Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 35 (1): 12–24, 2024
OPEN ACCESS
Available online at:
http://www.italian-journal-of-mammalogy.it
doi:10.4404/hystrix-00630-2024

Research Article

Revealing the cryptic diversity of the hosts of Rio Mamoré orthohantavirus complex, *Oligoryzomys microtis* (Allen 1916) (Rodentia: Cricetidae: Sigmodontinae), with the description of one new species with two subspecies

Cibele Rodrigues Bonvicino[1], Marcelo Weksler[2,*]

[1] *Instituto Oswaldo Cruz, FIOCRUZ*
[2] *Museu Nacional / UFRJ*

Keywords:
Oligoryzomys
new species
new subspecies
karyotype
morphology
molecular phylogeny

Article history:
Received: 6 April 2023
Accepted: 13 February 2024

Acknowledgements
We appreciated the collaboration in fieldwork by the field team of Secretaria de Vigilância em Saúde (SVS), Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, IOC, FIOCRUZ, and Laboratório de Vertebrados (UFRJ). 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. Weksler (440663/2015-6 and 309654/2020-3) and C. R. Bonvicino (304498/2014-9 and 312446/2018-7), and from the Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) to M. Weksler (E-26/110.505/2012 and E-26/201.232/2022) and C. R. Bonvicino (E26/201.200/2014 and E-26/210.047/2014). We also would like to thank the curators and staff from the AMNH (Robert S. Voss, Nancy Simmons, and Eileen Westwig), USNM (Alfred Gardner, Michael Carleton), and MN/UFRJ (João A. de Oliveira). We are grateful to one anonymous reviewer and P. Gaubert for fruitful comments on the original draft.

Abstract

Oligoryzomys is a widespread and speciose genus of Neotropical rodents of the subfamily Sigmodontinae, including several species that are natural reservoirs of hantavirus and other zoonotic pathogens. Although Sigmodontinae species are generally considered to be species-specific reservoirs of *Orthohantavirus*, *Oligoryzomys microtis* is an exception, as it is the reservoir of four different genotypes of the Rio Mamoré orthohantavirus: RIOMV, HTN-007, RIOMV-3, and RIOMV-4. Here we demonstrate, based on comparative morphology, karyology, and phylogenetic analyses of the mitochondrial gene cytochrome *b* and the intron 7 of the β-fibrinogen nuclear gene, that *O. microtis* is a cryptic species complex with three geographically structured lineages and two different karyotypes. The lineages are parapatric, with one occurring in western Amazonia and north of the Amazonas-Solimões River, the second in transitional areas (ecotones) from central Amazonia with the Cerrado of central Brazil, and the third in eastern Amazonia south of Amazonas River. We establish that one lineage of *O. microtis* is the reservoir of the Rio Mamoré orthohantavirus genotypes RIOMV, HTN-007, and RIOMV-3 from Peru, Bolivia, and the Brazilian states of Amazonas and Acre. The second lineage is the reservoir of orthohantavirus Rio Mamoré genotype RIOMV-4 from the Brazilian state of Rondônia, whereas no orthohantavirus has been associated with the third lineage. The second and third lineages differ from *O. microtis sensu stricto* in chromosomal fundamental numbers (64 versus 66). The three lineages form monophyletic units in the cytochrome *b* tree, each supported by several synapomorphies. However, the three forms are morphologically very similar regarding external, cranial, and dental traits. Based on these karyological, molecular, and morphological results, we describe a new species of *Oligoryzomys* with two subspecies, and discuss the implications of our taxonomic revision for the evolutionary history of Rio Mamoré orthohantavirus.

Introduction

With 26 recognized species, *Oligoryzomys* Bangs is a widespread and species-rich genus of Neotropical muroid rodents (Hurtado and D'Elía, 2018; da Cruz et al., 2019; Hurtado, 2021) distributed from Mexico to Tierra del Fuego (Weksler and Bonvicino, 2005). Ten *Oligoryzomys* species are recognized as reservoirs for *Orthohantavirus* genotypes in the Neotropics, with five of them having been found to be orthohantavirus positive in Brazil: *O. flavescens*, *O. mattogrossae*, *O. microtis, O. nigripes*, *O. utiaritensis* (Suzuki et al., 2004; Rosa et al., 2005; Oliveira et al., 2009; Rosa et al., 2010, 2011; Oliveira et al., 2011; González-Ittig et al., 2014; Mull et al., 2020).

Several species of *Oligoryzomys* are well adapted to invasion of altered areas, such as agricultural and pasture landscapes, and zoonotic spillover happens due to the frequent peridomiciliary contact in areas of environmental destruction (Mull et al., 2020). One of the most important areas of zoonotic interest in South America is the agricultural frontier of central Brazil and northeastern Bolivia into Amazon, in which extensive transformation of rainforest into (especially) soybean monocultures and cattle have led to an extensive number of Hantavirus pulmonary syndrome (HPS) cases (Oliveira et al., 2014).

Oligoryzomys microtis Allen 1916, the reservoir of Rio Mamoré orthohantavirus (Oliveira et al., 2014), is the most widespread species in the Amazon basin, being found in the Brazilian states of Acre, Amazonas, Mato Grosso, Rondônia and Pará, the Bolivian departments of Beni, Cochabamba, La Paz, Pando, and Santa Cruz, and the Peruvian departments of Amazonas, Loreto, Madre de Dios, Pasco, and Ucayali (Weksler and Bonvicino, 2005). The role of *Oligoryzomys microtis* in the transmission of Rio Mamoré orthohantavirus and its variants is well documented (Oliveira et al., 2014). Rio Mamoré virus was first described in *O. microtis* from El Beni and La Paz departments in Bolivia (Bharadwaj et al., 1997), and posteriorly identified in *O. microtis* specimens from Santa Cruz department in Bolivia (Carroll et al., 2005), Loreto region in Peru (Powers et al., 1999; Richter et al., 2010), and Amazonas, Acre, and Rondônia states in Brazil (Firth et al., 2012; Nunes et al., 2015). Concomitantly, human cases were registered in Peru (Castillo et al., 2012; Casapía et al., 2012) and Brazil (Oliveira et al., 2014). Among all reported cases, four variants of Rio Mamoré orthohantavirus have been identified: RIOMV in Bolivia; HTN-007 in Peru; RIOMV-3 in Acre and Amazonas states, Brazil; and RIOMV-4 in Rondônia state, Brazil (Powers et al., 1999; Firth et al., 2012; Oliveira et al., 2014; Guterres et al., 2015).

The taxonomy of *Oligoryzomys* is hampered by a high level of morphological similarity among distinct phylogenetic lineages. Furthermore, due to the superficial similarities among the chromosome com-

*Corresponding author
Email address: mweksler@mn.ufrj.br (Marcelo Weksler)

plements of several species, such as *O. microtis*, *O. mattogrossae* and *O. flavescens*, several mistaken associations between karyotypes and these species have been already produced (Weksler and Bonvicino, 2015). Several currently recognized species have been considered as junior synonyms of *O. microtis*, such as *O. mattogrossae, O. fornesi*, and *O. utiaritensis,* (see Agrellos et al., 2012; Weksler et al., 2017). However, despite the resolution of these taxonomic issues, the last taxonomic checklist of *Oligoryzomys* still considered *O. microtis* as a putative species complex (Weksler and Bonvicino, 2005), and several molecular analyses have indicated phylogenetic structuring of geographically separated individuals within the species (Weksler et al., 2017; da Cruz and Weksler, 2018; da Cruz et al., 2019; Hurtado and D'Elía, 2019, 2022).

Given the importance of correct taxonomic identification of reservoirs for a complete understanding of orthohantavirus transmission cycles, and for assessing their potential as host transmitters of orthohantavirus to humans, we herein review the taxonomy of *Oligoryzomys microtis*, the reservoir of Rio Mamoré orthohantavirus and related virus. In particular, we analyze the anatomical, morphometric, cytogenetic, and molecular variability among a geographically wide sample of *Oligoryzomys microtis*, including the forms recognized as candidate species in previous molecular studies (e.g., *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2 of Hurtado and D'Elía, 2022), referred here as *Oligoryzomys* sp. n.

Material and methods

Morphological analysis

Oligoryzomys microtis specimens were collected from the type locality and several other Brazilian localities in Cerrado and Amazonas (Fig.1, appendix 1). Collecting and permits were issued by SISBIO (System of Authorization and Information in Biodiversity) license numbers 13373 and 11375. The capture and handling of the specimens were under permission of the FIOCRUZ Ethics Committee (#1260/14) and followed the guidelines of the American Society of Mammalogists (Sikes et al., 2016). Animals were euthanized and voucher material and tissues were deposited in the mammal collections of Museu Nacional/UFRJ (MN) and COLMASTO (IOC/FIOCRUZ) (see appendix 1 for a list of specimens and locality information).

We examined additional *Oligoryzomys* specimens deposited in the mammals' collections of the following institutions: (1) MN - Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, (2) AMNH - American Museum of Natural History, New York, USA, including the type series of *O. utiaritensis*, *O. mattogrossae*, and *O. microtis*, (3) USNM - United States National Museum (Smithsonian Institution), Washington D.C., (4) COLMASTO - Coleção integrada de Mamíferos Silvestres e Reservatórios, IOC-Fiocruz, Rio de Janeiro, Brazil (note that SVS - Secretaria de Vigilância em Saúde - specimens are housed at LBCE). Among the analyzed specimens, four were positive carriers of *Orthohantavirus* (see appendix 1) as reported by Nunes *et al.* (2015). Information on collection locality data (Fig.1), museum acronyms and numbers are presented in appendix 1; see also Bonvicino and Weksler (1998), Weksler and Bonvicino (2005), Agrellos et al. (2012), and Weksler et al. (2017) for previously analyzed specimens of other *Oligoryzomys* species.

The terminology of characters herein analyzed follows previous studies (Reig, 1977; Voss, 1988; Carleton and Musser, 1989; Weksler, 2006). For color nomenclature, we followed Ridgway (1912) and Villalobos-Dominguez and Villalobos (1947). The following external dimensions were measured (in millimeters) in specimens collected by us, or obtained from original specimen tags: total length (ToL), head and body length (HBL), tail length (TL), ear length (Ear), hind foot length with claw (HF) and body mass (Wt). Whenever total length had been originally reported in specimen tags, HBL was estimated by subtracting tail length (TL) from total length. 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

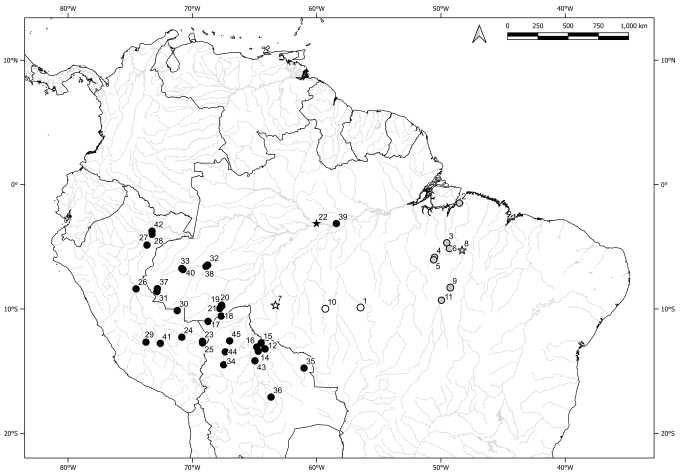

Figure 1 – Map showing the collecting localities of *O. microtis* (black symbols), and *Oligoryzomys sp. n.* (grey and white symbols); starts correspond to type localities. Numbers refer to localities listed in appendices 1 and 2 and table 1.

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 inter-researcher differences in paired *t* tests; data not shown).

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, $p < 0.05$; data not shown). We computed descriptive statistics (average, standard deviation, minimum and maximum) and employed Analysis of Variance (ANOVA) with TUKEY *post hoc* test (Sokal and Rohlf, 1994) and MANOVA, using logarithmic-transformed data to compare sets of populations of *O. microtis* from eastern, central and western Amazon (see map in Fig. 1); the geographic limits of the population sets were also based on previous karyotypic and molecular data (Weksler et al., 2017; da Cruz and Weksler, 2018; da Cruz et al., 2019; Hurtado and D'Elía, 2019). We adjusted the individual measurements' alpha using Holm´s Sequential Bonferroni correction to reflect an overall alpha of 0.05 (Holm, 1979; Rice, 1989). We also employed principal component analysis and discriminant canonical analysis (Strauss, 2010) to identify patterns of multivariate morphometric variation among the populations. Measurements were transformed to natural logs and covariance matrices were computed, considering all variables. All statistical analyses were performed in R version 4.0.2 using Rstudio (Rstudio Team, 2020) using the MASS and candisc packages (Friendly and Fox, 2010; Ripley et al., 2013). Because both PCA and DFA require complete data sets, missing values (2.1 % of the total dataset) were estimated from the existing raw data using the missMDA package (Josse and Husson, 2016) implemented in R.

Karyotype data and molecular phylogenetic analysis

We karyotyped eight specimens of *Oligoryzomys microtis* and 15 *Oligoryzomys* sp. n. (Table 1, appendix 1). Cell suspensions were obtained in the field with short-term bone marrow culture as previously reported (de Andrade and Bonvicino, 2003). Chromosomes were ordered according to morphology and decreasing size, and fundamental numbers refer to the count of autosomal (i.e., non-sex) chromosomes.

DNA was isolated from livers preserved in 100 % ethanol following the standard phenol-chloroform protocol (Sambrook and Russell, 2001). The entire cytochrome *b* gene (mt-Cytb; gene acronym 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 reac-

Table 1 – Karyotypic data available for *O. microtis, Oligoryzomys sp. n., O. mattogrossae* and *O. flavescens*, with diploid (2n) and autosome fundamental (FN) numbers, locality and reference (Ref). Numbers in parentheses (locs.) refer to sampling localities in map (Fig. 1). Brazilian (BR) states are Amazonas (AM), Pará (PA), Mato Grosso (MT), Goiás (GO), Paraná (PR), Santa Catarina (SC), Rio Grande do Sul (RS), Tocantins (TO), Bahia (BA), and Distrito Federal (DF). Argentinian (AR) provinces are Buenos Aires (BA), Córdoba (CD), Jujuy (JY), Tucumán (TM). Bolivia (BO), Peru (PE).

Taxon	As published	2n	FNa	Locality	Ref
O. flavescens	*O. flavescens*	64,66	66, 68, 70	AR: Boca Cerrada, Punta Lara. UR: Montevideo, Colonia, Maldonado, Artigas, Fray Bentos, Canelones	1
O. flavescens	*O. aff. flavescens*	66-68	68-70	AR: JY, Maimará; TM, El Infiernillo	2
O. flavescens	*O. flavescens*	64	66	AR: Boca Cerrada, Punta Lara, Villa Elisa. UR: Canelones, Colonia, Montevideo	3
O. flavescens	*O. flavescens*	64-66	66-68	BO: Tarija department	4
O. flavescens	*O. flavescens*	66,67	68,69	AR: BA, Paranã River Delta, Monte Hermoso, Capilla del Serior, Diego Gaynor; CD, Rio Cuarto	2
O. flavescens	*O. flavescens*	64-66	66-68	BR: PR, Ponta Grossa, Curitiba, Piraquara, RS, Esmeralda, Torres, Tramandai, Osório, Sapiranga, Mostardas, Pelotas, Taim	5
O. flavescens	*O. flavescens*	64-67	66-68	BR: SC, Costa de Dentro, Florianópolis; RS, Nonoai, Tainhas, Charqueadas	6
O. flavescens	*O. flavescens*	64-66	66-68	BR: PR, Piraquara, São José dos Pinhais, Curitiba, São Mateus do Sul, Vila Velha; SC, São Domingos	7
O. flavescens	*O. flavescens*	64	68	BR: MG, Parque Nacional de Caparaó, Viçosa	8
O. mattogrossae	*O. fornesi*	62	64	BR: GO, Teresina de Goiás, Corumbá de Goiás	8
O. mattogrossae	*O. fornesi*	62	64	BR: TO, Peixe	9
O. mattogrossae	*O. fornesi*	62	65	BR: DF, Brasília, Jardim Botânico de Brasília	10
O. mattogrossae	*O. fornesi*	62	64	BR: BA, Lençóis, Remanso	11
O. mattogrossae	*O. eliurus*	62	64,66	BR: GO, 40 km SW Minaçu, 55 km N Niquelândia, 20 km NW Colinas do Sul, 40 km NE Uruaçú, Ipameri, Caldas Novas, Corumbaíba	6
Oligoryzomys sp. n.		64	64	BR: RO, Alto Paraíso (loc. 7); TO, São Sebastião do Tocantins, Faz. Osara II (loc. 8) PA, Itupiranga (loc. 2)	TS
Oligoryzomys sp. n.	*O. flavescens*	64	64*	BR: TO, São Sebastião do Tocantins, Faz. Osara II (loc. 8), Couto Magalhães, Faz. do Zé Carlos (loc. 9)	12
Oligoryzomys sp. n.	*O. microtis*	64	64	BR: MT, Aripuanã (loc. 11)	9
O. microtis		64	66	BR: AM, Manacapuru (loc. 22, type locality); AC, Brasiléia (loc. 17), Porto Acre (loc. 19, 20)	TS
O. microtis	*O. microtis*	64	66	PE: Ucayali, Pucallpa (loc. 26), Loreto, Henaro Errera (loc. 27), Mishana Allpahuayo (loc. 28)	4
O. microtis	*O. microtis*	64	66	PE: Ayacucho, Hda. Luisiana (loc. 29), Ucayali, Balta, Rio Curanja (loc. 30)	13
O. microtis	*O. microtis*	64	66	BR: AC, Igarapé Porangaba (loc. 31), Jainu (loc. 32), Seringal Condor (loc. 33)	14

1= Brum-Zorilla et al. (1988), 2= Espinosa and Reig (1991), 3= Vidal-Rioja et al. (1988), 4= Aniskin and Volobouev (1999), 5= Sbalqueiro et al. (1991), 6= Andrades-Miranda et al. (2001), 7= Bordignon (2007), 8= Bonvicino and Weksler (1998), 9= Di-Nizo et al. (2015), 10= Bonvicino et al. (2014), 11= Pereira and Geise (2007), 12= Lima (2004), 13= Gardner and Patton (1976), 14= Patton et al. (2000), TS= this study. * Lima (2004) reported that the FN of these specimens was 66, but the karyotype of two offsprings of specimens from São Sebastião in Tocantins state showed 2n=64 and FN=64. In addition, analysis of the mitochondrial gene Cytochrome oxidase I (da Cruz et al., 2019) sequences of the specimens reported by Lima (2004) showed that it belongs to *Oligoryzomys sp. n.*. Differences in fundamental number in relation to Lima (2004) is due to the interpretation of the morphology of one small autosome pair.

tions 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 either with GFX® PCR DNA or 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 (Bonvicino and Moreira, 2001) and MVZ16 (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 1.45 (McCarthy, 1998).

We also amplified the intron 7 of the nuclear β-fibrinogen gene (i7-Fgb) of six *O. microtis* specimens with the primer pair β17-mammL and βfib-mammU as reported by Matocq et al. (2007). Amplifications were performed with 30 cycles of denaturation at 94 °C for 1 min, 60 °C for 30 s, and extension at 72 °C for 1 min, with an initial denaturation at 94 °C for 5 min and final extension at 72 °C for 7 min.

Additional mt-Cytb and i7-Fgb data from GenBank *Oligoryzomys* specimens were used for phylogenetic reconstructions (appendix 2). We also performed a combined analysis of mt-Cytb and i7-Fgb. For the combined analyses, we included only exemplars with both mt-Cytb and i7-Fgb, except for the outgroup *Hylaeamys megacephalus*, for which sequences of each gene are from different individuals (appendix 2). We employed nine oryzomyines and three non-oryzomyines sigmodontines as outgroup taxa (appendix 2) in all phylogenetic analyses, and rooted our trees using *Sigmodon hispidus*.

Maximum Likelihood (Felsenstein, 1981) and Bayesian analyses (Huelsenbeck et al., 2001) were carried out for phylogenetic reconstructions. The nucleotide evolution model was selected using Akaike Information Criteria (AICc) as estimated by Paup* 4.0a146 (Swofford, 2002; commands AutoModel modelset=j7). 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 proportion of invariant sites, was used for mt-Cytb, while GTR+G was used for i7-Fgb. Concatenated analyses employed un-

linked partitioned models. Maximum-likelihood trees were built with RaxML-NG (Kozlov and Stamatakis, 2019) and nodal bootstrap values (Felsenstein, 1985) were calculated using 1,000 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 of 10,000,000 generations each, with two heated chains sampling for trees and parameters every 10,000 generations. The first 10,000 generations were discarded as burn-in, and the remaining trees were used to estimate posterior probabilities for each node. Independent runs were combined with LogCombiner (version 2.6.6; Drummond and Rambaut, 2007). 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).

The Median-Joining (MJ) network (Bandelt et al., 1999) based on partial mt-Cytb sequences (801 bp) was reconstructed in the Network program (version 4.5.1.6) to evaluate the spatial and populational structuring of haplotypes. We retained only variable sites, and excluded any sites with missing data. Only specimens with sequences $\geq$ 777 bp were included (Appendix 3). To assess the genetic distinctiveness of the lineages within *O. microtis* species group, we calculated uncorrected genetic distances (*'p'*) between individuals.

Results

Karyotype

Karyotypic analysis of 15 specimens of *Oligoryzomys* sp. n. from Rondônia, Mato Grosso, and Tocantins states showed the same karyotype, 2n=64 and FN=64 (Table 1, Fig. 2B and 2D). The autosomal complement is composed of one small-sized biarmed chromosome, and 30 acrocentric pairs varying in size from large to small, plus a large-sized X chromosome. The karyotypic analysis of eight specimens of *O. microtis* from Acre and Amazonas states, including one topotype, showed 2n=64 and FN=66 (Table 1, Fig. 2A). The autosome complement is composed of two biarmed chromosomes, one very large (the largest of the chromosome complement) and one small sized, 29 pairs of acrocentric chromosomes, and a median sized X chromosome. These chromosomal complements have been previously reported in the literature (Table 1).

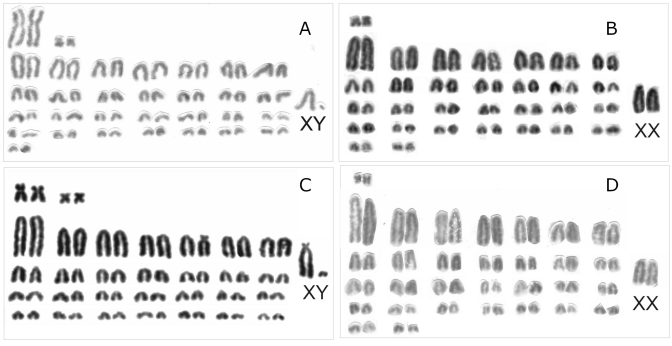

Figure 2 – Karyotypes in conventional coloration of (A) *O. microtis* topotype male MN84349 with 2n=64 and FN=66, (B) *Oligoryzomys sp. n.* female MN91085 from Central clade (Rondônia, Brazil), with 2n=64 and FN=64, (C) *O. mattogrossae* male CRB3141 from Brasília, Brazil with 2n=62 and FN=64, and (D) *Oligoryzomys sp. n.* female MN81643 from Eastern clade (Tocantins, Brazil) with 2n=64 and FN=64 .

Phylogenetic analyses

The ML and BA analyses based on the mt-Cytb recovered similar topologies, the differences among them being restricted to clades with low support. Both analyses recovered the clade containing *O. microtis* and *Oligoryzomys* sp. n. in the most basal dichotomy within *Oligoryzomys*, while all other 23 species were recovered in a poorly supported sister clade (Fig.3). Within the former clade, referred as *O. microtis* species group, two clades were recovered: one with specimens of *O. microtis sensu stricto*, from Peru, Bolivia, and the Brazilian states of Acre and Amazonas (western Amazon), including the topotype specimen MN84349; and the second with specimens of *Oligoryzomys* sp. n. from Tocantins, Mato Grosso and Rondônia states. This clade is further separated in two well supported subclades, structured geographically into samples from Mato Grosso and Rondônia in one side (south central Amazon, referred as Central clade), and samples from Tocantins (southeastern Amazon, referred as Eastern clade) in another clade.

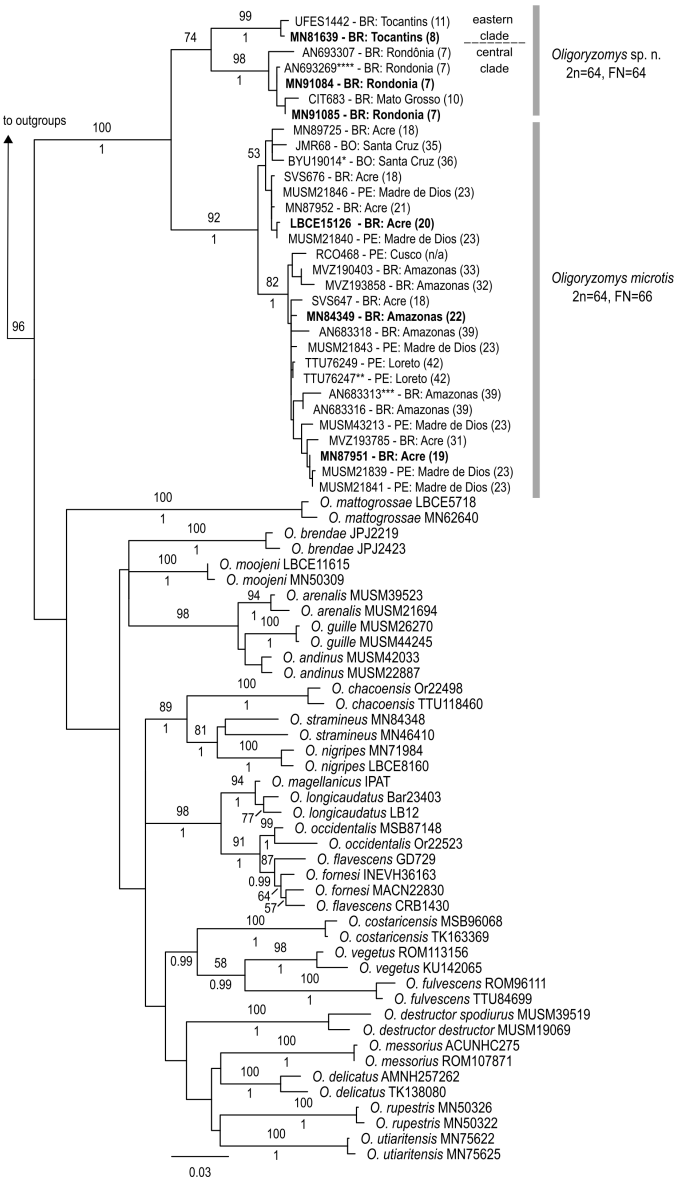

Figure 3 – Phylogenetic relationships among *Oligoryzomys* specimens based on maximum likelihood analyses of mt-Cytb. Bootstrap values (bs, %) are shown above branches; posterior probabilities of Bayesian analysis are shown below branches. Locality numbers for *O. microtis* and *Oligoryzomys sp. n.* are in parentheses; diploid number (2n) and fundamental number (FN) are based on karyotyped specimens marked in bold; specimens that were reported positive for virus-specific RNA hantavirus are marked with asterisks: * for RIOMV strain (Bharadwaj et al., 1997; Carroll et al., 2005); ** for strain HTN-007 (Powers et al., 1999; Oliveira et al., 2014); *** for RIOMV-3 (Firth et al., 2012); and **** for RIOMV-4 (Firth et al., 2012). See appendix 2 for outgroups and specimen information.

Combined analyses of mt-Cytb and i7-Fgb recovered the monophyly of *Oligoryzomys,* which was sister group of *Neacomys* (sup. Fig. 1). The ML and BI analyses converged in similar topologies, but the BI is less fully resolved, and disagreements are centered on poorly supported relationships. The first dichotomy within *Oligoryzomys* separates a clade containing *O. microtis* species group and *O. mattogrossae* from a clade containing the remaining 20 species; *O. microtis* is recovered with a deep split separating specimens from western amazon (MVZ193858 from Amazonas state in Brazil and MUSM21846 from Madre de Dios in Peru) from samples from central (MN91804 from

Rondônia) and eastern (MN81639 from Tocantins) Amazon. Remaining *Oligoryzomys* species are further divided into two subclades, but with lower support. Six clades have high levels of support: 1: (*O. stramineus* + *O. nigripes*); 2: (*O. moojeni* + *O. rupestris*); 3: (*O. messorius*, (*O. delicatus*, (*O. costaricensis*, (*O. vegetus* + *O. fulvescens*)))), with *O. utiaritensis* as sister group with low support; 4: ((*O. occidentalis* + *O. longicaudatus*), (*O. fornesi* + *O. flavescens*)), the latter species not recovered monophyletic; 5: (*O. chacoensis*, *O. destructor*); and 6: ((*O. arenalis* + *O. guille*), *O. andinus*), the latter species not recovered monophyletic.

The median-joining network with mt-Cytb delineated three major haplogroups (Fig. 4A; appendix 3): the first corresponds to *O. microtis s.s.,* with specimens from Bolivia, Peru, and the Brazilian states of Amazonas and Acre; the second group included specimens of *Oligoryzomys* sp. n. from the Brazilian state of Rondônia (corresponding to the Central clade of the phylogenetic analyses), while the third included specimens from Tocantins (Eastern clade). The latter two haplogroups were separated by 35 mutations and four median vectors, but the first haplogroup was separated from the latter two by at 46 and 51 mutations and four median vectors. The first haplogroup was further divided into two subgroups, one with specimens from Peru and the Brazilian states of Amazonas and Acre separated by 11 nucleotide substitutions and two median vectors from the cluster with specimens from Bolivia and the Brazilian state of Acre. Genetic distances (uncorrected *p*, average, minimum and maximum) using mt-Cytb sequences were (Fig. 1B): 7.4 % (6.8 % - 8.3 %) between *O. microtis* s.s. and *Oligoryzomys* sp. n. Eastern clade; 7.4% (6.3 %-9.5 %) between *O. microtis* s.s. and *Oligoryzomys* sp. n. Central clade; and 5.4 % (4.9 %-5.9 %) between the central and Eastern clades of *Oligoryzomys* sp. n.

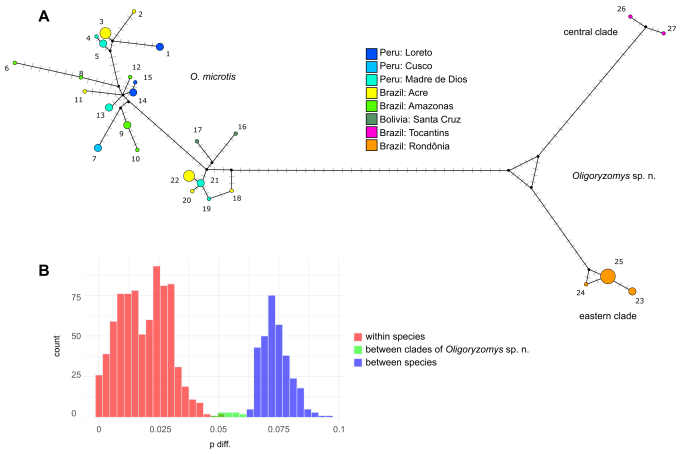

Figure 4 – (A) Median joining network with *O. microtis* and *Oligoryzomys sp. n.*. Circles are haplotypes proportional to number of shared sequences; small black circles are median vectors; small bars indicate nucleotide substitutions; numbers refer to haplotype numbers listed in appendix 3; see legend for geographic source of haplotypes. (B) Pairwise uncorrected (´p´) genetic distances for 3 contrasts: within species, between clades of *Oligoryzomys sp. n.* and between species.

Morphology

Specimens belonging to the different lineages of the *O. microtis* species group exhibit very similar integumental, cranial, and dental anatomy. In any case, specimens of *O. microtis* and *Oligoryzomys* sp. n from eastern and central Amazon present slight differences in external characters, the most notable being the length of tail and coloration of dorsal, lateral and ventral parts. However, most characters show intrapopulational variation.

The average HBL of the three populations groups are similar (Fig. 5A, table 2), but the tail length in specimens from the Eastern clade are significantly longer than in specimens from the Central clade and *O. microtis*, both in relative and absolute terms (Fig. 5B). The same is true for the length of the hindfeet (Fig. 5C), which also displays significative differences between the eastern group viz-a-viz central group and *O. microtis*

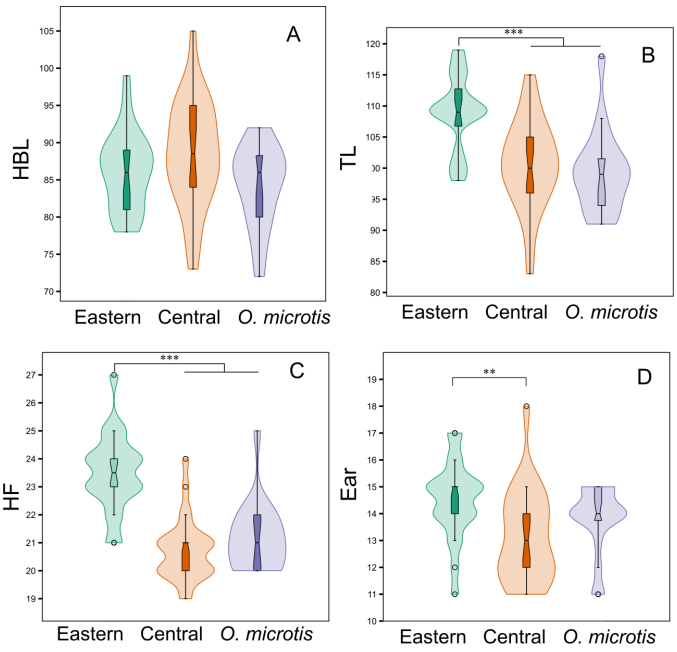

Figure 5 – Combined violin plot with box plot for external measurements for E of *Oligoryzomys microtis* complex. Violin plot shows kernel density plot from minimum to maximum value. The box plot shows the median, 25-75 percent quartiles (boxes), values less or more than 1.5 times the box height (whiskers), and outliers. Measurements are: (A) HBL: head-and-body length, (B) TL: tail length, (C) HF: hind-feet length, and (D) Ear: ear length. Lines above each graph show significant differences among groups: ** < 0.01, *** < 0.001.

In terms of coloration (Fig. 6), most individuals from eastern populations have an orange-brown coloration (Villalobos-Dominguez and Villalobos 1947: color range from O-8-8° to 8-11-7°; Ridgway 1912: antique brown, buckhorn brown), with dark base of guard-hairs distinct and heterogeneous overall coloration, while individuals from central Amazon and *O. microtis* have a slightly lighter coloration (Villalobos-Dominguez and Villalobos, 1947: color range from O-5-8° to 8-9-8°; Ridgway (1912): antique brown, brussels brown, raw umber). The ventral coloration of specimens from central Amazon and *O. microtis* vary from ochreous to white.

Oligoryzomys species are very similar cranially (Fig. 7), as most characters are either polymorphic within species or subtle variations of a general morphology, or both. In any case, the three lineages within *O. microtis* species group exhibit slight variation in a few characters that can be used for a differential diagnosis (Fig. 8 and sup. Fig. 2). Overall, members of the central populations are more dissimilar morphologically from Eastern clade and *O. microtis* specimens.

Most specimens (sup. Fig. 2) from Amazonas and Acre states (*O. microtis*) and from Pará and Tocantins (Eastern clade) have a narrow zygomatic notch, oriented postero-laterally (Fig. 8A), with the anterior border of the zygomatic plate flat, below or slightly in front of anterior margin of superior maxillary root of zygoma; in contrast, most specimens from Rondônia and Mato Grosso (Central clade) have a slightly broad and rounded zygomatic notch (Fig. 8B), and a zygomatic plate with anterodorsal margin smoothly curved.

The interorbital region of all specimens of the Central clade are symmetrically constricted without crests (hourglass shape; Fig. 8C), while in *O. microtis* and in the Eastern clade specimens can present either the amphoral morphology, or the interorbital region with margins slightly convergent anteriorly, with very weakly developed crests in their beaded supraorbital borders (cuneate shape; Fig. 8D). The same pattern of variation is observed for the interparietal width: while the members of *O. microtis* and the Eastern clade have either narrower interparietal narrower, apart from the squamosal (Fig. 8E) or a wide interparietal approaching the squamosal (Fig. 8F), all members of the Central clade have a wide interparietal.

The jugal bone is present in the lateral surface of the zygomatic arch, separating the maxillary and squamosal bones (Fig. 8G), in few specimens from all analyzed populations (sup. Fig. 2); in contrast, in most

Figure 6 – Dorsal, lateral and ventral views of skins of *Oligoryzomys sp. n.* from Eastern Clade (Tocantins State, MN76206), *Oligoryzomys sp. n.* from Central Clade (Rondônia State, MN8792l), and *O. microtis* (Acre State, MN87929).

specimens the jugal is usually absent laterally (Fig. 8H), or extremely reduced to bony sliver, resulting in the maxillary and squamosal in contact.

The shape of the incisive foramina is also variable among the lineages (Fig. 8I-K). Most members of *O. microtis* and *Oligoryzomys* sp. n. from Eastern clade present teardrop-shaped incisive foramina, with posterior margins rounded (Fig. 8I and K), while specimens from Central clade have oval-shaped foramina, with more pointed posterior margins (Fig. 8J). In terms of length, the foramina of specimens of all lineages of *O. microtis* are variable, not approaching the plane of M1 alveolus or barely approaching the line of M1 alveolus. Finally, the posterior extent of the palate is also slightly variable, with palate of intermediate length, mesopterygoid fossa extends up to 1/2 of M3 length between the maxillary bones (Fig. 8I), as observed in most specimens of Central clade and almost all from Eastern clade; or palate long, mesopterygoid fossa extend more than M3 length (Fig. 8J-K), as observed in more than half of specimens of *O. microtis*.

The descriptive statistics for cranial characters (Table 2) showed that members of the three geographic sets, *O. microtis* s.s., *Oligoryzomys* sp. n. from south-central Amazon, and *Oligoryzomys* sp. n from south-eastern Amazon, are similar in size, with considerable overlap on mean and range sizes. Four cranial measurements displayed significant differences among the three population sets in the ANOVA: PB ($p<0.001$), BIF, LM, and ZB ($p<0.05$); nevertheless, only the first variable was significant after Holm-Bonferroni correction. The MANOVA recovered significant variation among the population sets (Wilks = 0.355, approx. F = 3.5, num. DF = 24, den. DF = 124, p = 2.575e-06). Pairwise

Figure 7 – Dorsal, ventral, and lateral views of the skull of *Oligoryzomys sp. n.* from Central clade (Rondônia State, MN8792l), *Oligoryzomys sp. n.* from Eastern Clade (Tocantins State, MN76206).

Tukey tests showed that eastern populations of *Oligoryzomys* sp. n. to be significantly different ($p < 0.001$) from central populations of *Oligoryzomys* sp. n. in two variables (PB and LM). *Oligoryzomys microtis s.s.* did not differ significantly in any variable from central or eastern population sets.

The three population sets of *O. microtis* species group were also poorly differentiated by principal component analysis (Fig. 9 and appendix 4). The scatterplots of the first two principal components, which account for 83 % of the total variance, reveal an overall juxtaposition in the multivariate space (Fig. 9A). There is a large amount of variation on the first component (77.21 %), which is explained by variables associated to the cranial longitudinal axis, especially condylo-zygomatic length. Pairwise contrasts between the population sets (Fig. 9B-D) present the same pattern, with a slight separation between central and eastern forms of *Oligoryzomys sp. n.*, but with western *O. microtis* scores overlapping with central and eastern groups (*Oligoryzomys* sp. n.).

The discriminant canonical functions (Fig. 9E), in turn, reveal a significative separation among the three population sets (LR test = 0.577 approx. F = 3.8477, num. DF = 12, den. DF = 63, p = 0.0002), and is even more conspicuous when the contrasts are pairwise (Fig. 9F-H). Nevertheless, a considerable overlap among canonical function scores is observed in all contrasts.

Discussion

Karyotype variation

The karyotype of the central and eastern forms of *Oligoryzomys* sp. n., with 2n=64 and FN=64 is similar to the one of *O. microtis sensu stricto*, 2n=64 and FN=66 (Fig. 2, table 1). Although sharing the same diploid number, they differ in FN due to a pericentric inversion affecting the largest autosome pair of these karyotypes, being submetacentric in *O. microtis* and acrocentric in *Oligoryzomys* sp. n. (Fig. 2). This inversion is apparently fixed because heterozygous specimens for this inversion were neither found in the present study nor in previous reports (Gardner and Patton, 1976; Aniskin and Volobouev, 1999; Patton et al., 2000; Di-Nizo et al., 2015). The comparison of the G band karyotypes of *O. microtis* (2n=64 and FN=66, Aniskin and Volobouev 1999) and *Oligoryzomys* sp. n. (2n=64 and FN=64, Di-Nizo et al., 2015) allows us to infer homologies in large size pairs of the autosome complement, despite differences in the chromosome elongation. This comparison corroborates that these karyotypes differ by one pericentric inversion or centromere shift affecting the largest autosome pair.

A considerable amount of evidence suggests deleterious meiotic effects of pericentric inversions leading to a profound barrier in viability, acting as a significant post-mating isolating mechanism (King, 1993). Other examples of fixed pericentric inversion in congeneric sigmodontine species pairs are *Calomys tener* and *Calomys ex-*

Table 2 – Descriptive statistics of external and cranial measurements for *Oligoryzomys sp. n.* and *O. microtis*. Values are given as average ± standard deviation, minimum-maximum (sample size). See material and methods for measurements' acronyms.

Measurement	*Oligoryzomys* sp. n. eastern clade	*Oligoryzomys* sp. n. central clade	*O. microtis*
HBL	86 ± 5 78-99 (23)	89 ± 7 73-105 (25)	84 ± 5 72-92 (18)
TL	109 ± 6 98-119 (23)	101 ± 7 83-115 (25)	99 ± 7 91-118 (18)
HF	23 ± 1 21-27 (22)	21 ± 1 19-24 (26)	21 ± 1 20-25 (18)
Ear	15 ± 1 11-17 (22)	13 ± 2 11-18 (24)	14 ± 1 11-15 (18)
W	19 ± 5 12-29 (22)	19 ± 3 13-23 (26)	20 ± 5 8-28 (18)
CIL	21.02 ± 0.77 19.28-22.8 (34)	21.12 ± 0.73 19.44-22.1 (21)	20.80 ± 1.12 18.52-22.9 (35)
LD	5.77 ± 0.35 4.94-6.5 (33)	5.82 ± 0.32 5.02-6.42 (21)	5.70 ± 0.38 4.69-6.46 (43)
PB	4.15 ± 0.19 3.85-4.57 (34)	4.44 ± 0.2 4.12-4.84 (21)	4.30 ± 0.3 3.6-4.91 (41)
LIF	3.75 ± 0.29 3.18-4.37 (34)	3.70 ± 0.2 3.39-4.04 (21)	3.79 ± 0.24 3.37-4.48 (43)
BIF	1.61 ± 0.16 1.3-1.9 (34)	1.60 ± 0.14 1.35-1.86 (21)	1.68 ± 0.14 1.34-1.93 (41)
LM	3.19 ± 0.12 2.95-3.45 (33)	3.33 ± 0.14 3.09-3.68 (21)	3.21 ± 0.2 2.84-3.84 (43)
BM1	0.96 ± 0.04 0.89-1.05 (33)	0.96 ± 0.07 0.86-1.11 (21)	0.97 ± 0.07 0.82-1.14 (43)
M1M	4.35 ± 0.13 4.09-4.63 (34)	4.34 ± 0.16 3.94-4.55 (21)	4.29 ± 0.2 3.86-4.63 (43)
BRO	4.36 ± 0.2 3.9-4.76 (34)	4.45 ± 0.21 4.01-4.85 (20)	4.29 ± 0.29 3.87-5.03 (43)
ORL	8.08 ± 0.33 7.28-8.82 (34)	7.82 ± 0.43 7.08-8.56 (17)	7.95 ± 0.37 7.06-8.64 (42)
ZB	12.37 ± 0.44 11.3-13.26 (33)	12.31 ± 0.39 11.41-13.03 (21)	12.05 ± 0.54 10.84-12.85 (41)
BZP	2.26 ± 0.13 1.94-2.48 (33)	2.20 ± 0.13 1.9-2.38 (21)	2.22 ± 0.15 1.93-2.52 (43)

pulsus (Bonvicino and Almeida, 2000), *Cerradomys akroai* and *Cerradomys scotti* (Bonvicino et al., 2014), *Juliomys rimofrons* and *Juliomys ossitenuis* (Costa et al., 2007). Examples of pericentric inversion as polymorphism are in *Oligoryzomys nigripes* and *Akodon cursor* (Fagundes et al., 1998; Bonvicino et al., 2001).

The apparent similarity between the karyotype of *Oligoryzomys* sp. n. (2n=64 and FN=64) with those of *O. microtis* (2n=64 and FN=66), *O. mattogrossae* (2n=62 and FN=64), and *O. flavescens* (2n=64-66 and FN=66-68), has led to various incorrect associations (see Weksler and Bonvicino, 2015). The karyotype of *Oligoryzomys* sp. n. with 2n=64 and FN=64 has been attributed to *O. microtis* (Di-Nizo et al., 2015). Another chromosome complement with 2n=66 and FN=74 (Andrades-Miranda et al., 2001) was described from Amazonian *Oligoryzomys* specimens wrongly identified as *O. microtis*; this karyotype probably belongs to *O. messorius* (see Weksler and Bonvicino, 2015).

The chromosome complements of *O. microtis* (2n=64 and FN=66) and *O. flavescens* (2n=64 and FN=66), despite sharing the same 2n and FN, differ in the morphology of the largest autosome pair, which is metacentric in the *O. microtis* and acrocentric in *O. flavescens*, despite sharing the same G banding pattern (Figure 3 in Aniskin and Volobouev, 1999). The comparison of the complete G band karyotypes of *O. microtis* and *O. flavescens* shows variations in the morphology of the two largest autosome pairs. These differences arise from a centromeric shift and the addition of a heterochromatic arm, respectively, indicating that these chromosomal features are stable within each species (Aniskin and Volobouev, 1999). These karyotypes also differ from each other by the presence of supernumerary chromosomes in *O. flavescens*. Similarly, despite the apparent similarity between *O. mattogrossae* and *Oligoryzomys* sp. n. karyotypes, in situ hybridization clearly shows differences between the chromosome complements (Di-Nizo et al., 2015, species identified as *O. fornesi* and *O. microtis*, respectively). These findings also showed that these apparent similarities among *O. microtis*, *Oligoryzomys* sp. n., *O. mattogrossae*, and *O. flavescens* are superficial, and that the differences among these karyotypes are enough to reduce or prevent the fertility of hybrids.

Phylogenetic results

The phylogenetic analyses in this study, employing both Maximum Likelihood (ML) and Bayesian Analysis (BA) methods based on the mitochondrial cytochrome b gene (mt-Cytb) and the combined mt-Cytb and nuclear i7-Fgb, produced incongruent topologies, but the discrepancies were usually in clades with low support values. In the mt-Cytb-only analysis, the first split within *Oligoryzomys* separates the *O. microtis* species group from remaining species, while the combined analysis of mt-Cytb and the i7-Fgb gene reveals an initial dichotomy separating a clade with the *O. microtis* species group and *O. mattogrossae* from the remaining species. Four additional clades are strongly supported in both mt-Cytb and the combined analyses: 1) *O. stramineus* + *O. nigripes*, 2) *O. occidentalis* + *O. longicaudatus* + *O. flavescens* + *O. fornesi*, 3) *O. costaricensis* + *O. vegetus* + *O. fulvescens, O. destructor*,

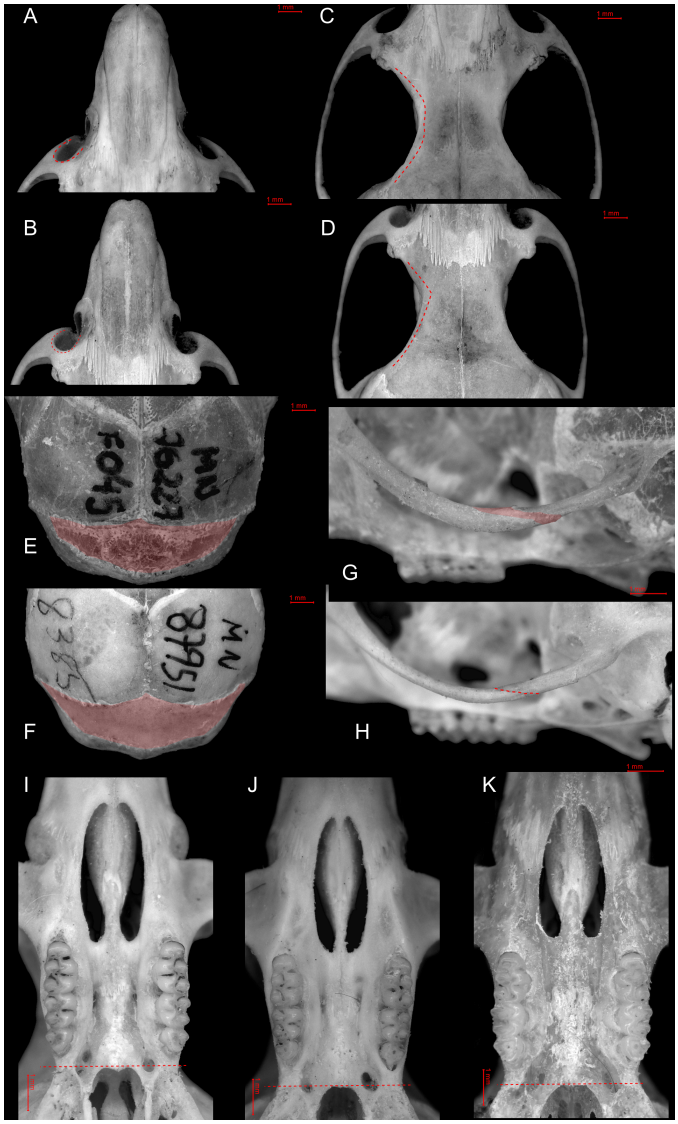

Figure 8 – Comparative plate of *Oligoryzomys* skulls, showing the variation of six selected qualitative traits: depth of the zygomatic notch (dorsal view; A-B), interorbital region (dorsal view, C-D), width of interparietal (dorsal view, E-F), presence of jugal (lateral view; G-H), and shape of incisive foramina and length of palate (ventral view; I-K). (A) *Oligoryzomys sp. n.,* central clade (MN87906); (B, D, F, H, I) *O. microtis* (MN87951); (C) *Oligoryzomys sp. n.,* central clade (MN87901); (E, G, K) *Oligoryzomys sp. n.,* eastern clade (MN76227); (J) *Oligoryzomys sp. n.,* central clade (MN87907).

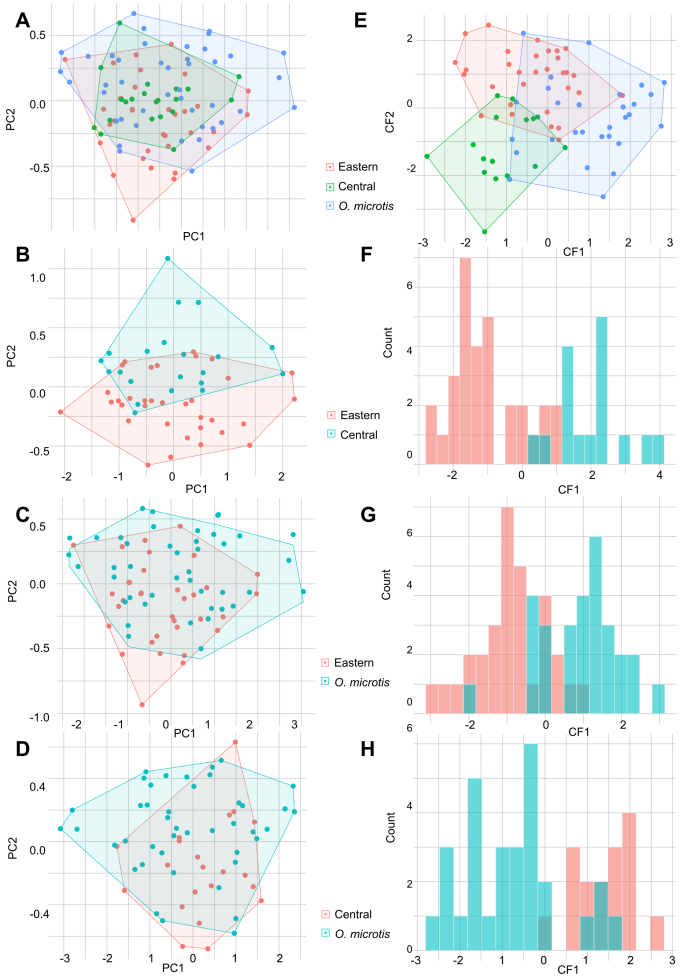

Figure 9 – Results of principal component analysis (A-D) and canonical discriminant analysis (E-H) of log-transformed cranial measurements. Scatterplots A and E include all analyzed specimens, while remaining graphs refer to pairwise contrasts between: (B and F) eastern and central clades of *Oligoryzomys sp. n.,* (C and G) O. microtis and eastern clade of *Oligoryzomys sp. n.,* and (D and H) *O. microtis* and central clade of *Oligoryzomys sp. n.*.

and 4) *O. arenalis* + *O. guille, O. andinus*. These findings provide insights into the phylogenetic relationships and genetic divergence within the *Oligoryzomys* genus, aligning with previous phylogenetic analyses of the genus (e.g., González-Ittig et al., 2010, González-Ittig et al., 2014, Weksler et al., 2017; da Cruz and Weksler, 2018; da Cruz et al., 2019; Hurtado and D'Elía, 2019, 2022).

The *O. microtis* species group, as identified in this study, comprises two primary clades. The first clade encompasses *O. microtis sensu stricto* specimens from Peru, Bolivia, and the Brazilian states of Acre and Amazonas within the western Amazon, including the topotype specimen MN84349. The second clade comprises specimens of *Oligoryzomys* sp. n. from Tocantins, Mato Grosso, and Rondônia. Significantly, this clade is further divided into two well-supported subclades, each characterized by distinct geographic distributions. The first subclade, referred to as the Central clade, includes samples from Mato Grosso and Rondônia, located in the south-central Amazon region, while the second subclade, known as the Eastern clade, encompasses specimens from Tocantins, positioned in the southeastern Amazon region.

Additionally, the median-joining network analysis of mt-Cytb data delineates three primary haplogroups. The first corresponds to *O. microtis* s.s., with specimens from Bolivia, Peru, and the Brazilian states of Amazonas and Acre. The second comprises specimens of *Oligoryzomys* sp. n. from the Brazilian state of Rondônia (Central clade), and the third includes specimens from Tocantins (Eastern clade). Within the first haplogroup, there is further subdivision into two subgroups. One subgroup contains specimens from Peru and the Brazilian states of Amazonas and Acre, while the other comprises specimens from Bolivia and the Brazilian state of Acre. Genetic distances, based on uncorrected p-distances using mt-Cytb sequences, reveal a 7.4 % difference between *O. microtis* s.s. and *Oligoryzomys* sp. n. Eastern clade, a 7.4 % difference between *O. microtis* s.s. and *Oligoryzomys* sp. n. Central clade, and a 5.4 % difference between the central and Eastern clades of *Oligoryzomys* sp. n. This intricate genetic structuring within the *O. microtis* species group alludes to potential historical isolation and differentiation events within these regions, underscoring the genetic distinctiveness of *Oligoryzomys microtis* from the western Amazon, including those from the type locality, in comparison to their counterparts in the south central and southeastern Amazon regions.

Morphological variation and cryptic species

Species of the genus *Oligoryzomys*, and in particular Amazonian forms, are extremely similar in their external and cranial anatomy, and thus very hard to tell apart; Hershkovitz (1966: 137), for instance, considered *O. flavescens* and *O. longicaudatus* as "races" of *O. nigripes*. Moreover, Voss et al. (2001: 119) stated that they "…found no obvious qualitative characters to distinguish *Oligoryzomys fulvescens* (as represented by … Mexican and central American exemplars) from typical *O. microtis*." Despite overall similarity, several morphological characters have been demonstrated to vary among species (Myers and

Carleton, 1981; Carleton and Musser, 1995; Weksler and Bonvicino, 2005; Machado et al., 2011; Agrellos et al., 2012; Weksler et al., 2017; Hurtado, 2021), and a few subtle differences were observed among the mitochondrial lineages detected here, such as configuration of interorbital region, incisive foramina, zygomatic plate, and jugal. In any case, *O. microtis* and *Oligoryzomys* sp. n. are so morphologically and morphometrically similar that they can be considered as cryptic species, at least in the character systems analyzed by us. Additional research in comparative morphology of other character systems, such as penial and stomach morphology, may reveal diagnostic characteristics for the species.

Numerous other *Oligoryzomys* species present taxonomic challenges as cryptic entities. These species exhibit limited and often polymorphic morphological variations while concurrently demonstrating significant divergence in karyological and molecular characteristics (González-Ittig et al., 2014; Rivera et al., 2018; da Cruz and Weksler, 2018). The complexities surrounding their identification hold substantial implications, particularly in the context of public health services, as several *Oligoryzomys* species serve as reservoirs for *Orthohantavirus* (Agrellos et al., 2012; Firth et al., 2012; Rivera et al., 2007; da Cruz et al., 2019).

Within rodents, and more broadly among mammals, the discovery of cryptic species currently lies on the application of molecular techniques, with "DNA barcoding" and automatic species detection (e.g., GMYC, b-PTP) standing as popular tools for unraveling genetic variations within seemingly indistinguishable populations (e.g., da Cruz et al., 2019; Ojeda et al., 2021; Di-Nizo et al., 2022; Quiroga-Carmona et al., 2022). Nevertheless, the central challenge in recognizing cryptic species lies in distinguishing between genetic structuring arising from geographical barriers within a species and the delineation of genuinely distinct evolutionary lineages that may exhibit morphological similarities. We contend that karyotypic data serves as an indispensable source of information for distinguishing between genuine cryptic entities and regional variants marked by genetic structuring. This rationale underpins the approach adopted in our current study, where we describe a new species possessing a distinctive karyotype in contrast to *O. microtis*, while the two new subspecies share the same karyotype and exhibit subtle morphological differences. We further emphasize the need for expanded and more geographically comprehensive sampling to validate our classification.

Biogeography

Oligoryzomys sp. n. predominantly inhabits the central Brazil Shield, while *O. microtis sensu stricto* is found in the western Amazonia lowlands and in the Mamoré-Madre de Dios Piedmont. The new lineage is currently separated from *O. microtis* in the northern part of its range by the Amazonas/Solimões River, and in the west by its tributary, the Madeira River. This distribution pattern is also observed in marsupials, as seen with *Monodelphis glirina* with distribution in the western Amazonia lowlands and its sister species, *M. maraxina*, in the central Brazil Shield (Bonvicino et al., 2023). The Amazonas/Solimões River also serves as a barrier for subspecies and sister species of various mammals, including rodents such as *P. steerei* in the south and *P. quadruplicatus* in the north (Patton and da Silva, 1998). Additionally, marsupials such as *Caluromys philander philander* are found in the north, while *C. philander affinis* and *C. philander dichurus* inhabit the south. In the case of species of *Marmosa (Micoureus)*, *M. demerarae* is found in the north of the Amazonas/Solimões River, while *M. constantiae* and *M. domina* are located in the south (Bonvicino et al., 2023).

There is evidence that the Madeira River has acted as a vicariance barrier for certain mammals and avian species, such as Primates like *Callicebus brunneus* and *Callicebus dub*ius (Santorelli et al. 2018), as well as birds like *Psophia viridis* and *Psophia leucoptera* (Ribas et al., 2011). However, its role as the limit of distribution was not supported for several species of mammals, birds and squamates (Santorelli et al., 2018).

The hypothesis of rivers serving as current barriers has been tested since its formulation in the 19th century (Wallace, 1853) and has become a valuable concept for understanding the delimitation of species and subspecies distribution. Riverine barriers can pose significant obstacles to several taxa, such as birds (Naka et al., 2022) and mammals (Ayres and Clutton-Brock, 1992). However, the role of rivers as a primary factor in speciation remains less established (Bonvicino and Weksler, 2012; Janiak et al., 2022). When assessing the role of rivers as geographic barriers, it is essential to consider various characteristics, not only of the rivers themselves (e.g., meandering rivers, depth, water speed) but also of the taxa under investigation, including their ability to disperse and swim. In the case of *Oligoryzomys* sp. n., the causative role of the Madeira River remains uncertain.

O. microtis taxonomy and implications for Rio Mamoré orthohantavirus

Karyotype differences were congruent with median-joining and phylogenetic analyses (Figs. 3 and 4), which showed *O. microtis* separated into two clades, the first with specimens from Brazilian Cerrado biome and transitions areas with Amazonas, including karyotyped animals of *Oligoryzomys* sp. n.; and a second clade with specimens from localities in the Bolivian, Peruvian and Brazilian Amazon biome, including karyotyped specimens, and a topotype, of *O. microtis*. The first clade was further divided into two subclades, one with specimens from southeastern Amazon (Tocantins state) and another with specimens from south central Amazon (Rondônia and Mato Grosso states).

Previous studies with *Orthohantavirus* sequences detected four variants in the Rio Mamoré orthohantavirus genotype (Richter et al., 2010; Firth et al., 2012; Guterres et al., 2015; Nunes et al., 2015): RIOMV in Bolivia (=OMM-556) and in Peru (=HTN-007), RIOMV-3 in Acre and Amazonas states, Brazil; and RIOMV-4 in Rondônia state, Brazil. Phylogenetic analysis of *Orthohantavirus* sequences (Firth et al., 2012) have demonstrated that these four lineages are highly divergent and do not form monophyletic group. These authors also associated the first three lineages of Rio Mamore orthohantavirus to *O. microtis* and one, RIOMV-4, to an unnamed species, which is described here (see also Figure 3 for identification of *Orthohantavirus* positive *Oligoryzomys* specimens).

The evidence presented here suggests that *O. microtis* and *Oligoryzomys* sp. n. belong to different evolutionary lineages, and thus they merit taxonomic recognition. Although the two forms are reciprocally monophyletic and differ in the chromosomal complement, they are morphologically similar, and thus could be considered as different cryptic species in a phylogenetic species concept (e.g., De Queiroz, 2007). Furthermore, we opted here for the recognition of two subspecies within the *Oligoryzomys* sp. n. lineage, corresponding to the Central and Eastern clades, due to sharing the same karyotype. We could not find non-overlapping discrete morphological diagnostic features between the two subspecies among analyzed features (skin, skull, and dentition), and thus taxonomic identification would be presently impossible without the use of DNA sequences, hindering ecological and epidemiological studies. Future morphological work in other systems may provide anatomical evidence for specific separation.

TAXONOMIC ACCOUNT

Oligoryzomys gri *sp. n.*

Figures 6, 7, and 8

Holotype. MN87921, an adult male collected on 2005, July 20 by Secretaria de Vigilância em Saúde (SVS, original field number SVS134/LBCE20531), at Fazenda do Seu Bento, Alto Paraíso, Rondônia state, Brazil (Fig. 7). The holotype consists of skin, skull, and liver tissue fixed in ethanol. External measurements of holotype (see material and methods for acronyms; all measurements in mm except weight): ToL = 185, TL = 101, HF = 20, Ear = 13, W = 13 g, CIL = 21.01, LD = 5.74, PB = 4.45, LIF = 3.57, BIF = 1.62, LM = 3.40, BM1 = 1.01, M1M = 4.25, BRO = 4.35, ORL = 8.05, ZB = 12.19, BZP = 2.17.

Paratypes. All from the type locality. MN91084, an adult male (original field number SVS003/LBCE7038), and MN91085, an adult female (original field number SVS004/LBCE7039), both collected by SVS on 2005, July 15, consisting of skin, skull (broken), cell suspension and liver tissue fixed in ethanol. MN87919 male (original field number SVS118/LBCE20515), collected by SVS on 2005, July 20, consisting of skin, skull, and liver tissue fixed in ethanol; MN91086 male (original field number SVS107), collected by SVS on 2005, July 19, consisting of skin, skull (broken), and liver tissue fixed in ethanol.

Etymology: the name *gri* means small or tiny in the Apinayé language (Albuquerque, 2012), as well as in proto-Macro-Jê (Nikulin, 2020), and refers to the smaller size of this species in relation to most *Oligoryzomys* species. We employed the Latin form 'gri', as employed in Albuquerque (2012), instead of 'ŋgri' (Nikulin, 2020) because the guttural sound represented by the letter 'ŋ' can be challenging to pronounce.

Type Locality: Brazil, Rondônia state, Alto Paraíso, Fazenda do Seu Bento (9°19'15"S, 63°19'15"W, 108 m a.s.l.).

Geographic Distribution: *Oligoryzomys gri* sp. n. occurs throughout the Southern border of the Amazon biome of central and northwest Brazil and in areas of ecotone between Amazon and Cerrado biomes (Fig. 1; appendix 1). In Brazil, the species has been reported in the states of Rondônia, Mato Grosso, Pará, and Tocantins (Table 1, Fig. 1), in the Madeira-Tapajos and Xingu-Tocantins interfluvial regions.

Diagnosis: A small-sized *Oligoryzomys* species (adult HBL varying from 73-105 mm) with slightly bicolored tail longer than the head-body size, incisive foramina posterior borders never extending posteriorly the plane of the alveolus of the first upper molars, palatal bridge broad and relatively short, with posterior portion extending beyond M3 plane less than half M3 length. In addition, all known karyotyped specimens share the same diploid number of 64 and fundamental autosome number of 64.

Description: Adult dorsal pelage yellowish to orangish brown (brussels brown, raw umber, antique brown, buckhorn brown in Ridgway (1912), composed of ca. 6-7 mm-long guard hairs and slightly shorter overhairs with a sub-apical brown-yellowish or brown-orangish band (Fig. 6). Lateral color lighter than in dorsum and with a defined limit with the ventral pelage. Ventral pelage coloration varies from light cream to white slightly tinged with ochre; younger animals have more ochraceous overtones. Ventral hairs are cream at their upper part and grey in the third or fifth basal part. Gular and urogenital region with pure cream hairs, without any basal grey band. Dorsal surface of pes with short pelage, with cream hairs. Short tufts of white ungual hairs at bases of claws on dII–dV. Plantar surface of pes with conspicuous scales and with six plantar pads. Internal hairs of the ear are light brown. Tail longer than combined length of head and body, scarcely covered with small brown light hairs, and covered with relatively conspicuous epidermal scales, lacking a long tuft of terminal hairs and weakly bicolored, dorsal surface dark grey and ventral surface light grey. Superciliary, genal, and mystacial vibrissae do not extend beyond ears. See table 2 for external measurements.

Delicate skull (Figs. 7 and 8), narrow rostrum, but slightly wider than interorbital constriction. Interorbital region hourglass-shaped or very slightly cuneate in eastern populations. Braincase without supraorbital (or weakly developed in eastern populations) and postorbital ridges. Interparietal bone as broad as anterior half of parietal. Relatively large zygomatic plate with shallow or moderate zygomatic notch. Jugal bone not detected in lateral view, resulting in zygomatic process of squamosal in contact with the zygomatic process of maxillary. Incisive foramina teardrop or round bracket shaped, the posterior borders not reaching or reaching (in eastern populations) the plane of the alveolus of the first upper molars, but never extending posteriorly. Palatal bridge broad and relatively short, with posterior portion extending beyond M3 plane, less than half M3 length. Palate with one single large, or two smaller, posterolateral palatal pits recessed, or not, in an incipient palatine fossa situated anterior to mesopterygoid fossa and posterior or lateral to M3. Bony roof of mesopterygoid fossa perforated by large sphenopalatine vacuities. Width of parapterygoid plate similar to the 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, reaching the carotid canal. Mastoid perforated by conspicuous postero-dorsal fenestra. In mandible, capsular process of lower incisor alveolus well developed; superior and inferior masseteric ridges converging anteriorly as open chevron below m1.

Upper and lower incisors opisthodont; molars pentalophodont. Superior molar rows parallel. Procingulum of first upper molar (M1) with anteromedian flexus only in young animals, with moderate wear lacking anteromediam flexus. A small anteroloph is present and separate from anterocone in young, but anteroloph is joined with anterocone in specimens with more advanced wear; posteroloph small joined to metacone in specimens with more advanced wear. Paracone connected to mesoloph, creating an internal mesofosseta. M2 with mesoloph, with or without a protoflexus. Third upper molar (M3) is reduced, and has a single posterior cusp, 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=64 and FN=64. Because of the poorly known taxonomy of this group of species, this karyotype has been previously associated with *O. microtis* (Di-Nizo et al., 2015), and *O. flavescens* (Lima, 2004, Table 1).

Habitat: *Oligoryzomys gri* sp. n. is an inhabitant of Cerrado and transition areas with Amazonas.

Comparisons: *Oligoryzomys* species are very similar one to another, and few characters allow the separation between them. *Oligoryzomys gri* sp. n. differs from all other *Oligoryzomys* species by its unique karyotype. In addition, *O. gri* sp. n. differs from *Oligoryzomys* species that occur in Brazil by a combination of other characters including (1) slightly bicolored tail, contrary to unicolored tail in *O. nigripes* and *O. rupestris* (other species of the genus also have slightly bicolored tails); (2) small-sized species (adult HBL between < 87 mm in average) as in *O. rupestris*, *O. microtis*, *O. moojeni*, *O. flavescens*, *O. delicatus*, *O. messorius*, *O. fornesi*, *O. mattogrossae*, opposed to large size species (adult HBL > 100 mm in average) as *O. nigripes*, *O. stramineus*, and *O. chacoensis*. *O. gri* sp. n. is different from *O. microtis* in the relatively smaller incisive foramen in relation to the diastema length. See also results above for more detailed morphological contrasts with *O. microtis.*

Conservation status: *Oligoryzomys gri* sp. n. inhabits the region of the ecotone between the Amazon rainforest and Cerrado of Central and Northern Brazil, currently undergoing massive development in the "agricultural frontier", where cases of Hantavirus pulmonary syndrome (HPS) have been reported (Oliveira et al., 2009, 2011; Rosa et al., 2005, 2010; Suzuki et al., 2004). This new species, as far as we know, is not uncommon at its sampling sites, with several specimens collected during field work. Despite its extensive geographic range (Fig. 1), sampling localities were relatively few and distant among them. We propose that the species be categorized as data-deficient until further information is acquired for a proper evaluation by IUCN criteria.

Remarks: Hurtado and D'Elía (2019) suggested the presence of two new candidate species within the *O. microtis* complex in their analysis of molecular variation and automatic species identification; the two candidate species would represent the Central and Eastern clades detected in our phylogenetic analyses and considered here as subspecies of *Oligoryzomys gri* sp. n.: *O. gri gri,* and *O. gri apinaye,* described below, respectively.

Specimens Examined: See appendix 1.

***Oligoryzomys gri apinaye* subsp. n.**

Figures 6, 7 and 8

Holotype: MN76206 an adult male, collected on September 1997 by Laboratório de Vertebrados, UFRJ (original field number FO19), at Fazenda Osara II, São Sebastião do Tocantins, Tocantins state, Brazil (Fig. 7). The holotype consists of skin, skull, and liver tissue fixed in ethanol. External measurements of holotype (see material and methods for acronyms; all measurements in mm except weight): ToL = 193, TL = 103, HF = 23, Ear = 14, W = 23 g, CIL = 21.52, LD = 5.77, PB = 3.89, LIF = 4.28, BIF = 1.79, LM = 3.37, BM1 = 0.95, M1M = 4.23, BRO = 4.35, ORL = 7.98, ZB = 12.64, BZP = 2.29.

Paratypes: All from type locality consisting of skin, skull, and tissues. MN76192 (original field number FO05), MN76194 (FO07), MN76198 (FO10), MN76200 (FO13), MN76203 (FO16), MN75205 (FO18), MN76207 (FO20), MN76209 (FO22), MN76210 (FO23), MN76212 (FO25), MN76213 (FO26), MN76216 (FO29), MN76217 (FO30), MN76223 (FO36), MN81726 (FO41), MN76226 (FO43), MN81727 (FO44), MN76227 (FO45), MN80436 (FO47), MN80431 (FO39). Skin, skull, tissue and cells suspension of MN81639 (offspring of MN81726), MN81640 (offspring of MN81726), MN81641 (offspring of MN81727), MN81642 (offspring of MN81727), MN81643 (offspring of MN81726), and MN81644 (offspring of MN81726).

Etymology: The name refers to the Apinayé people of the Macro-Jê linguistic trunk, who are the native inhabitants of the north of the State of Tocantins, mainly around the rivers Araguaia and Tocantins.

Type locality: Brazil, Tocantins state, São Sebastião do Tocantins municipality, Fazenda Osara II (5º16'S, 48º21'W).

Geographic distribution: *Oligoryzomys gri apinaye* ssp. n. occurs in south-eastern Amazon, in the moist and semi-deciduous forests of the Xingu-Tocantins/Araguaia interfluvial region and in areas of ecotone between Amazon and Cerrado biomes, in the Brazilian states of Tocantins and Pará (Fig. 1).

Diagnosis: A small-sized *Oligoryzomys* taxon (adult HBL varying from 78-99 mm) with tail longer than the head-body size, and characterized by the combination of the following morphological characteristics: interorbital region cuneate with weakly developed supraorbital ridges; large zygomatic plate with deep zygomatic notch; palatal bridge broad and long, with posterior portion extending beyond M3 plane by half M3 length.

Description: External morphology as in *Oligoryzomys gri* (Fig. 6), except for characters differentiated in the diagnosis (see also Fig. 5). See table 2 for external measurements. Skull similar to *O. gri*, except in the following characters (Fig. 7 and Fig. 8): interorbital region cuneate; supraorbital ridges weakly developed. Relatively large zygomatic plate with deep zygomatic notch. Incisive foramina reaching the plane of the alveolus of the first upper molars, but never extending posteriorly. Palatal bridge broad and long, with posterior portion extending beyond M3 plane by half M3 length. Long mesopterygoid fossa exposing a relatively larger portion of the presphenoid.

Karyotype: This species is characterized by 2n=64 and FN=64 (Fig. 2), sharing the same chromosome complement with *Oligoryzomys gri gri*.

Habitat: *Oligoryzomys gri apinaye* subsp. n. is an inhabitant of Cerrado and transition areas with the Amazon.

Comparisons: See comparisons above for contrasts with other species. *Oligoryzomys gri apinaye* ssp. n. differs from *Oligoryzomys gri gri* by its smaller skull size (Table 2), deeper zygomatic notch and longer interparietal and the cuneate supraparietal region with more developed crests (Figs. 7 and 8). In ventral view, *O. gri apinaye* differs from both *O. gri gri* and *O. microtis* in longer incisive foramen, resulting in a shorter palatal bridge, and a mesopterygoid fossa extending anteriorly closer to M3 plane (less than M3 length; Fig. 8).

Remarks: See above in remarks for *Oligoryzomys gri* sp. n..

Specimens Examined: This subspecies corresponds to *Oligoryzomys* sp. in Hurtado and D'Elía (2019) and to clade 2 of *O. microtis* in da Cruz et al. (2019).

References

Agrellos R., Bonvicino C.R., Rosa E.S.T., Marques A.A.R., D'Andrea P.S., Weksler M., 2012. The taxonomic status of the Castelo dos Sonhos Hantavirus reservoir, *Oligoryzomys utiaritensis* Allen 1916 (Rodentia, Cricetidae, Sigmodontinae). Zootaxa 3220: 1–28.

Albuquerque F.E., 2012. Dicionário escolar Apinayé. Editora da Faculdade de Letras da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

Almendra A.L., Rogers D.S., González-Cózatl F.X., 2014. Molecular phylogenetics of the *Handleyomys chapmani* complex in Mesoamerica. J. Mammal. 95**:** 26–40.

Andrades-Miranda J., Oliveira L.F.B., Lima-Rosa C.A.V., Nunes A.P., Zanchin N.I.T., Mattevi M.S., 2001. Chromosome studies of seven species of *Oligoryzomys* (*Rodentia, Sigmodontinae*) from Brazil. J. Mammal. 82(4): 1080–1091. 10.1644/1545-1542(2001)082<1080:CSOSSO>2.0.CO;2

Aniskin V.M., Volobouev V.T., 1999. Comparative chromosome banding of two South-American species of rice rats of the genus *Oligoryzomys* (*Rodentia, Sigmodontinae*). Chromosome Res. 7: 557–562. 10.1023/a:1009245729902

Ayres J. M., Clutton-Brock T. H., 1992. River boundaries and species range size in Amazonian Primates. Amer. Natural. 140(3): 531 –537.

Bandelt H.J., Forster P., Röhl A., 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16(1): 37–48.

Bharadwaj M., Botten J., Torrez-Martinez N., Hjelle B., 1997. Rio Mamore virus: genetic characterization of a newly recognized hantavirus of the pygmy rice rat, *Oligoryzomys microtis*, from Bolivia. Am. J. Trop. Med. Hyg. 57:368–374. 10.4269/ajtmh.1997.57.368

Bonvicino C.R., Almeida F.C., 2000. Karyotype, morphology and taxonomic status of *Calomys expulsus* (*Rodentia: Sigmodontinae*). *Mammalia* 64(3): 339–351. 10.1515/mamm.2000.64.3.339

Bonvicino C.R., Moreira M.A., 2001. Molecular phylogeny of the genus *Oryzomys* (*Rodentia: Sigmodontinae*) based on cytochrome b DNA sequences. Mol. Phylogen. Evol. 18: 282–92.

Bonvicino C.R., Weksler M., 1998. A new species of *Oligoryzomys* (*Rodentia, Sigmodontinae*) from northeastern and central Brazil. Z. Saügetierk. 63: 90–103.

Bonvicino C.R., Weksler M., 2012. Speciation in Amazonia: Patterns and Predictions of a Network of Hypotheses. In: Patterson B.D., Costa E.P. (Eds.) Bones Clones and Biomes. University of Chicago Press, Chicago, Il. 283-306.

Bonvicino C.R., Casado F., Weksler M., 2014. A new species of *Cerradomys* (*Mammalia: Rodentia: Cricetidae*) from central Brazil, with remarks on the taxonomy of the genus. Zoologia (Curitiba) 31(6): 525–540. 10.1590/S1984-46702014000600002

Bonvicino C.R., D'Andrea P.S., Borodin P., 2001. Pericentric inversions: a study in natural populations of *Oligoryzomys nigripes* (*Rodentia: Sigmodontinae*). Genome 44: 791–796. 10.1139/g01-080

Bonvicino C.R., Lazar A., Freitas T., Lanes R.O., D'Andrea PS, 2023. Diversification of the Marsupials (Didelphimorphia) of South America. In: Cáceres N.C., Dickman C. R. (Eds.) American and Australasian Marsupials. An Evolutionary, Biogeographical, and Ecological Approach. Springer Nature, Cham, Switzerland.

Bordignon S.E., 2007. Análise da variabilidade cromossômica e distribuição geográfica de duas espécies de *Oligoryzomys* (*Rodentia, Cricetidae*) ocorrentes nos Estados de Santa Catarina e Paraná. Honors Thesis, Universidade Federal do Paraná, Curitiba, Brazil.

Brum-Zorilla N., Fronza T.G., Wainberg R., Vidal-Rioja I., Zwinrger N., 1988. *Oryzomys flavescens* and *O delticola* chromosomes (*Rodentia, Cricetidae*) from Uruguay and Argentina. Caryologia 41: 275–288. 10.1080/00087114.1988.10797868

Canon C., Mir D., Pardiñas U.F.J., Lessa E.P., D'Elía G., 2014. A multilocus perspective on the phylogenetic relationships and diversification of rodents of the tribe Abrotrichini (Cricetidae: Sigmodontinae). Zool. Scr. 43: 443–454.

Carleton M.D., Musser G.G., 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bull. Am. Mus. Nat. Hist. 191: 1–83.

Carleton, M.D., Musser, G.G. 1995. Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegetus* (Bangs, 1902). Proc. Biol. Soc. Wash. 108(2): 338–369.

Carroll D.S., Mills J.N., Montgomery J.M, Bausch D.G., Blair P.J., Burans J.P., Felices V, Gianella A., Iihoshi N., Nichol S.T., Olson J.G., Rogers D.S., Salazar M., Ksiazek T.G., 2005. Hantavirus pulmonary syndrome in central Bolivia: relationships between reservoir hosts, habitats, and viral genotypes. Am. J. Trop. Med. Hyg. 72: 42–46.

Casado F., Bonvicino C.R., Nagle C., Comas B., Manzur T.D., Lahoz M.M., Seuánez H.N., 2010. Mitochondrial divergence between 2 populations of the hooded capuchin, *Cebus* (*Sapajus*) *cay* (*Platyrrhini, Primates*). J. Hered. 101: 261–269.

Casapía M., Mamani E., García M.P., Miraval M.L., Valencia P., Quino A.H., Donaires L.F., 2012. Síndrome pulmonar por Hantavirus (Virus Río Mamoré) en la Amazonía Peruana. Rev. Peru. Med. Exp. Salud. Pub. 29:390–395. 10.1590/s1726-46342012000300016

Castillo Oré R.M., Forshey B.M., Huaman A., Villaran M.V., Long K.C., Kochel T.J., Guevara C., Montgomery J.M., Alvarez C.A., Vilcarromero S., Morrison A.C., Halsey E.S., 2012. Serologic Evidence for Human Hantavirus Infection in Peru. Vector-Borne Zoonotic Dis. 12(8) : 683–689. 10.1089/vbz.2011.0820

Costa L.P., Pavan S.E., Leite Y.L.R., Fagundes V., 2007. A new species of *Juliomys* (*Mammalia: Rodentia: Cricetidae*) from the Atlantic Forest of southeastern Brazil. Zootaxa 1463: 21–37.

da Cruz M.O.R., Weksler M., Bonvicino C.R., Bezerra A.M.R., Prosdocimi F., Furtado C., Geise L, Catzeflis F., Thoisy B. de, Oliveira L.F.B. de, Silva C., Oliveira J.A. 2019. DNA barcoding of the rodent genus *Oligoryzomys* (*Cricetidae: Sigmodontinae*): mitogenomic-anchored database and identification of nuclear mitochondrial translocations (Numts). Mitochondrial DNA Part A 17:1–11. 0.1080/24701394.2019.1622692

da Cruz M.O.R., Weksler M., 2018. Impact of tree priors in species delimitation and phylogenetics of the genus *Oligoryzomys* (*Rodentia: Cricetidae*). Mol. Phylogenet. Evol. 119: 1–12. 10.1016/j.ympev.2017.10.021

de Andrade A.F.B., Bonvicino C.R., 2003. A new karyologic variant of *Oecomys* (*Rodentia: Sigmodontinae*) and its phylogenetic relationship based on molecular data. Genome 46(2): 195–203. 10.1139/g02-123

D'Elía G., Hanson J.D., Mauldin M.R., Teta T., Pardiñas U.F.J., 2015. Molecular systematics of South American marsh rats of the genus *Holochilus* (*Muroidea, Cricetidae, Sigmodontinae*). J. Mammal. 96 (5): 1081–1094. 10.1093/jmammal/gyv115

De Queiroz K. 2007. Species Concepts and Species Delimitation. Syst. Biol. 56(6): 879–886. 10.1080/10635150701701083

Di-Nizo C.B., Ventura K., Ferguson-Smith M.A., O'Brien P.C.M., Yonenaga-Yassuda Y., Silva M.J., 2015. Comparative Chromosome Painting in Six Species of *Oligoryzomys*

(*Rodentia, Sigmodontinae*) and the Karyotype Evolution of the Genus. PLoS ONE 10(2): e0117579. 10.1371/journal. pone.0117579
Di-Nizo C.B., Suárez-Villota E.Y., Silva M.J.J., 2022. Species limits and recent diversification of *Cerradomys* (*Sigmodontinae: Oryzomyini*) during the Pleistocene. PeerJ 10: e13011. 10.7717/peerj.13011
Drummond A. J., Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7(1): 214.
Eppig J.T., Blake J.A., Bult C.J., Kadin J.A., Richardson J.E., The Mouse Genome Database Group. 2015. The Mouse Genome Database (MGD): facilitating mouse as a model for human biology and disease. Nucleic Acids Res. 28: D726–36.
Espinosa M.B., Reig O.A., 1991. Cytogenetics and karyosystematics of South American oryzomyine rodents (Cricetidae, Sigmodontinae) III. Banding karyotypes of Argentinian *Oligoryzomys*. Z. Säugetierk. 56: 306–317.
Fagundes V., Christoff A.U., Yonenaga-Yassuda, Y., 1998. Extraordinary chromosomal polymorphism with 28 different karyotypes in the neotropical species Akodon cursor (Muridae, Sigmodontinae), one of the smallest diploid number in rodents (2n=16, 15 and 14). Hereditas 129: 263–274. 10.1111/j.1601-5223.1998.00263.x
Felsenstein J., 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. J. Mol. Evol. 17: 368–76.
Felsenstein J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evol. 39: 783–791.
Firth C., Tokarz R., Simith D.B., Nunes M.R.T., Bhat M., Rosa E.S.T., Medeiros D.B., Palacios G., Vasconcelos P.F.C., Lipkin W.I., 2012. Diversity and distribution of hantaviruses in South America. J. Virol. 86: 13756–66.
Friendly M., and Fox J., 2010. Candisc: R package for canonical discriminant analysis.
Gardner A.L., Patton J.L., 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. Occ. Pap. Mus. Zool., La. State Univ. 49: 1–47.
González-Ittig, R.E., Salazar-Bravo J., Barquez R.M., Gardenal C.N., 2010. Phylogenetic relationships among species of the genus *Oligoryzomys* (*Rodentia, Cricetidae*) from Central and South America. Zool. Scr. 39: 511–526.
González-Ittig R.E., Rivera P.C., Levis S.C., Calderón G.E., Gardenal C. N., 2014. The molecular phylogenetics of the genus *Oligoryzomys* (*Rodentia: Cricetidae*) clarifies rodent host–hantavirus associations. Zool. J. Linn. Soc. 171 (2): 457–474.
Guterres A., de Oliveira R.C., Fernandes J., Schrago C.G., de Lemos E.R.S., 2015. Detection of different South American hantaviruses. Virus Res. 210: 106–113. 10.1016/j.virusres.2015.07.022
Hall T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41: 95–98.
Hanson J.D., 2008. Molecular phylogenetics of the tribe Oryzomyini: does a multi-gene approach help resolve a systematic conundrum? Ph.D. Thesis, Texas Tech University, Lubbock, Tx.
Hanson J.D., A. Utrera, Fulhorst C.F., 2011. The delicate pygmy rice rat (*Oligoryzomys delicatus*) is the principal host of Maporal Virus (Family Bunyaviridae, Genus Hantavirus). Vector-Borne and Zoonotic Dis. 11(6): 691–696.
Hershkovitz P., 1966. South American Swamp and fossorial rats of the Scapteromyine group (Cricetinae, Muridae), with comments on the glans penis in murid taxonomy. Z. Säugetierk. 31: 81–149.
Holm S., 1979. A simple sequential rejective multiple test procedure. Scand. J. Stat. 6: 65–70.
Huelsenbeck J.P., Ronquist F., Nielsen R., Bollback J.P., 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294: 2310–2314.
Hurtado N., 2021. A new species of the genus *Oligoryzomys* (*Rodentia: Cricetidae*) from Peru. J. Mammal. 102(3): 931–946. 10.1093/jmammal/gyab030
Hurtado N., and D'Elía G., 2018. A new species of long-tailed mouse, genus *Oligoryzomys* Bangs, 1900 (*Rodentia: Cricetidae*), from the Bolivian Yungas. Zootaxa 4500(3): 341–362. 10.11646/zootaxa.4500.3.3
Hurtado N., D'Elía G., 2019. An assessment of species limits of the South American mouse genus *Oligoryzomys* (*Rodentia, Cricetidae*) using unilocus delimitation methods. Zool. Scr. 48(5): 557–570.
Hurtado, N., and D'Elía, G. 2022. Historical biogeography of a rapid and geographically wide diversification in Neotropical mammals. J. Biogeog. 49(5): 781–793.
Irwin D.M., Kocher T.D., Wilson A.C., 1991. Evolution of the cytochrome b gene of mammals. J. Mol. Evol. 32: 128–144.
Janiak M.C., Silva F.E., Beck R.M.D., Vries D. de, Kuderna L.F.K., Torosin N.S., Melin A.D., Marquès- Bonet T., Goodhead I.B., Messias M., da Silva M.N..F, Sampaio I., Farias I.P., Rossi R., Melo F.R. de, Valsecchi J., Hrbek T., Boubli J.P., 2022. Two hundred and five newly assembled mitogenomes provide mixed evidence for rivers as drivers of speciation for Amazonian primates. Mol. Ecol. 31: 3888-3902. 10.1111/mec.16554
Josse J., Husson F., 2016. missMDA: A Package for Handling Missing Values in Multivariate Data Analysis. Journal of Statistical Software 70(1): 1–31. 10.18637/jss.v070.i01
King M., 1993. Species evolution: the role of chromosome change. Cambridge University Press, Cambridge.
Kozlov A.M., Stamatakis, A., 2019. Using RAxML-NG in Practice. Preprints.org, 2019050056. 10.20944/preprints201905.0056.v1
Lima J.F.S., 2004. Diversidade cariológica de roedores de pequeno porte do estado de Tocantins. PhD thesis, Instituto de Biociências, Universidade Estadual de São Paulo, Rio Claro, Brazil.
Machado L.F., Paresque R., Christoff A.U., 2011. Anatomia comparada e morfometria de *Oligoryzomys nigripes* e *O. flavescens* (*Rodentia, Sigmodontinae*) no Rio Grande do Sul, Brasil. Pap. Avulsos Zool. (São Paulo) 51(3): 29-47. 10.1590/S0031-10492011000300001
Machado L.F., Leite Y.L., Christoff A.U., Giugliano L.G., 2014. Phylogeny and biogeography of tetralophodont rodents of the tribe Oryzomyini (Cricetidae: Sigmodontinae). Zool. Scr. 43: 119–130.
Matocq M.D., Shurtliff Q.R., Feldman, C.R., 2007. Phylogenetics of the woodrat genus *Neotoma* (*Rodentia: Muridae*): Implications for the evolution of phenotypic variation in male external genitalia. Mol. Phylogen. Evol. 42(3): 637–652. 10.1016/j.ympev.2006.08.011
McCarthy C., 1998. Chromas version 1.45 (32-bit).
Milazzo M. L., Cajimat M.N., Hanson J.D., Bradley R.D., Quintana M., Sherman C., Velásquez R.T., Fulhorst C.F., 2006. Catacamas virus, a hantaviral species naturally associated with *Oryzomys couesi* (*Coues' oryzomys*) in Honduras. Am. J. Trop. Med. Hyg. 75: 1003–1010.
Miller M.A., Pfeiffer W., Schwartz T., 2010. Creating CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshops (GCE), New Orleans, La., 1–8.
Mull N., Jackson R., Sironen T., Forbes K.M., 2020. Ecology of neglected rodent-borne American orthohantaviruses. Pathogens 9(5): 325. 10.3390/pathogens9050325
Myers P., Carleton M.D., 1981. The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "rat sixieme ou rat à tarse noir". Misc Publ. Mus. Zool. Univ. Mich. 161:1–41.
Naka L.N., da Silva Costa B.M., Lima G.R., Claramunt S., 2022. Riverine Barriers as Obstacles to Dispersal in Amazonian Birds. Front. Ecol. Evol. 10: 84697.
Nikulin A., 2020. Proto-Macro-Jê: um estudo reconstrutivo. PhD Thesis, Departamento de Linguística, Português e Línguas Clássicas, Universidade de Brasília, Brasília, Brazil.
Nunes M.L., Oliveira S.V. de, Elkhoury M. da R., Fonseca L.X., Pereira S.V.C., Caldas E.P., Guimarães J.C.N., Rosa E.S.T., Bonvicino C.R., D'Andrea, P.S., 2015. Evidência de circulação de hantavirus em área silenciosa da Região Amazônica. Rev. Pan-Amaz. Saude 6(4): 63–67. 10.5123/S2176-62232015000400009
Ojeda, A.A., Teta, P., Pablo Jayat, J., Lanzone, C., Cornejo, P., Novillo, A., Ojeda, R.A., 2021. Phylogenetic relationships among cryptic species of the *Phyllotis xanthopygus* complex (*Rodentia, Cricetidae*). Zool. Scr. 50(3): 269–281. 10.1111/zsc.12472
Oliveira J.A., Strauss R.E., Reis S.F., 1998. Assessing relative age and age structure in natural populations of *Bolomys lasiurus* (*Rodentia: Sigmodontinae*) in Northeastern Brazil. J. Mammal. 79: 1170–1183.
Oliveira R.C, Teixeira B.R., Mello F.C., Pereira A.P., Duarte A.S., Bonaldo M.C., Bonvicino C.R., D'Andrea P.S., de Lemos E.R.S., 2009. Genetic characterization of a Juquitiba-like viral lineage in *Oligoryzomys nigripes* in Rio de Janeiro, Brazil. Acta Tropica 112: 212–318.
Oliveira R.C., Padula P.J., Gomes R., Martinez V.P., Bellomo C., Bonvicino C.R., Freire e Lima D.I., Bragagnolo C, Caldas A.C.S, D'Andrea P.S, de Lemos E.R.S., 2011. Genetic characterization of hantaviruses associated with sigmodontine rodents in an endemic area for hantavirus pulmonary syndrome in southern Brazil. Vector Borne Zoonotic Dis. 11: 301–314.
Oliveira R.C., Guterres A., Fernandes J., D'Andrea P.S., Bonvicino C.R., de Lemos E.R.S., 2014. Hantavirus reservoirs: current status in the world with an emphasis on data from Brazil. Viruses 6(5): 1929–1973.
Oliveira da Silva W., Rosa C.C., Ferguson-Smith M.A., O'Brien P.C.M., Saldanha J., Rossi R.V., Pieczarka J.C., Nagamachi C.Y. 2022. The emergence of a new sex-system (XX/XY1Y2) suggests a species complex in the "monotypic" rodent *Oecomys auyantepui* (*Rodentia, Sigmodontinae*). Sci. Rep. 12(1): 8690. 10.1038/s41598-022-12706-3
Palma R.E., Cancino R.A., Rodríguez-Serrano E., 2010a. Molecular systematics of *Abrothrix longipilis* (*Rodentia: Cricetidae: Sigmodontinae*) in Chile. J. Mammal. 91: 1102–1111.
Palma R.E., Rivera-Milla E., Salazar-Bravo J., Torres-Pérez F., Pardiñas U.F.J., Marquet P.A., Spotorno A.E., Meynard A.P., Yates T. 2005. Phylogeography of *Oligoryzomys longicaudatus* (*Rodentia: Sigmodontinae*) in temperate South America. J. Mammal. 86(1): 191–200.
Palma R.E., Rodríguez-Serrano E., Rivera-Milla E., Hernandez C.E., Salazar-Bravo J., Carma M.I., Belmar-Lucero S., Gutierrez-Tapia P., Zeballos H., Yates T.L., 2010b. Phylogenetic relationships of the pygmy rice rats of the genus *Oligoryzomys* Bangs, 1900 (*Rodentia, Sigmodontinae*). Zool. J. Linnean Soc. 160: 551–566.
Patton J.L., 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. Proc. Biol. Soc. Washington 108 (2): 319–337.
Patton J.L., M.N.F. da Silva, 1998. Molecular phylogeography and the evolution and conservation of Amazonian mammals. Mol. Ecol. 7(4): 475-86.
Patton J.L., da Silva M.N.F., Malcolm J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bull. Am. Mus. Nat. Hist. 244: 1–306.
Percequillo A.R., Weksler M., Costa L.P., 2011. A new genus and species of rodent from the Brazilian Atlantic Forest (Rodentia: Cricetidae: Sigmodontinae: Oryzomyini), with comments on oryzomyine biogeography. Zool. J. Linnean Soc. 161 (2): 357–390.
Pereira L.G., Geise L., 2007. Karyotype composition of some rodents and marsupials from Chapada Diamantina (Bahia, Brazil). Braz. J. Biol. 67(3): 509–518.
Powers A.M., Mercer D.R., Watts D.M., Guzman H., Fulhorst C.F., Popov V.L., Tesh R.B., 1999. Isolation and genetic characterization of hantavirus (Bunyaviridae: Hantavirus) from a rodent, *Oligoryzomys microtis* (*Muridae*), collected in northeastern Peru. Am. J. Trop. Med. Hyg. 61: 92–98.
Quiroga-Carmona M., Abud C., Lessa E.P., D'Elía G., 2022. The mitochondrial Genetic diversity of the Olive Field Mouse *Abrothrix olivacea* (*Cricetidae; Abrotrichini*) is latitudinally structured across its geographic distribution. J. Mammal. Evol. 29(2): 413–430. 10.1007/s10914-021-09582-5
Rambaut A., Drummond A., 2007. Tracer v1.4. 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). J. Zool. 181: 227–241.
Ribas C., Aleixo A., Nogueira A., Miyaki C., Cracraft J., 2011. A paleobiogeographic model for biotic diversification within Amazonia over the past three million years. Proceedings of the Royal Society B 279(1729):681–689. 10.1098/rspb.2011.1120
Rice W., 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.
Richter M.H., Hanson J.D., Cajimat M.N., Milazzo M.L., Fulhorst C.F., 2010. Geographical range of Rio Mamore virus (family Bunyaviridae, genus *Hantavirus*) in association with the small-eared pygmy rice rat (*Oligoryzomys microtis*). Vector Borne Zoonotic Dis. 10: 613–620.
Ridgway, R., 1912. Color standards and color nomenclature. The author, Washington.
Ripley B., Venables B., Bates D.M., Hornik K., Gebhardt A., Firth D., Ripley M.B. 2013. Package 'mass.' Cran r 538: 113–120.
Rivera P.C., González-Ittig R.E., Fraire H.J.R., Levis S. Gardenal C.N., 2007. Molecular identification and phylogenetic relationships among the species of the genus *Oligoryzomys* (*Rodentia, Cricetidae*) present in Argentina, putative reservoirs of hantaviruses. Zool. Scripta. 36(3): 231–239. 10.1111/j.1463-6409.2007.00273.x
Rivera P.C., González-Ittig R.E., Robainas Barcia A., Trimarchi L.I., Levis S., Calderón G.E., Gardenal C.N., 2018. Molecular phylogenetics and environmental niche modeling reveal a cryptic species in the *Oligoryzomys flavescens* complex (*Rodentia, Cricetidae*). J. Mammal. 99(2): 363–376. 10.1093/jmammal/gyx186
RStudio: integrated development environment for R. Boston, MA: RStudio, PBC

Rocha R.G., Ferreira E., Costa B., Martins I., Leite Y.L., Costa L.P., Fonseca C., 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., Oliver J.L., Marín A., Medina J.R., 1990. The general stochastic model of nucleotide substitution. J. Theoret. Biol. 142: 485–501.

Rogers D.S., Arenas E.A., González-Cózatl F.X., Hardy D.K., Hanson J.D., Lewis-Rogers N., 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 (Eds.) 60 años de la Colección Nacional de Mamíferos del Instituto de Biología, UNAM. Aportaciones al Conocimiento y Conservación de los Mamíferos Mexicanos. Universidad Autonoma de México, D.F., México. 209–222.

Ronquist F., Huelsenbeck J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Rosa E.S.T., Mills J.N., Padula P.J., Elkhoury M.R., Ksiazek T.G., Mendes W.S., Santos E.D., Araujo G.C., Martinez V.P., Rosa J.F., Edelstein A., Vasconcelos P.F.C., 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 Zoonotic Dis. 5: 11–19.

Rosa E.S.T., de Lemos E.R.S., Medeiros D.B.A., Simith D.B., Pereira A.S., Elkhoury M.R., Mendes W.S., Vidigal J.R., Oliveira R.C., D'Andrea P.S., Bonvicino C.R., Cruz A.C., Nunes M.R., Vasconcelos P.F.C., 2010. Hantaviruses and hantavirus pulmonary syndrome, Maranhão, Brazil. Emerging Infect. Dis. 16: 1952–1955.

Rosa E.S.T., Medeiros D., Nunes M.R., Simith D.B., Pereira A.S., Elkhoury M.R., Nunes M.R., Marques A., Via A., D'Andrea P.S., Bonvicino C.R., de Lemos E.R.S., Vasconcelos P.F.C., 2011. Pygmy rice rat as potential host of Castelo dos Sonhos Hantavirus. Emerging Infect. Dis. 17(8): 1527–1530.

Sambrook J., Russell D.W., 2001. Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Santorelli S., Magnusson W.E., Deus C.P., 2018. Most species are not limited by an Amazonian river postulated to be a border between endemism areas. Sci. Rep. 8: 2294.10.1038/s41598-018-20596-7

Sbalqueiro I.J., Mattevi M.S., de Oliveira L.F.B., Solano M.J.V., 1991. B chromosome system in populations of *Oryzomys flavescens* (*Rodentia, Cricetidae*) from southern Brazil. Acta Theriol. 36: 193–199.

Sikes, R.S. and the Animal Care and Use Committee of the American Society of Mammalogists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education: J. Mammal. 97(3): 663–688. 10.1093/jmammal/gyw078

Smith M.F., Patton J.L., 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biol. J. Linnean Soc. 50: 149–177.

Sokal R.R., Rohlf F.J., 1994. Biometry: The principles and practice of statistics in biological research. W. H. Freeman, New York, NY.

Strauss, R.E., 2010. Discriminant groups of organisms. In: Elewa A.M.T. (Ed.) Morphometrics for Nonmorphometricians (Lecture Notes in Earth Sciences vol. 124). Springer-Verlag, Berlin. 73–91.

Suzuki A., Bisordi I., Levis I., Garcia J., Pereira P.E., Souza R.P., Sugahara T.K., Pini N., Enria D., Souza L.T., 2004. Identifying Rodent Hantavirus Reservoirs, Brazil. Emerging Infect. Dis. 10: 2127–2134.

Swofford D.L., 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), v. 4.0. Sinauer Associates, Sunderland, Ma.

Teta P., Jayat J.P., Ortiz P.E., D'Elía G., 2013. The taxonomic status of *Oligoryzomys brendae* Massoia, 1998 (Rodentia, Cricetidae), with comments on the availability of this name. Zootaxa, 3641(4): 433–447.

Vidal-Rioja L., Fronza T.G. de, Wainberg R., Brum-Zorilla N., Wallace F., Zambelli A., 1988. C-banding pattern and satellite DNA localization on the chromosomes of *Oryzomys flavescens* (*Rodentia, Cricetidae*). Caryologia 41: 323–328. 10.1080/00087114.1988.10797872

Villalobos-Dominguez, C., Villalobos, J., 1947. Atlas de los Colores. (Colour Atlas). With 7,279 illustrations on 38 colour plates. El Ateneo, Buenos Aires.

Voss, R.S., 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bull. Am. Mus. Nat. Hist. 188: 260–493.

Voss R.S., Lunde D.P., Simmons, N.B., 2001. The mammals of Paracou, French Guiana: A neotropical lowland rainforest fauna. Part 2. Nonvolant species. Bull. Am. Mus. Nat. Hist. 263: 1–236.

Wallace A.R., 1853. On the monkeys of the Amazon. Ann. Mag. Nat. Hist. 14(3): 451 –454. 10.1080/037454809494374

Weksler M., 2006. Phylogenetic relationships of oryzomine rodents (Muroidea, Sigmodontinae): separate and combined analyses of morphological and molecular data. Bull. Am. Mus. Nat. Hist. 296: 1–149.

Weksler M., Bonvicino C.R., 2005. Taxonomy of pigmy rice rats genus *Oligoryzomys* Bangs, 1900 (*Rodentia, Sigmodontinae*) of the Brazilian Cerrado, with the description of two new species. Arquivos Mus. Nac. 63: 113–130.

Weksler M., Bonvicino C.R., 2015. Genus *Oligoryzomys* Bangs. In Patton J.L., Pardiñas U.F.J., D'Elía G. (Eds.) Mammals of South America. Volume 2 Rodents. University of Chicago Press, Chicago, Il. 417– 437.

Weksler M., de Lemos E.M.S., D'Andrea P.S., Bonvicino, C.R. 2017. The Taxonomic status of *Oligoryzomys mattogrossae* (Allen 1916) (Rodentia: Cricetidae: Sigmodontinae), reservoir of Anajatuba Hantavirus. Amer. Mus. Novitates 3880(3880): 1–32. 10.1206/3880.1

Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. J. Mol. Evol. 39: 306–314.

Associate Editor: Gaubert

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Appendix 1 Supplemental Material S1.
Appendix 2 Supplemental Material S2.
Appendix 3 Supplemental Material S3.
Appendix 4 Supplemental Material S4.