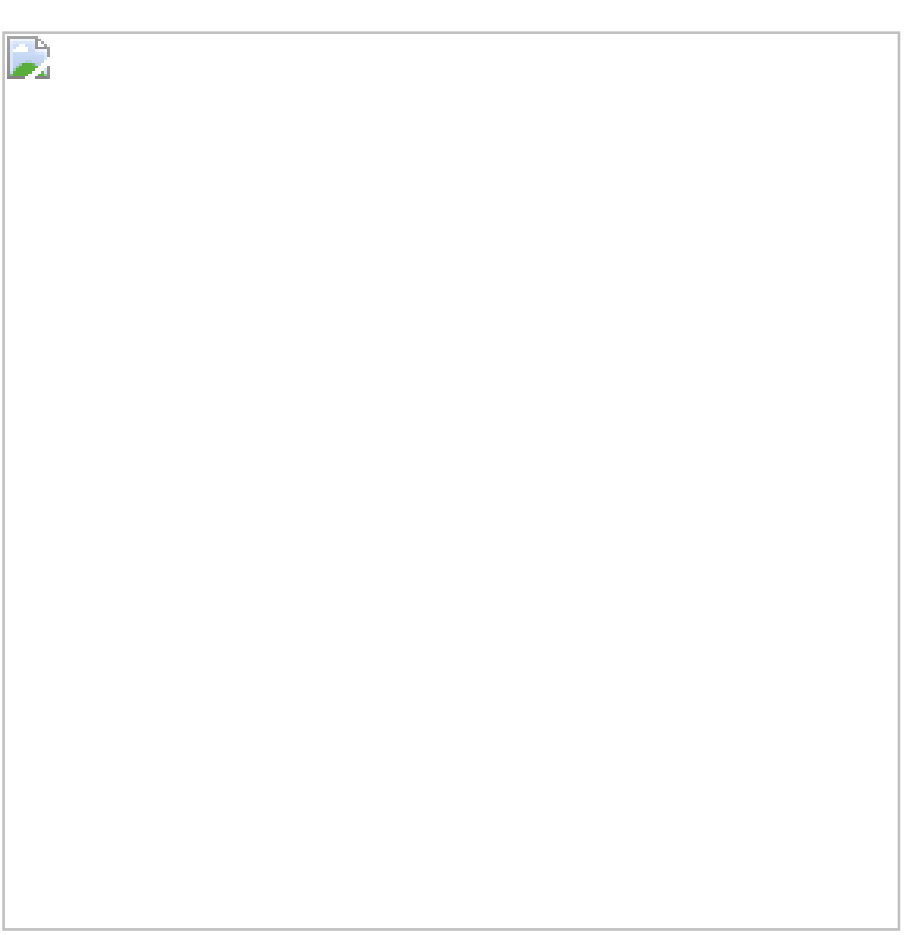

The Taxonomic Status of Oligoryzomys mattogrossae (Allen 1916) (Rodentia: Cricetidae: Sigmodontinae), Reservoir of Anajatuba Hantavirus

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

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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

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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 (*colalargas* 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. mattogrossae* (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

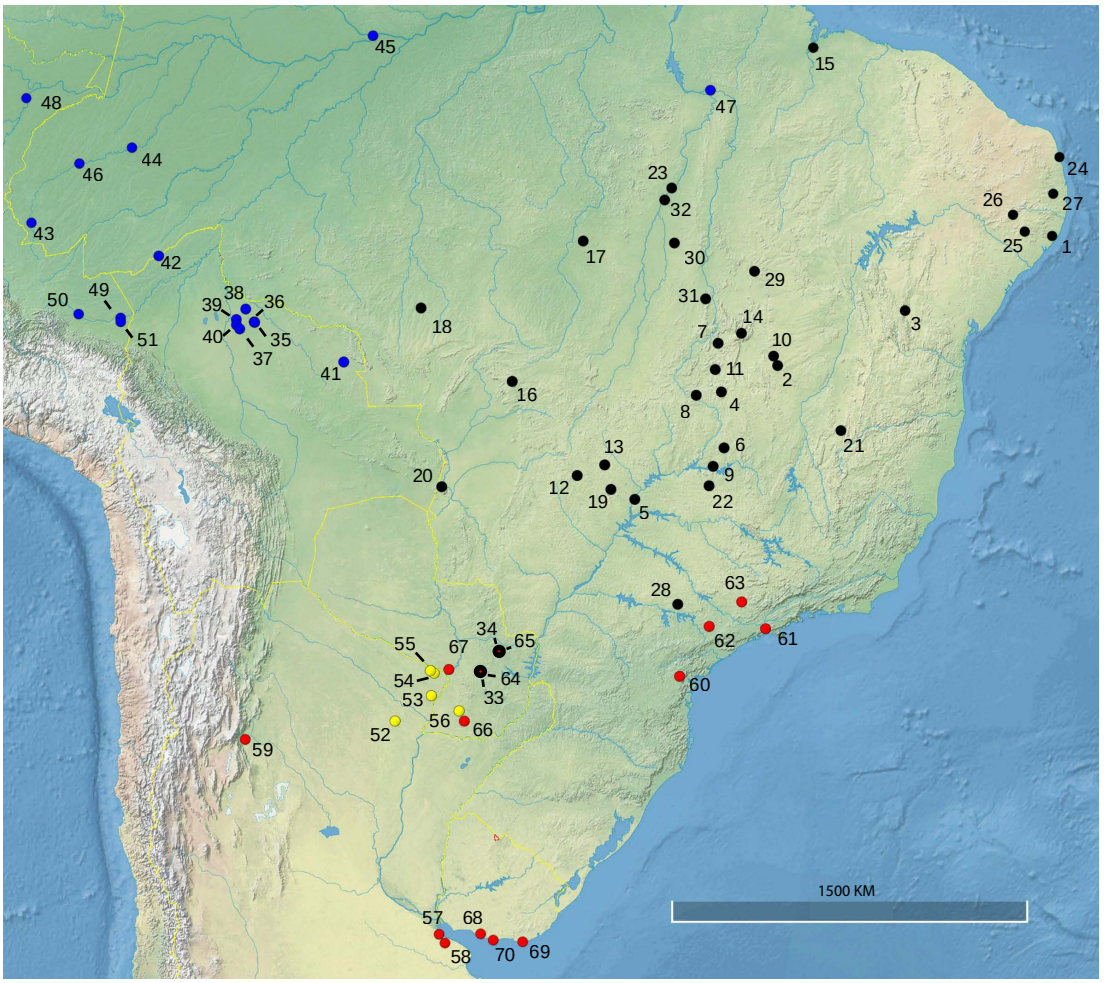


FIGURE 1. Map of central portion of South America showing the localities of analyzed specimens of *O. mattogrossae* (black), *O. fornesi* (yellow), *O. microtis* (blue), and *O. flavescens* (red). Localities are listed in appendix 1.

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′–CGAAGCTTGATATGAAAAACCATCGTTG–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′–TAGGAARTATCAYTCTGGTTTRAT–3′; Smith and Patton, 1993). Sequencing reactions were run in an ABI3130*xl* (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: [a] Present study; [b] Massoia (1973); [c] Weksler and Bonvicino (2005); [d] Agrellos et al. (2012); and [e] Myers and Carleton (1981). Remaining information is from specimens listed in appendix 1, type material, and from the above-mentioned sources.

Character/Species	*mattogrossae*	*fornesi*	*flavescens*	*microtis*	*rupestris*	*moojeni*	*utiaritensis*	*chacoensis*	*nigripes*	*stramineus*
Greatest skull length (range, in mm)	20.6–25.0[a]	21.9–23.7[b]	20.1–24.3[c]	21.2–25.5[a]	22.7–25.2[c]	22.1–25.0[c]	21.3–26.7[d]	22.1 – 27.8[e]	23.1–28.4[c]	23.3–28.3[c]
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, orange pectoral streaks sometimes present	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.*

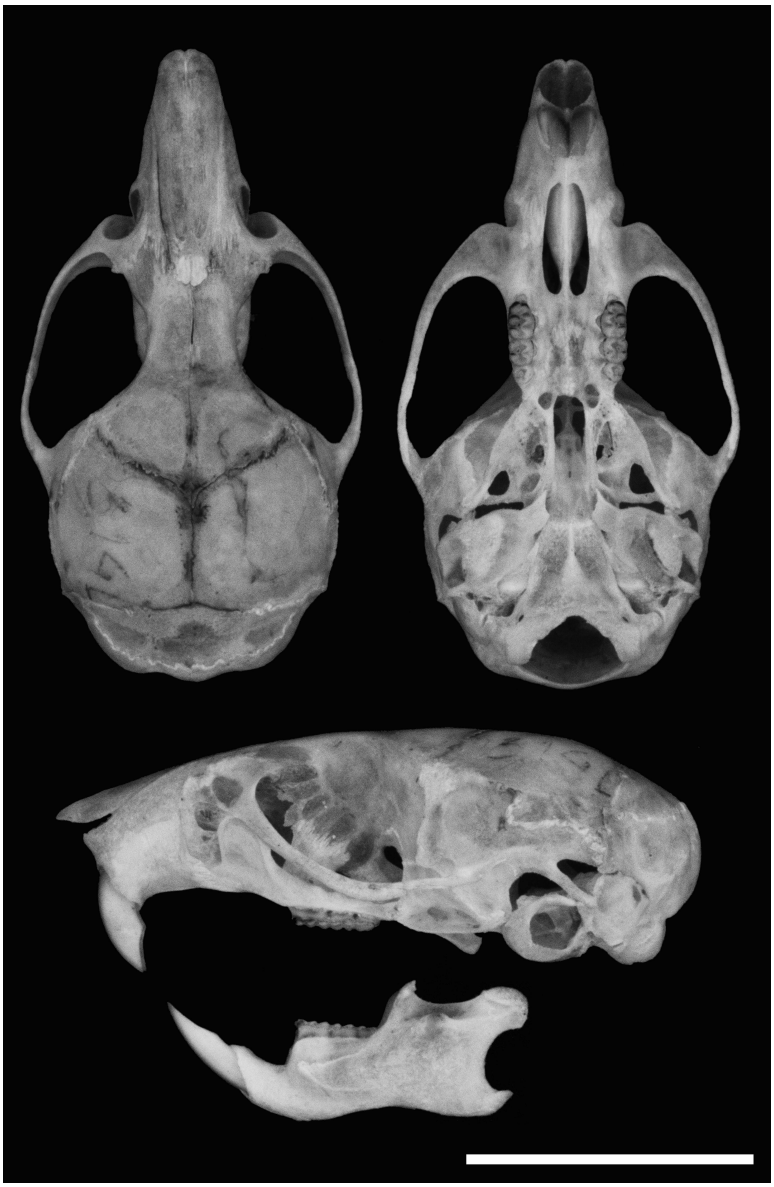


FIGURE 3. Dorsal, ventral, and lateral views of the skull and mandible of a recently collected specimen of *O. mattogrossae* (CRB3141). Bar scale = 10 mm.

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*

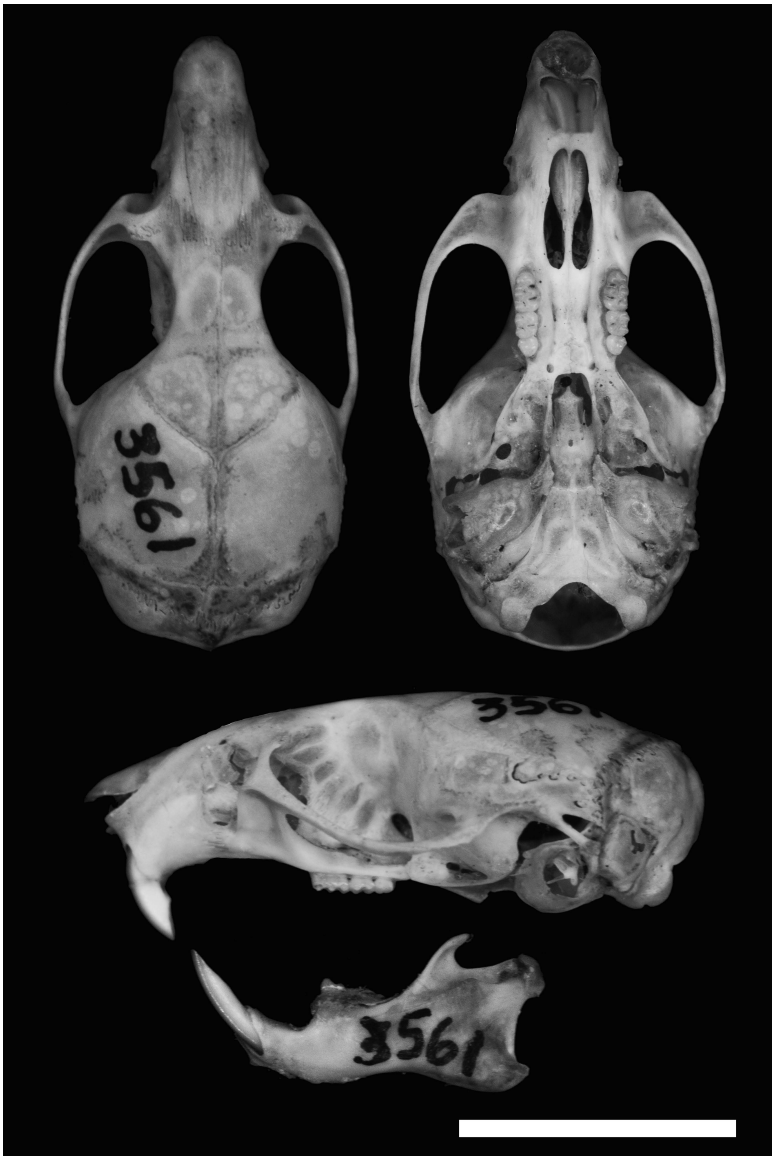


FIGURE 4. Dorsal, ventral, and lateral views of the skull (and mandible) of the holotype of *O. fornesi* (CEM3561). Bar scale = 10 mm.

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

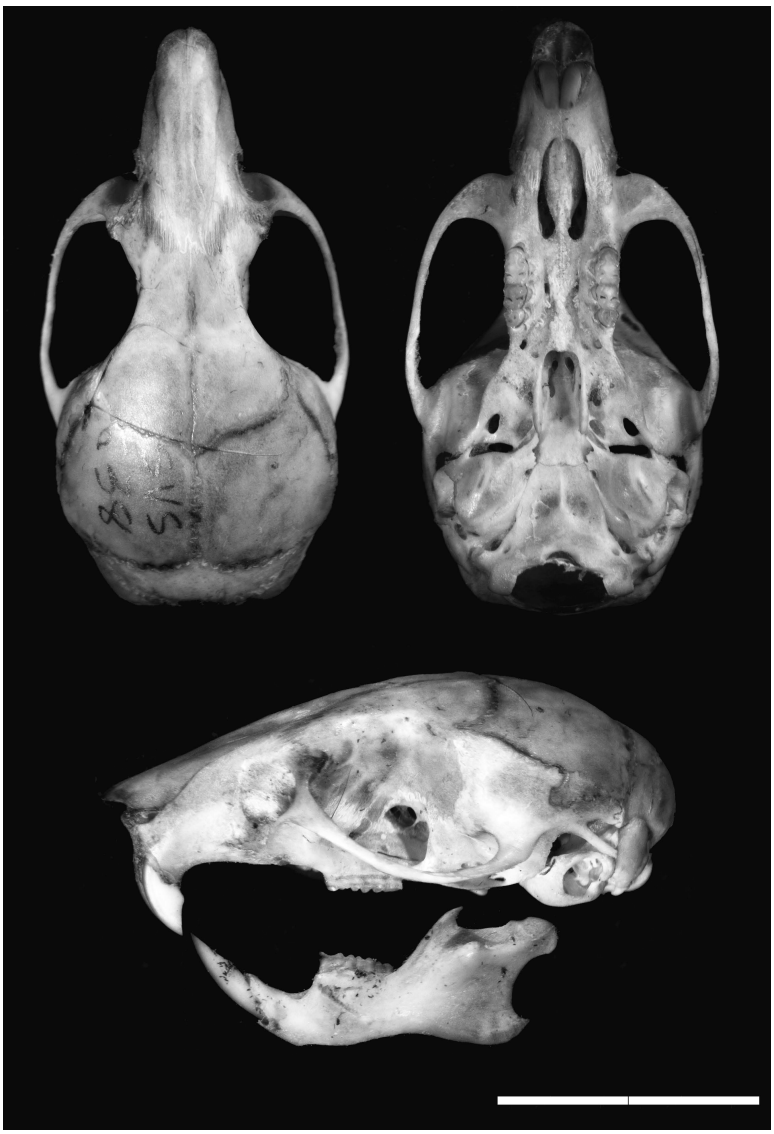


FIGURE 5. Dorsal, ventral, and lateral views of the skull and mandible of a recently collected specimen of *O. microtis* (SVS638). Bar scale = 10 mm.

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	*O. mattogrossae* (*N* = 17)	1.7																		
2	*O. microtis* (9)	11.9	3.1																	
3	*O. destructor* (2)	11.7	12.7	0.2																
4	*O. costaricensis* (2)	10.2	12.6	9.8	2.4															
5	*O. brendae* (2)	10.7	11.7	11.2	10.0	0.5														
6	*O. vegetus* (2)	9.6	11.6	11.5	8.2	8.4	0.8													
7	*O. fulvescens* (2)	10.3	12.5	12.2	9.8	8.8	7.2	2.2												
8	*O. moojeni* (2)	10.6	9.7	8.9	7.9	6.9	7.7	9.1	0.0											
9	*O. rupestris* (2)	12.2	12.8	9.3	9.2	9.3	9.8	9.3	7.6	0.7										
10	*O. magellanicus* (1)	10.5	10.6	9.5	7.0	10.3	8.6	9.4	6.4	8.4	0.0									
11	*O. longicaudatus* (2)	11.0	11.6	9.8	7.7	10.2	9.3	8.9	7.2	8.4	1.1	0.5								
12	*O. flavescens* (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	*O. fornesi* (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	*O. chacoensis* (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	*O. stramineus* (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	*O. nigripes* (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	*O. utiaritensis* (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	*O. delicatus* (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	*O. messorius* (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

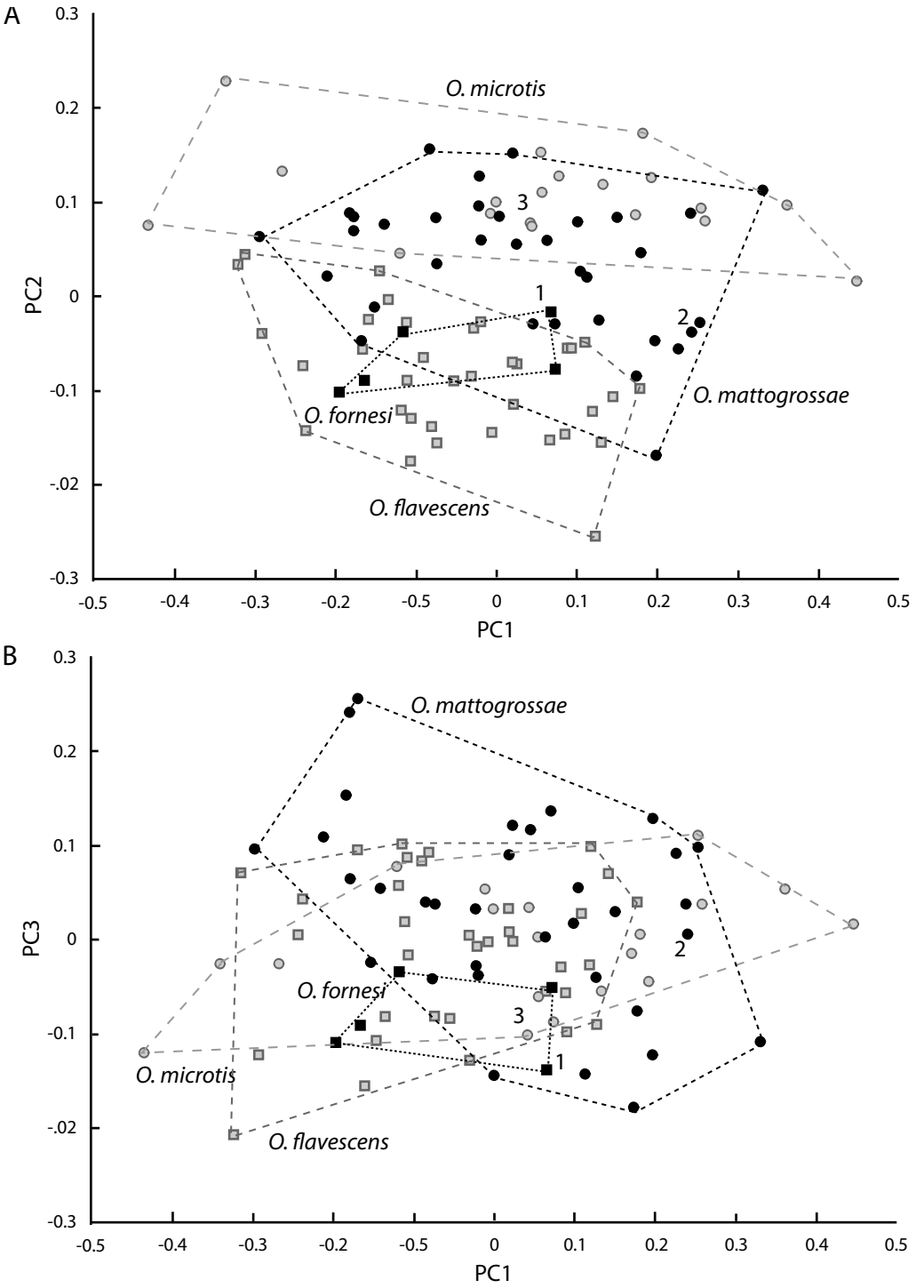
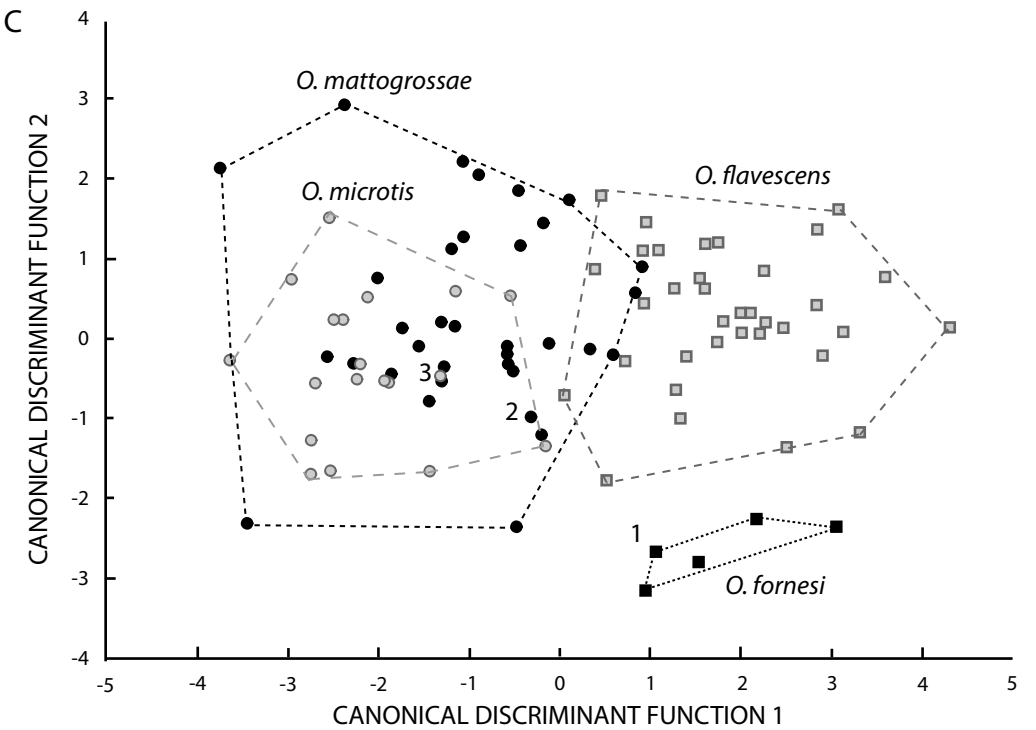
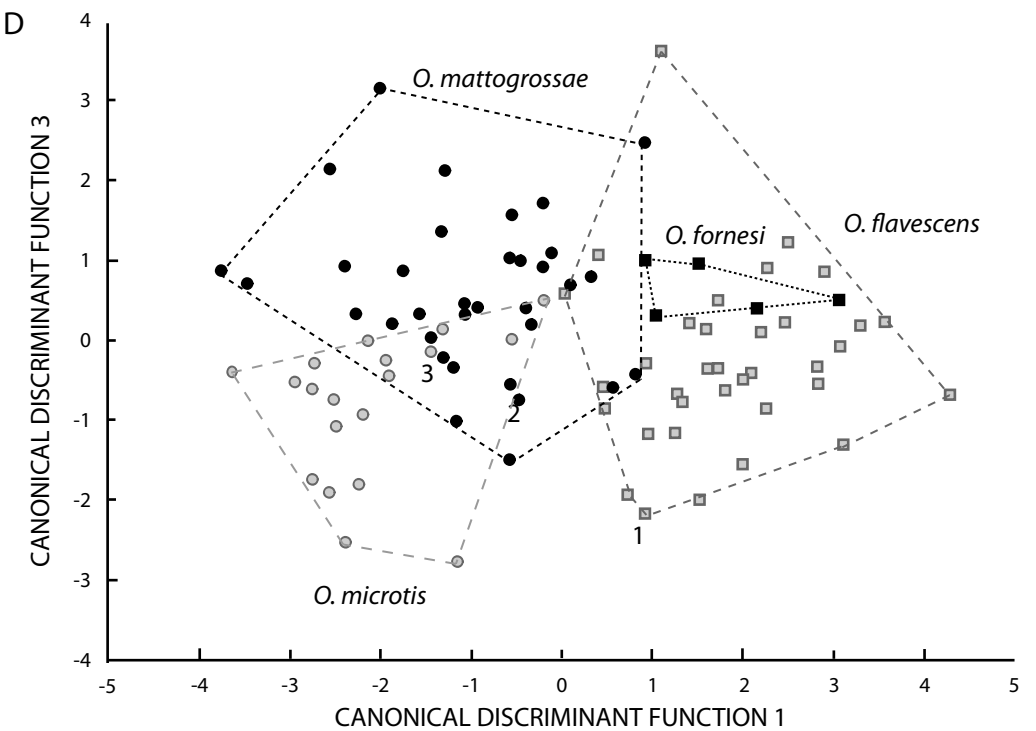
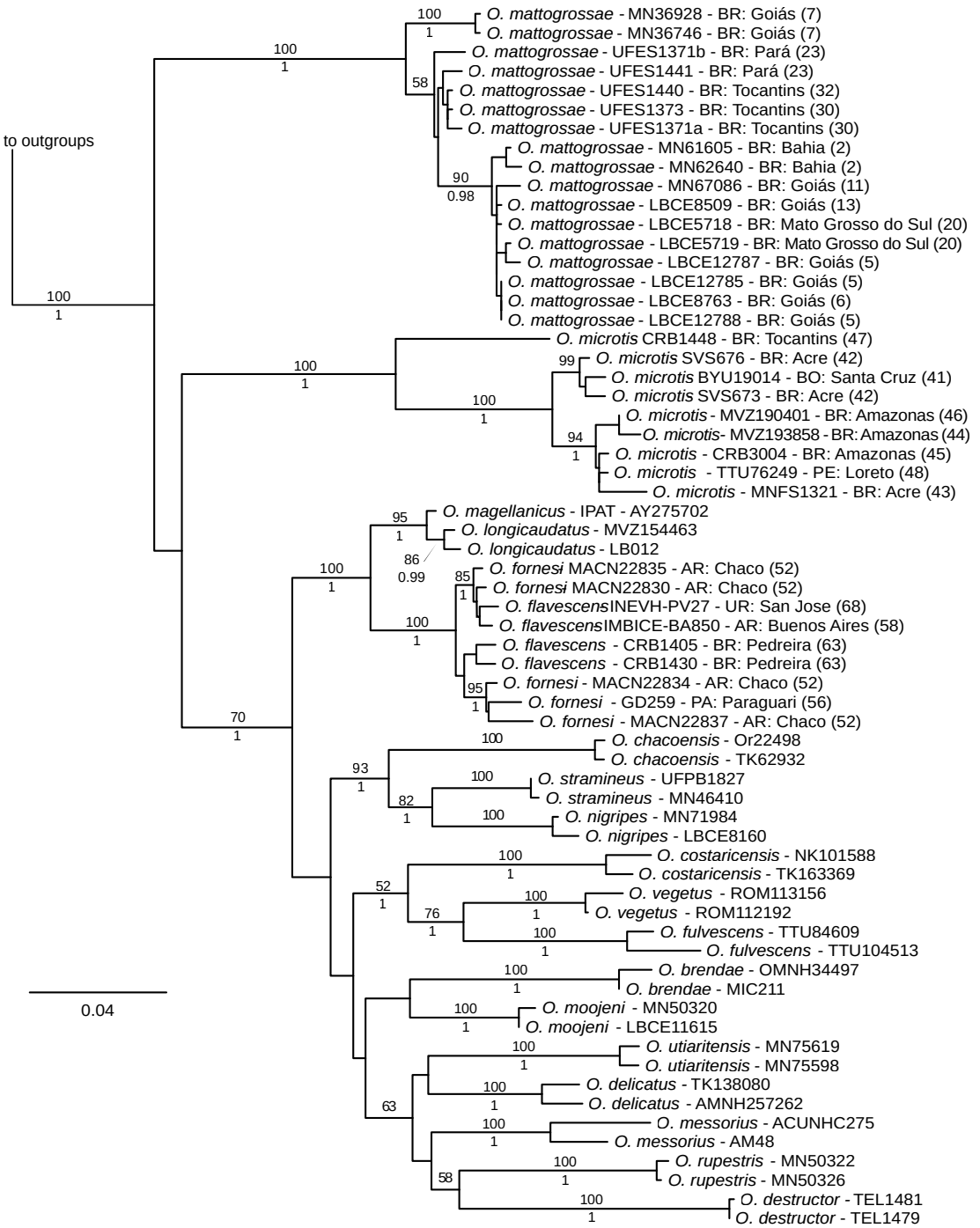


FIGURE 6. Scatterplot results of principal component analysis (A and B, *above*) and canonical discriminant analysis (C and D, *opposite page*) of log-transformed cranial measurements. Numbers indicate holotypes: **1**, *O. fornesi* (CFA3561); **2**, *O. mattogrossae* (AMNH37542), and **3**, *O. microtis*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

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 (Carmingnotto 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

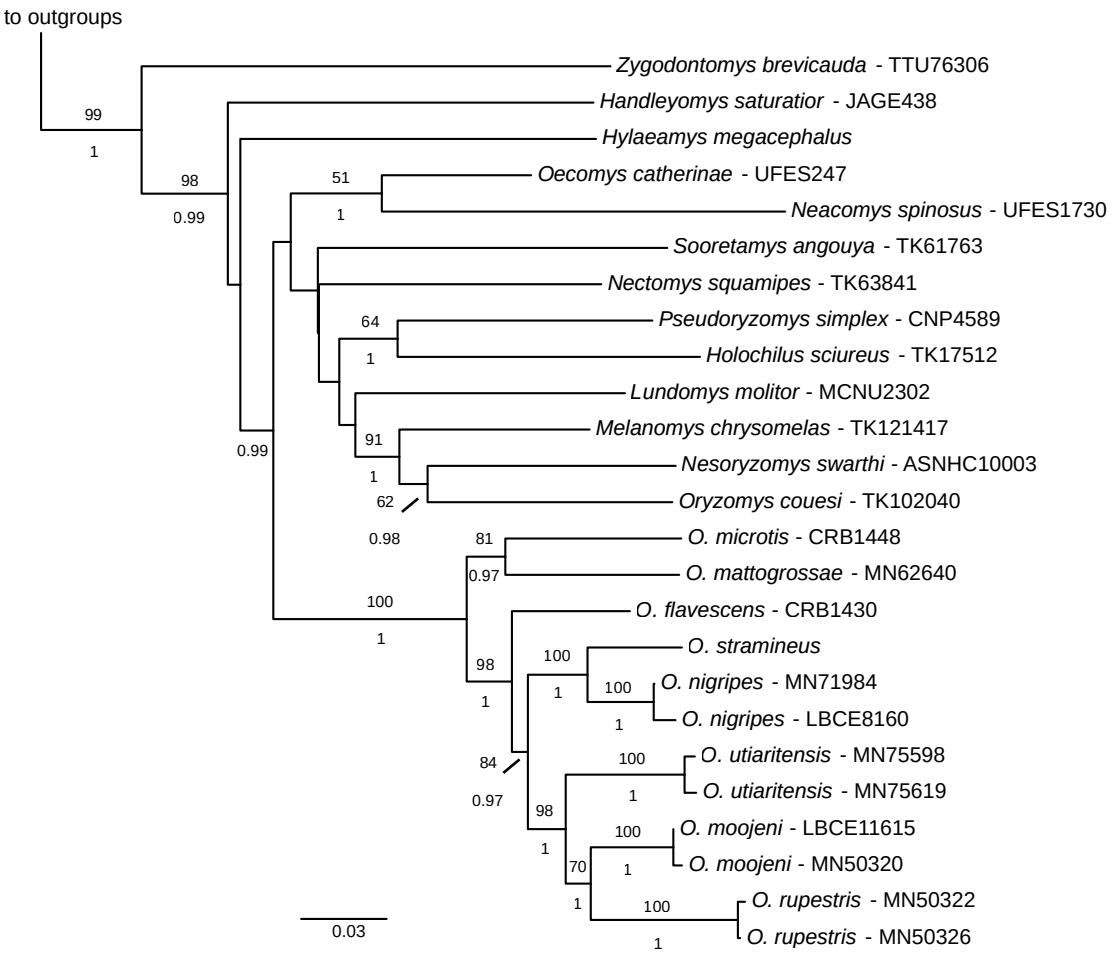


FIGURE 8. Phylogenetic relationships among *Oligoryzomys* specimens based on a maximum-likelihood analysis of the combined genetic matrix (mt-Cytb and i7-Fgb) using a partitioned GTR-G model with unlinked substitution parameters. Bootstrap values are shown above branches, and posterior probabilities 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 ± standard deviation (minimum-maximum) sample size (when different from overall *N*). See Material and Methods for measurements acronyms.

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

[a] Except as indicated.

Upper and lower incisors opisthodont; molars pentalophodont. 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 mattogrossae* 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. mattogrossae* (Allen, 1916), but the vegetation along the Papagaio River, including the Utiariti region, is gallery forest.

Comparisons: *Oligoryzomys mattogrossae* differs from all other *Oligoryzomys* species by its unique karyotype. In addition, *O. mattogrossae* 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. utiaritensis,* 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. mattogrossae* differs from *O. utiaritensis* by its karyotype with $2n = 62$ and FNa = 64 (*O. utiaritensis* $2n = 70$ and FNa = 74), and a combination of morphological characters including (1) yellowish ventral pelage, contrary whitish ventral coloration in *O. utiaritensis*, (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. utiaritensis* (fig. 2). *O. mattogrossae* and *O. utiaritensis* are also readily distinguished by size, as *O. utiaritensis* is a larger species (see Agrellos et al., 2012, for measurements of other *Oligoryzomys* species).

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

Specimens Examined: See appendix 1.

Remarks: *Oligoryzomys mattogrossae* was described by Allen (1916) based on two specimens, the holotype from Utiariti, 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.

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APPENDIX 1

List of Localities and Examined Specimens of *Oligoryzomys*

Specimens are tagged as karyotyped (marked with superscript ^{K}), used in morphometric analyses (^{M}), and/or in phylogenetic analyses (^{P}). 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 Biologia 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 mattogrossae: BRAZIL: Alagoas: (1) 6 km SSL of Matriz de Camaragipe: UFPB977^{M}. Bahia: (2) Jaborandi: MN61605^{P}, MN62637^{M}, MN62640^{P}; (3) Lençois, Remanso: MZUSP33816^{K}. Distrito Federal: (4) Brasília, Fazenda Água Limpa: UNB288^{M}, UNB289^{M}, UNB290^{M}, UNB291^{M}, UNB294^{M}, UNB931^{M}, UNB979^{M}, UNB1212^{M}; Estação Ecológica do Jardim Botânico: CRB3141^{K}, CRB3299^{K}; Parque Nacional de Brasília: UNB965^{M}. Goiás: (5) Aporé, UHE Espora: LBCE5450^{M}, LBCE9438^{M}, LBCE10900^{M}, LBCE12785^{P}, LBCE12787^{P}, LBCE12788^{P}; (6) Campo Alegre de Goiás: LBCE8763^{P}; (7) Colinas do Sul, Rio Tocantizinho:

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

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

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

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

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

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

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

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

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