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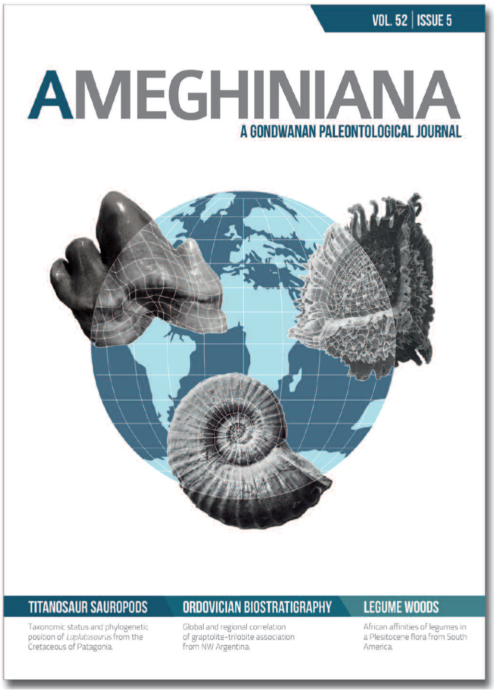

FIRST FOSSIL RECORD OF SIGMODONTINE RODENTS (MAMMALIA: CRICETIDAE) FOR PARAGUAY: TAXONOMY AND LATE PLEISTOCENE ENVIRONMENTS

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FIRST FOSSIL RECORD OF SIGMODONTINE RODENTS (MAMMALIA: CRICETIDAE) FOR PARAGUAY: TAXONOMY AND LATE PLEISTOCENE ENVIRONMENTS

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Key words. Vallemí. Paraguay. Muroidea. Quaternary. Cerrado.

Pleistocene records of South American vertebrates are diverse, especially for mammals (*e.g.*, Paula Couto, 1979; Marshall, 1985; Tonni *et al.*, 1999). However, knowledge of their spatial distribution is uneven, with most known fossil localities restricted to open, temperate to cold areas at medium to high latitudes (*e.g.*, Marshall *et al.*, 1984). By contrast, in tropical and subtropical areas such data are limited, notwithstanding that the knowledge about the Neogene of this region of the continent began accumulating more than 175 years ago, with the pioneer studies of P. Lund and H. Winge (*e.g.*, Lund, 1838; Winge, 1887; Paula Couto, 1950) in the limestone caves of Lagoa Santa (Minas Gerais, Brasil). Even though large mammals (mass > 1 ton) received more attention from researchers (*cf*. Cartelle, 1999), most of these caves are characterized by a richness of small mammal remains, especially rodents and bats (*e.g.*, Winge, 1887; Voss and Carleton, 1993; Czaplewski and Cartelle, 1998; Auler *et al.*, 2006; Hadler *et al.*, 2008; Pardiñas *et al.*, 2008).

Mammal paleontological data from Paraguay are scarce (*e.g.*, Hoffstetter, 1978; Carlini and Tonni, 2000; Ríos *et al.*, 2014) and in the case of small mammals completely absent. Considering that micromammals are suitable indicators to reconstruct environmental conditions, the study of fossil assemblages from cavern systems is an appropriate method for inferring paleoenvironmental conditions in areas where other traditional paleoclimatic archives are scarce or absent (*e.g.*, Andrews, 1990; Hadly, 1996; Pardiñas and Teta, 2013). The aims of this work are to describe the first assemblage of small mammals recovered in a cave in eastern Paraguay, and to consider its environmental implications for our understanding of Late Pleistocene evolution.

Risso cave (22° 17′ 49″ S; 57° 52′ 33″ W, Vallemí, San Lázaro District, Concepción Department; Fig. 1.1) is located in the northernmost extreme of the eastern half of Paraguay, near the confluence of the Apa and Paraguay rivers. Geographically, the area lies in the Campos Cerrados ecoregion (Hayes, 1995), although this region also includes elements of adjacent biomes such as the Interior Atlantic Forest (IAF), Chaco, and Pantanal. Thus, this area is biogeographically complex, due to possible interplay among these biomes throughout the fluctuating climatic conditions of the Quaternary. Risso cave is developed in carbonate and siliciclastic rocks of the Itapucumi Group (Campanha *et al.*, 2010) and it is filled by clastic sediments, mostly fine-grained sands. From top to bottom, cave sediments are organized in sequence of medium- to fine-grained sand covered by clay and silt (Fig. 1.2).

The small mammal remains examined in this study were obtained by sieving the sediments associated with a skeleton of the extinct ground sloth *Catonyx* Ameghino,

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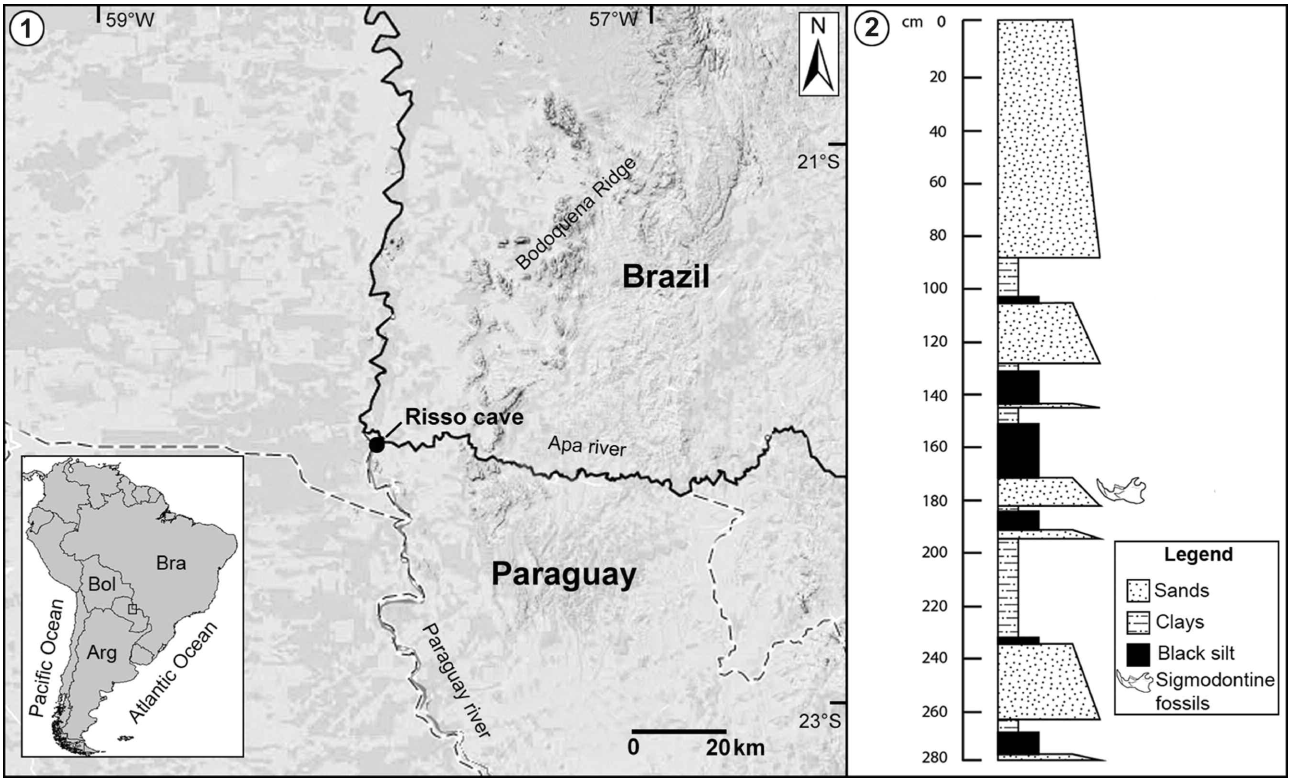

Figure 1. 1, Topographic map showing the location of Risso cave; **2,** Stratigraphic section of sediments inside Risso cave. **Arg=** Argentina, **Bol=** Bolivia and **Bra=** Brazil.

1891 (Mylodontidae, Scelidotheriinae), which was extracted from Risso cave through an excavation conducted during the second half of 2012. The small-mammal material shows marks in the enamel of molars and incisors that are characteristic of those produced by owls during digestion (Andrews, 1990; Pardiñas, 2000); coupled with the taxonomic affinities of the remains it appears that the assemblage was originated by the trophic activity of avian predators. Based on the low degree of corrosion of dental elements, we believe that the species involved in the genesis of the sample was a relatively non-destructive predator, such as *Tyto alba* (Andrews, 1990). Owls, in addition, typically prey on small mammals with weights <200 g, such as those found in the Risso Cave assemblage. Chronologically, we estimate that these fossils are Late Pleistocene–Early Holocene because they were recovered closely associated with the bones of *Catonyx*.

Taxonomic identifications were made through comparisons with Recent specimens housed at the Museo Nacional de Historia Natural del Paraguay; anatomical descriptions follow Hershkovitz (1962) and Pardiñas and Galliari (1998). Dental terminology was taken from Reig (1977).

Institutional abbreviation. **FVR** ("FaCEN-vert-roed")**,** Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Asunción, Paraguay.

Anatomical abbreviations. **BM/Bm,** breadth of upper/lower molars; **LM/Lm,** length upper/lower molars; **M1–3/m1–3,** length from anterior edge of M1/m1 to posterior edge of M3/m3.

SYSTEMATIC PALEONTOLOGY

Family Cricetidae Fischer, 1817
Subfamily Sigmodontinae Wagner, 1843
Tribe Oryzomyini Vorontsov, 1959

Genus ***Holochilus*** Brandt, 1835

Type species. *Holochilus sciureus* Wagner, 1842.

Holochilus chacarius Thomas, 1906
Figure 2.1–2; Table 1

Referred material. FVR-1, right maxillary with M2–3; FVR-2, left maxillary with M1; FVR-3, left mandible with m1–2; FVR-4, right mandible with the incisor and m1 (Fig. 2.1); FVR-5, right mandible with m2–3 (Fig. 2.2); FVR-6, 7, two left M1; FVR-8, 9, two left M2 ; FVR-10, 11, two left M3; FVR-12, 13, two right m2; FVR-14, left m3.

Description. The mandible is robust and high; main molar cusps are arranged in alternate pairs; the procingulum of m1 has a large labially displaced anterofossetid; the metaflexid reaches the midline of the tooth; the mesoflexid is transverse; the proto- and hypoconid are subrectangular in outline; the m2 is subquadrate in outline and the hypoflexid reaches the midline of the tooth; the m3 has a distinctive S-shaped pattern, produced by deeply interpenetrating folds (Fig. 2.1–2).

Comments. These materials are referred to *Holochilus chacarius* due to morphology (*i.e.*, well laminated molars, absence of mesoloph/id) and measurements (Tab. 1; *cf*. Pardiñas and Teta, 2011).

Genus ***Oligoryzomys*** Bangs, 1900

Type species. *Oryzomys navus* Bangs, 1900.

Oligoryzomys sp.
Figure 2.3; Table 1

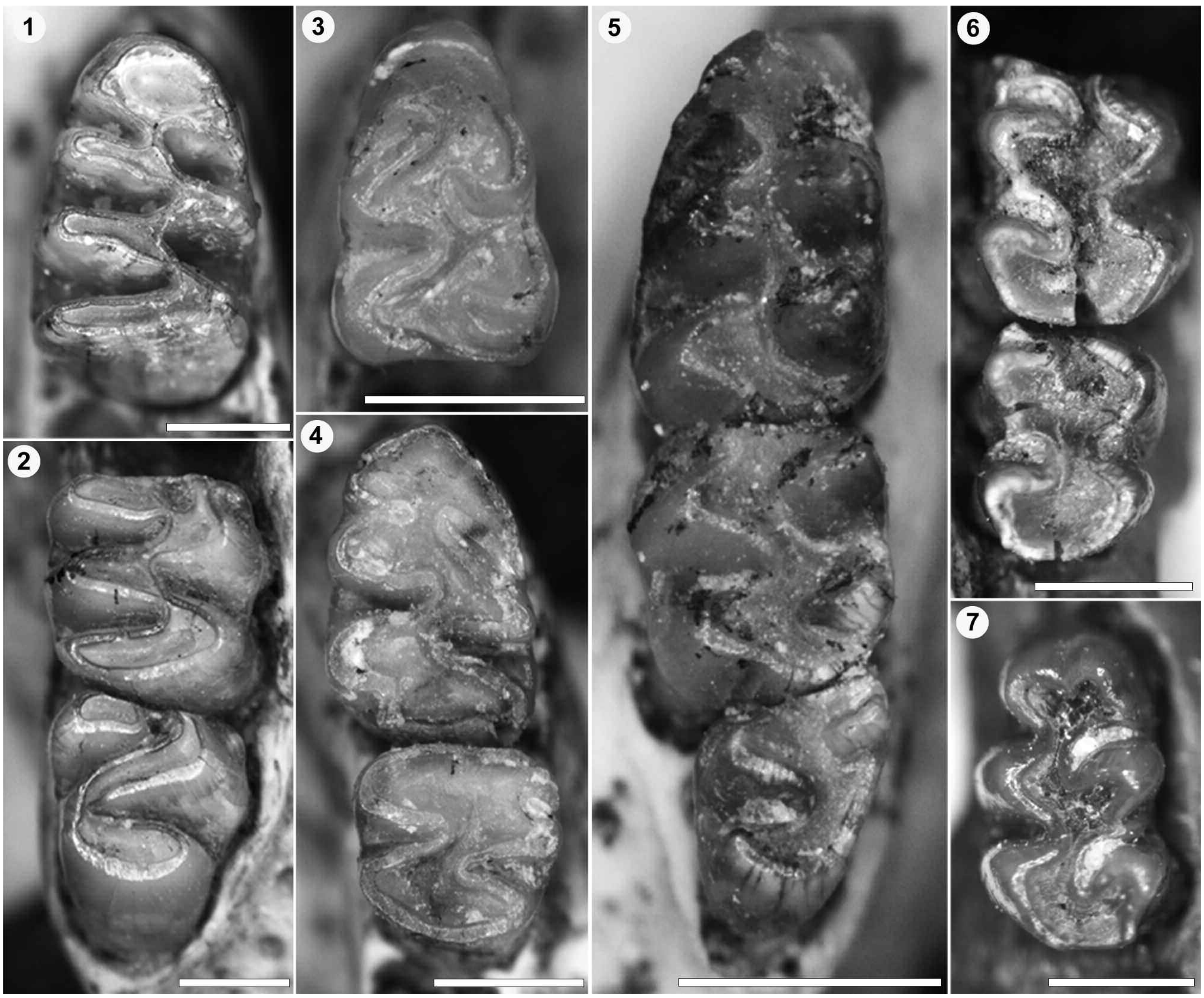

Figure 2. Oclussal views of molars. **1–2,** ***Holochilus chacarius*****; 1, FVR**-4, m1 of right mandible; **2, FVR-**5, m2–3 of right mandible. **3,** ***Oligoryzomys*** sp. (**FVR**-26), m1 of left mandible. **4,** ***Graomys*** **cf.** ***G. chacoensis*** (**FVR**-16), m1–2 of right mandible. **5,** ***Calomys*** sp. (**FVR**-25), m1–3 of left mandible. **6–7,** ***Akodon*** **cf.** ***A. toba*****; 6, FVR**-20, M1 (without procingulum) and M2 of right maxillary; **7, FVR**-21, M1 left maxillary. Scale bars= 1 mm.

TABLE 1 - Measurements in millimeters of sigmodontine fossils of Risso cave.

	FVR	M1-3	LM1	BM1	LM2	BM2	LM3	BM3	m1-3	Lm1	Bm1	Lm2	Bm2	Lm3	Bm3
Holochilus chacarius	1	-	-	-	-	-	-	-	-	-	-	2.27	1.94	2.13	-
Holochilus chacarius	2	-	2.95	2.1	-	-	-	-	-	-	-	-	-	-	-
Holochilus chacarius	3	-	-	-	-	-	-	-	-	2.91	1.95	2.3	2.05	-	-
Holochilus chacarius	4	-	-	-	-	-	-	-	-	3.05	2	-	-	-	-
Holochilus chacarius	5	-	-	-	-	-	-	-	-	-	-	2.15	2.05	2.05	2
Holochilus chacarius	6	-	3.15	2.3	-	-	-	-	-	-	-	-	-	-	-
Holochilus chacarius	7	-	3.1	2.1	-	-	-	-	-	-	-	-	-	-	-
Holochilus chacarius	8	-	-	-	1.9	2	-	-	-	-	-	-	-	-	-
Holochilus chacarius	9	-	-	-	2	2.05	-	-	-	-	-	-	-	-	-
Holochilus chacarius	10	-	-	-	-	-	2.25	1.75	-	-	-	-	-	-	-
Holochilus chacarius	11	-	-	-	-	-	2.1	1.45	-	-	-	-	-	-	-
Holochilus chacarius	12	-	-	-	-	-	-	-	-	-	-	2.1	2.2	-	-
Holochilus chacarius	13	-	-	-	-	-	-	-	-	-	-	2.05	2.05	-	-
Holochilus chacarius	14	-	-	-	-	-	-	-	-	-	-	-	-	2.1	2.05
G. *cf*. G. chacoensis	15	6	2.55	1.7	-	-	-	-	-	-	-	-	-	-	-
G. *cf*. G. chacoensis	16	-	-	-	-	-	-	-	-	2.6	1.6	1.7	1.7	-	-
G. *cf*. G. chacoensis	17	-	-	-	-	-	-	-	-	2.4	1.6	-	-	-	-
Akodon *cf*. A. toba	18	-	-	-	-	-	-	-	-	1.8	1.1	1.6	1.1	-	-
Akodon *cf*. A. toba	19	-	2.4	1.4	-	-	-	-	-	-	-	-	-	-	-
Akodon *cf*. A. toba	20	-		1.3	1.45	1.1	-	-	-	-	-	-	-	-	-
Akodon *cf*. A. toba	21	-	2.25	1.3	-	-	-	-	-	-	-	-	-	-	-
Calomys *sp.*	22	-	1.6	0.9	-	-	-	-	-	-	-	-	-	-	-
Calomys *sp.*	23	3.55	-	-	1	0.79	-	-	-	-	-	-	-	-	-
Calomys *sp.*	24	-	-	-	-	-	-	-	-	1.39	0.62	1	0.96	-	-
Calomys *sp.*	25	-	-	-	-	-	-	-	3.75	1.48	0.89	0.99	0.92	0.89	0.73
Oligoryzomys *sp.*	26	-	-	-	-	-	-	-	3.4	1.55	0.99	-	-	-	-
Oligoryzomys *sp.*	27	-	-	-	-	-	-	-	3.55	-	-	-	-	-	-
Oligoryzomys *sp.*	28	-	-	-	-	-	-	-	4.3	-	-	-	-	-	-
Oligoryzomys *sp.*	29	-	-	-	-	-	-	-	3.85	-	-	-	-	-	-
Oligoryzomys *sp.*	30	-	1.65	1.1	-	-	-	-	-	-	-	-	-	-	-

Referred material. FVR-26, left mandible with m1 (Fig. 2.3); FVR-27, left mandible without molars; FVR-28, right mandible with incisor and without molars; FVR-29, right mandible without incisor and molars; FVR-30, right M1.
Description. The mandible is short and high, with the upper and lower ridges of the masseteric crest converging anteriorly below the m1; the m1 is subrectangular in outline; the procingulum is rounded and lacks an anteromedian flexid; the metaflexid is obliterated and the posteroflexid barely visible; the hypoflexid and mesoflexid are deep and reach the midline of the teeth; the mesolophid is present (Fig. 2.3).
Comments. Based on measurements, these materials can be ascribed to a medium to large-sized species of the genus, probably *Oligoryzomys chacoensis* or *O. nigripes* (*cf*. Myers and Carleton, 1981). However, the fragmentary nature of the fossils examined, and the difficulty of identifying these taxa based solely on dentary remains (*e.g.*, Teta *et al.*, 2009) prevent a specific assignation.

Tribe Phyllotini Vorontsov, 1959

Genus ***Graomys*** Thomas, 1916

Type species. *Mus griseoflavus* Waterhouse, 1837.

Graomys cf. ***G. chacoensis*** (Allen, 1901)
Figure 2.4; Table 1

Referred material. FVR-15, right maxillary with M1; FVR-16, right mandible with m1–2 (Fig. 2.4); FVR-17, right m1.
Description. The mandible is medium sized, robust, and relatively high; the lower ridge of the masseteric crest is evident and ends just below the anterior plane of the m1; the molars are hypsodont; the m1 is planate, with its procingulum labially compresed and the anterolabial conulid continued through a cingulum; the metaconid and entoconid are rounded, while the protoconid and hypoconid are subtriangular in shape; the posterolophid is very small; the mesoflexid and hypoflexid are deep and reach the midline of the teeth; the m2 is squared in outline, with opposite cusps and deep hypo- and entoflexid (Fig. 2.4).
Comments. Based on size (Tab. 1), general morphology (*cf*. Ferro and Martínez, 2009), and distribution, the materials are referred to cf. *G. chacoensis*.

Genus ***Calomys*** Waterhouse, 1837

Type species. *Mus bimaculatus* Waterhouse, 1837.

Calomys sp.
Figure 2.5; Table 1

Referred material. FVR-22, left maxillary with M1; FVR-23, left maxillary with M2; FVR-24, right mandible with m1–2; FVR-25, left mandible with m1–3 (Fig. 2.5).
Description. The mandible is delicate and relatively high; the upper and lower ridges of the masseteric crest converge anteriorly forming a conspicuous excrescence just below the anterior border of the m1; the capsular projection is conspicuous and lies just below the sigmoid notch; the molars are crested, with the main cusps exhibiting slight wearing and arranged in alternate pairs; the m1 is subrectangular in outline, with the procingulum divided by a shallow anteromedian flexid; the flexids are deep and patent, except that the metaflexid is less developed; m2 is square in outline with well excavated hypo-, meso- and posteroflexid; the mesolophid is absent; the m3 is small and subtriangular, with the hypoflexid deep and the mesoflexid almost obliterated (Fig. 2.5).
Comments. *Calomys* is one of the most complex and widespread genera of Phyllotini; its alpha taxonomy, including the status of several cryptic species, is still pending a comprehensive study (Musser and Carleton, 2005). Based on size, we are confident that these remains belong to a small-sized species, such as *Calomys laucha* or *C. tener*, the latter currently recorded in eastern Paraguay (González-Ittig *et al.*, 2014).

Tribe Akodontini Vorontsov, 1959

Genus ***Akodon*** Meyen, 1833

Type species. *Akodon boliviensis* Meyen, 1833.

Akodon cf. ***A. toba*** Thomas, 1921
Figure 2.6–7; Table 1

Referred material. FVR-18, left mandible with m1–2; FVR-19, left maxillary with M2–3; FVR-20, right maxillary with

M1 (without procingulum) and M2 (Fig. 2.6); FVR-21, left maxillary with M1 (Fig. 2.7).

Description. Main cusps of M1 are arranged in opposite pairs; the procingulum is divided by a marked anteromedian flexus; the paraflexus and metaflexus are well developed; the anteroloph, mesoloph and posteroloph are small (Fig. 2.6–7); the M2 is subquadrate in outline, with a well-developed metaflexus and hypoflexus.

Comments. Based mostly on size (Tab. 1) and tooth morphology (*cf*. Myers, 1989) these specimens are referred to cf. *A. toba*.

DISCUSSION

Recent sigmodontine assemblages in northernmost eastern Paraguay (east of the Paraguay River) include a mixture of species that inhabit forests (*e.g.*, *Oligoryzomys nigripes*, *Oecomys* spp.), grasslands (*e.g.*, *Necromys lasiurus*) and wetlands (*e.g.*, *Holochilus chacarius*), with affinities with the Chacoan fauna (*e.g.*, *Graomys chacoensi*s), Cerradoan fauna (*Cerradomys* spp.), and Atlantic forest fauna (*e.g.*, *Akodon montensis*) ecoregions (Myers, 1982). The sigmodontine assemblage from Risso Cave includes five species with widespread distributions in open to forested areas, such as semiarid grasslands and woodlands of the Chaco and Cerrado ecoregions. Both *Graomys* and *Oligoryzomys* are present in thorn forests, low trees and shrubby areas of western Paraguay (Hershkovitz, 1962; Myers and Carleton, 1981; Bonvicino and Weksler, 1998). *Akodon toba* occupies several kinds of habitats, including patches of forests intermingled with palm savannas, marshlands, thorn forests, semiarid scrublands, and gallery forest (Massoia, 1971; Myers, 1989; Pardiñas and Teta, 2005). *Holochilus chacarius* inhabits wetlands and flooded grasslands in open, mostly non-forested habitats, being strongly associated with grazing areas with high amounts of litter and deep herbaceous ground cover (Yahnke, 2006).

In summary, the sigmodontine assemblage of Risso cave is in accordance with a landscape of open grasslands and wetlands, intermixed with low trees and thorn forest islands. General conditions were perhaps slightly more xeric than present, as inferred from the absence of species that typically inhabit humid grasslands, such as *Akodon azarae* or *Necromys lasiurus*. Other notable absences, also in agreement with the proposed paleoenvironmental scenario, are species associated with forested areas in the eastern Paraguayan region, such as the oryzomyines *Hylaeamys megacephalus* and *Sooretamys angouya* or the akodontine *A. montensis*, all of which are presently common in the IAF of eastern Paraguay.

In agreement with our results, studies based in pollen sequences suggest drier and cooler climatic conditions for the Late Pleistocene in south and southeastern Brazil, which triggered the advance of Cerrado environments over humid forests and grassland (Ledru, 1993; Behling, 2002). A scenario consistent with this hypothesis can be drawn from the mammalian faunas found at three caves in Serra da Bodoquena, Brazil (ca. 160 km northeast from our study site), where species adapted to open to shrubby physiognomies dominate the samples, while forest dwellers were almost absent (*cf*. Salles *et al*., 2006).

The small amount of fossil material recovered, as well as our poor knowledge about the natural history of the mammals currently living in this area, limit the precision of our interpretation. Additional samples, with more accurate stratigraphical and chronological control are much needed to test the hypothesis presented here. However, the evidence reported here is promising, considering that paleontological evaluation of the Paraguayan karstic system is only in its initial stages.

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