

## **The Taxonomic Status of *Oligoryzomys mato Grossoe* (Allen 1916) (Rodentia: Cricetidae: Sigmodontinae), Reservoir of Anajatuba Hantavirus**

Authors: Weksler, Marcelo, Lemos, Elba M.S., D'Andrea, Paulo Sérgio, and Bonvicino, Cibele Rodrigues

Source: American Museum Novitates, 2017(3880) : 1-32

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3880.1>

---

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## The taxonomic status of *Oligoryzomys mattogrossae* (Allen 1916) (Rodentia: Cricetidae: Sigmodontinae), reservoir of Anajatuba Hantavirus

MARCELO WEKSLER,<sup>1,2</sup> ELBA M.S. LEMOS,<sup>3</sup> PAULO SÉRGIO D'ANDREA,<sup>4</sup> AND CIBELE RODRIGUES BONVICINO<sup>4,5</sup>

### ABSTRACT

Species of the cricetid genus *Oligoryzomys* are found across most Neotropical biomes, and several of them play important roles as natural reservoirs of hantaviruses and arenaviruses. Here we demonstrate that *O. mattogrossae*, previously considered a junior synonym of *O. microtis*, is a valid species, and that it is the oldest available name for specimens previously identified as *O. fornesi* from Brazil and northern Paraguay. Comparative morphology and phylogenetic analyses based on mitochondrial (cytochrome *b*) and nuclear (intron 7 of beta-fibrinogen) genes show that *O. mattogrossae* differs from its sister species *O. microtis* and from other forms of the genus, corroborating previously published karyological data. *Oligoryzomys mattogrossae* occurs in Cerrado and Caatinga habitats throughout central and northeastern Brazil and Paraguay, whereas distribution of *O. fornesi* is apparently restricted to southern Paraguay and northernmost Argentina. Specimens of *O. mattogrossae* were found to be the natural reservoir of the Anajatuba genotype of hantavirus in northeastern Brazil. Therefore, continuing

---

<sup>1</sup> Museu Nacional, Universidade Federal do Rio de Janeiro, Departamento de Vertebrados, Rio de Janeiro, Brazil.

<sup>2</sup> FIOCRUZ, Instituto Oswaldo Cruz, Laboratório de Eco-Epidemiologia de Doença de Chagas, Rio de Janeiro, Brazil.

<sup>3</sup> FIOCRUZ, Instituto Oswaldo Cruz, Laboratório de Hantavirose e Rickttioses, Rio de Janeiro, Brazil.

<sup>4</sup> FIOCRUZ, Instituto Oswaldo Cruz, Laboratório de Biologia e Parasitologia de Mamíferos, Rio de Janeiro, Brazil.

<sup>5</sup> Instituto Nacional de Câncer, Genetics Division, Rio de Janeiro, Brazil.

efforts to delimit *Oligoryzomys* species and facilitate their identification are important for zoonotic monitoring.

## INTRODUCTION

Members of the genus *Oligoryzomys* Bangs, commonly known as pygmy rice rats (*colalar-gas* or *colilargos* in Spanish), are found from northeastern Mexico to extreme southern Chile and Argentina, and occur in several Neotropical biomes, including open vegetation formations such as Cerrado, Pampa, Llano, and Chaco, as well as lowland and montane forests and drier environments, such as Patagonia, Caatinga, and the Peruvian Pacific Coast (Weksler and Bonvicino, 2015). *Oligoryzomys* is among the most speciose genera of the neotropical subfamily Sigmodontinae, with 22 currently recognized species.

Recent phylogenetic studies of this genus (Rivera et al., 2007; Rogers et al., 2009; Miranda et al., 2009; Palma et al., 2010a; González-Ittig et al., 2010, 2014; Hanson et al., 2011; Agrellos et al., 2012; Teta et al., 2013) have shown that *Oligoryzomys* systematics is still controversial, probably due to the high phenotypic similarity between species, which makes diagnosis and species identification difficult (see Carleton and Musser, 1989, 1995; Weksler and Bonvicino, 2005, 2015, for historical accounts of the generic taxonomy). In addition, molecular studies not employing morphological examination of specimens hinders further advance of the systematics of the genus, as specific names have been attached to several exemplars without a proper morphological assessment or that are based solely on geographic proximity of species ranges or type localities.

Species of *Oligoryzomys* are reservoirs of several hantaviruses and arenaviruses, and so work in the systematics of the genus is important for public health policy (Suzuki et al., 2004; Rosa et al., 2005, 2010; Oliveira et al., 2009, 2011, 2014). Six Brazilian *Oligoryzomys* species are known as hantavirus reservoirs: *O. nigripes* (Olfers, 1818), the host of Juquitiba and Itapua viruses (Suzuki et al., 2004; Oliveira et al., 2009); *O. flavescens* (Waterhouse, 1837) the host of Central Plata virus (Delfraro et al., 2003); *O. fornesi* (Massoia, 1973), the host of Anajatuba virus (Rosa et al., 2005) and Juquitiba virus (Guterres et al., 2014); *O. microtis* (Allen, 1916), the host of Rio Mamoré virus (Ritcher et al., 2010); *O. utiaritensis* (Allen, 1916) the host of Castelo dos Sonhos virus (Agrellos et al., 2012), and *O. chacoensis* (Myers and Carleton, 1981) of Bermejo virus (Oliveira et al., 2014). Other *Oligoryzomys* species with distribution out of Brazil are also hantavirus reservoirs: *O. fulvescens* (Saussure, 1860) is the reservoir of Choco virus, *O. delicatus* (Allen and Chapman, 1897) of Maporal virus, *O. longicaudatus* (Bennett, 1832) virus of Andes, and *O. brendae* Massoia, 1988, of Oran virus (see Teta et al., 2013, for identification of the latter reservoir species).

In this study, we analyze the taxonomic status of two forms of *Oligoryzomys* that are associated with hantaviruses, *O. mottogrossae* (Allen 1916) and *O. fornesi* (Massoia 1973). We provide evidence that *O. fornesi*, the currently recognized host species for the Anajatuba hantavirus genotype, is a form restricted to its type locality and vicinity in Argentina and Paraguay, within the *O. flavescens* species complex, as proposed by Gonzalez-Ittig et al. (2014). We report mor-

phological, karyological, and molecular data showing that *O. mattogrossae* is the valid name for the species that is the host for that hantavirus, providing an emended diagnosis and redescription of the taxon.

## MATERIAL AND METHODS

We examined *Oligoryzomys* specimens deposited in the mammal collections of Museu Nacional, Universidade Federal do Rio de Janeiro (MN), Rio de Janeiro, Brazil; American Museum of Natural History (AMNH), New York (including the type series of *O. utiaritensis*, *O. mattogrossae*, and *O. microtis*); Fundacion de Historia Natural Félix de Azara (FHN), Universidad Maimónides, Buenos Aires, Argentina (including the type series of *O. fornesi*); Instituto Evandro Chagas (IEC), Belém, Brazil, and Laboratório de Biologia e Parasitologia de Mamíferos Reservatórios Silvestres (LBCE), IOC-Fiocruz, Rio de Janeiro, Brazil. Two analyzed specimens were positive carriers of Anajatuba hantavirus, as reported by Rosa et al. (2010): IEC19491 and IEC19540. Information on collection locality data (fig. 1) and museum acronyms and numbers are presented in appendix 1; see also Bonvicino and Weksler (1998), Weksler and Bonvicino (2005), and Agrellos et al. (2012) for previously analyzed specimens of other *Oligoryzomys* species. In addition to museum specimens, we report here several new *Oligoryzomys* individuals collected in localities of the Brazilian Cerrado (appendix 1).

The terminology and illustrations of characters herein analyzed were reported by Reig (1977), Voss (1988), Carleton and Musser (1989), and Weksler (2006). The following external dimensions were measured (in mm) in specimens collected by us or obtained from original specimen tags: head and body length (HBL), tail length (LT), ear length (Ear), hind foot length with claw (HF) and body mass (Wt). Whenever a total length had been originally reported on specimen tags, HBL was estimated by subtracting tail length (T) from total length (TL). Cranial measurements were taken with digital calipers to the nearest 0.01 mm. For morphometric analyses, we employed 12 cranial dimensions following Bonvicino and Weksler (1998): condylo-incisive length (CIL), length of diastema (LD), palatal bridge (PB), length of maxillary molars (LM), breadth of first maxillary molar (BM1), external alveolar breadth (M1M), length of incisive foramen (LIF), breadth of incisive foramen (BIF), rostrum breadth (BRO), orbital length (ORL), zygomatic breadth (ZB), and breadth of zygomatic plate (BZP). These dimensions were chosen because they provided consistent estimates by different investigators (i.e., did not display significant interresearcher differences in a paired *t*-test).

**STATISTICAL ANALYSES:** Morphometric analyses of skull characters were performed for adult specimens, i.e., specimens with all teeth erupted and with at least minimal wear (Oliveira et al., 1998); males and females were grouped due to lack of sexual dimorphism (*t*-tests, *p* < 0.05; not shown). Analysis of variance (ANOVA) with Tukey post hoc test (Sokal and Rohlf, 1994), and MANOVA using logarithmic-transformed data were carried out for comparing *O. mattogrossae* with *O. microtis*, *O. flavescens*, and *O. fornesi*. We adjusted the individual measurements' alpha (level of significance) using sequential Bonferroni correction to reflect an overall



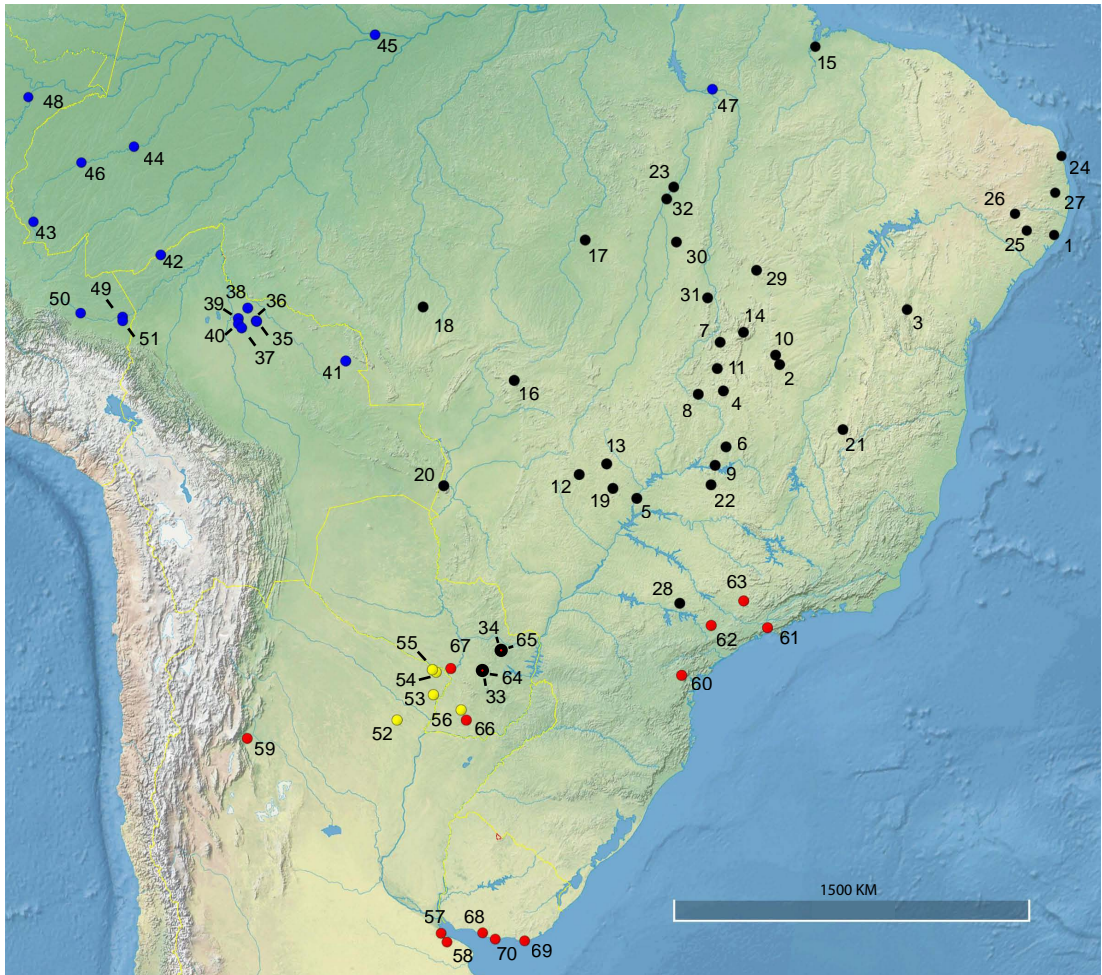


FIGURE 1. Map of central portion of South America showing the localities of analyzed specimens of *O. mottogrossae* (black), *O. fornesi* (yellow), *O. microtis* (blue), and *O. flavesceus* (red). Localities are listed in appendix 1.

alpha of 0.05 (Rice, 1989). We used two multivariate approaches to identify patterns of morphometric variation among these species: principal component analysis based on the covariance matrix, and discriminant analysis with estimation of canonical functions (Strauss, 2010); both analyses used logarithmic-transformed data. All statistical analyses were performed in R environment (R Core Team, 2014).

**MOLECULAR DATA:** DNA was isolated from livers preserved in 95%–100% ethanol following the standard phenol-chloroform protocol (Sambrook and Russell, 2001). A fragment containing the full-length cytochrome *b* gene (mt-Cytb; genes' acronyms following *Mus musculus* nomenclature of Eppig et al., 2015) was amplified with primers L14724 (5'–CGAAGCTTGATATGAAAACCATCGTTG–3'; Irwin et al., 1991) and Citb-Rev (5'–GAATATCAGCTTTGGGTGTTGRTG–3'; Casado et al., 2010) by standard PCR procedures.

Amplifications were performed in 50 µL reactions with Platinum® Taq Polymerase (Invitrogen™) and recommended concentrations of primers and templates. Reactions were run for 35 cycles at 94° C for 30 s, 58° C for 30 s, and extension at 72° C for 90 s, with initial denaturation at 94° C for 2 min and final extension at 72° C for 7 min.

Amplicons were purified with GFX® PCR DNA and Gel Band Purification Kit (GE™ Healthcare) and sequenced with the same primers used in the PCR amplification and additional internal primers for mt-Cytb: MEU1 (5′–ACAACCATAGCAACAGCATTCGT–3′; Bonvicino and Moreira, 2001) and MVZ16 (5′–TAGGAARTATCAYTCTGGTTTTRAT–3′; Smith and Patton, 1993). Sequencing reactions were run in an ABI3130xl (Applied Biosystems) platform and electropherograms were manually checked and aligned using BioEdit 8.0 (Hall, 1999) and Chromas v. 1.45 (Technelysium). (McCarthy, 1998).

Additional mt-Cytb data from other GenBank *Oligoryzomys* specimens (appendix 2) were used for phylogenetic reconstructions; we included only those sequences with at least 750 bp (65% of completeness). We also performed a combined analysis of mt-Cytb and the nuclear intron 7 of the nuclear β-fibrinogen gene (i7-Fgb) previously employed by Agrellos et al. (2012). For the combined analyses, we included only exemplars with both mt-Cytb and i7-Fgb, except for *O. stramineus*, for which we combined sequences from two individuals from the same locality (Terezina de Goiás; appendix 2). We employed 13 oryzomyines and 3 non-oryzomyines sigmodontines as outgroup taxa (appendix 2) in all phylogenetic analyses, and rooted our trees using *Sigmodon hispidus*.

**PHYLOGENETIC ANALYSES:** Maximum-likelihood estimation (Felsenstein, 1981) and Bayesian analysis (Huelsenbeck et al., 2001) were carried out for phylogenetic reconstructions. A nucleotide evolution model was evaluated using Akaike Information Criteria (AICc) as estimated by PAUP\* 4.0a146 (Swofford, 2002; commands AutoModel modelset=j7 invarSites IplusG). The GTR model of nucleotide substitution (Rodríguez et al., 1990), corrected for site-specific rate heterogeneity using gamma distribution with four classes (Yang, 1994) and invariable sites (i.e., GTR+G+I) was selected as the best model for cytochrome *b* (mt-Cytb), while the HKY+G was selected for i7-Fgb (GTR+G+I was close to the best model, with delta AICc = 4.937). The GTR+G+I was used for all phylogenetic analyses, and the combined analyses used a gene-partitioned model. Maximum-likelihood trees were calculated with RaxML (Stamatakis, 2006, 2014) and nodal bootstrap values (Felsenstein, 1985) were calculated using 1000 pseudoreplicates. Bayesian analyses were performed using Markov chain Monte Carlo (MCMC) sampling as implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Uniform interval priors were assumed for all parameters except base composition, for which we assumed a Dirichlet prior. We performed four independent runs, each with 2 heated chains and 10,000,000 generations, and sampling for trees and parameters every 10,000 generations. The first 10% generations were discarded as burn-in, and the remaining trees were used to estimate posterior probabilities for each node. All analyses were checked for convergence by plotting the log-likelihood values against generation time for each run with Tracer 1.4 (Rambaut and Drummond, 2007), and all parameters had an effective sample size (ESS) over 500. Phylogenetic analyses were run in the CIPRES Science Gateway (Miller et al., 2010).

## RESULTS

The holotype and paratype of *O. mattogrossae* share distinctive features of the external (fig. 2) and cranial (fig. 3) anatomy with *Oligoryzomys* specimens from the Cerrado and Caatinga, previously referred as *O. fornesi* (Bonvicino and Weksler, 1998): (1) yellowish ventral pelage, with yellowish hair tips and gray base; (2) absence of a well-defined limit between ventral and lateral pelage; (3) incisive foramen almost reaching the level of the alveoli of the first molar, or barely reaching but not advancing posteriorly beyond it; (4) position of posterolateral palatal pits lateral to the mesopterygoid fossa; and (5) posterior extension of palatal bridge beyond the last molar smaller than the size of M3. Although each of these features have been found in other *Oligoryzomys* species (table 1), this character combination is found only in this *Oligoryzomys* form, which we hereafter refer as *O. mattogrossae*.

*Oligoryzomys mattogrossae* specimens differs from *O. fornesi* (type series; figs. 2, 4) in the following characters: (1) the incisive foramen of *O. fornesi* is long and teardrop shaped, while *O. mattogrossae* specimens have parallel-sided foramina; (2) the posterolateral pits are between the mesopterygoid fossa and M3 in *O. fornesi* and lateral to the fossa mesopterygoid in *O. mattogrossae*; (3) and the posterior extension of the palatal bridge is longer than the M3 length in *O. fornesi*, and smaller than M3 in *O. mattogrossae*. Externally, the *O. fornesi* holotype and paratypes of *O. fornesi* also possess yellowish ventral pelage with subtle limits between ventral and lateral pelage, as *O. mattogrossae*.

*Oligoryzomys mattogrossae* differs from *Oligoryzomys microtis* (figs. 2, 5) in the following characters: (1) the dorsal coloration does not have a defined limit with the ochraceous or yellow ventral pelage color in *O. mattogrossae*, in comparison with a whitish venter with a well-defined limit between lateral and ventral coloration in most adult specimens of *O. microtis*; although the venter in some specimens of *O. microtis* may also be ochraceous, it will still have strong countershading; (2) the posterior terminus of the incisive foramina of *O. microtis* is anterior to the M1 alveolar line, whereas in *O. mattogrossae* the foramina reach, but not extend posteriorly past the alveolar line; (3) the posterolateral pits are between the mesopterygoid fossa and M3 in *O. microtis* and lateral to the fossa mesopterygoid in *O. mattogrossae*; and (4) the posterior extension of the palatal bridge is longer than the M3 length in *O. fornesi*, and smaller than M3 in *O. mattogrossae*.

Only five of 12 measurements displayed significant differences among analyzed species in the ANOVA: PB, LIF, BIF, LIB ( $p < 0.001$ ), and LM ( $p < 0.01$ ); the MANOVA also recovered significant variation among species ( $p < 0.001$ ). Pairwise Tukey tests showed *O. mattogrossae* to be significantly different ( $p < 0.05$ ) from *O. fornesi* in 2 variables (LIF and LIB), from *O. microtis* in 2 variables (BIF and LIB), and from *O. flavescens* in 3 variables (PB, LIB and LIF). *O. fornesi* and *O. flavescens* did not differed significantly in any variable, while *O. flavescens* differed from *O. microtis* in 5 variables. The four *Oligoryzomys* species were also poorly differentiated by multivariate analyses (fig. 6). The biplot of the first 3 principal components, which account for 73% of the total variance, reveal an overall juxtaposition in the multivariate space (fig. 6A, B). *O. microtis* is separated from *O. fornesi* and *O. flavescens* in the second component, but *O. mattogrossae* scores overlap with all other species. The discriminant canonical functions (fig. 6C,

TABLE 1. Variation of morphological characters of *Oligoryzomys* species occurring in the open vegetation belt of South America, and neighboring biomes. Sources of greatest skull length are from: <sup>a</sup> Present study; <sup>b</sup> Massoia (1973); <sup>c</sup> Weksler and Bonvicino (2005); <sup>d</sup> Agrellos et al. (2012); and <sup>e</sup> Myers and Carleton (1981). Remaining information is from specimens listed in appendix 1, type material, and from the above-mentioned sources.

| Character/Species  | <i>mattogrossae</i>                          | <i>fornei</i>                   | <i>flavescens</i>               | <i>microtis</i>                                     | <i>rupestris</i>                    | <i>mojoeni</i>                       | <i>utianiensis</i>                 | <i>chacoensis</i>              | <i>nigripes</i>              | <i>stramineus</i>        |
|--|--|---------------------------------|---------------------------------|---|-------------------------------------|--------------------------------------|------------------------------------|--------------------------------|------------------------------|--------------------------|
| Greatest skull length (range, in mm)                         | 20.6–25.0 <sup>a</sup>                       | 21.9–23.7 <sup>b</sup>          | 20.1–24.3 <sup>c</sup>          | 21.2–25.5 <sup>a</sup>                              | 22.7–25.2 <sup>c</sup>              | 22.1–25.0 <sup>c</sup>               | 21.3–26.7 <sup>d</sup>             | 22.1 – 27.8 <sup>e</sup>       | 23.1–28.4 <sup>c</sup>       | 23.3–28.3 <sup>c</sup>   |
| Ventral color  | yellowish or ochraceous buffy with gray base | ochraceous buffy with gray base | ochraceous buffy with gray base | pure white, or whitish or ochraceous with gray base | whitish with gray base              | cream with gray base                 | whitish with gray base             | whitish with gray base         | whitish with gray base       | whitish with gray base   |
| Dorsal color   | rufous yellowish-brown                       | chestnut-brown - yellowish      | bright brownish-orange          | dull yellowish brown                                | grizzled yellowish-brown, gray head | grizzled reddish- to yellowish-brown | grizzled yellowish-brown           | clay, heavily lined with black | dark-brown to dark-yellowish | pale grayish-yellow      |
| Strong dorsal and ventral coloration contrast                | no   | no                              | no                              | yes   | no                                  | no                                   | yes                                | yes                            | yes                          | yes                      |
| Tail color pattern   | weakly bicolored                             | weakly bicolored                | weakly bicolored                | weakly bicolored                                    | unicolored                          | weakly bicolored                     | weakly bicolored                   | weakly bicolored               | unicolored                   | weakly bicolored         |
| Posterior terminus of incisive foramina relative to M1 level | not extended posteriorly                     | not extended posteriorly        | posterior                       | anterior  | not extended posteriorly            | anterior                             | not extended posteriorly           | not extended posteriorly       | not extended posteriorly     | not extended posteriorly |
| PPP position relative to mesopterygoid fossa (MF)            | lateral to MF                                | between MF and M3               | between MF and M3               | between MF and M3                                   | between MF and M3                   | between MF and M3                    | lateral to MF or between MF and M3 | between MF and M3              | between MF and M3            | between MF and M3        |
| Posterior extension of palatal bridge beyond M3              | less than M3 length                          | more than M3 length             | more than M3 length             | more than M3 length                                 | more than M3 length                 | more than M3 length                  | less than M3 length                | more than M3 length            | less than M3 length          | less than M3 length      |
| Carotid circulation (Voss, 1988)                             | pattern 2                                    | pattern 2                       | pattern 2                       | pattern 2   | pattern 3                           | pattern 2                            | pattern 2                          | pattern 2                      | pattern 2                    | pattern 2                |





FIGURE 2. Ventral views of the skin of the type specimens of *Oligoryzomys*. **A**, From left to right, *Oligoryzomys mattogrossae* (AMNH37542, holotype; HBL = 95 mm), *O. microtis* (AMNH37090, holotype; HBL = 93 mm), and *O. utiaritensis* (AMNH37541, holotype; HBL = 100 mm); **B**, *O. fornesi* (CEM3562, paratype; HBL = 82 mm).

D), in turn, reveal a separation of *O. microtis* and *O. mattogrossae* from *O. fornesi* and *O. flavescens* in the first function, while the latter two species are separated in the second function; *O. microtis* and *O. mattogrossae* are partially discriminated in the third function.

Maximum-likelihood estimation (ML) and Bayesian inference (BI) based on cytochrome *b* data showed the same topology (fig. 7). *Oligoryzomys* was shown to be monophyletic, with bootstrap support (*bs*) of 100% in ML and posterior probability (*pp*) of 1.0 in BI. All species with more than one exemplar were recovered as monophyletic with high nodal support, except *O. flavescens*, which was paraphyletic in relation to *O. fornesi*. Most interspecific relationships received low nodal support, except for 4 clades with high support (*bs*>80 or *pp*>0.95): (1) *O. stramineus* and *O. nigripes*; (2) *O. magellanicus*, *O. longicaudatus*, *O. flavescens*, and *O. fornesi*; (3) *O. utiaritensis*, *O. messorius*, *O. destructor*, and *O. rupestris*; and (4) *O. costaricensis*, *O.*



FIGURE 3. Dorsal, ventral, and lateral views of the skull and mandible of a recently collected specimen of *O. mattogrossae* (CRB3141). Bar scale = 10 mm.

*vegetus*, and *O. fulvescens*. The lineage leading to *O. mattogrossae* is the first to split within the genus, followed by *O. microtis* lineage, but this resolution has low nodal support.

Combined analyses of mt-Cytb and i7-Fgb recovered a fully resolved and highly supported tree within *Oligoryzomys*, but not for *Oryzomyini* generic relationships (fig. 8). The first dichotomy within *Oligoryzomys* separates a strongly supported clade containing *O. microtis* and *O. mattogrossae* from a clade containing the remaining species; the lineage leading to *O. flavescens*



FIGURE 4. Dorsal, ventral, and lateral views of the skull (and mandible) of the holotype of *O. fornesi* (CEM3561). Bar scale = 10 mm.

is part of the most basal split within this latter clade, which is then divided into two clades: (1) *O. nigripes* and *O. stramineus*; and (2) *O. utiaritensis*, *O. moojeni*, and *O. rupestris*.

#### DISCUSSION

Almost a century after its original description, the identity of *O. mattogrossae* is still controversial. This is due to overall similarity among small-sized *Oligoryzomys* species from cis-Andean Neotropics, especially eastern and central South America. There are seven recognized



FIGURE 5. Dorsal, ventral, and lateral views of the skull and mandible of a recently collected specimen of *O. microtis* (SVS638). Bar scale = 10 mm.

species of small-sized *Oligoryzomys* occurring in this region: *O. fornesi*, *O. flavescens*, *O. microtis*, *O. utiaritensis*, *O. moojeni*, *O. rupestris*, and now *O. mattogrossae*. We recognize the last-named species based on the examination of its holotype, which shares the same morphological traits of specimens of *Oligoryzomys* from the Cerrado and Caatinga of Brazil that form a well-supported clade within *Oligoryzomys* (figs. 7, 8) and that have a unique karyotype.

Cabrera (1961:396) considered *O. mattogrossae* as a junior synonym of *O. microtis*, a position followed by Carleton and Musser (1989) and Musser and Carleton (2005). The two species are morphometrically extremely similar with only subtle morphological differences (see above). Nevertheless, they form clearly independent lineages in the phylogenetic analyses of both mito-



chondrial and nuclear genes (figs. 7, 8). The mt-Cytb recovered the two species in sequential nodes at the stem of *Oligoryzomys* in a poorly supported resolution; the combined analyses, in turn, place the two taxa as sister species, with high nodal support. Although one of the arguments presented by Weksler and Bonvicino (2015: 431) for the recognition of *O. mattogrossae* was their nonsister species status relative to *O. microtis*, the molecular distance between the species (average  $p = 11.9\%$  for mt-Cytb) is very suggestive of their distinctiveness (see table 2); the distance is higher than the mean pairwise comparisons among all *Oligoryzomys* species pairs ( $p = 8.9\%$ ; min = 1.1% between *O. longicaudatus* and *O. magellanicus*; max = 12.8% between *O. microtis* and *O. rupestris*), and especially among sister species ( $p = 6.1\%$ ). In addition, there are 38 putative molecular apomorphies for both *O. mattogrossae* and *O. microtis* based on parsimony optimization of characters in the combined tree.

The two species also possess distinct karyotypes, with *O. mattogrossae* presenting  $2n = 62$  and FN = 64 (Bonvicino and Weksler, 1998) and *O. microtis* presenting  $2n = 64$  and FN = 66 (Gardner and Patton, 1976, as *Oryzomys* (*Oligoryzomys*) *longicaudatus*, variant 2; Aniskin and Volobouev, 1999; Patton et al., 2000); this latter karyotype was confirmed in a topotype of *O. microtis* (unpublished data). Another karyotype with  $2n = 64$  and FN = 64 was also attributed to *O. microtis* (Di-Nizo et al., 2015), but the taxonomic status of this lineage needs to be assessed. Besides differences in diploid and fundamental numbers, suggesting a major chromosomal rearrangement between the species, the morphology of the autosomal chromosomes is also distinctive between the *O. microtis* and *O. mattogrossae*; although the two species have two biarmed autosome pairs, in the former the largest autosome is a metacentric, while in the later species it is an acrocentric chromosome; in contrast, *O. mattogrossae* has a medium-sized biarmed chromosome, that is probably homologous to an acrocentric in *O. microtis*. This suggests at least two pericentric inversions to derive one karyotype from another. The  $2n = 62$  and FN = 64 karyotype has also been attributed to *O. eliurus* (Svartman, 1989; Andrades-Miranda et al., 2001), but morphological examination and sequencing of some of the karyotyped specimens listed by these authors (MN36928, MN36746) confirm they are *O. mattogrossae*.

Our results confirmed the need for analyzing additional loci to obtain a more complete understanding of *Oligoryzomys* phylogeny, mainly because analyses exclusively based on mt-Cytb did not provide a sufficient phylogenetic signal for a robust resolution of intrageneric relationships. Our combined analysis of mt-Cytb and i7-Fgb, albeit with a more restricted taxonomic coverage, provided a robust hypothesis for the relationships of the genus, and was similar to the previous study that employed the i7-Fgb nuclear marker (Agrellos et al., 2012; in that study, the specimen referred as *O. fornesi*, MN62640, is here treated as *O. mattogrossae*). The only difference between the results is the position of *O. flavescens*, which in our present analyses receives high support for its placement (fig. 8). Some clades recovered in the present study, both in the mt-Cytb only and in combined analyses, are generally coincident with recent studies of *Oligoryzomys* (Palma et al., 2005, 2010a; Francés and D'Elía, 2006; Rivera et al., 2007; Rogers et al., 2009; Miranda et al., 2009; Richter et al., 2010; González-Ittig et al., 2010, 2014).

Sequences of *O. mattogrossae* have been attributed to *O. fornesi* (e.g., Agrellos et al., 2012; Teta et al., 2012) or considered as NUMTs (Gonzales-Ittig et al., 2014) in previous molecular



TABLE 2. Average pairwise nucleotide divergence (uncorrected *p*, in percentage) among species. The diagonal contains intraspecific nucleotide variation, but note that most species have 2 samples (in parentheses).

|  | 1    | 2    | 3    | 4    | 5    | 6   | 7    | 8   | 9    | 10  | 11  | 12  | 13  | 14   | 15  | 16  | 17  | 18  | 19  |
|--|------|------|------|------|------|-----|------|-----|------|-----|-----|-----|-----|------|-----|-----|-----|-----|-----|
| 1 <i>O. mattogrossae</i><br>( <i>N</i> = 17) | 1.7  |      |      |      |      |     |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 2 <i>O. microtis</i> (9)                     | 11.9 | 3.1  |      |      |      |     |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 3 <i>O. destructor</i> (2)                   | 11.7 | 12.7 | 0.2  |      |      |     |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 4 <i>O. costaricensis</i> (2)                | 10.2 | 12.6 | 9.8  | 2.4  |      |     |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 5 <i>O. brendae</i> (2)                      | 10.7 | 11.7 | 11.2 | 10.0 | 0.5  |     |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 6 <i>O. vegetus</i> (2)                      | 9.6  | 11.6 | 11.5 | 8.2  | 8.4  | 0.8 |      |     |      |     |     |     |     |      |     |     |     |     |     |
| 7 <i>O. fulvescens</i> (2)                   | 10.3 | 12.5 | 12.2 | 9.8  | 8.8  | 7.2 | 2.2  |     |      |     |     |     |     |      |     |     |     |     |     |
| 8 <i>O. moojeni</i> (2)                      | 10.6 | 9.7  | 8.9  | 7.9  | 6.9  | 7.7 | 9.1  | 0.0 |      |     |     |     |     |      |     |     |     |     |     |
| 9 <i>O. rupestris</i> (2)                    | 12.2 | 12.8 | 9.3  | 9.2  | 9.3  | 9.8 | 9.3  | 7.6 | 0.7  |     |     |     |     |      |     |     |     |     |     |
| 10 <i>O. magellanicus</i> (1)                | 10.5 | 10.6 | 9.5  | 7.0  | 10.3 | 8.6 | 9.4  | 6.4 | 8.4  | 0.0 |     |     |     |      |     |     |     |     |     |
| 11 <i>O. longicaudatus</i> (2)               | 11.0 | 11.6 | 9.8  | 7.7  | 10.2 | 9.3 | 8.9  | 7.2 | 8.4  | 1.1 | 0.5 |     |     |      |     |     |     |     |     |
| 12 <i>O. flavescens</i> (4)                  | 10.9 | 10.8 | 9.5  | 7.0  | 9.8  | 8.3 | 9.4  | 6.8 | 8.7  | 3.2 | 3.5 | 1.0 |     |      |     |     |     |     |     |
| 13 <i>O. fornesi</i> (5)                     | 11.2 | 10.9 | 9.4  | 7.1  | 10.0 | 8.6 | 10.1 | 6.8 | 9.0  | 3.5 | 3.7 | 1.4 | 1.1 |      |     |     |     |     |     |
| 14 <i>O. chacoensis</i> (2)                  | 12.2 | 12.6 | 10.9 | 9.9  | 10.8 | 9.0 | 9.6  | 8.3 | 10.1 | 9.1 | 9.4 | 8.0 | 8.7 | 0.5  |     |     |     |     |     |
| 15 <i>O. stramineus</i> (2)                  | 11.5 | 11.9 | 9.4  | 9.0  | 9.4  | 8.0 | 9.2  | 7.4 | 8.7  | 7.7 | 7.9 | 7.1 | 7.2 | 6.9  | 0.3 |     |     |     |     |
| 16 <i>O. nigripes</i> (2)                    | 11.2 | 12.6 | 9.7  | 8.9  | 9.9  | 8.4 | 9.4  | 7.5 | 8.2  | 7.1 | 7.8 | 7.8 | 8.3 | 7.8  | 5.2 | 0.7 |     |     |     |
| 17 <i>O. utiariensis</i> (2)                 | 11.8 | 11.1 | 9.6  | 10.3 | 9.1  | 9.6 | 10.0 | 6.1 | 8.2  | 7.9 | 8.4 | 8.9 | 8.9 | 10.6 | 8.7 | 8.9 | 1.0 |     |     |
| 18 <i>O. delicatus</i> (2)                   | 11.1 | 11.1 | 8.8  | 7.4  | 9.3  | 7.9 | 8.2  | 5.6 | 6.5  | 6.6 | 6.8 | 6.7 | 6.9 | 9.1  | 7.9 | 7.6 | 5.7 | 2.0 |     |
| 19 <i>O. messorius</i> (2)                   | 9.9  | 11.3 | 9.1  | 8.6  | 9.1  | 9.6 | 9.2  | 7.6 | 7.5  | 8.0 | 8.2 | 8.1 | 8.2 | 9.9  | 9.7 | 9.0 | 6.4 | 6.0 | 3.6 |

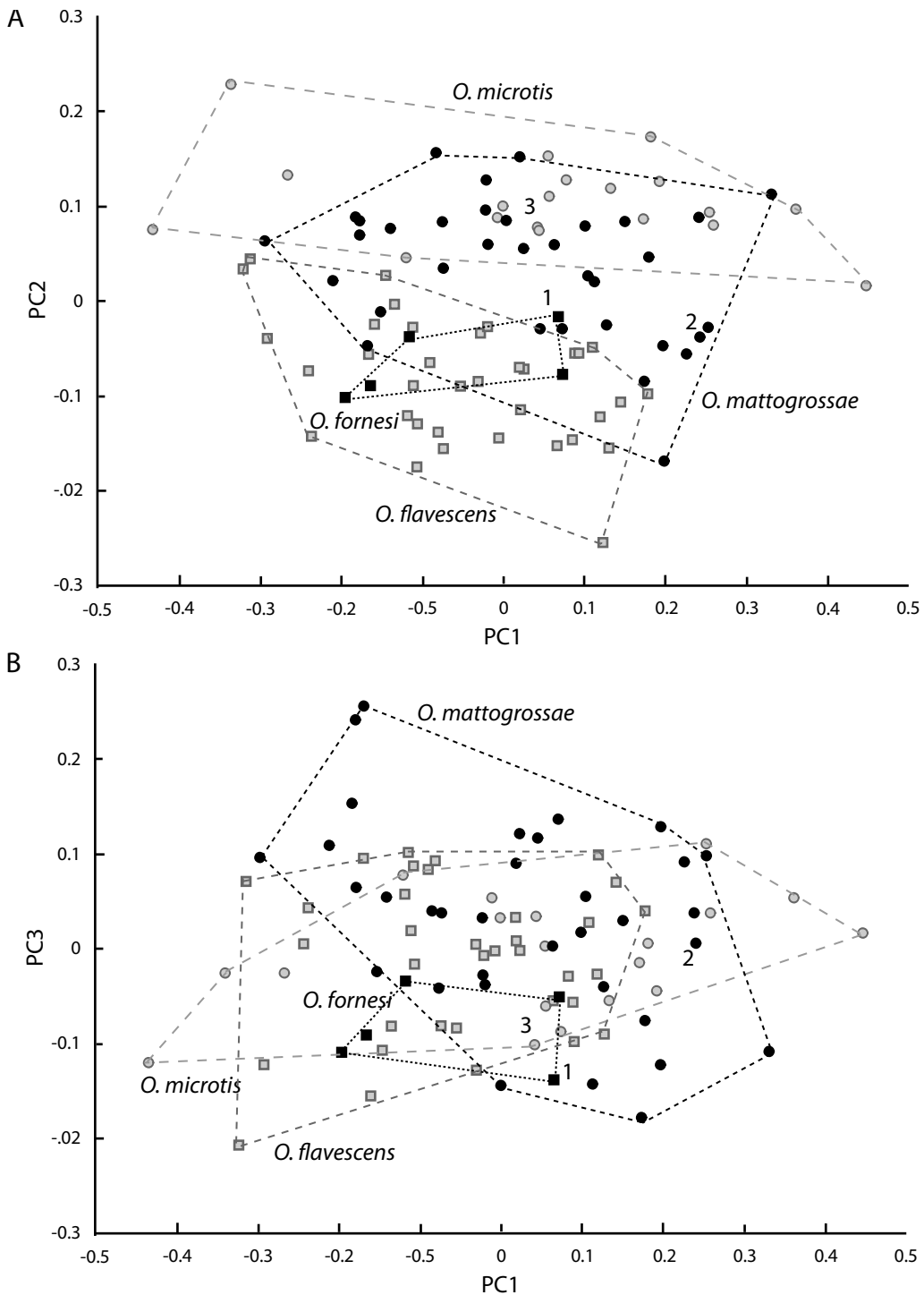
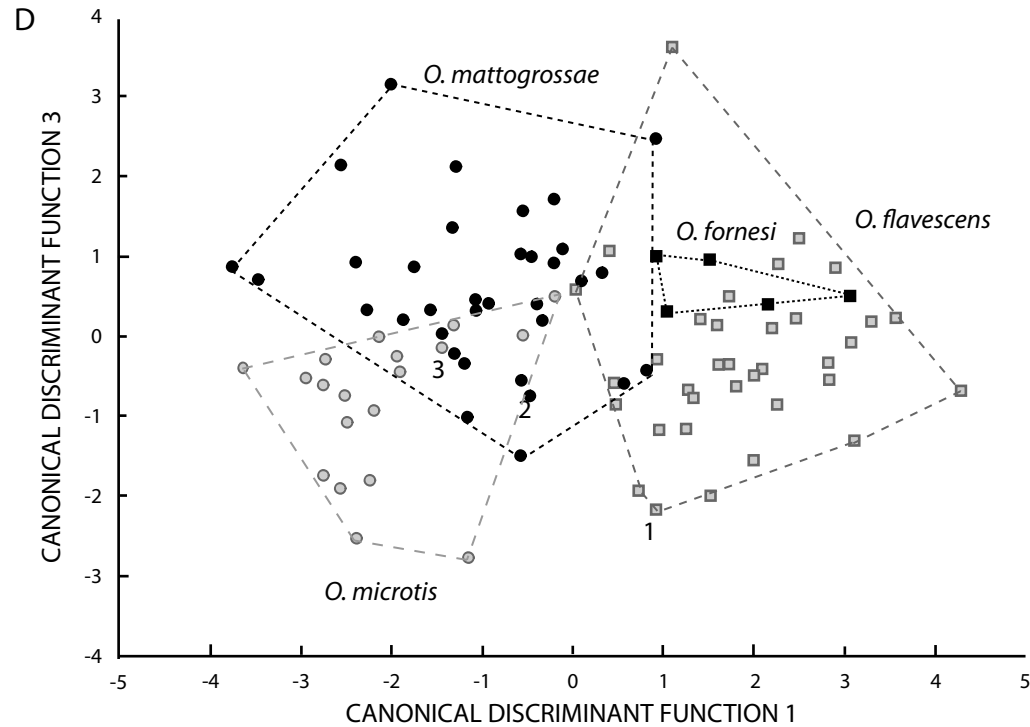
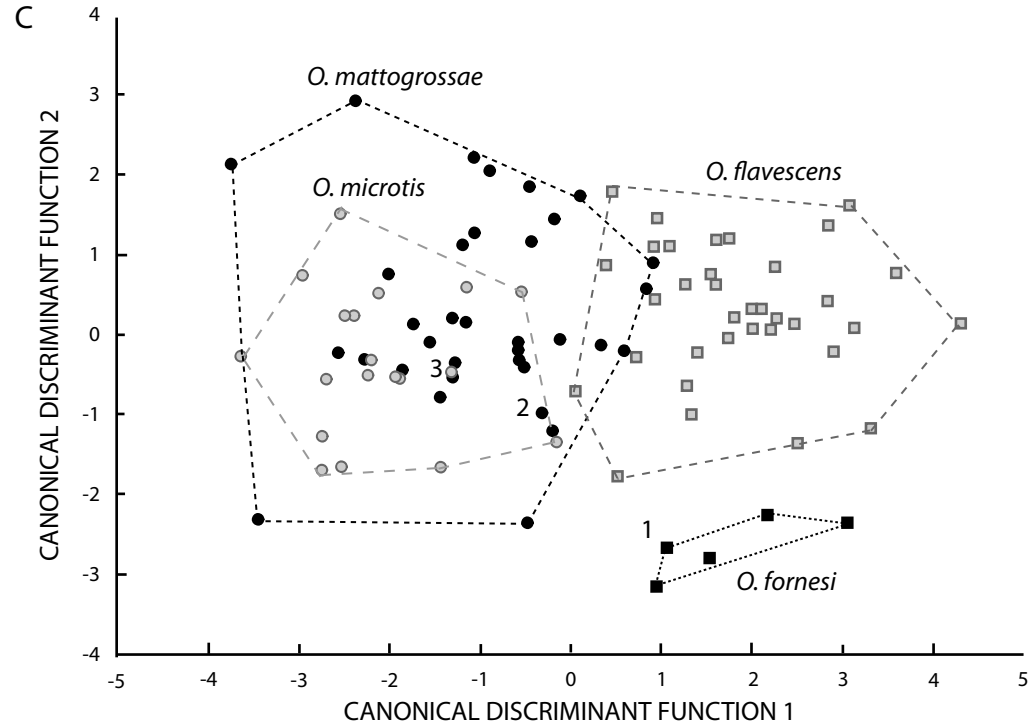
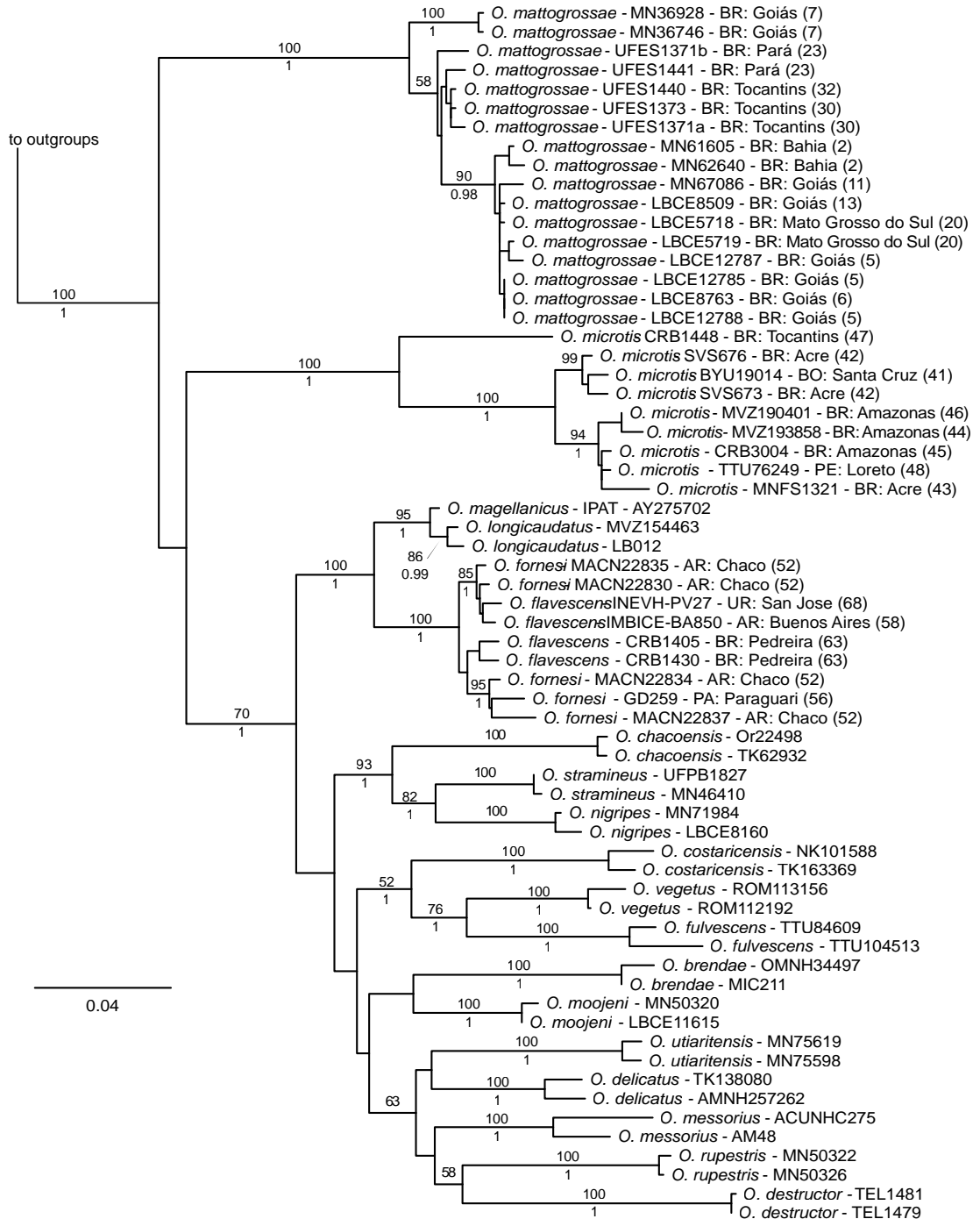


FIGURE 6. Scatterplot results of principal component analysis (A and B, *above*) and canonical discriminant analysis (C and D, *opposite page*) of log-transformed cranial measurements. Numbers indicate holotypes: 1, *O. fornesi* (CFA3561); 2, *O. mattogrossae* (AMNH37542), and 3, *O. microtis* (AMNH37090).





phylogenetic analyses. It is important to note that we did not observe any characteristics of NUMT pseudogenes, such as a stop codon or frame shifts, in any mt-Cytb sequence of this taxon. Our phylogenetic analyses also show that specimens from Argentina and southern Paraguay, recognized here as *O. fornesi*, do not cluster with *O. mattogrossae*; instead, they are members of two clades within *O. flavescens*, rendering both taxa as paraphyletic and strongly suggesting that the two forms belong to a single evolutionary lineage. Our morphometric analyses corroborate this pattern, as the type series of *O. fornesi* is morphometrically similar to *O. flavescens*.

The sister species *O. microtis* and *O. mattogrossae* occupy distinct habitats throughout their parapatric distributional ranges (fig. 1): although also found in the Cerrado-Amazonian ecotone in Para and Mato Grosso, *O. mattogrossae* is mostly found in open vegetation biomes such as Cerrado and Caatinga; *O. microtis* is found only in forested environments throughout the Amazon basin (Weksler and Bonvicino, 2005). In turn, *O. mattogrossae* is sympatric with *O. flavescens* in two localities in Paraguay (Curuguaty and Carayaó); the sympatric forms were identified based on karyotyped specimens (Bonvicino and Weksler, 1998) and the discriminant analysis separates the exemplars. *O. nigripes* was also collected in these localities (Myers and Carleton, 1981), another example of cooccurrence of three sympatric forms of the genus in the ecotone of the Cerrado and other biomes (Weksler and Bonvicino, 2015).

We conclude that our data corroborate the valid taxonomic status of *O. mattogrossae*, the correct name for the *Oligoryzomys* with small body size, yellow belly, and  $2n = 62$  and  $FN = 64$  karyotype, found in the Cerrado and Caatinga domains of Brazil and northern Paraguay, and previously identified by us as *O. fornesi* (e.g., Bonvicino and Weksler 1998; Weksler and Bonvicino, 2005). This finding is relevant for governmental agencies, such as the Brazilian Ministry of Health, given that *O. mattogrossae* specimens have been identified as seropositive for Anajatuba hantavirus in Maranhão state in Brazil (Rosa et al., 2010) and its correct taxonomic identification is extremely important for the implementation of public policies of hantavirus control. The redescription of *O. mattogrossae* is herein provided.

## TAXONOMIC ACCOUNT

### *Oligoryzomys mattogrossae* (J.A. Allen, 1916)

Figures 2 and 3

**HOLOTYPE:** AMNH37542 adult male; measurements of holotype in mm (see Material and Methods for acronyms): TL = 210, HBL = 95, T = 115, PB = 4.08, LIF = 4.48, BIF = 1.61, LM

FIGURE 7. Phylogenetic relationships among *Oligoryzomys* specimens based on maximum-likelihood analyses of mt-Cytb sequences. The tree shows complete separation of specimens from central Brazil (*O. mattogrossae*) and specimens from Paraguay and Argentina identified as *O. fornesi*. Bootstrap values are shown above branches, and posterior probabilities of Bayesian analyses are shown below branches. For the focal species of this study, *O. mattogrossae*, *O. fornesi*, *O. microtis*, and *O. flavescens*, terminal labels also include the following locality data: country code (AR: Argentina, BO: Bolivia; BR: Brazil; PA: Paraguay; PE: Peru); state, department, or province; and locality number (map 1 and appendix 1).



= 3.30, BM1 = 0.97, M1M = 4.50, BRO = 4.56, LIB = 3.45, ORL = 8.05, BZP = 2.4. The holotype corresponds to an old adult individual, i.e., with advanced wear of molars and large skull measurements (table 3), and has a severely damaged skull.

TYPE LOCALITY: Brazil, Mato Grosso state, Rio Papagaio, Utiriti.

GEOGRAPHIC DISTRIBUTION: *Oligoryzomys mattogrossae* occurs throughout the Cerrado and Caatinga biomes of central and northeastern Brazil and Paraguay, as well as in the Cerrado-Amazonia ecotone between Mato Grosso and Pará states, and between the Pantanal region of Corumbá in Mato Grosso do Sul state (fig. 1). In Brazil, the species has been recently reported in the states of Mato Grosso do Sul (Carmignotto et al., 2014), São Paulo (Vivo et al., 2011), Tocantins (Di-Nizo et al., 2015), Pará (Rocha et al., 2011), and Bahia (Pereira and Geise, 2009). Therefore, *O. mattogrossae* is found in the Brazilian Caatinga (Bahia, Alagoas, Pernambuco, Paraíba states) and Cerrado (Distrito Federal, São Paulo, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Goiás, Tocantins, Bahia, and Maranhão states). *O. mattogrossae* also possibly occurs in Bolivia (e.g., Santa Cruz specimens listed as *O. microtis* in Olds and Anderson, 1987, and Anderson, 1997), but voucher material still needs to be analyzed to confirm identification. See appendix 1 for specific localities and examined material.

EMENDED DIAGNOSIS: A small-sized *Oligoryzomys* species (adult HBL <96 mm in average) characterized by the combination of the following morphological characteristics: (1) rufous tone in dorsum, especially on the rump, (2) underparts light ochraceous buff instead of grayish white, (3) dorsal and ventral coloration without a well-defined limit, (4) position of posterolateral pits lateral to the mesopterygoid fossa; and (5) posterior extension of palatal bridge smaller than the size of M3. In addition, all known karyotyped specimens share the same diploid number of 62 and fundamental autosome number of 64.

DESCRIPTION: Adult dorsal pelage grizzled yellowish, between Antique Brown and Dresden Brown (Ridgway, 1912), composed of long guard hairs and slightly shorter overhairs with a subapical brown-yellowish band. Lateral color lighter than in dorsum and without a clearly defined limit with the yellowish ventral pelage. Ventral hair upper half yellowish, gray at base. Short tufts of white ungual hair at base of claws on dII–dV. Tail longer than combined length of head and body, sparsely haired, and covered with more or less conspicuous epidermal scales, lacking a long tuft of terminal hairs and weakly bicolored, dorsal surface dark gray and ventral surface light gray. Superciliary, genal, and mystacial vibrissae not extending beyond ears. Presence of eight mammae in inguinal, abdominal, postaxial, and pectoral positions.

Delicate skull, narrow rostrum, but slightly wider than interorbital constriction. Interorbital region hourglass shaped. Braincase without supraorbital and postorbital ridges and with weakly developed lambdoidal ridge. Interparietal bone as broad as anterior half of parietal. Relatively large zygomatic plate with zygomatic notch intermediate between deep and shallow. Jugal bone absent, resulting in zygomatic process of squamosal in contact with the zygomatic process of maxillary. Incisive foramina with almost parallel margins, the posterior borders reaching or almost reaching the plane of alveolus of the first upper molars, but never extending posteriorly. Palate with a single large or two posterolateral palatal pits not recessed in palatine fossa, lateral to mesopterygoid fossa. Palatal bridge broad and long. Bony roof of

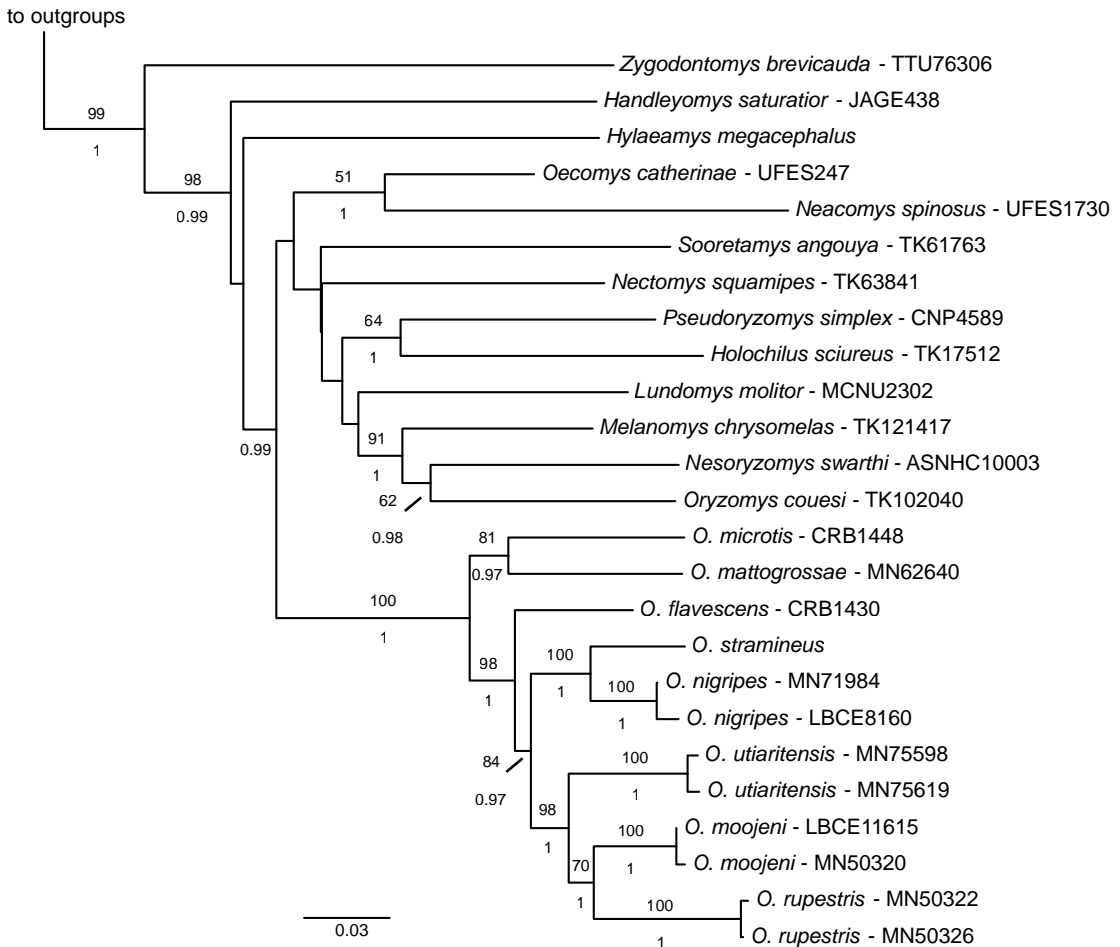


FIGURE 8. Phylogenetic relationships among *Oligoryzomys* specimens based on a maximum-likelihood analysis of the combined genetic matrix (mt-Cytb and i7-Fgb) using a partitioned GTR-G model with unlinked substitution parameters. Bootstrap values are shown above branches, and posterior probabilities of Bayesian analyses are shown below branches.

mesopterygoid fossa perforated by large sphenopalatine vacuities. Width of parapterygoid plate slightly greater than width of mesopterygoid fossa. Alisphenoid strut absent (buccinator-masticatory foramen and accessory foramen ovale confluent), alisphenoid canal with large anterior opening. Stapedial foramen and the posterior opening of the alisphenoid canal large, but squamosal-alisphenoid groove and sphenofrontal foramen absent (= carotid circulatory pattern 2 of Voss, 1988). Posterior suspensory process of the squamosal absent. Large subsquamosal fenestra, slightly smaller than postglenoid foramen. Periotic exposed posteromedially between ectotympanic and basioccipital, not reaching the carotid canal. Mastoid perforated by conspicuous posterodorsal fenestra. In mandible, capsular process of lower incisor alveolus well developed in most adults; superior and inferior masseteric ridges converging anteriorly as open chevron below m1.

TABLE 3. Skull measurements (in mm) of the type specimens of *O. mattogrossae* and descriptive statistics for populations of *O. mattogrossae* and *O. fornesi*. Locality numbers (appendix 1) of measured specimens are provided in parentheses. Values are given as average  $\pm$  standard deviation (minimum-maximum) sample size (when different from overall *N*). See Material and Methods for measurements acronyms.

| <i>O. mattogrossae</i> |   |   |  |   |  |                                     | <i>O. fornesi</i>                   |
|------------------------|---|---|--|---|--|-------------------------------------|-------------------------------------|
| Locality               | Holotype<br>AMNH37542<br>Brazil,<br>Utiariti (18) | Paratype<br>AMNH37100<br>Brazil,<br>Guatsué | Central Brazil (2,<br>4-5, 8, 10, 13-14)<br><i>N</i> = 27 <sup>a</sup> | Northeast<br>Brazil (1, 25)<br><i>N</i> = 4 | Brazil, Minas<br>Gerais (21)<br><i>N</i> = 3 | Paraguay<br>(33-34)<br><i>N</i> = 3 | Paraguay<br>(53-55)<br><i>N</i> = 5 |
| CIL                    | –   | 22.03                                       | 19.98 $\pm$ 0.86<br>(18.39–21.47)                                      | 20.34 $\pm$ 0.72<br>(19.56–20.99)<br>3      | 20.07 $\pm$ 0.78<br>(19.24–20.79)            | 20.81 $\pm$ 1.17<br>(19.46–21.56)   | 20.05 $\pm$ 0.62<br>(19.49–20.92)   |
| LD                     | –   | 5.85  | 5.59 $\pm$ 0.32<br>(4.98–6.18) 26                                      | 5.68 $\pm$ 0.18<br>(5.57–5.94)              | 5.40 $\pm$ 0.19<br>(5.27–5.62)               | 5.66 $\pm$ 0.45<br>(5.18–6.07)      | 5.56 $\pm$ 0.21<br>(5.3–5.82)       |
| PB                     | 4.08  | 4.08  | 3.99 $\pm$ 0.23<br>(3.52–4.36)   | 3.98 $\pm$ 0.23<br>(3.66–4.15)              | 4.00 $\pm$ 0.13<br>(3.86–4.11)               | 4.31 $\pm$ 0.27<br>(4–4.49)         | 3.74 $\pm$ 0.22<br>(3.44–3.96)      |
| LIF                    | 4.48  | 4.36  | 3.72 $\pm$ 0.32<br>(3.17–4.41)   | 4.19 $\pm$ 0.26<br>(3.81–4.37)              | 4.42 $\pm$ 0.56<br>(3.8–4.9)                 | 3.83 $\pm$ 0.07<br>(3.75–3.89)      | 4.32 $\pm$ 0.11<br>(4.14–4.42)      |
| BIF                    | 1.61  | 1.74  | 1.51 $\pm$ 0.13<br>(1.24–1.75)   | 1.73 $\pm$ 0.07<br>(1.63–1.78)              | 1.72 $\pm$ 0.2<br>(1.5–1.86)                 | 1.71 $\pm$ 0.05<br>(1.66–1.76)      | 1.57 $\pm$ 0.11<br>(1.46–1.75)      |
| LM                     | 3.3   | 3.22  | 3.19 $\pm$ 0.22<br>(2.84–3.64)   | 3.02 $\pm$ 0.09<br>(2.94–3.15)              | 3.5 $\pm$ 0.18<br>(3.3–3.63)                 | 3.23 $\pm$ 0.06<br>(3.19–3.29)      | 3.03 $\pm$ 0.1<br>(2.91–3.14)       |
| BM1                    | 0.97  | 1.06  | 0.96 $\pm$ 0.09<br>(0.81–1.2)  | 0.92 $\pm$ 0.04<br>(0.86–0.96)              | 0.99 $\pm$ 0.07<br>(0.92–1.05)               | 0.95 $\pm$ 0.06<br>(0.88–1)         | 0.89 $\pm$ 0.04<br>(0.83–0.95)      |
| M1M                    | 4.5   | 4.37  | 4.16 $\pm$ 0.2<br>(3.85–4.51) 26                                       | 4.30 $\pm$ 0.05<br>(4.24–4.37)              | 4.32 $\pm$ 0.18<br>(4.12–4.43)               | 4.18 $\pm$ 0.2<br>(4.02–4.4)        | 4.14 $\pm$ 0.23<br>(3.95–4.53)      |
| BRO                    | 4.56  | 4.19  | 4.04 $\pm$ 0.32<br>(3.38–4.54)   | 4.16 $\pm$ 0.05<br>(4.11–4.23)              | 4.21 $\pm$ 0.2<br>(3.98–4.35)                | 4.24 $\pm$ 0.32<br>(3.92–4.56)      | 3.90 $\pm$ 0.41<br>(3.45–4.43)      |
| LIB                    | 3.45  | 3.62  | 3.57 $\pm$ 0.14<br>(3.32–3.92) 26                                      | 4.02 $\pm$ 0.11<br>(3.92–4.18)              | 3.80 $\pm$ 0.09<br>(3.71–3.89)               | 3.56 $\pm$ 0.14<br>(3.4–3.68)       | 3.32 $\pm$ 0.06<br>(3.25–3.41)      |
| ORL                    | 8.05  | 8.46  | 7.72 $\pm$ 0.41<br>(6.79–8.61)   | 7.72 $\pm$ 0.23<br>(7.51–7.96)              | 7.72 $\pm$ 0.3<br>(7.4–8)                    | 7.92 $\pm$ 0.27<br>(7.67–8.2)       | 7.44 $\pm$ 0.31<br>(7.13–7.92)      |
| ZB                     | –   | 12.51                                       | 11.75 $\pm$ 0.59<br>(10.57–12.71)                                      | 11.84 $\pm$ 0.96<br>(10.4–12.44)            | 11.99 $\pm$ 0.49<br>(11.65–12.55)            | 11.99 $\pm$ 0.46<br>(11.5–12.4)     | 11.41 $\pm$ 0.47<br>(10.91–12.03)   |
| BZP                    | 2.43  | 2.54  | 2.20 $\pm$ 0.15<br>(1.94–2.47) 26                                      | 2.30 $\pm$ 0.1<br>(2.22–2.44)               | 2.16 $\pm$ 0.12<br>(2.08–2.3)                | 2.27 $\pm$ 0.08<br>(2.18–2.33)      | 2.16 $\pm$ 0.13<br>(2.01–2.35)      |

<sup>a</sup> Except as indicated.

Upper and lower incisors opisthodont; molars pentalphodont. Superior molar rows parallel. Procingulum of first upper molar (M1) with anteromedian flexus only in young animals, specimens with moderate wear do not present anteromedian flexus. Anteroloph present and separate from anterocone in young, but anteroloph joining with anterocone in specimens with more advanced wear; posteroloph small joined to metacone in specimens with more advanced wear. Paracone of M1 with small crest that joins the mesoloph, creating an internal fosseta. M2 with mesoloph, with or without a protoflexus. The third upper molar (M3) is reduced, and has a single posterior cup, which we equate to the hypocone; hypoflexus is diminutive. The anteroconid of the first lower molar (m1) is without an anteromedian flexid; the mesolophid is distinct on unworn m1 and m2; m2 and m3 with anterolabial cingulum.

**KARYOTYPE:** This species is characterized by  $2n = 62$  and  $FNa = 64$ . This karyotype has been formerly associated with other epithets besides *O. fornesi*, such as *O. eliurus* (Wagner, 1845) and *O. flavescens* (Myers and Carleton 1981; Svartman 1989; Andrades-Miranda et al., 2001; Pereira and Geise, 2009; Di-Nizo et al., 2015).

**HABITAT:** *Oligoryzomys mottogrossae* is an inhabitant of open vegetation biomes such as the Cerrado and Caatinga, but can also be found in formations in the transition with Amazonian forest. No information about the vegetation of the type locality was provided in the description of *O. mottogrossae* (Allen, 1916), but the vegetation along the Papagaio River, including the Utariti region, is gallery forest.

**COMPARISONS:** *Oligoryzomys mottogrossae* differs from all other *Oligoryzomys* species by its unique karyotype. In addition, *O. mottogrossae* differs from other *Oligoryzomys* that occur in Brazil by a combination of other characters including (1) yellowish ventral pelage and (2) dorsal coloration without a defined limit with ventral pelage color, in comparison to a whitish venter with defined limit between lateral and ventral coloration in adult specimens of *O. nigripes*, *O. microtis*, *O. utaritensis*, and *O. stramineus* (see table 1); (3) slightly bicolored tail, contrary to unicolored tail in *O. nigripes* and *O. rupestris* (other species of the genus also have slightly bicolored tails); (4) small size species (adult HBL <96 mm in average) as in *O. rupestris*, *O. microtis*, *O. moojeni*, *O. flavescens*, *O. delicatus*, *O. messorius*, *O. fornesi*, opposed to large size species (adult HBL >100 mm in average) as *O. nigripes*, *O. stramineus*, and *O. chacoensis*. See table 1 for other comparisons.

Despite sharing the same type locality, *O. mottogrossae* differs from *O. utaritensis* by its karyotype with  $2n = 62$  and  $FNa = 64$  (*O. utaritensis*  $2n = 70$  and  $FNa = 74$ ), and a combination of morphological characters including (1) yellowish ventral pelage, contrary whitish ventral coloration in *O. utaritensis*, (2) dorsal coloration without a defined limit with ventral pelage color, in comparison to a whitish venter with defined limit between lateral and ventral coloration in adult specimens of *O. utaritensis* (fig. 2). *O. mottogrossae* and *O. utaritensis* are also readily distinguished by size, as *O. utaritensis* is a larger species (see Agrellos et al., 2012, for measurements of other *Oligoryzomys* species).

**ETYMOLOGY:** *Oligoryzomys mottogrossae* was named by J.A. Allen based on its type locality in Mato Grosso state.

**SPECIMENS EXAMINED:** See appendix 1.

**REMARKS:** *Oligoryzomys mottogrossae* was described by Allen (1916) based on two specimens, the holotype from Utariti, and one paratype from “Guatsué”; the latter locality was not located, but Paynter and Traylor (1991) suggest that it is presumably on middle Rio Papagaio in Mato Grosso state.

#### ACKNOWLEDGMENTS

We appreciated the facilities provided by the owners of the Fazenda Caetitu in Sapezal (MT), Fazendas Campo Belo, Ponte Senada, Itamarati, Ouro Verde II, and Alvorada in Campo Novo do Parecis (MT), and the secretaries of health of the state of Mato Grosso (especially

Alberto Aparecido Marques and Alba Valeria Melo) and of the municipalities of Sapezal and Campo Novo do Parecis. The collaboration in fieldwork by the field team of Secretaria de Vigilância em Saúde (SVS) and Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, IOC, FIOCRUZ, was most useful. Instituto Chico Mendes de Conservação da Natureza (ICMBio) granted license to collect the specimens. Work was supported by grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to M.W. (440663/2015-6), C.R.B. (473687/2013-5 and 304498/2014-9), and P.S.D., and from the Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) to M.W. (E-26/110.505/2012) and C.R.B. (E-26/201-200/2014). We also would like to thank the curators and staff from the AMNH (Robert S. Voss, Nancy Simmons, and Eileen Westwig), MN/UFRJ (João A. de Oliveira and Stella Franco), and FHN (Sérgio Bogan) who generously allowed and helped us to analyze the specimens under their care; Pablo Teta for kindly photographing type specimens at the FHN; Guillermo D'Elia and Jorge Salazar-Bravo for comments and corrections that greatly improved the manuscript; and Mauro Elkoury and Marilia Lavocat, for providing facilities and hard work for the project development.

#### REFERENCES

- Agrellos R., et al. 2012. The taxonomic status of the Castelo dos Sonhos hantavirus reservoir, *Oligoryzomys utiaritensis* Allen 1916 (Rodentia, Cricetidae, Sigmodontinae). *Zootaxa* 3220: 1–28.
- Allen, J.A. 1916. Mammals collected on the Roosevelt Brazilian Expedition, with field notes by Leo E. Miller. *Bulletin of the American Museum of Natural History* 35 (30): 559–610.
- Allen, J.A., and F.M. Chapman. 1897. On a second collection of mammals from the island of Trinidad, with descriptions of new species, and a note on some mammals from the island of Dominica, W.I. *Bulletin of the American Museum of Natural History* 9 (2): 13–30.
- Almendra, A.L., D.S. Rogers, and F.X. González-Cózatl. 2014. Molecular phylogenetics of the *Handleyomys chapmani* complex in Mesoamerica. *Journal of Mammalogy* 95: 26–40.
- Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History* 231: 1–652.
- Andrades-Miranda, J., et al. 2001. Chromosome studies of seven species of *Oligoryzomys* (Rodentia: Sigmodontinae) from Brazil. *Journal of Mammalogy* 82: 1080–1091.
- Aniskin, V.M., and V.T. Volobouev, 1999. Comparative chromosome banding of two South-American species of rice rats of the genus *Oligoryzomys* (Rodentia, Sigmodontinae). *Chromosome Research* 7: 557–562.
- Bennett, E.T. 1832. Characters of a new species of otter (*Lutra*, Erxl.) and of a new species of mouse (*Mus*, L.) collected in Chili by Mr. Cuming. *Proceedings of the Committee of Science and Correspondence of the Zoological Society of London*, part 2 (1832): 1–4.
- Bonvicino, C.R., and M.A. Moreira. 2001. Molecular phylogeny of the genus *Oryzomys* (Rodentia: Sigmodontinae) based on cytochrome *b* DNA sequences. *Molecular Phylogenetics and Evolution* 18: 282–92.
- Bonvicino, C.R., and M. Weksler. 1998. A new species of *Oligoryzomys* (Rodentia, Sigmodontinae) from northeastern and central Brazil. *Zeitschrift für Säugetierkunde* 63: 90–103.



- Bonvicino, C.R., F. Casado, and M. Weksler. 2014. A new species of *Cerradomys* (Mammalia: Rodentia: Cricetidae) from Central Brazil, with remarks on the taxonomy of the genus. *Zoologia* 31: 525–540.
- Cabrera, A. 1961. Catalogo de los mamiferos de America del Sur. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 4: 309–732.
- Canon, C., D. Mir, U.F.J. Pardiñas, E.P. Lessa, and G. D'Elía. 2014. A multilocus perspective on the phylogenetic relationships and diversification of rodents of the tribe Abrotrichini (Cricetidae: Sigmodontinae). *Zoologica Scripta* 43: 443–454.
- Carleton, M.D., and G.G. Musser. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. *Bulletin of the American Museum of Natural History* 191: 1–83.
- Carleton, M.D., and G.G. Musser. 1995. Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegetus* (Bangs, 1902). *Proceedings of the Biological Society of Washington* 108: 338–369.
- Carmignotto, A.P., A.M. Bezerra, and F.H. Rodrigues. 2014. Nonvolant small mammals from a southwestern area of Brazilian Cerrado: diversity, habitat use, seasonality, and biogeography. *Therya* 5 (2): 535–558.
- Carroll, D.S., et al. 2005. Hantavirus pulmonary syndrome in central Bolivia: relationships between reservoir hosts, habitats, and viral genotypes. *American Journal of Tropical Medicine and Hygiene* 72: 42–46.
- Casado, F., et al. 2010. Mitochondrial divergence between two populations of the hooded capuchin, *Cebus (Sapajus) cay* (Platyrrhini, Primates). *Journal of Heredity* 101: 261–269.
- Coyner, B.S., J.K. Braun, M.A. Mares, and R.A. Van Den Bussche. 2013. Taxonomic validity of species groups in the genus *Akodon* (Rodentia, Cricetidae). *Zoologica Scripta* 42: 335–350.
- Delfraro, A., et al. 2003. Yellow pigmy rice rat (*Oligoryzomys flavescens*) and hantavirus pulmonary syndrome in Uruguay. *Emerging Infectious Diseases* 9: 846–852.
- D'Elía, G., J.D. Hanson, M.R. Mauldin, P. Teta, and U.F.J. Pardiñas. 2015. Molecular systematics of South American marsh rats of the genus *Holochilus* (Muroidea, Cricetidae, Sigmodontinae). *Journal of Mammalogy* 96 (5): 1081–1094.
- Di-Nizo, C.B., et al. 2015. Comparative chromosome painting in six species of *Oligoryzomys* (Rodentia, Sigmodontinae) and the karyotype evolution of the genus. *PloS One* 10 (2): e0117579.
- Eppig, J.T., J.A. Blake, C.J. Bult, J.A. Kadin, and J.E. Richardson. 2015. The mouse genome database (MGD): facilitating mouse as a model for human biology and disease. *Nucleic Acids Research* 28: D726–36.
- Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 17: 368–76.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Francés, J., and G. D'Elía. 2006. *Oligoryzomys delticola* es sinónimo de *O. nigripes* (Rodentia, Cricetidae, Sigmodontinae). *Mastozoología Neotropical* 13: 123–131.
- Gardner, A.L., and J.L. Patton. 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. *Occasional Papers Museum Zoology, Louisiana State University* 49: 1–47.
- González-Ittig, R.E., J. Salazar-Bravo, R.M. Barquez, and C.N. Gardenal. 2010. Phylogenetic relationships among species of the genus *Oligoryzomys* (Rodentia, Cricetidae) from Central and South America. *Zoologica Scripta* 39: 511–526.

- González-Ittig, R.E., P.C. Rivera, S.C. Levis, G.E. Calderón, and C.N. Gardenal. 2014. The molecular phylogenetics of the genus *Oligoryzomys* (Rodentia: Cricetidae) clarifies rodent host—hantavirus associations. *Zoological Journal of the Linnean Society* 171 (2): 457–474.
- Guterres, A., et al. 2014. Characterization of Juquitiba virus in *Oligoryzomys fornesi* from Brazilian Cerrado. *Viruses* 6 (4): 1473–1482.
- Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hanson, J.D. 2008. Phylogenetic relationships of the Oryzomyini: use of multiple datasets to resolve a systematic conundrum. Department of Biological Sciences, Ph.D. dissertation, Texas Tech University.
- Hanson, J.D., A. Utrera, and C.F. Fulhorst. 2011. The delicate pygmy rice rat (*Oligoryzomys delicatus*) is the principal host of Maporal Virus (Family Bunyaviridae, Genus *Hantavirus*). *Vector-Borne and Zoonotic Diseases* 11 (6): 691–696.
- Huelsenbeck, J.P., F. Ronquist, R. Nielsen, and J.P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310–2314.
- Irwin, D.M., T.D. Kocher, and A.C. Wilson. 1991. Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution* 32: 128–144.
- Machado, L.F., Y.L. Leite, A.U. Christoff, and L.G. Giugliano. 2014. Phylogeny and biogeography of tetralophodont rodents of the tribe Oryzomyini (Cricetidae: Sigmodontinae). *Zoologica Scripta* 43: 119–130.
- Massoia, E. 1973. Descripción de *Oryzomys fornesi*, nueva especie y nuevos datos sobre algunas especies y subespecies argentinas del subgénero *Oryzomys* (*Oligoryzomys*) (Mammalia-Rodentia-Cricetidae). *Revista de Investigaciones Agropecuarias INTA Serie I Biología y Producción Animal* 10: 21–37.
- Milazzo, M.L., et al. 2006. Catacamas virus, a hantaviral species naturally associated with *Oryzomys couesi* (Coues' oryzomys) in Honduras. *American Journal of Tropical Medicine and Hygiene* 75: 1003–1010.
- Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshops (GCE)*, New Orleans: 1–8.
- Miranda, G.B., et al. 2009. Phylogenetic and phylogeographic patterns in sigmodontine rodents of the genus *Oligoryzomys*. *Journal of Heredity* 100: 309–321.
- Musser, G.G., and M.D. Carleton. 2005. Superfamily Muroidea. In D.E. Wilson and D.M. Reeder (editors), *Mammal species of the world, a taxonomic and geographic reference*, 3rd ed.: 894–1531. Baltimore: Johns Hopkins University Press.
- Myers, P., and M.D. Carleton. 1981. The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixième ou Rat à Tarse Noir. *Miscellaneous Publications of the Museum of Zoology University of Michigan* 161: 1–41.
- Olds, N., and S. Anderson. 1987. Notes on Bolivian mammals. 2. Taxonomy and distribution of rice rats of the subgenus *Oligoryzomys*. *Fieldiana Zoology (new series)* 39: 261–281.
- Olfers, I. von. 1818. Bemerkungen zu Illiger's *Ueber-blick der Säugthiere, nach ihrer Vertheilung über die Welttheile*, rücksichtlich der südamerikanischen Arten (Species). In W.L. von Eschwege (editor), *Journal von Brasilien, oder vermischte Nachrichten auch Brasilien, auf wissenschaftlichen Reisen gesammelt*: 192–237. Weimar: Im Verlage des Gr. H.S. priv. Landes-Industrie-Comptoirs.

- Oliveira, J.A., R.E. Strauss, and S.F. Reis. 1998. Assessing relative age and age structure in natural populations of *Bolomys lasiurus* (Rodentia: Sigmodontinae) in Northeastern Brazil. *Journal of Mammalogy* 79: 1170–1183.
- Oliveira, R.C., et al. 2009. Genetic characterization of a Juititaba-like viral lineage in *Oligoryzomys nigripes* in Rio de Janeiro, Brazil. *Acta Tropica* 112: 212–318.
- Oliveira, R.C., et al. 2011. Genetic characterization of hantaviruses associated with sigmodontine rodents in an endemic area for hantavirus pulmonary syndrome in southern Brazil. *Vector Borne and Zoonotic Diseases* 11: 301–314.
- Oliveira, R.C., et al. 2014. Hantavirus reservoirs: current status in the world with an emphasis on data from Brazil. *Viruses* 6 (5): 1929–1973.
- Palma, R.E., et al. 2005. Phylogeography of *Oligoryzomys longicaudatus* (Rodentia: Sigmodontinae) in temperate South America. *Journal of Mammalogy* 86: 191–200.
- Palma, R.E., et al. 2010a. Phylogenetic relationships of the pygmy rice rats of the genus *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae). *Zoological Journal of the Linnean Society* 160: 551–566.
- Palma, R.E., R.A. Cancino, and E. Rodríguez-Serrano. 2010b. Molecular systematics of *Abrothrix longipilis* (Rodentia: Cricetidae: Sigmodontinae) in Chile. *Journal of Mammalogy* 91: 1102–1111.
- Patton, J.L. and M.N.F. da Silva. 1995. A review of the spiny mouse genus *Scolomys* (Rodentia: Muridae: Sigmodontinae) with the description of a new species from the western Amazon of Brazil. *Proceedings of the Biological Society of Washington* 108 (2): 319–337.
- Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244: 1–306.
- Paynter, R.A., and M.A. Traylor. 1991. *Ornithological gazetteer of Brazil*. Cambridge, MA: Harvard University, Museum of Comparative Zoology (Bird Department).
- Percequillo, A.R., M. Weksler, and L.P. Costa. 2011. A new genus and species of rodent from the Brazilian Atlantic Forest (Rodentia: Cricetidae: Sigmodontinae: Oryzomyini), with comments on oryzomyine biogeography. *Zoological Journal of the Linnean Society* 161 (2): 357–390.
- Pereira, L.G., and L. Geise. 2009. Non-flying mammals of Chapada Diamantina (Bahia, Brazil). *Biota Neotropica* 9 (3): 185–196.
- R Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online resource (<http://www.R-project.org/>).
- Rambaut, A., and A. Drummond. 2007. Tracer v1.4. Online resource (<http://beast.bio.ed.ac.uk/Tracer>).
- Reig, O.A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *Journal of Zoology* 181: 227–241.
- Rice, W. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Richter, M.H., J.D. Hanson, M.N. Cajimat, M.L. Milazzo, and C.F. Fulhorst. 2010. Geographical range of Rio Mamore virus (family Bunyaviridae) genus *Hantavirus*, in association with the small-eared pygmy rice rat (*Oligoryzomys microtis*). *Vector Borne and Zoonotic Diseases* 10: 613–620.
- Ridgway, R. 1912. *Color standards and color nomenclature*. Washington, D.C.: [published by the author].
- Rivera, P.C., R.E. González-Ittig, H.J.R. Fraire, S. Levis, and C.N. Gardenal. 2007. Molecular identification and phylogenetic relationships among the species of the genus *Oligoryzomys* (Rodentia, Cricetidae) present in Argentina, putative reservoirs of hantaviruses. *Zoologica Scripta* 36: 231–239.
- Rocha, R.G., et al. 2011. Small mammals of the mid-Araguaia River in central Brazil, with the description of a new species of climbing rat. *Zootaxa* 2789: 1–34.

- Rodríguez, F., J.L. Oliver, A. Marín, and J.R. Medina. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* 142: 485–501.
- Rogers, D.S., et al. 2009. Molecular phylogenetics of *Oligoryzomys fulvescens* based on cytochrome *b* gene sequences, with comments on the evolution of the genus *Oligoryzomys*. In F.A. Cervantes (editor), 60 años de la colección nacional de mamíferos del Instituto de Biología, UNAM. Aportaciones al Conocimiento y Conservación de los Mamíferos Mexicanos: 209–222. México, D.F.: Universidad Autónoma de México.
- Ronquist, F., and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Rosa, E.S.T., et al. 2005. Newly recognized hantaviruses associated with hantavirus pulmonary syndrome in northern Brazil: partial genetic characterization of viruses and serologic implication of likely reservoirs. *Vector Borne and Zoonotic Diseases* 5: 11–19.
- Rosa, E.S.T., et al. 2010. Hantaviruses and hantavirus pulmonary syndrome, Maranhão, Brazil. *Emerging Infectious Diseases* 16: 1952–1955.
- Sambrook, J., and D.W. Russell. 2001. *Molecular cloning: a laboratory manual*. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- Saussure, H. de 1860. Note sur quelques mammifères du Mexique. *Revue et Magasin de Zoologie (série 2)* 12: 97–110.
- Smith, M.F., and J.L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of the Linnean Society* 50: 149–177.
- Smith, M.F., and J.L. Patton. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. *Journal of Mammalian Evolution* 6: 89–128.
- Sokal, R.R., and F.J. Rohlf. 1994. *Biometry: the principles and practice of statistics in biological research*. New York: W.H. Freeman.
- Stamatakis, A. 2006. Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A. 2014. RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 2014: 30 (9): 1312–1313.
- Strauss, R.E. 2010. Discriminating groups of organisms. In A.M.T. Elewa (editor), *Morphometrics for nonmorphometricians (Lecture Notes in Earth Sciences 124)*: 73–91. Berlin: Springer-Verlag.
- Suzuki, A., et al. 2004. Identifying rodent hantavirus reservoirs, Brazil. *Emerging Infectious Diseases* 10: 2127–2134.
- Svartman, M. 1989. Levantamento cariotípico de roedores da região do Distrito Federal. Master's thesis, Universidade de São Paulo.
- Swofford, D.L. 2002. PAUP\*. Phylogenetic analysis using parsimony (\*and other methods), v. 4.0. Sunderland, MA: Sinauer Associates.
- Teta, P., J.P. Jayat, P.E. Ortiz, and G. D'Elía. 2013. The taxonomic status of *Oligoryzomys brendae* Massoia, 1998 (Rodentia, Cricetidae), with comments on the availability of this name. *Zootaxa* 3641 (4): 433–447.
- Vivo, M., et al. 2011. Checklist dos mamíferos do Estado de São Paulo, Brasil. *Biota Neotropica* 11 (suppl. 1): 111–131.
- Voss, R.S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188 (2): 260–493.

- Waterhouse, G.R. 1837. Characters of new species of the genus *Mus*, from the collection of Mr. Darwin. Proceedings of the Zoological Society of London 1837, part 5: 15–21.
- Weksler, M. 2006. Phylogenetic relationships of oryzomine rodents (Muroidea, Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296: 1–149.
- Weksler, M., and C.R. Bonvicino. 2005. Taxonomy of pigmy rice rats genus *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) of the Brazilian Cerrado, with the description of two new species. Arquivos do Museu Nacional 63: 113–130.
- Weksler, M., and C.R. Bonvicino. 2015. Genus *Oligoryzomys* Bangs. In J.L. Patton, U.F.J. Pardiñas, and G. D'Elía (editors), Mammals of South America. Vol. 2, rodents: 417–437. Chicago: University of Chicago Press.
- Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. Journal of Molecular Evolution 39: 306–314.

## APPENDIX 1

### LIST OF LOCALITIES AND EXAMINED SPECIMENS OF *OLIGORYZOMYS*

Specimens are tagged as karyotyped (marked with superscript <sup>K</sup>), used in morphometric analyses (<sup>M</sup>), and/or in phylogenetic analyses (<sup>P</sup>). Numbers in parentheses refer to sampling localities in map (fig. 1). Museum and collectors acronyms are: AMNH (American Museum of Natural History), BYU (Monte L. Bean Museum, Brigham Young University, Provo, UT), CFA (Collection Felix Azara, Universidade de Maimónides, Buenos Aires, Argentina), CRB (Cibele Rodrigues Bonvicino), LBCE (mammals collections of Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, FIOCRUZ, Rio de Janeiro, Brazil), GD (Guillermo D'Elía), IMBICE (Instituto Multidisciplinario De Biología Celular, La Plata, Argentina), INEVH (*Instituto Nacional de Enfermedades Virales Humanas* “Dr. Julio I. Maiztegui,” Buenos Aires, Argentina), MACN (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina), MN (Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil), MNFS (Maria Nazaré F. da Silva), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), NHM (Natural History Museum, Vienna, Austria), SVS (Serviço de Vigilância em Saúde, Ministry of Health, Brazil), TTU (The Museum, Texas Tech University, Lubbock), UFPB (mammal collection, Universidade Federal da Paraíba, João Pessoa, Brazil), UNB (mammal collection, Universidade de Brasília, Brazil), UFES (mammal collection, Universidade Federal do Espírito Santo, Vitória, Brazil), and USNM (U.S. National Museum of Natural History).

*Oligoryzomys mottogrossae*: BRAZIL: Alagoas: (1) 6 km SSL of Matriz de Camaragipe: UFPB977<sup>M</sup>. Bahia: (2) Jaborandi: MN61605<sup>P</sup>, MN62637<sup>M</sup>, MN62640<sup>P</sup>; (3) Lençóis, Remanso: MZUSP33816<sup>K</sup>. Distrito Federal: (4) Brasília, Fazenda Água Limpa: UNB288<sup>M</sup>, UNB289<sup>M</sup>, UNB290<sup>M</sup>, UNB291<sup>M</sup>, UNB294<sup>M</sup>, UNB294<sup>M</sup>, UNB931<sup>M</sup>, UNB979<sup>M</sup>, UNB1212<sup>M</sup>; Estação Ecológica do Jardim Botânico: CRB3141<sup>K</sup>, CRB3299<sup>K</sup>; Parque Nacional de Brasília: UNB965<sup>M</sup>. Goiás: (5) Aporé, UHE Espora: LBCE5450<sup>M</sup>, LBCE9438<sup>M</sup>, LBCE10900<sup>M</sup>, LBCE12785<sup>P</sup>, LBCE12787<sup>P</sup>, LBCE12788<sup>P</sup>; (6) Campo Alegre de Goiás: LBCE8763<sup>P</sup>; (7) Colinas do Sul, Rio Tocantinho:



MN36928<sup>K,P</sup>, MN36746<sup>K,P</sup>; (8) Corumbá de Goiás, Morro dos Cabeludos: MN34440<sup>M</sup>; (9) Cumari: LBCE15961<sup>K</sup>; (10) Mambai: LBCE10859<sup>M</sup>, LBCE10851<sup>M</sup>, LBCE10852<sup>M</sup>, LBCE10880<sup>M</sup>, LBCE10885<sup>M</sup>, LBCE10887<sup>M</sup>; (11) Mimoso de Goiás, Fazenda Cadoz: MN67086<sup>P</sup>; (12) Parque Nacional das Emas: MZUSP-APC565<sup>K</sup>; (13) Serranópolis, UHE Espora: LBCE8509<sup>M</sup>, LBCE6789<sup>M</sup>, LBCE6859<sup>M</sup>, LBCE6862<sup>M</sup>; (14) Teresina de Goiás, Fazenda Vão dos Bois: CRB733<sup>M</sup>, CRB747<sup>M</sup>, CRB768<sup>M</sup>. Maranhão: (15) Anajatuba: IEC19241, IEC19248, IEC19491, IEC19527, IEC19540. Mato Grosso: (16) Campo Verde, Assentamento Taperinha: SVS884<sup>M</sup>; (not plotted) Guatsué: AMNH37100<sup>M</sup> (paratype); (17) São José do Xingu, Fazenda São Luiz: CRB2823<sup>K</sup>; (18) Rio Papagaio, Utariiti: AMNH37542<sup>M</sup> (holotype); Mato Grosso do Sul: (19) Cassilândia, PCH Planalto: LBCE12070<sup>K</sup>, LBCE12071<sup>K</sup>, LBCE12794<sup>K</sup>, LBCE11950<sup>K</sup>; (20) Corumbá, Fazenda Alegria: LBCE5718<sup>P</sup>, LBCE5719<sup>P</sup>. Minas Gerais: (21) Montes Claros, Fazenda Canoas: MN-FC51<sup>M</sup>, MN-FC37<sup>M</sup>, MN-FC73<sup>M</sup>; (22) Uberlândia: LBCE18172<sup>K</sup>, LBCE18183<sup>K</sup>; (23) Pará, Santana do Araguaia: UFES1371b<sup>P</sup>, UFES1441<sup>P</sup>. Paraíba: (24) Mamanaguape: UFPB-MPS78<sup>M</sup>. Pernambuco: (25) Bom Conselho: UFPB-PMN60<sup>M</sup>, UFPB-PMN61<sup>M</sup>, UFPB-PMN63<sup>M</sup>; (26) Buique: UFPB1893<sup>M</sup>; (27) Macaparana: UFPB-MPS34<sup>M</sup>; São Paulo: (28): Águas de Santa Barbara: MZUSP-APC1135<sup>K</sup>; Tocantins: (29) Dianópolis, PCH Porto Franco: LBCE12883<sup>K</sup>, LBCE12834<sup>K</sup>, LBCE12839<sup>K</sup>, LBCE12832<sup>K</sup>, LBCE12837<sup>K</sup>, LBCE12843<sup>K</sup>, LBCE12847<sup>K</sup>; (30) Lagoa da Confusão: UFES1371a<sup>P</sup>, UFES1373<sup>P</sup>; (31) Peixe: MZUSP-APC839<sup>K</sup>; (32) Pium: UFES1440<sup>P</sup>. PARAGUAY: (33) Caaguazú, 24 km NNW Carayaó: UMMZ133819<sup>K,M</sup>, UMMZ133818<sup>K,M</sup>; (34) Canendeyu, Curugaty: UMMZ124218<sup>K,M</sup>.

*Oligoryzomys microtis*: BOLIVIA: Beni: (35) Boroica: USNM460740<sup>M</sup>; (36) Chachuelita: USNM460739<sup>M</sup>; (37) Chaco Lejo: USNM391295<sup>M</sup>, USNM391296<sup>M</sup>, USNM391297<sup>M</sup>; (38) Las Penas: USNM460741<sup>M</sup>; (39) San Joaquin: USNM364738<sup>M</sup>, USNM391299<sup>M</sup>, USNM460273<sup>M</sup>, USNM460742<sup>M</sup>; USNM364923<sup>M</sup>, USNM460743<sup>M</sup>; (40) Totai: USNM364948<sup>M</sup>; Santa Cruz, (41) El Refugio: BYU19014<sup>P</sup>. BRAZIL, Acre, (42) Capixaba: SVS638<sup>M</sup>, SVS673<sup>P</sup>, SVS676<sup>P</sup>; (43) Igarapé Porangaba: MNFS1321<sup>P</sup>; Amazonas, (44) Jaiú: MVZ193858<sup>P</sup>; (45) Manacapuru: AMNH37091<sup>M</sup> (holotype), AMNH37157<sup>M</sup> (paratype), AMNH37096<sup>M</sup> (paratype), CRB3004<sup>B,K</sup>; (46) Seringal Condor, left bank Rio Juruá: MVZ190401<sup>P</sup>; Tocantins, (47) São Sebastião do Tocantins: CRB1448<sup>P</sup>. PERU: Loreto, (48) Iquitos, Zona Marina: TTU76249<sup>P</sup>. Madre de Dios: (49) Puerto Maldonado: USNM390112<sup>M</sup>, USNM390117<sup>M</sup>, USNM390119<sup>M</sup>; USNM390115<sup>M</sup>, USNM390116<sup>M</sup>, USNM390118<sup>M</sup>; (50) Rio Manu, 57 km above mouth: USNM559399<sup>M</sup>, USNM559403<sup>M</sup>; USNM559400<sup>M</sup>, USNM559401<sup>M</sup>, USNM559402<sup>M</sup>; (51) Río Tambopata, 30 km above mouth: USNM530925<sup>M</sup>.

*Oligoryzomys fornesi*: ARGENTINA: Chaco, (52) Parque Nacional Chaco: MACN22830<sup>P</sup>, MACN22834<sup>P</sup>, MACN22835<sup>P</sup>, MACN22837<sup>P</sup>. Formosa: (53) Estancia Guayacolec: CFA-CO2594<sup>M</sup>, CFA-CO2588<sup>M</sup>; Pilcomayo, Ceibo 13, (54) Nainek: CFA3562<sup>M</sup>, CFA3561<sup>M</sup> (holotype); Pilcomayo, (55) Laguna Branca: CFA3436<sup>M</sup>. PARAGUAY: Paraguari, (56) Costa del Río Tebicuary: GD259<sup>P</sup>.

*Oligoryzomys flavescens*: ARGENTINA: Buenos Aires: (57) 25 km SE of Buenos Aires: USNM331059<sup>M</sup>; (58) La Plata IMBICE-BA850<sup>P</sup>. Tucuman: (59) Concepcion: USNM259289<sup>M</sup>; USNM259287<sup>M</sup>; USNM259291<sup>M</sup>. BRAZIL: Paraná, (60) Campina Grande do Sul: LBCE11206<sup>M</sup>,

LBCE11208<sup>M</sup>. São Paulo: (61) Casa Grande: USNM461991<sup>M</sup>, USNM484123<sup>M</sup>; USNM484122<sup>M</sup>, USNM484124<sup>M</sup>, USNM484125<sup>M</sup>; (62) Itapetininga: USNM460516<sup>M</sup>, USNM460517<sup>M</sup>, USNM461049<sup>M</sup>, USNM461050<sup>M</sup>, USNM461054<sup>M</sup>, USNM461055<sup>M</sup>, USNM484127<sup>M</sup>, USNM484128<sup>M</sup>, USNM461051<sup>M</sup>, USNM461052<sup>M</sup>, USNM461053<sup>M</sup>, USNM461993<sup>M</sup>, USNM461994<sup>M</sup>, USNM484126<sup>M</sup>, USNM484129<sup>M</sup>, USNM484130<sup>M</sup>, USNM484131<sup>M</sup>, USNM484132<sup>M</sup>, USNM484133<sup>M</sup>, USNM485056<sup>M</sup>; (63) Pedreira CRB1405<sup>P</sup>, CRB1430<sup>P</sup>. PARAGUAY: Caaguazú, (64) 24 km NNW Carayaó: UMMZ133817<sup>M</sup>, UMMZ133816<sup>M</sup>; Canendeyu, (65) Curuguaty: UMMZ124216<sup>M</sup>, UMMZ124255<sup>M</sup>, UMMZ124217<sup>M</sup>, UMMZ124222<sup>M</sup>; Misio- nes, San Pablo, (66) 20 km W San Ignacio: USNM390122<sup>M</sup>; Pres. Hayes, (67) 24 km NW Villa Hayes: UMMZ133833<sup>M</sup>, UMMZ134342<sup>M</sup>, UMMZ134341<sup>M</sup>. URUGUAY: San Jose, (68) Puntas de Valdez: INEVH-PV27<sup>P</sup>. (69) Maldonado, Maldonado: USNM259599<sup>M</sup>; (70) Montevideo, Montevideo: USNM174937<sup>M</sup>.

## APPENDIX 2

### SPECIMEN DATA

Including Museum and/or Collector Number, GenBank Accession Number  
and Locality of the Specimens Used in the Molecular Analysis

Numbers after localities of *O. fornesi* and *O. mato Grossoe* refer to collecting sites in the map (fig. 1). Reference codes are: **1**, Carroll et al. (2005), **2**, Miranda et al. (2009), **3**, Palma et al. (2005), **4**, Coyner et al. (2013), **5**, Rogers et al. (2009), **6**, Percequillo et al. (2011), **7**, Agrellos et al. (2012) **8**, Hanson et al. (2011), **9**, González-Ittig et al. (2010), **10**, Oliveira et al. (2009), **11**, Rocha et al. (2011), **12**, Patton and Silva (1995), **13**, Ritcher et al. (2010), **14**, D'Elia et al. (2015), **15**, Palma et al. (2010b), **16**, Almendra et al., 2014), **17**, Bonvicino et al. (2014), **18**, Machado et al. (2014), **19**, Milazzo et al. (2006), **20**, Hanson (2008), **21**, Smith and Patton (1999), **22**, Canon et al. (2014), **23**, This study. Museum and collector acronyms are: AMNH (American Museum of Natural History), ASNHC (Angelo State Natural History Collections, San Angelo, TX), BYU (Monte L. Bean Museum, Brigham Young University, Provo, UT), CM (Carnegie Museum of Natural History, Pittsburgh, PA), CRB (Cibele Rodrigues Bonvicino), GD (Guillermo D'Elia), IMBICE (Instituto Multidisciplinario de Biología Celular, La Plata, Argentina), INEVH (*Instituto Nacional de Enfermedades Virales Humanas* "Dr. Julio I. Maiztegui," Buenos Aires, Argentina), LB (Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina), LBCE (Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, FIOCRUZ, Rio de Janeiro, Brazil), LF (Luís Flamarion), MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina), MCNU (Museu de Ciencias Naturais da Ulbra, Brazil), MN (Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil), MNFS (Maria Nazaré F. da Silva), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), NK (Museum of Southwestern Biology, University of New Mexico, Albuquerque), OMNH (Sam Noble Museum, University of Oklahoma, Norman), SVS (Serviço de Vigilância em Saúde, Ministry of Health, Brazil), TTU (The Museum, Texas

Tech University, Lubbock), UFPB (Universidade Federal da Paraíba, João Pessoa, Brazil), UFES (Universidade Federal do Espírito Santo, Vitória, Brazil). n/a = not applicable.

| Taxon                   | Locality  | Voucher Number | CYTB     | I7FGB    | Ref.  |
|-------------------------|---|----------------|----------|----------|-------|
| <i>O. brendae</i>       | Argentina, Salta  | OMNH34497      | KC841389 | N/A      | 4     |
| <i>O. brendae</i>       | Argentina, Catamarca, Las Juntas                        | MIC211         | EU192168 | N/A      | 8     |
| <i>O. chacoensis</i>    | Paraguay, Boqueron                                      | TK62932        | EU258543 | N/A      | 5     |
| <i>O. chacoensis</i>    | Argentina, Salta  | INEVH-Or22498  | GU185904 | N/A      | 9     |
| <i>O. costaricensis</i> | Panama, Los Santos                                      | NK101588       | EU192164 | N/A      | 8     |
| <i>O. costaricensis</i> | Panama, Gamboa  | TK163369       | GU393988 | N/A      | 8     |
| <i>O. delicatus</i>     | Venezuela, Portuguesa, Hato Maporal near Caño Delgadito | TK138080       | DQ227457 | N/A      | 5     |
| <i>O. delicatus</i>     | Venezuela, Sucre, Finca Vuelta Larga                    | AMNH257262     | GU126529 | N/A      | 6     |
| <i>O. destructor</i>    | Ecuador, Pichincha                                      | TEL1479        | EU258544 | N/A      | 5     |
| <i>O. destructor</i>    | Ecuador, Pichincha                                      | TEL1481        | GU393991 | N/A      | 8     |
| <i>O. flavescens</i>    | Argentina, Buenos Aires, La Plata (58)                  | IMBICE-BA850   | GU185925 | N/A      | 9     |
| <i>O. flavescens</i>    | Brazil, São Paulo, Pedreira (63)                        | CRB1405        | EU258545 | N/A      | 5     |
| <i>O. flavescens</i>    | Brazil, São Paulo, Pedreira (63)                        | CRB1430        | JQ013746 | JQ282855 | 7     |
| <i>O. flavescens</i>    | Uruguay, San Jose, Puntas de Valdez (68)                | INEVH-PV27     | GU185921 | N/A      | 9     |
| <i>O. fornesi</i>       | Argentina, Chaco, Parque Nacional Chaco (52)            | MACN22835      | GU185919 | N/A      | 9     |
| <i>O. fornesi</i>       | Argentina, Chaco, Parque Nacional Chaco (52)            | MACN22830      | GU185920 | N/A      | 9     |
| <i>O. fornesi</i>       | Argentina, Chaco, Parque Nacional Chaco (52)            | MACN22837      | GU185918 | N/A      | 9     |
| <i>O. fornesi</i>       | Argentina, Chaco, Parque Nacional Chaco (52)            | MACN22834      | GU185917 | N/A      | 9     |
| <i>O. fornesi</i>       | Paraguay, Paraguari, Costa del Rio Tebicuary (56)       | GD259          | EU192158 | N/A      | 8     |
| <i>O. fulvescens</i>    | Honduras, Olancho, 4 km E Catcamas                      | TTU84609       | EU258547 | N/A      | 5     |
| <i>O. fulvescens</i>    | Mexico, Chiapas, Mapastepec, Tutuan, El Rancho Trébol   | TTU104513      | EU258548 | N/A      | 5     |
| <i>O. longicaudatus</i> | Argentina, Neuquén                                      | LB012          | AY275702 | N/A      | 3     |
| <i>O. longicaudatus</i> | Argentina, Rio Negro                                    | MVZ154463      | GU393998 | N/A      | 8     |
| <i>O. magellanicus</i>  | Chile, Magallanes                                       | IPAT           | AY275705 | N/A      | 3     |
| <i>O. mattogrossae</i>  | Brazil, Bahia, Jaborandi (2)                            | MN62640        | KY952261 | JQ282862 | 23, 7 |
| <i>O. mattogrossae</i>  | Brazil, Bahia, Jaborandi (2)                            | MN61605        | KY952260 | N/A      | 23    |
| <i>O. mattogrossae</i>  | Brazil, Goiás, Aporé (5)                                | LBCE12787      | KY952254 | N/A      | 23    |
| <i>O. mattogrossae</i>  | Brazil, Goiás, Aporé (5)                                | LBCE12788      | KY952255 | N/A      | 23    |
| <i>O. mattogrossae</i>  | Brazil, Goiás, Aporé (5)                                | LBCE12785      | KY952253 | N/A      | 23    |
| <i>O. mattogrossae</i>  | Brazil, Goiás, Campo Alegre de Goiás (6)                | LBCE8763       | KY952259 | N/A      | 23    |

|                        |   |           |          |          |       |
|------------------------|---|-----------|----------|----------|-------|
| <i>O. mattogrossae</i> | Brazil, Goiás, Colinas do Sul, Rio Tocantizinho (7)                 | MN36928   | DQ826023 | N/A      | 2     |
| <i>O. mattogrossae</i> | Brazil, Goiás, Colinas do Sul, Rio Tocantizinho (7)                 | MN36746   | DQ826022 | N/A      | 2     |
| <i>O. mattogrossae</i> | Brazil, Goiás, Mimoso de Goiás (11)                                 | MN67086   | KY952262 | N/A      | 23    |
| <i>O. mattogrossae</i> | Brazil, Goiás, Serranópolis (13)                                    | LBCE8509  | KY952258 | N/A      | 23    |
| <i>O. mattogrossae</i> | Brazil, Mato Grosso do Sul, Corumbá (20)                            | LBCE5718  | KY952256 | N/A      | 23    |
| <i>O. mattogrossae</i> | Brazil, Mato Grosso do Sul, Corumbá (20)                            | LBCE5719  | KY952257 | N/A      | 23    |
| <i>O. mattogrossae</i> | Brazil, Pará, Santana do Araguaia (23)                              | UFES1371b | HM594621 | N/A      | 11    |
| <i>O. mattogrossae</i> | Brazil, Pará, Santana do Araguaia (23)                              | UFES1441  | HM594623 | N/A      | 11    |
| <i>O. mattogrossae</i> | Brazil, Tocantins, Lagoa da Confusão (30)                           | UFES1371a | HM594619 | N/A      | 11    |
| <i>O. mattogrossae</i> | Brazil, Tocantins, Lagoa da Confusão (30)                           | UFES1373  | HM594620 | N/A      | 11    |
| <i>O. mattogrossae</i> | Brazil, Tocantins, Pium (32)  | UFES1440  | HM594622 | N/A      | 11    |
| <i>O. messorius</i>    | Venezuela, Amazonas, Pozon, 50 km NE Puerto Ayacucho                | ACUNHC275 | EU258537 | N/A      | 5     |
| <i>O. messorius</i>    | Brazil, Amapá, Porto Grande   | AM48      | KY952250 | N/A      | 23    |
| <i>O. microtis</i>     | Bolivia, Santa Cruz, El Refugio (41)                                | BYU19014  | AY439000 | N/A      | 1     |
| <i>O. microtis</i>     | Brazil, Acre, Capixaba (42)   | SVS673    | KY952263 | N/A      | 23    |
| <i>O. microtis</i>     | Brazil, Acre, Capixaba (42)   | SVS676    | KY952264 | N/A      | 23    |
| <i>O. microtis</i>     | Brazil, Acre, Igarapé Porangaba (43)                                | MNFS1321  | U58381   | N/A      | 12    |
| <i>O. microtis</i>     | Brazil, Amazonas, Jaiú (44)   | MVZ193858 | EU258549 | N/A      | 5     |
| <i>O. microtis</i>     | Brazil, Amazonas, Manacapurú (45)                                   | CRB3004   | KY952252 | N/A      | 23    |
| <i>O. microtis</i>     | Brazil, Amazonas, Seringal Condor (46)                              | MVZ190401 | HM594624 | N/A      | 11    |
| <i>O. microtis</i>     | Brazil, Tocantins, São Sebastião do Tocantins (47)                  | CRB1448   | KY952251 | JQ282857 | 23, 7 |
| <i>O. microtis</i>     | Peru, Loreto, Zona Marina (48)                                      | TTU76249  | FJ374766 | N/A      | 13    |
| <i>O. moojeni</i>      | Brazil, Goiás, Sítio D' Abadia                                      | LBCE11615 | JQ013771 | JQ282874 | 7     |
| <i>O. moojeni</i>      | Brazil, Goiás, Cavalcante, Parque Nacional da Chapada dos Veadeiros | MN50320   | JQ013769 | JQ282849 | 7     |
| <i>O. nigripes</i>     | Brazil, Santa Catarina, Jaborá                                      | LBCE8160  | JQ013778 | JQ282873 | 7     |
| <i>O. nigripes</i>     | Brazil, Rio de Janeiro, Parque Nacional da Serra dos Órgãos         | MN71984   | GQ259905 | JQ282868 | 10, 7 |
| <i>O. rupestris</i>    | Brazil, Goiás, Alto Paraíso   | MN50326   | JQ013764 | JQ282851 | 7     |
| <i>O. rupestris</i>    | Brazil, Goiás, Alto Paraíso   | MN50322   | JQ013763 | JQ282850 | 7     |
| <i>O. stramineus</i>   | Brazil, Goiás, Fazenda Regalito                                     | UFPB1827  | DQ826027 | N/A      | 2     |
| <i>O. stramineus</i>   | Brazil, Goiás, Terezina de Goiás                                    | MN46410   | JQ013747 | N/A      | 7     |
| <i>O. stramineus</i>   | Brazil, Goiás, Terezina de Goiás                                    | MN34439   | N/A      | JQ282842 | 7     |
| <i>O. utiariensis</i>  | Brazil, Mato Grosso, Campo Novo do Parecis                          | MN75619   | JQ013749 | JQ282888 | 7     |

|                               |   |              |          |          |        |
|-------------------------------|---|--------------|----------|----------|--------|
| <i>O. utiaritensis</i>        | Brazil, Mato Grosso, Sapezal, Fazenda Begolim | MN75598      | JQ013760 | JQ282882 | 7      |
| <i>O. vegetus</i>             | Costa Rica, Cartago, Volcan Irazu             | ROM113156    | EU258541 | N/A      | 5      |
| <i>O. vegetus</i>             | Nicaragua, Rivas                              | ROM112192    | EU258538 | N/A      | 5      |
| OUTGROUPS                     |   |              |          |          |        |
| <i>Abrothrix longipilis</i>   | Chile, Aysen                                  | NK160649     | GU564074 | GU564103 | 15     |
| <i>Thomasomys aureus</i>      | Peru, Cusco                                   | MVZ170076    | U03540   | KJ614620 | 21, 22 |
| <i>Sigmodon hispidus</i>      | Mexico, Tamaulipas                            | TK137315     | EU073177 | EU652895 | 20     |
| <i>Handleyomys saturator</i>  | Nicaragua, Matagalpa                          | CURN JAGE438 | KF658386 | KF658445 | 16     |
| <i>Holochilus sciureus</i>    | Suriname, Paramaribo                          | TK17512      | KP970145 | KP970209 | 14     |
| <i>Hylaeamys megacephalus</i> | Brazil, Goiás                                 | LBCE18571    | KP122250 | N/A      | 17     |
| <i>Hylaeamys megacephalus</i> | Brazil, Brasília                              | UNB3069      | N/A      | JQ966815 | 18     |
| <i>Lundomys molitor</i>       | Brazil, Rio Grande do Sul                     | MCNU2302     | JQ966241 | JQ966825 | 18     |
| <i>Melanomys chrysomelas</i>  | Nicaragua, Atlantico Norte                    | TK121417     | EU340017 | KP970194 | 14     |
| <i>Neacomys spinosus</i>      | Brazil  | UFES1730     | JQ966232 | JQ966811 | 18     |
| <i>Nectomys squamipes</i>     | Paraguay, Paraguari                           | TTU82920     | EU074634 | KP970195 | 14     |
| <i>Nesoryzomys swarthi</i>    | Ecuador, Galapagos                            | ASNHC10003   | EU340014 | KP970196 | 14     |
| <i>Oecomys catherinae</i>     | Brazil, Tocantins                             | UFES247      | JQ966233 | JQ966813 | 18     |
| <i>Oryzomys couesi</i>        | Honduras, Olancha                             | TK102040     | DQ185383 | EU652903 | 19, 20 |
| <i>Pseudoryzomys simplex</i>  | Argentina, Chaco                              | CNP4589      | KP970127 | KP970198 | 14     |
| <i>Sooretamys angouya</i>     | Paraguay, Ñembucu                             | TK61763      | KP970128 | KP970200 | 14     |

All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:

<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications  
Central Park West at 79th Street  
New York, NY 10024

Ⓢ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).