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New and noteworthy records of Rodentia (Erethizontidae, Sciuridae, and Cricetidae) from Paraguay

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Abstract

Extensive field work conducted in Paraguay since 1995 allowed us to present the first records for this country of the family Sciuridae (*Sciurus urucumus*), the genus *Bibimys* (*B. chacoensis*), and the species *Akodon paranaensis*, in addition to the first formal mention of *Oxymycterus misionalis*, and noteworthy records of *Cerradomys maracajuensis*, *Pseudoryzomys simplex*, and *Sphiggurus spinosus*. These records demonstrate that the mammal fauna of the Paraguayan Oriental Region is more similar in species richness and composition to that of adjacent regions of Argentina and Brazil than previously realized.

Key words: *Akodon*, Atlantic forest, *Bibimys*, *Cerradomys*, Chaco, *Oxymycterus*, *Pseudoryzomys*, *Sciurus*, Sigmodontinae, *Sphiggurus*

Resumen

Un extenso trabajo de campo realizado en Paraguay desde 1995 nos permitió brindar los primeros registros para el país de la familia Sciuridae (*Sciurus urucumus*), el género *Bibimys* (*B. chacoensis*) y la especie *Akodon paranaensis*, además de la primera mención formal de *Oxymycterus misionalis* y registros novedosos de *Cerradomys maracajuensis*, *Pseudoryzomys simplex* y *Sphiggurus spinosus*. Estos registros indican que la mastofauna de la Región Oriental de Paraguay es en términos de riqueza específica y composición, más similar a las zonas adyacentes de Argentina y Brasil de lo considerado previamente.

Palabras claves: *Akodon*, *Bibimys*, Bosque Atlántico, *Cerradomys*, Chaco, *Oxymycterus*, *Pseudoryzomys*, *Sciurus*, Sigmodontinae, *Sphiggurus*

Introduction

Paraguay is one of two landlocked countries of South America, lying in the center of the continent (S 19º to 28º, W 54º to 63º). Its 406,752 km^2 are subdivided by the large Paraguay River into two distinctive regions. The Chaco west of the Paraguay River consists of a mosaic of grasslands, palm savannas, open woodlands and xeric thorn forests. This region represents about 60% of the land area of Paraguay and holds fewer than 100,000 human inhabitants. The region east of the Paraguay River, known as the Oriental Region, represents about 40% of the land area and contains about 98 % of the country's human population. The Oriental Region

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is composed of grasslands and tropical semi-deciduous forest, which represents the westernmost reaches of the Interior Atlantic Forest ecoregion. Rates of deforestation are alarming; Paraguay lost about two thirds of its Atlantic forest between 1973 and 2000 (Huang *et al*. 2007).

Paraguay harbors around 160 mammal species grouped in 30 families and 9 orders (Myers *et al*. 2002). Although the mammal fauna of Paraguay was one of the first of the New World to be studied by naturalists (e.g., Azara 1801, 1802; Rengger 1830; for a historical account of Paraguayan mammalogy see Myers *et al*. 2002), the current knowledge of it is far from thorough. For most species, what is known is little more than preliminary data on habitat preference and activity patterns, and a rough approximation of their distributions, which reflect a marked distinction between the mammal communities east and west of the Paraguay River (Myers, 1982). Auspiciously, in the last decade a renewed interest in prospecting and studying the mammal fauna of Paraguay is changing this scenario (e.g., Frutos & van den Bussche 2002; Stevens *et al*. 2004; Yahnke 2006). Among important recent advances deserving mention is the first citation for the country of four bat and one marsupial species (Lopez-González *et al*. 1998; de la Sancha *et al*. 2007). In the same vein, we present herein the first citations for Paraguay of three rodent species, including one new family and one new genus, and noteworthy records of four other species.

Material and methods

We have been conducting field work in Paraguay since 1995, sampling all regions of the country, including grasslands, wetlands, tropical humid forest, and both Humid and Dry Chaco. Collections were made using Sherman and snap traps, a shotgun, and by hand. The voucher specimens that constitute the basis of this report are (or will be) deposited in the following collections: Argentina—Colección Contreras (CE; to be catalogued at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina); Paraguay—field numbers of The Museum, Texas Tech University, Lubbock (TK) and field numbers of Guillermo D'Elía (GD), to be catalogued at the Museo Nacional de Historia Natural del Paraguay, San Lorenzo; United Kingdom—Natural History Museum, London (BMNH); United States of America: field numbers of The Museum, Texas Tech University (TK), to be catalogued at The Museum, Texas Tech University, Lubbock; The University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Museum of Natural History, University of Kansas (KU).

Standard external measures, sex, and reproductive condition were taken from specimen labels and collector field catalogs. Measurements (in mm) are as follows: total body length (TBL); tail length (TL); hind foot length (including the claw) (HF); ear length (EL); and weight (W) (gm).

Specimen determinations were made on the basis of morphological comparisons with reference material and literature descriptions. In two cases genetic comparisons using partial sequences of the gene that codes for cytochrome *b* (cyt *b*) were also carried out. In one case, the morphological determination was complemented with phylogenetic analyses based on cyt *b* sequences. Sequences were taken from GenBank or generated by us (n=7; accession numbers: EF621302-7, EU449517) following protocols detailed in D'Elía *et al*. (2003). Sequence alignment was done by eye. Percentage of observed sequence divergence was estimated with PAUP* (Swofford 2000) ignoring sites with missing data. Maximum parsimony analyses (MP; Farris 1982) with characters equally weighted and treated as unordered were performed with PAUP* with 200 replicates of heuristic searches, random addition of sequences and tree bisection reconnection branch swapping. One thousand parsimony jackknife (JK; Farris *et al*. 1996) replications with 5 addition sequence replicates each and the deletion of one third of the character data were performed.

In the following accounts the heading "distribution" refers to the known distribution of the species excluding our records. Division of Rodentia into suborders follows Carleton & Musser (2005). New locality records (Fig. 1) are numbered in the order that they are presented in the text.

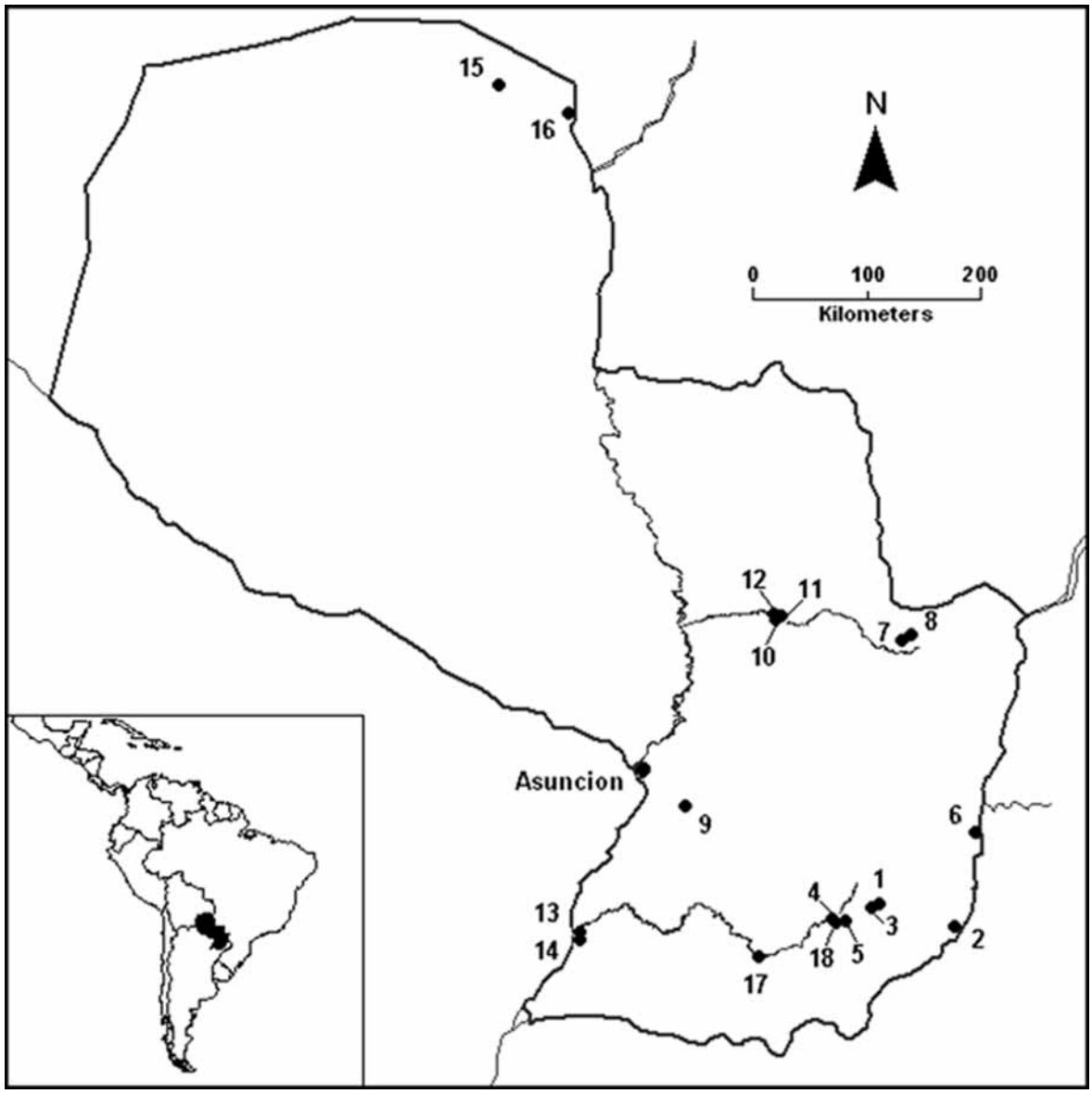

FIGURE 1. Map of Paraguay indicating the localities where the specimens reported here were collected. Locality numbers refer to those of the text.

Results

Family Cricetidae Fischer

Subfamily Sigmodontinae Wagner

Tribe Akodontini Vorontzov (sensu D'Elía, 2003)

Genus *Akodon* Meyen

***Akodon paranaensis* Christoff *et al*.**
Fig. 2. Table 1.

Type Locality: Piraquara (Estacão Ecológica Canguiri), Paraná, Brazil.

Distribution: Extreme northeastern Misiones Province in northeastern Argentina, and southeastern Brazil.

FIGURE 2. Dorsal, ventral and lateral views of the cranium and mandible of *Akodon paranaensis* from Paraguay (TK 66278). Scale bar = 5 mm.

New records: 1) ITAPUA, Estancia Parabel, 0.3 km E of houses, 26º 20.91' S 55º 30.75' W, 420 m (TK 66185, TK 66278). Figure 1.

Taxonomy: *Akodon* is the most diverse genus of Sigmodontinae with around 42 forms currently considered as valid species, and with several more taxonomic forms considered as subspecies or full synonymies of the valid forms (Musser & Carleton 2005). As expected given these numbers, several aspects of the *Akodon* alpha taxonomy remain confused and poorly addressed. Among them are the distinction of *A. paranaensis* and *A. reigi* Gonzalez *et al*. These two species are very similar morphologically, share the same diploid complement of 2n = 44, show complementary distributions, and are sister to each other in phylogenetic analyses (Fig, 3; see also Gonçalves *et al*. 2007). Remarkably, in the description of *A. paranaensis* (Christoff *et al*. 2000), no comparison with *A. reigi* was made. Moreover, the same populations in southern Rio Grande do Sul (southern Brazil) were allocated to both species in their original descriptions (Gonzalez *et al*. 1998; Christoff *et al*. 2000). Our analysis includes a haplotype recovered from a paratype of *A. reigi* (MNHNA 3682), but lacks haplotypes from the type locality of *A. paranaensis* as well as from intermediate areas of Rio Grande do Sul. Therefore, we recognize for the moment both forms as valid species, and since the Paraguayan haplotypes fall in the northern clade (i.e, *A. paranaensis*; Fig. 3), we allocate the Paraguayan specimens to *A. paranaensis*. Haplotypes recovered from populations assigned to *A. paranaensis* (i.e., those from Brazil, northern Argentina, and Paraguay) and to *A. reigi* (those from Uruguay), which form reciprocally monophyletic groups, differ on average by 5.93 % (observed divergence: range 4.37 – 10.62 %, n=12). Observed variation within *A. paranaensis* ranges from 1.0 to 9.48 %, while that observed between the available pair of haplotypes of *A. reigi* is 3.8 %.

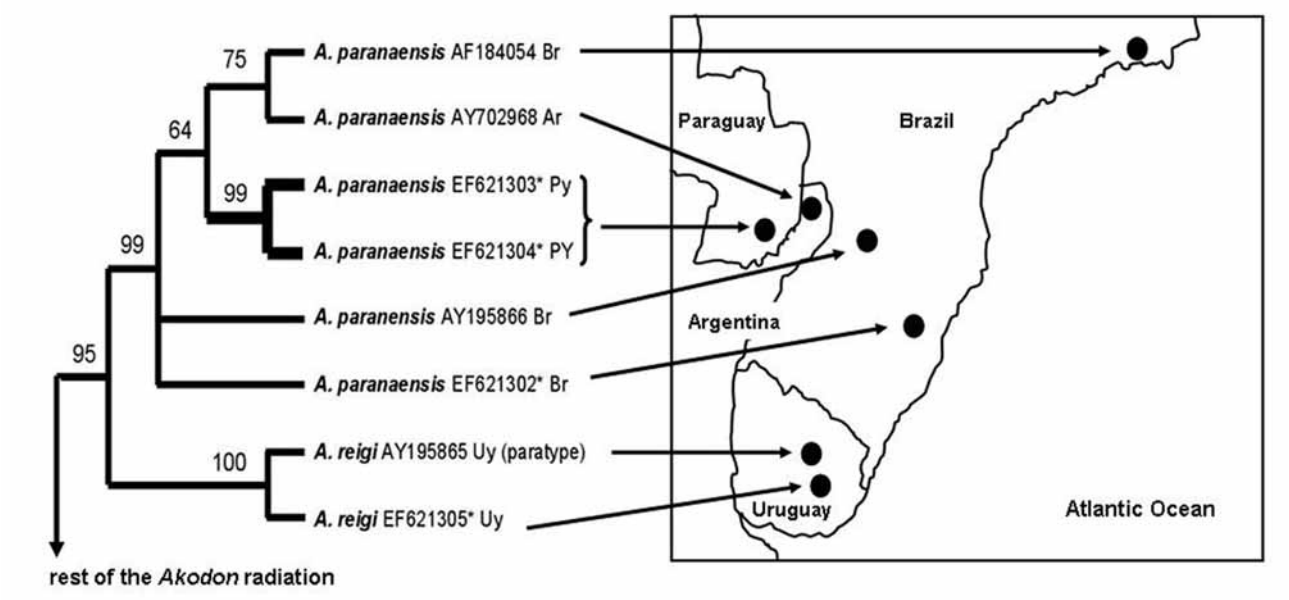

FIGURE 3. Partial phylogenetic hypothesis of *Akodon* (strict consensus of 2 most parsimonious trees: 531 steps; IC=0.571; IR=0.568) showing the relationships of cytochrome *b* haplotypes recovered from specimens assigned to *A. paranaemsis* and *A. reigi*. Numbers at nodes indicate jackknife support values. Genbank accession numbers are listed next to species names. Arrows indicate the localities where the specimens were collected. The Paraguayan locality corresponds to locality 1 in Figure 1. * indicates that the sequence was generated in this study.

Comments: These specimens constitute the first citation of *A. paranaensis* for Paraguay; which elevates to four the number of *Akodon* species (*A. azarae*, *A. montensis*, and *A. toba* in addition to *A. paranaensis*) known for the country (Myers *et al*. 2002). The Paraguayan records expand to the west the known distribution of *A. paranaensis*. These specimens were collected in primary tropical forest as well as in secondary forest. Importantly, these records indicate that *A. paranaensis* also inhabits forested areas, in addition to grasslands.

The specimens reported here were collected in the month of October (1998) and were males with scrotal testes. Other small mammal species collected in the same traplines as the *A. paranaensis* reported here include the sigmodontines *Akodon montensis*, *Bibimys chacoensis* (Shamel), *Oligoryzomys nigripes* (Olfers), and *Thaptomys nigrita* (Lichtenstein), and the small didelphid *Monodelphis sorex* (Hensel).

TABLE 1. Measurements (mm), weight (gm), and sex of specimens representing new or noteworthy records from Paraguay. Data were taken from specimen tags and field catalogs. TBL, total body length; TL, tail length; HF, hind foot length (including the claw); EL, ear length; W: weight.

Species	Catalog number	sex	TBL	TL	HF	EL	W
Akodon paranaensis	TK 66185	♂	203	95	25	18	39.1 g
A. paranaensis	TK 66278	♂	231	107	29	18	42.4 g
Bibimys chacoensis	GD 153	♀	185	80	23	18	40.5 g
B. chacoensis	TK 65978	♂	163	80	21	16	19.2 g
B. chacoensis	TK 66294	♂	161	74	25	16	20.4 g
B. chacoensis	TK 66400	♂	178	81	20	16	24.8 g
B. chacoensis	TK 66401	♂	(132)	(37)	21	16	23.5 g
B. chacoensis	TK 66436	♂	179	76	22	16	33.1 g
B. chacoensis	TK 132621	♀	(142)	(35)	21	16	39 g
Oxymycterus misionalis	TK 130587	♀	303	135	36	25	121 g
O. misionalis	TK 121751	♀	(277)	(132)	35	26	87 g
O. misionalis	TK 121752	♂	(281)	(151)	36	26	140 g
Cerradomys maracajuensis	GD 371	♀	378	207	40	21	115 g
C. maracajuensis	GD 372	♀	383	206	40	22	120 g
C. maracajuensis	GD 373	♀	366	202	39	22	94.5 g
C. maracajuensis	GD 389	♀	244	142	31	14	25.5 g
C. maracajuensis	GD 390	♂	396	212	41	22	135 g
Pseudoryzomys simplex	GD 065	♀	252	132	30	16	38.4 g
P. simplex	TK 61744	♂	247	128	30	17	38.5 g
Sciurus urucumus	TK 67300	♀	467	234	63	33	352 g
Sphiggurus spinosus	GD 252	♀	547	214	61	17	1040 g
S. spinosus	UMMZ 174975	♀	615	236	58	26	?

Genus *Bibimys* Massoia

***Bibimys chacoensis* (Shamel)**
Fig. 4. Table 1

Type Locality: Las Palmas, Chaco, Argentina.

Distribution: Known from the Argentinean provinces of Chaco, Formosa and Misiones.

New records: ITAPUA: 1) Estancia Parabel, 0.3 km E of house, 26º 20.91' S 55º 30.75' W, 420 m (TK 66294); 2) 3.2 km N, 0.4 km E Ape Aimé 26 32.13' S 54 50.44' W (TK 65978); 3) Estancia Parabel, 5.8 km SW of house (by road), 26º 23.34' S 55º 32.25' W, 360 m (TK 66400, TK 66401, TK 66436); 4) Estancia San Isidro, 5.18 km NW of houses, 26º 29.284' S; 55º 53.803' W (GD 153); 5) Parque Nacional San Rafael 26º 30’ 14.2’’ S 55º 47’ 32.5’’ W, 134 m (TK 132621). Figure 1.

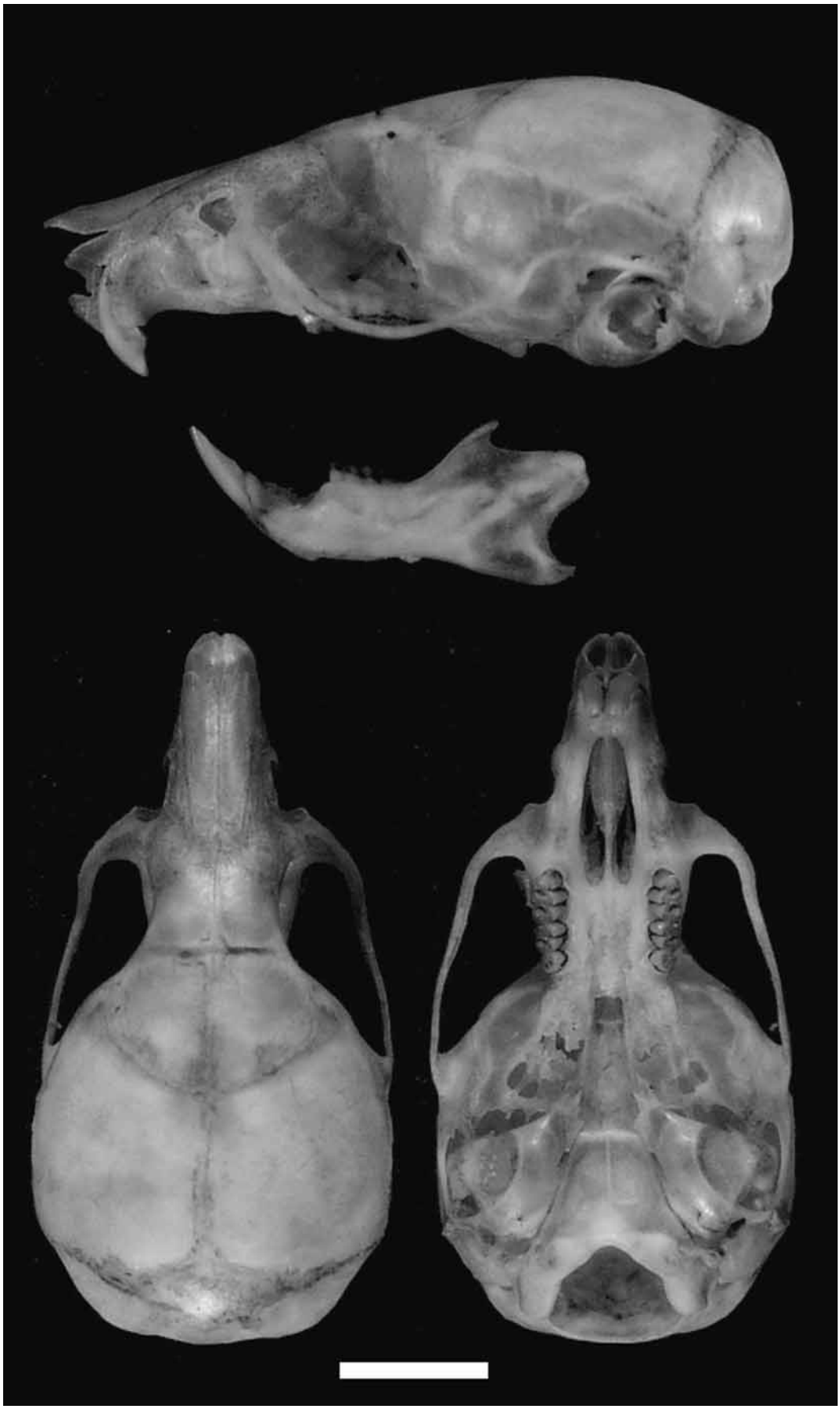

FIGURE 4. Dorsal, ventral and lateral views of the cranium and mandible of *Bibimys chacoensis* from Paraguay (TK 132621). Scale bar = 5 mm.

Taxonomy: The genus *Bibimys* was recently revised by D'Elía *et al*. (2005). Results of analyses of morphological and molecular geographic variation that included individuals assigned to the three currently recognized species of *Bibimys* (*B. chacoensis*, *B. labiosus* [Winge], *B. torresi* Massoia) question the distinctiveness of these forms. However, no formal change in the taxonomy of *Bibimys* species was proposed.

Comments: These records constitute the first formal mention of the genus *Bibimys* for Paraguay, and the specimens are referred to *B. chacoensis*. These records partially fill the gap in the previous known distribution of the species, which had been reported from the Argentinean provinces of Chaco and Formosa in the west, and Misiones in the east (D'Elía *et al*. 2005; Pardiñas & Teta 2005). Field notes available for some of the Paraguayan specimens of *Bibimys* indicate that they were trapped in small patches of humid grassland near or inside remnants of tropical forest. Four of the specimens were males collected from July to September (1998) that presented scrotal testes. A female collected in January (2007) had a closed vagina, while another collected in November (1999) was lactating and had an open vagina. Other mammal species collected in the same trap lines as the specimens of *Bibimys* were *Akodon montensis*, *A. paranaensis*, *Monodelphis sorex*, *Necromys lasiurus* (Lund), *Nectomys squamipes* (Brants), and *Oligoryzomys fornesi* (Massoia).

Genus *Oxymycterus* Waterhouse

***Oxymycterus misionalis* Sanborn**
Fig. 5. Table 1

Type Locality: Río Paranay, Misiones, Argentina; restricted to the confluence of the Paranay Guazú and Paraná Rivers, General San Martín, Misiones by Pardiñas et al. (2007).

Distribution: Known from the Argentinean province of Misiones and from Alto Paraná in Paraguay.

New records: ALTO PARANA: 6) Puerto Bertoni, 25º.38' S 54º.40' W, 91 m (BMNH 21.4.21.4). CANINDEYU: 7) Colonia Britez Cue, 24º 15' 05.2'' S 55º 18' 24.1'' W, 222 m (TK 130587); 8) Colonia Britez Cue, 24º 14' 21'' S 55º 16' 04'' W, 266 m (TK 121751, TK 121752, TK 141169). Figure 1. The record from Alto Paraná was taken from the unpublished dissertation of Joäo A. Oliveira (1998).

Taxonomy: In spite of recent advances (e.g. Oliveira 1998; Hoffmann et al., 2002), the alpha taxonomy of *Oxymycterus* remains confused in several aspects, and as explained below, difficult issues continue to arise. Our records may play a key role to solve a complex *Oxymycterus* nomenclatorial and taxonomic issue, as they approximate the probable collection locality of the type of *O. rufus* (Fischer) and by extension, the population which should be ascribed to this taxon. By their morphology, our specimens belong to the species presently bearing the name *O. misionalis*, not to *O. rufus* as it is currently understood (for a detailed revision of *Oxymycterus* see Oliveira 1998). However, they may in fact represent the latter taxon. Fischer (1814) named *Oxymycterus rufus* on the basis of Azara's (1801) description of the "rat roux" (Contreras & Teta 2003). Azara based his description on a mouse sent to him by his friend Pedro Blas Noceda, a priest that practiced at the towns of Santiago, Santa María de Fe, and San Ignacio, in southern Paraguay. This convinced Galliari *et al*. (1996) to restrict the type locality of *O. rufus* to San Ignacio in the Department of Misiones, Paraguay. By the same line of reasoning, more than 150 years earlier, Rengger (1830) restricted the type locality of *O. rufus* to an area (Ñu Guazu) near Asunción, the Paraguayan capital. The view that the type locality of *O. rufus* lies in Paraguay was followed, sometimes with simplifications, by later authors (e.g., Gyldenstolpe 1932 indicated only "Paraguay" as the type locality; Cabrera 1961). The actual place where Noceda collected the specimens, however, remains unknown. This uncertainty, in conjunction with two other issues, has led most authorities of sigmodontine taxonomy during the last two decades to consider the *terra typica* of *O. rufus* to lie in Argentina rather than Paraguay (e.g., Hershkovitz 1994, Oliveira 1998; Musser and Carleton 2005; but see Contreras & Teta 2003). The first of these issues is that a second specimen of *Oxymycterus* ("hocicudo") described by Azara (1802) was incorrectly assumed to be the same individual that served as the diagnosis basis of the rat

roux (see details in Contreras & Teta 2003). In his 1802 book, Azara provided latitudinal information (32 ½ degrees) for the collection site of the hocicudo. Musser and Carleton (1993) and Hershkovitz (1994) assumed that the hocicudo and the rat roux were the same specimen and as a result, erroneously suggested that the bibliographical type of *O. rufus* was collected at that latitude, which falls outside of Paraguayan borders. Moreover, it was assumed that Paraguay was inhabited only by a blackish form of *Oxymycterus* described as *O. delator* Thomas (a report by de Roguin, 1986:1819-1829, of a reddish specimen collected in 1982 near Ciudad del Este in eastern Paraguay, and identified as *O. rutilans* --a synonym of *O. rufus*-- was overlooked.) As a result, currently most authorities list the type locality of *O. rufus* as lying outside Paraguay. Our records, together with the observation of de Roguin (1986), of a relatively reddish form from Paraguay suggest, in accordance with Contreras and Teta (2003), among others, that Azara may indeed have used a Paraguayan mouse to describe the rat roux. In turn, this implies that the type locality of *O. rufus* may be restricted to a location within Paraguay. We note that our records are about 275 and 340 km from San Ignacio, the area to which Galliari *et al*. (1996) restricted the type locality of *O. rufus*, but more than likely in Azara's time forest habitats were continuous between the two areas.

We are aware of the important nomenclatorial changes that the scenario we pose would cause in *Oxymycterus* taxonomy. But we also note that that taxonomy would revert, at least in part (i.e., the placement of the *O. rufus* type locality within Paraguay), to a scenario that was abandoned only recently (i.e., Musser & Carleton 1993; Hershkovitz 1994). Here, we do not innovate in this respect and refer these Paraguayan specimens to *O. misionalis*, preferring to reserve further treatment of this problem for an upcoming contribution focused on *Oxymycterus* systematics by D'Elía and collaborators.

On a related issue, Musser and Carleton (2005) considered *O. misionalis* and *O. judex* as junior synonyms of *O. quaestor* Thomas. It is worth noting that a cyt *b* haplotype recovered from the Paraguayan specimen TK 12151 (EU449517) is only 0.5 % divergent from *O. misionalis* (one specimen) from Argentina and from *O. judex* (two specimens) from Brazil, and is 2.8 – 2.9 % divergent with haplotypes referred to *O. quaestor* (three specimens) from Brazil. We recognize that the relationship among *misionalis*, *judex*, and *quaestor* is yet another unresolved taxonomic issue within the genus *Oxymycterus*, and therefore, pending further study, we prefer to follow the most recent reviews (Oliveira, 1998 and Hoffmann *et al.* 2002), in recognizing *O. misionalis* as a valid species.

Comments: These records constitute the first citation of the *O. misionalis* for Paraguay (but see above, especially concerning the specimen reported by de Roguin 1986). This report confirms that two species of *Oxymycterus* inhabit Paraguay; these are currently referred to as *O. delator* and *O. misionalis*. Specimens of the latter were collected in low secondary forest and abandoned crop fields. A female and a male collected in February (2007) had vagina open and scrotal testes, respectively. An adult female collected in June (2006) had the vagina closed. Others (all adults) captured and released in June included one female with vagina closed, three males with testes scrotal, and one with testes abdominal. Other sigmodontines collected in the same trap lines with *O. misionalis* include *Akodon montensis*, *Calomys callosus* (Rengger), and *Necromys lasiurus*.

Tribe Oryzomyini Vorontsov (sensu Voss and Carleton, 1993)

Genus *Cerradomys* Weksler *et al.*

***Cerradomys maracajuensis* (Langguth and Bonvicino, 2002)**
Table 1

Type Locality: Brazil, Mato Grosso do Sul: Municipality of Maracaju (approx. 21°38'S, 55°09'W) Fazenda da Mata.

FIGURE 5. Dorsal, ventral and lateral views of the cranium and mandible of *Oxymycterus misionalis* from Paraguay (TK 121752). Scale bar = 5 mm.

Distribution: Known from the type locality, in the Brazilian state of Mato Grosso do Sul, Municipality of Maracaju (approx. 21º38'S, 55º09'W), Fazenda da Mata and from one specimen (CE 2589) from Paraguay with unpublished locality data.

New records: PARAGUARI: 9) Paraguari (CE-2584). SAN PEDRO: 10) Ganadera La Carolina, 1.5 KM SO de las casas, 24º 06.169´ S 56º 25.624´ W (GD 371, GD 372, GD 373, GD 374, GD 375, GD 376); 11) Ganadera La Carolina, 745 m O de las casas 24º 05.698' S 56º 25.439' W (GD 390); 12) Ruta 3 sobre margen norte del Río Jejui Guazu 24º 04.979' S 56º 26.222' W (GD 389). Figure 1.

Taxonomy: This species was recently described and to date no geographic variation has been reported.

Comments: The first mention of *C. maracajuensis* for Paraguay was given by Pardiñas and Teta (2005) who mentioned specimen CE 2589 without giving locality data. This specimen was collected at Luque in the Department of Central (Pablo Teta, com. pers.). Our records expand to the northeast and southeast the known distribution of this species in Paraguay. A female collected in March (2001) gave birth to three young (measurements of one young were TBL=89, TL=36, HF=12, EL=5, W=6g). Other females collected at the same time had open or closed vagina. Specimens in San Pedro were collected with traps set on the ground in riparian forest and in nearby grasslands together with *Akodon montensis*, *Calomys callosus*, *Didelphis albiventris* Lund, and *Oligoryzomys nigripes.*

Genus *Pseudoryzomys* Hershkovitz

***Pseudoryzomys simplex* (Winge)**
Fig. 6. Table 1

Type Locality: Lagoa Santa, Minas Gerais, Brasil.

Distribution: Southern Peru, Eastern Bolivia, eastern and central Brazil, western Paraguay, and northeastern Argentina.

New records: ÑEEMBUCU: 13) Estancia Yacaré, Puesto San Fernando 26º 35.511' S 58º 08.329´ W (GD 065); 14) Estancia Yacaré, 26 38.05' S 58 08.27' W, 60 m (TK 61744). Figure 1.

Taxonomy: *Oryzomys wavrini* Thomas (type locality in the Paraguayan Chaco) and *P. wavrini reigi* Pine and Wetzel are considered synonyms of *P. simplex* (Voss & Myers 1991).

Comments: These specimens constitute the first record of the genus east of the large Paraguay River (Paraguayan Oriental Region). Moreover, these records are the first example of *P. simplex* east of the Paraguay-Paraná rivers system in Argentina and Paraguay (see Pardiñas *et al*. 2004). A cyt *b* haplotype (773 bp) of one of the specimens (GD 065: EF621306) from Ñeembucu differs by 1.4 % from a haplotype of a Chacoan specimen (TK 62425: EF621307) collected across the Paraguay River and about 600 km to the northwest in Alto Paraguay (21º 17.93' S 59º 33.87' W). A female collected in September (1999) had a closed vagina. Specimens in Ñeembucu were collected with traps set on the ground in humid grassland along with specimens of *Akodon azarae* and *Holochilus chacarius* Thomas.

Family Sciuridae Fischer

Subfamily Sciurinae Fischer

Genus *Sciurus* Linnaeus

***Sciurus urucumus* Allen**
Fig. 7. Table 1

FIGURE 6. Dorsal, ventral and lateral views of the cranium and mandible of *Pseudoryzomys simplex* from eastern Paraguay (TK 61744). Scale bar = 5 mm.

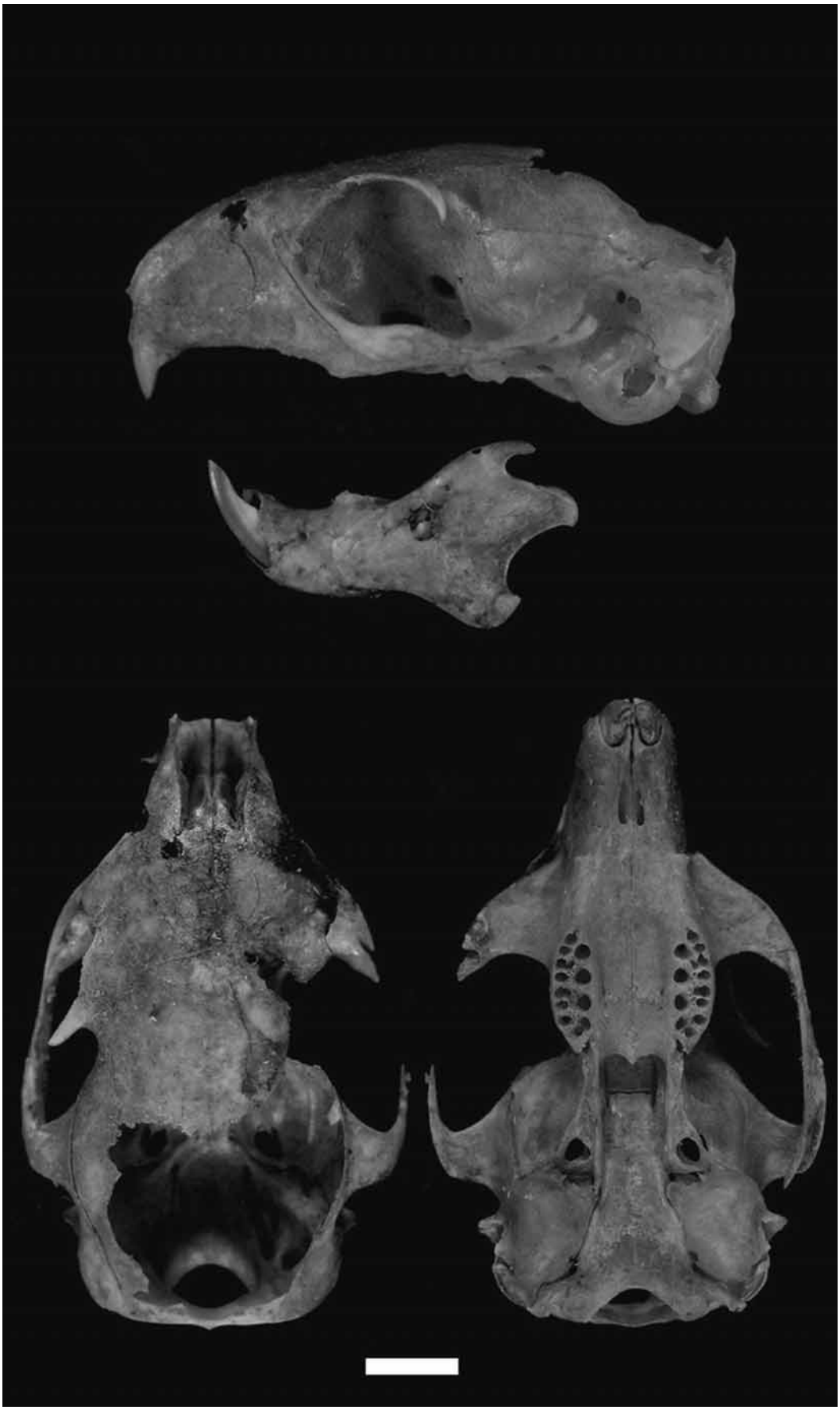

FIGURE 7. Dorsal, ventral and lateral views of the cranium and mandible of *Sciurus urucumus* from Paraguay (TK 67300). Scale bar = 5 mm.

Type Locality: Urucum (altitude 400 feet), Rio Paraguay (at mouth of Rio Tacuari), State of Mato Grosso do Sul, Brazil.

Distribution: Known from the region around the type locality in Brazil (e.g., Tapiropoan by the Sepotuba River).

New record: ALTO PARAGUAY: 15) Parque Nacional Rio Negro, Estancia Kamba Aka, 19° 50.342' S 58° 45.302' W (TK 67300); Figure 1.

Taxonomy: *Sciurus urucumus* was originally described as a subspecies of *S. langsdorffii* Brandt, which is currently regarded as a synonym of *Sciurus spadiceus* Olfers (e.g., Thorington & Hoffmann 2005). However, a revision currently underway of the species of South American Sciuridae indicates that *S. urucumus* represents a valid species (de Vivo, pers. com.).

Comments: This specimen represents the first citation of the family Sciuridae for Paraguay. The locality is about 140 km SW of the type locality (Fig. 1). The specimen is a female with vagina open (date of collection: January 12, 2003), collected with a shotgun near midday in Chiquitano forest. The specimen was in a tree about eight m from the ground. Field observations show that in the area *S. urucumus* feeds on fruits of the palm *Copernicia alba*.

We examined a second specimen of *Sciurus* from Paraguay, from W Bank Rio Negro, 8 km above mouth, 20° 05.919' S 58° 08.764' W (locality 16, Fig. 1) (KU 165551). This specimen, consisting of a skin from what seems to be a juvenile individual, appears not to be referable to *S. urucumus*; however, we are unable to determine its specific identity.

Family Erethizontidae Bonaparte

Subfamily Erethizontinae Bonaparte, 1845

Genus *Sphiggurus* F. Cuvier

***Sphiggurus spinosus* (F. Cuvier)**
Table 1

Type Locality: Paraguay, along the Paraná River.

Distribution: Northeast Argentina, southeastern Brazil, Paraguay, northeastern Uruguay.

New records: CAAZAPA: 17) Estancia Dos Marías, 12.2 Km SSO de las casas, Costa del Río Tebicuary, 26º 47.719’ S 56º 32.979´ W (UMMZ 174975). ITAPUA: 18) Estancia San Isidro, 6.6 km NE of houses, 26º 31.372’ S, 55º 51.767´ W (GD 252). Figure 1.

Taxonomy: *Sphiggurus* is a taxon in need of revision. Problems range from its distinction from *Coendou* Lacépède to the limits of its species, including *S. spinosus*. Although morphologically *Sphiggurus* is similar to *Coendou* (e.g., Handley & Pine 1992; but see Massoia & Vaccaro 1991), recent phylogenetic analysis of molecular data indicates that both constitute independent lineages (Bonvicino *et al*. 2002).

Comments: To our knowledge, these specimens constitute the first records corroborated by voucher specimens for these departments of the Paraguayan Oriental Region. The specimen from Caazapá was collected in riparian forest of the Tebicuary River; the specimen from Itapúa was caught by hand in an artificial prairie about 300 m from the closest forest island.

Discussion

The Paraguayan mammal fauna is diverse and, since the pioneering work of Felix de Azara (1801, 1802), has attracted the attention of generations of naturalists and mammalogists. Much remains to be learned about this

community, however, including in some cases such basic aspects as the identity of its members and their distributions. The results presented here contribute to filling several gaps in our understanding of this diverse fauna. With those taxa cited here for the first time, the known sigmodontine fauna of Paraguay includes 29 species and 18 genera (Table 2). Similarly, if one considers Myocastoridae and Hydrochoeridae as valid (e.g., Woods and Kilpatrick, 2005), the number of native rodent families present in Paraguay is 11.

TABLE 2. Sigmodontinae species known from Paraguay.

	Genus	species	Region
1	*Akodon*	*azarae*	Chaco and Oriental
2	*Akodon*	*montensis*	Oriental
3	*Akodon*	*paranaensis*	Oriental
4	*Akodon*	*toba*	Chaco
5	*Andalgalomys*	*pearsoni*	Chaco
6	*Bibimys*	*chacoensis*	Oriental
7	*Calomys*	*callosus*	Chaco and Oriental
8	*Calomys*	*laucha*	Chaco and Oriental
9	*Calomys*	*musculinus*	Chaco and Oriental
10	*Cerradomys*	*maracajuensis*	Oriental
11	*Euryoryzomys*	*russatus*	Oriental
12	*Graomys*	*griseoflavus*	Chaco
13	*Holochilus*	*chacarius*	Chaco and Oriental
14	*Holochilus*	*brasiliensis*	Chaco and Oriental
15	*Hylaeamys*	*megacephalus*	Oriental
16	*Necromys*	*lasiurus*	Chaco and Oriental
17	*Necromys*	*lenguarum*	Chaco
18	*Nectomys*	*squamipes*	Oriental
19	*Oecomys*	*mamorae*	Chaco and Oriental
20	*Oligoryzomys*	*chacoensis*	Chaco and Oriental
21	*Oligoryzomys*	*flavescens*	Oriental
22	*Oligoryzomys*	*fornesi*	Chaco and Oriental
23	*Oligoryzomys*	*nigripes*	Oriental
24	*Oxymycterus*	*delator*	Oriental
25	*Oxymycterus*	*misionalis*	Oriental
26	*Pseudoryzomys*	*simplex*	Chaco and Oriental
27	*Scapteromys*	*aquaticus*	Chaco and Oriental
28	*Sooretamys*	*angouya*	Chaco and Oriental
29	*Thaptomys*	*nigrita*	Oriental

The extensions of known species distributions due to our new records are also of importance for understanding the biogeographic history of the region. Our records of *Akodon paranaensis*, *Bibimys chacoensis*, and *Oxymycterus misionalis* are from the Oriental Region of Paraguay, which is northwest of the Parana River, traditionally considered to be a substantial biogeographic barrier for small non-volant mammals (e.g., Galliari & Goin 1993). Previously these species were understood to inhabit forested and neighboring areas to the southeast of the Paraná River in Argentina, and in the case of *A. paranaensis*, Brazil (see comments under

O. misionalis about its distinction from Brazilian *O. quaestor*). Although several other taxa are known only from the Argentinean and Brazilian Atlantic forest southeast of the Paraná River (e.g., the genera *Abrawayaomys* Souza Cunha and Cruz, *Blarinomys* Thomas, and *Delomys* Thomas), our new records demonstrate that the mammal fauna of the Paraguayan Oriental Region is more similar in species richness and composition to that of adjacent regions of Argentina and Brazil than previously realized. In this vein, it is interesting to note that apparently the Paraná River has not molded the genetic structure of *A. paranaensis*; some haplotypes east of the river are more related to those found to the west of the river in Paraguay than to those from eastern localities. Denser geographic sampling is needed to allow better estimation of the phylogeographic structure of this species.

Within Paraguay there are marked differences between the mammal communities found west and east of the Paraguay River (Myers 1982; Myers *et al*. 2002; López-González, 2004). Within Sigmodontinae, *Akodon toba*, *Andalgalomys pearsoni* (Myers), and *Graomys griseoflavus* (Waterhouse) are only known from the Chaco, whereas *Oxymycterus delator* and *Thaptomys nigrita*, among others, are known only from the Oriental Region. Previously, Argentinean and Paraguayan populations of *Pseudoryzomys simplex* were understood to be restricted to the Chaco; i.e., all populations of *P. simplex* at these latitudes were thought to be west of the axis formed by the large Paraguay and Paraná Rivers (Myers 1982; Pardiñas *et al*. 2004; see Fig. 1). In contrast, our specimens were collected east of the Paraguay River, close to one of its main tributaries, the Tebicuary River, in Ñeembucú (southern Paraguay). These records may indicate that the biogeographic history of the Ñeembucú region is more complex than previously recognized. These records also suggest that Paraguayan assemblages of small non-volant mammals on both sides of the Paraguay River are more similar than previously envisioned (Myers 1982; see also Myers and Carleton 1981). We note that *Calomys callosus* and *C. laucha* (Fischer), previously considered being exclusively chacoan species (e.g., Myers 1982), have also now been recorded in eastern Paraguay (Salazar-Bravo *et al*. 2002; Myers *et al*. 2002; our unpublished data). Similarly, *C. musculinus* (Thomas), previously known only from eastern Paraguay (e.g., Myers 1982), has been found to be abundant in the Chaco (Yahnke et al., 2001). Still, the mammal faunas on both sides of the Paraguay River are markedly different; of the 29 sigmodontine species recorded for Paraguay, 13 are distributed on both sides of River, four are exclusively found in the Chaco, while the remaining 12 are found exclusively in the Oriental Region (Table 2).

Finally, the records presented here, which include among others the first Paraguayan record of a family of mammals (Sciuridae), unquestionably highlight the need for continuing specimen collections in that country. It is important to note that the majority of the specimens that constitute the base of our records were recently collected by us, rather than being encountered among earlier collections. Although new records continue to be found among earlier collections (e.g, a second species of *Cerradomys*; Percequillo *et al*., pers. com.), we expect that additional collecting, including the usage of collection methodologies that have not been broadly employed in Paraguay (e.g., pit fall and arboreal traps), will also provide additional new records for the country. Finally, we note that the alarming rate of human induced habitat alteration occurring in Paraguay (Di Bitetti *et al*. 2003; Fragano & Clay, 2003; Huang *et al*. 2007) implies that the proposed collection work and its implication in the better knowledge of the Paraguayan small mammal community does not admit delays.

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References

Azara, F. de. (1801) Essais sur l´Historie Naturelle des Quadrupédes de la Province du Paraguay. Tome Second. Imprière C. Pougens, Paris.

Azara, F. de. (1802) Apuntamientos para la historia natural de los quadrúpedos del Paraguay y Río de La Plata. Tomo segundo. Imprenta de la Viuda de Ibarra, Madrid.

Bonvicino, C.R., Penna-Firme, V., & Braggio, E. (2002) Molecular and karyologic evidence of the taxonomic status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). *Journal of Mammalogy*, 83, 1071–1076.

Cabrera, A. (1961) Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Zoología*, 4, 309–732.

Carleton, M.D. & Musser, G.M. (2005) Order Rodentia. *In*: Wilson, D.E. & Reeder, D.M. (Eds.) *Mammal species of the world: A taxonomic and geographic reference*. 3rd edition, vol. 2. The John Hopkins University Press, Baltimore, 745–752.

Christoff, A.U., Fagundes V., Sbalqueiro, I.J., Mattevi, M.S. & Yonenaga-Yassuda, Y. (2000) Description of a new species of *Akodon* (Rodentia: Sigmodontinae) from southern Brazil. *Journal of Mammalogy*, 81, 838–851.

Contreras, J.R. & Teta, P. (2003) Acerca del estatus taxonómico y de la localidad típica de *Oxymycterus rufus* (Fisher, 1814) (Rodentia: Muridae: Sigmodontinae). *Nótulas Faunísticas*, 14, 1–5.

de la Sancha, N., Solari, S. & Owen, R.D. (2007) First records of *Monodelphis kunsi* Pine (Didelphimorphia, Didelphidae) from Paraguay, with an evaluation of its distribution. *Mastozoologia Neotropical*, 14, 241–247.

D'Elía, G. (2003) Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. *Cladistics*, 19, 307–323.

D'Elía, G., González, E. & Pardiñas, U.F.J. (2003) Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. *Mammalian Biology*, 68, 351–364.

D'Elía, G., Pardiñas, U.F.J. & Myers, P. (2005) An introduction to the genus *Bibimys* (Rodentia: Sigmodontinae): phylogenetic position and alpha taxonomy. *In:* Lacey, E. & Myers, P. (Eds.) *Mammalian Diversification: From Chromosomes to Phylogeography.* University of California Publications in Zoology series 133, Berkeley, 211–246.

de Roguin, L. 1986. Les Mammifères du Paraguay dans les collections du Muséum de Genève. *Revue Suisse de Zoologie*, 93, 1009–1022.

Di Bitetti, M.S., Placci, G. & Dietz, L.A. (2003) *Una Visión de Biodiversidad para la Ecoregion del Bosque Atlántico del alto Paraná: Diseño de un Paisaje para la Conservación de la Biodiversidad y Prioridades para las Acciones de Conservación.* Washington, D.C., World Wildlife Fund.

Farris, J.S. (1982) The logical basis of phylogenetic analyis. *In*: Platnick N. & Funk V. (Eds.) *Advances in Cladistics: Proceedings of the Second Meeting of the Willi Hennig Society.* Columbia University Press, New York, 7–36.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12, 99–124.

Fisher, G. (1813-1814). *Zoognosia tabulis Synopsis Illustrata*. Nicolai Sergeidis Vsevolozsky, Moscow 3 vols. (3–1814).

Fragano, F., & Clay, R. (2003). Biodiversity status of the interior Atlantic forest of Paraguay. *In*: C. Galindo-Leal & I.d.G. Camara (Eds.), *The Atlantic forest of South America: Biodiversity status, threats, and outlook*. Island Press,

Washington, 288-309.
Frutos, S.D. & van den Bussche, R.A. (2002) Genetic diversity and gene flow in nine-banded armadillos in Paraguay. *Journal of Mammalogy*, 83, 815–823.
Galliari, C.A. & Goin, F.J. (1993) Conservación de la biodiversidad en la Argentina: el caso de los mamíferos. *In*: Goin F.J. & Goñi, R. (Eds.) *Elementos de Política Ambiental*. Honorable Cámara de Diputados de la Provincia de Buenos Aires, Buenos Aires, 367–400.
Galliari, C.A., Pardiñas, U.F.J. & Goin, F.J. 1996. Lista comentada de los mamíferos argentinos. *Mastozoología Neotropical*, 3, 39–61.
Gonçalves, P.R., Myers, P., Vilela, J.F. & Oliveira, J.A. (2007) Systematics of species the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern Brazil and implications for the biogeography of the campos de altitude. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 197, 1–24.
González, E.M., Langguth, A. & de Oliveira L.F. (1998) A new species of *Akodon* from Uruguay and Southern Brazil (Mammalia: Rodentia: Sigmodontinae). *Comunicaciones Zoológicas del Museo de Historia Natural, Montevideo*, 191, 1–8.
Gyldenstolpe, N. (1932) A Manual of Neotropical Sigmodont Rodents. *Kungli Svenska Vetenskapsakademiens Handligar*, 11, 1–164.
Handley, C.O. Jr. & Pine R.H. (1992) A new species of *Coendou* Lacépède, from Brazil. *Mammalia*, 56, 237–244.
Hershkovitz, P. (1994) The description of a new species of South American hocicudo, or long-nose mouse, genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. *Fieldiana: Zoology. New Series*, 79, 1–43.
Hoffmann, F.G., Lessa, E.P. & Smith, M.F. (2002) Systematics of *Oxymycterus* with description of a new species from Uruguay. *Journal of Mammalogy*, 83, 408–420.
Huang, C., Kim, S., Altstatt, A., Townshend J.R.G., Davis, P., Song, K., Tucker, C.J., Rodas, O., Yanosky, A., Clay, R. & Musinsky, J. (2007) Rapid loss of Paraguay's Atlantic forest and the status of protected areas – A Landsat assessment. *Remote Sensing of Environment*, 106, 460–466.
López-González, C. (2004) Ecological zoogeography of the bats of Paraguay. *Journal of Biogeography*, 31, 33-45.
López-González, C., Presley, S.J., Owen, R.D., Willig, M.R. & Gamarra de Fox, I. (1998) Noteworthy records of bats (Chiroptera) from Paraguay. *Mastozoología Neotropical*, 5, 41–45.
Massoia, E. & Vaccaro, O.B. (1991) El estado sistemático de los géneros *Sphiggurus* F. Cuvier, 1825 y *Coendou* Lacépède, 1799 (Mammalia, Rodentia, Histricomorpha, Erethizontidae). *Boletín Científico, APRONA*, 19, 47-52.
Musser, G.G. & Carleton, M.D. (1993). Family Muridae. *In*: Wilson, D.E. & Reeder, D.M. (Eds.) *Mammal species of the world: a taxonomic and geographic reference. 2nd Edition.* Smithsonian Institution Press, Washington, D.C., 501–755.
Musser, G.G. & Carleton, M.D. (2005) Superfamily Muroidea. *In*: Wilson, D.E. & Reeder, D.M. (Eds.) *Mammal species of the world: a taxonomic and geographic reference. 3rd edition, vol. 2.* The John Hopkins University Press, Baltimore, 894–1531.
Myers, P. (1982) Origins and affinities of the mammal fauna of Paraguay. *In*: Mares, M.A. & Genoways, H. (Eds.) *Mammalian biology in South America*. Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania, 6, 85–93.
Myers, P., & Carleton, M.D. (1981). The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixième ou Rat à Tarse Noir". Miscelaneous Publications of the Museum of Zoology University of Michigan, Ann Arbor, 161:1–41.
Myers, P., Taber, A. & Gamarra de Fox, I. (2002) Mamíferos de Paraguay. *In*: Ceballos, G., & Simonetti J.A. (Eds.). *Diversidad y Conservación de los Mamíferos Neotropicales*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico, D. F., 453–502.
Oliveira, J.A. (1998) Morphometric assessment of species groups in the South American rodent genus *Oxymycterus* Sigmodontinae, with taxonomic notes based on the analysis of type material. Unpublished Ph.D. Thesis, Texas Tech University, Lubbock.
Pardiñas, U.F.J. & Teta, P. (2005) Roedores Sigmodontinos del Chaco Húmedo de Formosa: aspectos taxonómicos y distribución geográfica. *In*: Di Giacomo, A.G. & Krapovickas, S.F. (Eds.) *Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo*. Temas de Naturaleza y Conservación 4. Aves Argentinas / Asociación Ornitológica del Plata, Buenos Aires. 501–517.
Pardiñas, U.F.J., Cirignoli, S. & Galliari, C.A. (2004) Distribution of *Pseudoryzomys simplex* (Rodentia: Cricetidae) in Argentina. *Mastozoología Neotropical*, 11, 105–108.
Pardiñas, U.F.J., Teta, P., D'Elía, G., Cirignoli, S., & Ortiz, P.E. (2007). Resolution of some problematic type localities for sigmodontine Rodents (Cricetidae, Sigmodontinae). *In*: Kelt D.A., Lessa, E., Salazar-Bravo, J.A. & Patton. J.L. (Eds.) *The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson*. University of California Publications in Zoology, Berkeley, 391–416.

Rengger, J.R. (1830) *Naturgeschichte der Säugethiere von Paraguay.* Schweghauserschen Buchhandlung, Basel.
Salazar-Bravo, J., Dragoo, J.W., Bowen, M.D., Peters, C.J., Ksiazek, T.G. & Yates, T.L. (2002) Natural nidality in Bolivian Hemorrhagic Fever and the systematics of the reservoir species. *Infection, Genetics and Evolution*, 1, 191–199.
Stevens R.D., Willig, M.R. & Gamarra de Fox, I. (2004) Comparative community ecology of bats in Eastern Paraguay: taxonomic, ecological, and biogeographic perspectives. *Journal of Mammalogy*, 85, 698–707.
Swofford, D. (2000) *PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4.0.* Sinauer Associates Inc., Sunderland.
Thorington, R.W. & Hoffmann, R.S. (2005) Family Sciuridae. *In*: Wilson, D.E. & Reeder, D.M. (Eds.) *Mammal species of the world: A taxonomic and geographic reference.* 3rd edition, vol. 2. The John Hopkins University Press, Baltimore, 754–818.
Voss, R.S. & Carleton, M. (1993) A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. *American Museum Novitates*, 3085, 1–39.
Voss, R.S. & Myers, P. (1991) *Pseudoryzomys simplex* (Rodentia: Muridae) and the significance of Lund´s collections from the caves of Lagoa Santa, Brazil. *Bulletin American Museum of Natural History*, 206, 414–432.
Woods, C.A., & Kilpatrick, C.W. (2005) Infraorder Hystricognathi. *In*: Wilson, D.E. & Reeder, D.M. (Eds.) *Mammal species of the world: A taxonomic and geographic reference.* 3rd edition, vol. 2. The John Hopkins University Press, Baltimore, 1538-1600.
Yahnke, C.J. (2006) Habitat use and natural history of small mammals in the central Paraguayan chaco. *Mastozoología Neotropical*, 13, 103–116.
Yahnke, C.J., Meserve, P.L., Ksiazek, T.G. & Mills, J.N. (2001) Patterns of infection with Laguna Negra virus in wild populations of *Calomys laucha* in the central Paraguayan chaco. *American Journal of Tropical Medicine and Hygiene*, 65, 768–776.