2, one right and one left dentary with m1, one left dentary with m2, two right and three left dentaries with m1–m2, one right and one left dentary with m1–m3; FUMDHAM 444-78435-2B, one left dentary with m1–m3; FUMDHAM 444-78660-3A, FUMDHAM 444-79089-1B, fragment of right dentary with m1–m2; FUMDHAM 444-79156-4B, two left dentaries with m1, one right dentary with m1–m3; FUMDHAM 444-79156-2C, four isolated right m1; FUMDHAM 444-78903-1A, one right dentary with m1–m2, and one right dentary with m1. **Toca do Serrote das Moendas.** FUMDHAM 113-137855-2, one left dentary with m1; FUMDHAM 113-137866-2, one right dentary with m1–m2; FUMDHAM 113-137942, one right dentary with m1. ***Pseudoryzomys simplex*. Toca do Barrigudo.** FUMDHAM 444-78429-6F, one right and one left dentary without molars; FUMDHAM 444-78903-3A, FUMDHAM 444-79156-4D, one left dentary without molars; FUMDHAM 444-79089-1D, one left dentary with m2–m3, and one left dentary with m3; FUMDHAM 444-76164-1C, one right dentary with m1–m3; FUMDHAM 444-76185-1E, one left maxilla with M1–M3, one left isolated m2, one left and one right isolated m1, one fragment of right dentary with m1, one right dentary with m2, two right and three left dentaries without molars; FUMDHAM 444-76184-2B, one left dentary without molars. **Toca do Serrote das Moendas.** FUMDHAM 113-137813-2B, one right dentary with m1, one left dentary with m1–m2, one right dentary with m1–m3, and one right dentary without molars; FUMDHAM 113-137847-2C, one right maxilla with M1–M3, one right and two left dentaries without molars; FUMDHAM 113-137852-2B, one right dentary with m1 and one right dentary without molars; FUMDHAM 113-137855-2A, two right dentaries with m1–m3, one right and left dentary without molars; FUMDHAM 113-137864-2B, cranial fragment with right M1–M3, one right dentary with m1–m3 and one left dentary without molars; FUMDHAM 113-137887-2C, two right dentaries without molars; FUMDHAM 113-137857-2B, one right dentary with m1–m2; FUMDHAM 113-137882-2A, one right maxilla with M1–M2 and one left dentary without molars; FUMDHAM 113-137884-2A, one right maxilla with M2, one right dentary with m1–m3, and three right dentaries without molars; FUMDHAM 113-143300-2, one cranial fragment with left m1–m3; FUMDHAM 113-123253-2B, one right maxilla with M1–M3, and one right dentary with m1–m3. ***Wiedomys* sp. Toca do Barrigudo.** FUMDHAM 444-77709-2A, one left dentary without molars; FUMDHAM 444-77715-3C and FUMDHAM 444-78438-6C, one right dentary without molars; FUMDHAM 444-78424-4B, one right and one left dentary with m1, one right dentary with m1–m2, one left dentary with m1–m3, and one left dentary without molars; FUMDHAM 444-78429-6C, two right dentaries with m2–m3; one left dentary with m1–m2, one left dentary with m1, three right and three left dentaries without molars; FUMDHAM 444-78435-2A, one left dentary with m1–m2; FUMDHAM 444-79156-4C, one right and two left dentaries with m1, one right dentary with m1–m2, one left dentary with m2–m3, three right and five left dentaries without molars. **Toca do Serrote das Moendas.** FUMDHAM 113-137864-2D, one right dentary with m2, FUMDHAM 113-137887-2A, one left maxilla with M1–M2; FUMDHAM 113-145351-4, one left dentary with m1.

Appendix 2. Comparative specimens examined in this study.

Akodon azarae. UFSC 5469; ***Akodon cursor.*** MCN-M 2030; UFPE 468, UFPE 486, UFPE 809, UFPE 813, UFPE 866; UFPE 869, UFPE 870, UFPE 1096, UFPE 1097, UFPE 1300, UFPE 1301, UFPE 1302, UFPE 1659, UFPE 1660, UFPE 1738, UFPE 1739, UFPE 1913, UFPE 2729; ***Akodon montensis.*** UFSC 222, UFSC 288; ***Akodon paranaensis.*** UFSC 3631, UFSC 3628; ***Akodon reigi.*** UFSC 2621; ***Castoria angustiden.*** UFSC 3803; ***Akodon* sp.** UFSC 2655; ***Calomys laucha.*** MCN-M 270, MCN-M 698, MCN-M 687; ***Calomys tener.*** UFSC 5490; ***Calomys* sp.** UFSC 5708; ***Cerradomys subflavus*.** UFPE 714, UFPE 783, UFPE 792, UFPE 901, UFPE 989, UFPE 1299, UFPE 1428, UFPE 1429, UFPE 1430, UFPE 1431, UFPE 2788; ***Cerradomys* sp.** UFSC 5223; ***Delomys dorsalis*.** UFSC 521, UFSC 613; ***Delomys sublineatus*.** UFSC 710, UFSC 3287; ***Holochilus sciureus*.** UFPE 2464, UFPE 2465, UFPE 2467, UFPE 2471, UFPE 2486, UFPE 2488, UFPE 2495; ***Necromys lasiurus.*** UFPE 469, UFPE 475, UFPE 488, UFPE 487, UFPE 489, UFPE 499, UFPE 510, UFPE 694, UFPE 695, UFPE 716, UFPE 717, UFPE 726, UFPE 741, UFPE 779, UFPE 814, UFPE 1087, UFPE 1120, UFPE 1306, UFPE 1914, UFPE 2994, UFPE 2995 UFPE 2996, UFSC 3876, UFSC 4815; ***Necromys* sp.** UFSC 4714; UFSC 5212; ***Oecomys* sp.** UFPE 1896, UFPE 1897, UFSC 5213; ***Oligoryzomys flavescens*.** MCN-M 474, MCN-M 3606, MCN-M 3607, MCN-M 3609, MCN-M 3611, UFSC 4399, UFSC 4802; ***Oligoryzomys nigripes*.** MCN-M 3106, MCN-M 3110, MCN-M 3138, MCN-M 3143, MCN-M 3153, MCN-M 3170, MCN-M 3179, UFPE 815, UFPE 816; UFPE 1113, UFSC 3707, UFSC 3950, UFSC 3951, UFSC 4803; ***Oligoryzomys* sp.** UFPE 1759, UFPE 1762, UFPE 1763, UFPE 1764, UFPE 1831, UFPE 1855, UFPE 2959; ***Oxymycterus nasutus*.** UFSC 955; ***Oxymycterus quaestor*.** UFSC 4817; ***Rhipidomys* sp.** UFPE 648, UFPE 1323, UFPE 1432, UFPE 2833, UFPE 2834, UFSC 4719; ***Scapteromys meridionalis*.** UFSC 2662, UFSC 2671, UFSC 3597, UFSC 3819, UFSC 4989; ***Scapteromys tumidus*.** UFSC 2648; ***Wiedomys pyrrhorhinos*.** UFPE 556, UFPE 1131, UFPE 1132, UFPE 1135, UFPE 1136, UFPE 1146, UFPE 1148, UFPE 1149, UFPE 1152, UFPE 1310, UFPE 1420, UFPE 1606, UFPE 1760, UFPE 1856, UFPE 1871, UFPE 2713, ;UFPE 2987, UFSC 2823, UFSC 2827, UFSC 2828.