UNIVERSIDADE FEDERAL DE MATO GROSSO
INSTITUTO DE BIOCIÊNCIAS
CURSO DE DOUTORADO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

RELAÇÕES FILOGENÉTICAS EM *Oecomys* THOMAS, 1906, COM ÊNFASE EM SISTEMÁTICA E DIVERSIFICAÇÃO DO COMPLEXO *Oecomys catherinae* THOMAS, 1909 (RODENTIA, SIGMODONTINAE)

JULIANE SALDANHA DA SILVA

CUIABÁ - MT
2020

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Relações filogenéticas em *Oecomys* Thomas, 1906, com ênfase em sistemática e diversificação do complexo *Oecomys catherinae* Thomas, 1909 (Rodentia, Sigmodontinae)

JULIANE SALDANHA DA SILVA

Tese apresentada ao Curso de Pós-Graduação, do Instituto de Biociências, para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

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RESUMO

Roedores do gênero *Oecomys* Thomas, 1906, possuem ampla distribuição em biomas brasileiros, com a maior diversidade relatada para a região Amazônica. Entretanto, a identificação da diversidade e os limites de espécies no gênero ainda são confusos. Atualmente, são reconhecidas 18 espécies, cujas relações interespecíficas ainda não são amplamente conhecidas. A grande diversidade de *Oecomys* é relatada em estudos sobre a existência de complexos de espécies, com linhagens que podem representar novas espécies. Com isso, o objetivo deste estudo é avaliar e descrever a diversidade taxonômica e as relações filogenéticas de espécies de *Oecomys*, com ênfase no mais diverso complexo de espécies – *Oecomys catherinae* – com ampla distribuição em três biomas brasileiros. Para isso, inicialmente realizamos análises filogenéticas com base em marcador molecular mitocondrial e nuclear para elucidar a diversidade e as relações entre as espécies do gênero da bacia do Tapajós e o papel dos rios na distribuição das espécies. Posteriormente, para o complexo *O. catherinae* apresentamos análises moleculares de delimitação de espécies, assim como análises morfológicas e morfométricas. Além disso, apresentamos uma abordagem genômica sobre as relações filogenéticas e diversificação das linhagens que compõem o complexo com base representação genômica de ddRADseq. Nossas hipóteses filogenéticas sobre o gênero *Oecomys* revelam grande diversidade de espécies para a região da bacia do Tapajós, com a distribuição de algumas espécies moldada pelo rio Tapajós. Além disso, nossos dados indicam que o rio Teles Pires não atua como barreira para o fluxo gênico. As análises de delimitação de espécies, morfologia e morfometria indicam a existência de uma nova espécie do complexo *O. catherinae* para esta região, descrita neste estudo. Além disso, com a abordagem genômica, apontamos as divergências e diversidade entre as demais linhagens do complexo de espécies *O. catherinae*, com indícios da existência de duas espécies distintas e a comprovação de linhagens crípticas com ocorrência na Mata Atlântica e Cerrado. As diversificações entre linhagens do complexo foram estimadas para o Pleistoceno, em grande parte moldada pelos refúgios e glaciações deste período.

Palavras-chave: Fluxo gênico, diversidade críptica, Taxonomia, ddRADseq.

ABSTRACT

The arboreal rat *Oecomys* Thomas, 1906 are widely distributed in Brazilian biomes, with the greatest diversity reported for the Amazonia region. Currently, 18 species are recognized. However, the real diversity and species boundaries in the genus remains uncertain., and the interspecific relationships still poorly known. The great diversity of *Oecomys* is reported in studies about species complex, with lineages that may represent new species. The aim of this study is to evaluate the taxonomic diversity and phylogenetic relationships of *Oecomys* species, with emphasis on the most diverse species complex – *Oecomys catherinae* – which is widely distributed in Brazilian biomes. We performed phylogenetic analyses based on mitochondrial and nuclear marker to elucidate the diversity and relationships between *Oecomys* species of Tapajós basin and the role of Amazonian rivers in the species distribution. For the *O. catherinae* complex, we performed molecular analyses of species delimitation, and morphological and morphometric analyses. In addition, we used a genomic representation of ddRADseq to evaluate the phylogenetic relationships and diversification of the lineages of the complex. Our phylogenetic hypotheses for *Oecomys* genus reveal great species diversity for the Tapajós basin, with the distribution of some species shaped by the Tapajós river, but the Teles Pires river does not act as a barrier to gene flow for other species. The species delimitation, morphology and morphometric analyses indicate the existence of a new species of the *O. catherinae* complex for this region, described in this study. The genomic approach reveals the divergences and diversity between the other lineages of the *O. catherinae* complex, with evidence of two distinct species in Amazonia, and cryptic species occurring in the Atlantic Forest and Cerrado biomes. The diversifications between lineages of the complex were estimated for the Pleistocene, largely shaped by the refuges and glaciations of this period.

Keywords: Gene flow, Cryptic diversity, Taxonomy, ddRADseq.

1. INTRODUÇÃO GERAL

A subfamília Sigmodontinae é a representante da maior diversidade de roedores cricetídeos, dividida em sete tribos. Entre elas está a tribo Oryzomyini, na qual a maioria das espécies possui hábito terrícola, porém algumas são arborícolas, como as do gênero *Oecomys* Thomas, 1906 (Oliveira & Bonvicino 2011; Hershkovitz 1960). Representantes deste gênero possuem comprimento da cabeça e corpo entre 71 e 176 mm, comprimento da cauda entre 80 e 192 mm, pelagem macia variando de castanha-escura a castanha-avermelhada no dorso, e ventre esbranquiçado/amarelado com ou sem pelos de base cinza; possuem vibrissas longas, patas traseiras curtas e largas com dedos relativamente longos, cauda moderadamente mais longa que a cabeça e corpo, com a porção terminal pilosa em algumas espécies, e quatro pares de mamas: peitoral, pós-axial, abdominal e inguinal. (Carleton & Musser 2015; Oliveira & Bonvicino 2011; Bonvicino et al. 2008).

Na taxonomia, os nomes mais antigos ligados ao gênero *Oecomys* são *Hesperomys concolor* Wagner, 1845 e *Hesperomys bicolor* Tomes, 1860. Estas espécies foram listadas por Trouessart (1898) como membro do gênero *Rhipidomys*. No entanto, em 1906, Thomas determinou os caracteres para a definição do gênero *Rhipidomys* e alocou as espécies arborícolas com palato longo em *Oecomys* como um subgênero de *Oryzomys*, designando como espécie tipo *Rhipidomys benevolens* (= *Hesperomys bicolor*) (Musser & Carleton 2005; Hershkovitz 1960; Tate 1932). Em seguida, Thomas (1909) percebeu que, diferentemente de *Oryzomys*, o gênero *Oecomys* possui placa externa da raiz anterior do zigomático mal projetada anteriormente, e elevou *Oecomys* à categoria de gênero.

Ellerman (1941) discordou do arranjo de Thomas (1909) afirmando que este não poderia ser considerado mais do que um subgênero, pois a única característica do grupo era a cauda ligeiramente provida de tufo (Hershkovitz 1960). Com a revisão de Hershkovitz (1960), *Oecomys* foi consolidado como um subgênero de *Oryzomys* incluindo as vinte e cinco espécies associadas ao gênero em apenas duas espécies politípicas, sendo *O. bicolor* considerada a espécie "com porte menor", com quatro subespécies, e *O. concolor* a espécie "com porte maior", com cinco subespécies.

Somente com a revisão publicada por Musser & Carleton (1993) o status genérico de *Oecomys* foi reconhecido e posteriormente corroborado por análises moleculares, sendo a primeira destas realizadas por Patton & Da Silva (1995). Estes autores avaliaram as relações filogenéticas dentro da tribo Oryzomyini, incluindo o gênero *Oecomys*, apontando que este constitui um grupo monofilético, tal como outros autores posteriormente.

Embora o monofiletismo do gênero esteja comprovado, as informações sobre as relações filogenéticas entre as espécies de *Oecomys* e a distribuição geográfica das mesmas são pouco conhecidas (Rocha et al. 2011; Musser & Carleton, 2005; Patton et al. 2000). Mesmo nos estudos com uma filogenia mais completa para o gênero, existem evidências de complexos de espécies dentro de *Oecomys* (Suárez-Villota et al. 2018; Rocha et al. 2018; Malcher et al. 2017; Rosa et al. 2012).

Atualmente, o gênero possui 18 espécies válidas, das quais uma recentemente descrita e outra revalidada (Rocha et al. 2018; Pardiñas et al. 2016; Carleton & Musser 2015). A distribuição do gênero geralmente é associada à floresta tropical de baixa altitude, e a maior diversidade de espécies está concentrada na Bacia Amazônica (Carleton & Musser 2015; Oliveira & Bonvicino 2011; Bonvicino et al. 2008). Em um dos recentes estudos sobre a sistemática de *Oecomys*, Suárez-Villota et al. (2018) reúnem representantes de 14 espécies de localidades da Amazônia, Cerrado, Pantanal e Mata Atlântica. Os autores confirmam sete espécies válidas, sendo elas *O. auyantepui*, *O. concolor*, *O. rex*, *O. rutilus*, *O. superans O. sydandersoni e O. trinitatis*; três não descritas (*Oecomys* sp.1– 3); e cinco complexos de espécies, com linhagens que podem corresponder a 15 espécies: duas do grupo *O. bicolor / O. cleberi*, duas de *O. franciscorum / O. mamorae*, três de *O. paricola*, três de *O. roberti* e cinco em *O. catherinae*.

Entre os complexos de espécies mencionados, *O. catherinae* é o mais diverso em número de linhagens que podem representar novas espécies. As linhagens deste complexo apresentam ampla distribuição que inclui os biomas florestais Mata Atlântica e Amazônia, além de florestas de galeria no bioma Cerrado. Descrita por Thomas (1909) para Joinville, estado de Santa Catarina, *O. catherinae* teve sua distribuição ampliada para regiões amazônicas e florestas de galeria do Cerrado no Brasil Central (Saldanha et al. 2019; Asfora et al. 2011). No entanto, Malcher et al. (2017) levantaram a possibilidade de *O. catherinae* se tratar de um complexo de espécies, dada a existência de variações cromossômicas significativas entre as populações da Amazônia e da Mata Atlântica. Estas variações indicam a ausência de fluxo gênico entre as referidas populações, porém a divergência genética de Citocromo b entre elas é de 1,7%, valor considerado baixo quando comparado às divergências entre as demais espécies do gênero.

Comparações morfológicas e moleculares dos trabalhos de Suárez-Villota et al. (2018) são exemplos de como a diversidade específica deste gênero foi subestimada em estudos anteriores. Estes são indicativos da necessidade de estudos mais amplos no gênero *Oecomys*. Além de indicarem maior diversidade dentro do gênero, outros trabalhos que

envolvem análises moleculares e cariotípicas ainda refletem na distribuição geográfica mais ampla de algumas espécies (Malcher et al. 2017; Rosa et al. 2012; Rocha et al. 2011; Asfora et al. 2011).

Com isso, este estudo visa ampliar o conhecimento sobre a diversidade de *Oecomys*, com ênfase no complexo *O. catherinae*. No capítulo 1 são apresentas as relações filogenéticas entre as espécies e a diversidade deste gênero na região da bacia do Tapajós, assim como o papel de rios como barreira para o fluxo gênico nesta região. No capítulo 2 é apresentada uma análise integrativa de dados moleculares e morfológicos com a descrição de uma das linhagens do complexo *Oecomys catherinae* como uma nova espécie. Já no capítulo 3 são investigadas as relações filogenéticas e diversificação das linhagens do complexo *Oecomys catherinae*, com uma abordagem genômica.

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CAPÍTULO I

Genetic diversity of *Oecomys* (Rodentia, Sigmodontinae) from the Tapajós River basin and the role of rivers as barriers for the genus in the region

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Genetic diversity of *Oecomys* (Rodentia, Sigmodontinae) from the Tapajós River basin and the role of rivers as barriers for the genus in the region

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Abstract

The genus *Oecomys* is one of the most speciose within the subfamily Sigmodontinae, with most species found in the Amazon region. Recent studies have shown that the diversity, recognition of specific boundaries and geographical distribution is still imprecise for the genus. Herein, we investigate the genetic diversity of *Oecomys* in the Tapajós River basin and determine whether its rivers (Tapajós, Teles Pires, and Juruena) act as barriers for some species or populations in this genus based on phylogenetic analyzes with the mitochondrial marker cytochrome b (cytb) and the nuclear marker intron 7 β-fibrinogen, and on populational analysis with cytb. The phylogenetic relationships showed the presence of seven species in the region, namely *O*. *bicolor*, *Oecomys* aff. *catherinae*, *O*. *catherinae*, *O*. *cleberi*, *O*. *paricola*, *O*. *roberti*, and *O*. *tapajinus*. The geographic distributions of *O*. *bicolor* and *O*. *cleberi* seem to be shaped by the Tapajós and Teles Pires Rivers, with the former species occurring on the right bank and the latter species on the left bank of both rivers. Moreover, *O*. *cleberi* was the only *Oecomys* species to be recorded on the left bank of the Tapajós River. Our results also indicate that gene flow occurs between *O*. *cleberi* populations from the west Juruena and Tapajós Rivers and is absent between opposite banks of the Juruena River. The isolation by distance was discarded for this species. No evidence of gene flow was found for *O*. *bicolor* populations, and the isolation by distance was positive for this species. The spatial distribution of specimens and haplotypes of *O*. *paricola* indicates that the Teles Pires River does not act as a barrier for this species. Finally, Fs test significant results for

O. *cleberi* and *O*. *paricola* showed that species population expansion cannot be discarded for these species.

Key-words: Phylogeny, Geographic distribution, Gene flow, Teles Pires River, Juruena River.

Introduction

Knowledge about species richness of genus *Oecomys*, has increased considerably in recent years through the use of chromosomal and molecular analyses, revealing new species and greater geographic distribution for the genus (Asfora et al., 2011; Malcher et al., 2017; Rocha et al., 2011, 2018; Rosa et al., 2012; Suárez-Villota et al., 2018). Currently, the genus comprises eighteen species, one of which was recently described and another recently revalidated (Pardiñas et al., 2017; Rocha et al., 2018).

Richness estimates of *Oecomys* in any region are still unreliable due to the difficulty in defining the morphological limits and geographical distribution of the species. The majority of *Oecomys* species occur in the Amazon basin (Bonvicino et al., 2008; Carleton and Musser, 2015; Oliveira and Bonvicino, 2011; Paglia et al., 2012), which is considered one of the most biodiverse regions on the planet. Among the various hypotheses that try to explain the origin of the high mammal diversity in the Amazonia, the presence of rivers as barriers (Wallace, 1852) is one of the most studied (Antonelli et al., 2010). According to Patton et al. (2000), Wallace´s hypothesis was based on distribution patterns, but also implies that rivers from the Amazonia not only separate distinct faunas but may strongly reduce gene flow between populations of opposite banks, and thus have promoted speciation.

Evidences that river dynamics contribute to the Amazonian diversification have been pointed out by Ribas et al. (2012), who linked the development of rivers to the isolation and delimitation of endemic areas for birds of the genera *Psophia*. Conversely, Oliveira et al. (2017) claimed that Amazonian rivers do not demarcate areas of endemism, but act as dispersal barriers for some species, resulting in areas with different species compositions.

The Tapajós River has been recognized as a biogeographical barrier that separates two Amazonian centers of endemism (Silva et al., 2005). The Tapajós River basin covers about 492,200 km^2 in the south-central part of the Amazon and

includes the Teles Pires and Juruena Rivers as tributaries (PERH-MDA, 2011). According to and Carleton and Musser (2015) and Pardiñas et al. (2017), four species of *Oecomys* are expected to occur in the Tapajós River basin, namely *O*. *bicolor*, *O*. *paricola*, *O*. *roberti*, and *O*. *trinitatis*. More recently, Suárez-Villota et al. (2018) pointed out the occurrence of seven evolutionary lineages for the region, probably representing different species associated to the complexes *O*. *bicolor*/*O*. *cleberi*, *O*. *catherinae*, *O*. *paricola*, and *O*. *roberti*. Finally, the recently revalidated species *O*. *tapajinus* was recognized for the region by Rocha et al. (2018).

These recent findings confirm the difficulty in determining species limits and geographical distributions of *Oecomys* species in the Tapajós River basin. A great sample of *Oecomys* sequences obtained by us provided the chance to investigate the genetic diversity of this genus in the region and evaluate if the Tapajós River and two major tributaries – the Teles Pires and the Juruena Rivers – act as barriers for some species or populations of *Oecomys*, based on phylogenetic and population analyses using the mitochondrial marker cytochrome b and the nuclear marker intron 7 β-fibrinogen.

Materials and Methods

Sampling

In this study, sequences were generated from 101 specimens of *Oecomys* from 21 localities on the banks of the Tapajós, Juruena, and Teles Pires Rivers (Fig. 1), as well as two *Oecomys rex* specimens and one *Euryoryzomys macconnelli* specimen from the State of Pará (Supplementary Material, Table 1). The muscle tissue aliquots were extracted from samples preserved in 100% alcohol and stored at -20º C in the Zoological Collection at the Universidade Federal de Mato Grosso (UFMT), Universidade Federal do Pará (UFPA), and Universidade do Estado de Mato Grosso (Unemat). The sampling of the genus was complemented with sequences of 67 *Oecomys* specimens from the GenBank, 21 of which come from five localities in the Tapajós River basin (Fig. 1 and Supplementary Material, Table1).

DNA extraction, amplification and sequencing

The total DNA was obtained using the saline extraction protocol with modifications by Aljanabi and Martinez (1997) and was visualized in 1% agarose gel stained with red gel to verify its integrity. For molecular analyses, we used the

mitochondrial cytochrome gene b (cytb) and the nuclear marker intron 7 β-fibrinogen (i7-fgb).

The cytb mitochondrial gene was amplified using the Polymerization Chain Reaction (PCR) technique, using the MVZ05 (CGAAGCTTGATATGAAAAACCATCGTTG) and MVZ16 (AAATAGGAARTATCAYTCTGGTTTRAT) initiators (Smith and Patton, 1993). The PCRs were carried out with a final volume of 13.5 µl, containing 1.5 µl de dNTP (1.25 mM), 1.25 µl 10x buffer, 1 µl of the initiator MVZ05 (2 mM), 1µl of the initiator MVZ16 (2 mM), 0.4 to 0.65 µl de $MgCl_2$ (50 mM), 0.2 µl of Taq DNA Polimerase (Ludwig, 5U/µl), 1 µl of DNA, and autoclaved Milli-Q filtered H_2O until the final volume. The reactions were processed in a thermocycler (Applied Biosystems, Veriti), with initial denaturation at 94°C for 5 minutes, followed by 30 cycles of denaturation at 94°C for 30 seconds, annealing at 45°C to 52°C for 45 seconds, extension at 72°C for 45 seconds, and final extension at 72°C for 5 minutes.

The nuclear marker i7-fgb was amplified with the initiators βI7-mammL (ACCCCAGTAGTATCTGCCGTTTGGATT) and βfib-mammU (CACAACGGCATGTTCTTCAGCAC) (Matocq et al., 2007). The PCR's were carried out with a final volume of 35 µl, containing 4 µl of dNTP (1.25 mM), 3.5 µl 10x buffer, 2 µl of the initiator βI7-mammL (2 mM), 2 µl of the initiator βfib-mammU (2 mM), 2 µl of $MgCl_2$ (50 mM), 0.3 µl of Taq DNA Polimerase (Ludwig, 5 U/µl), 1µl of DNA, and autoclaved Milli-Q filtered H_2O until the final volume. The reactions were processed in a thermocycler (Applied Biosystems, Veriti), with initial denaturation at 93°C for 5 minutes, followed by 35 cycles of denaturation at 93°C for 1 minute, annealing 55°C for 1 minute, extension at 72°C for 2 minutes and 45 seconds, and final extension at 72°C for 2 minutes.

PCR products were purified using the enzyme method with EXO-SAP (Affymetrix). The two tapes (forward and reverse) were sequenced for the two genes, cytb and i7-fgb, with the same initiators used in the PCR and BigDye ® Terminator v 3.1 Cycle Sequencing kit, following the manufactures' protocol for the Sequencer ABI 3500 (Applied Biosystems ®).

The sequences obtained were displayed and aligned to assemble the consensus sequence in the Geneious ® program. Subsequently, the sequences were edited and aligned by the ClustalW tool in the BioEdit 7.0.5.2 program (Hall,

1999). These sequences were also subjected to a saturation test implemented in the DAMBE5 program (Xia, 2013).

Phylogenetic analysis and diversity

In order to assess the relationships of *Oecomys* specimens from the Tapajós River basin with other congeners, phylogenetic analyses were carried out using partial sequences of the cytb gene (801 base pairs) from 170 individuals (Supplementary Material, Table 1), including representatives of all currently recognized species, except for *O*. *flavicans*, *O*. *phaeotis*, and *O*. *speciosus*, which had no available sequences. *Euryoryzomys macconnelli* (this study), *Handleyomy intectus*, "*Handleyomys" melanotis* (species provisionally allocated under *Handleyomys*; see Pardiñas et al., 2017), and *Oligoryzomys utiaritensis* (GenBank sequences) were employed as external group. Phylogenetic analyses were also performed using the concatenated sequences of cytb and i7-fgb (736 base pairs) from 77 specimens of *Oecomys* and sequences of *Handleyomys melanotis* and *Oligoryzomys utiaritensis* as external group (Supplementary Material, Table 1). Lineage names were defined according to Suaréz-Villota et al. (2018) and Rocha et al. (2018).

The evolutionary models that best represented the data matrix were generated in the JModeltest program (Posada, 2008). The model that best represented the cytb data matrix was the GTR+I+G. The matrix of concatenated data was best represented by the GTR+I+G model for the partition of cytb and TIM2+I+G for the partition of the i7-fgb marker. The data matrix for analysis based on the cytb and the i7-fgb presented 311 and 93 nucleotide substitutions, respectively. The data did not show saturation (cytb: transition R^2= 0.9629 transversion R^2= 0.9348; i7-fgb: transition R^2= 0.9387 transversion R^2= 0.8956).

The Bayesian Inference (BI) analyses were carried out in the MrBayes 3.1.2 program (Ronquist and Huelsenbeck, 2003), with four chains, 20 million generations, a sampling tree every 100 generations and 25% burn-in. Maximum Likelihood (MV) analyses were carried out in the Garli 2.0 program (Zwickl, 2006), with bootstrap support of 1000 replicas. The trees obtained in the Garli program were summarized by majority consensus in the SumTrees program. The trees obtained from MV and BI were viewed and edited in the program Figtree version 1.4.3 (Rambaut, 2016). The

genetic distances between and within the clades were calculated in the MEGA7 (Kumar et al., 2016) using the Kimura 2 parameters (K2p) method.

Populational analyses and structure

Population analyses were carried out using *O*. *bicolor* and *O*. *cleberi* samples together to investigate genetic variability and geographical structuring in the *O*. *bicolor*/*O*. *cleberi* species complex. Population analyses were also carried out with the samples of *O*. *paricola*, whose species served as a model to investigate if the rivers acted as barriers to gene flow, given its geographical distribution in the Tapajós River basin region. For these analyses, the number of haplotypes (H) was generated in the DnaSP V6 program (Rozas et al., 2017) and the relationships between haplotypes were evaluated through the networks with cytb data by the Median-Joining method (Bandelt et al., 1999) in the PopArt program (http://popart.otago.ac.nz). The differentiation of populations into hierarchical levels was calculated by the Molecular Variance Analysis (AMOVA) (Excoffier et al., 1992) and, for the *O*. *bicolor*/*O*. *cleberi* species complex, these levels were considered two distinct groups. The population structure was verified based on the genetic differences between populations by comparing the F_{ST} (Weir and Cockerham, 1984). Both analyses were calculated in the Arlequin 3.5 program (Excoffier and Lischer, 2010). To test the isolation by distance, the Mantel test was carried out in the Alleles in Space program (Miller, 2005).

The mismatch distribution analysis in the DnaSP v6 program was used to test population expansion (Rozas et al., 2017), which compared the observed and expected distribution in an expansion model. In this model, the statistical test for deviations was the raggedness index (Harpending, 1994), in which an expanding population generates distributions of regular and unimodal mismatch. For demographic pattern description, we verified haplotype (h) and nucleotide (π) diversity values. The deviations of neutrality were verified by D (Tajima, 1989) and Fs (Fu, 1997) tests, which were carried out in the Arlequin 3.5 program (Excoffier and Lischer, 2010).

Results

Diversity of Oecomys in the Tapajós River basin

From the 101 samples analyzed in the present study, it was verified that there are either six or seven species with occurrence for the Tapajós River basin (Figs. 2 and 3). BI analysis with cytb recognized six highly supported lineages, namely *O*. *bicolor*/*O*. *cleberi*, *Oecomys* aff. *catherinae*, *O*. *catherinae*, *O*. *paricola*, *O*. *roberti*, and *O*. *tapajinus* (Fig. 2) with genetic mean distances of 5.64% to 10.54% (Supplementary Material, Table 2). BI analysis with concatenated data recognized seven highly supported lineages, with *O*. *bicolor* and *O*. *cleberi* recovered as distinct lineages (Fig. 3). Genetic mean distances varied from 4.84% to 11.68% among the lineages recovered in the concatenated data analysis (Supplementary Material, Table 3).

Specimens of *O*. *cleberi*, *O*. *roberti* and *O*. *tapajinus* from the Tapajós River basin were not recovered as monophyletic groups (Fig. 2). In the BI analysis with cytb, *O*. *cleberi* specimens from Aripuanã and Cotriguaçu (localities 23 and 24, respectively; Figs. 1 and 2) grouped in a clade with individuals from south-central Brazil (States of Goiás and São Paulo, and the Federal District). In addition, *O*. *cleberi* specimens from the east bank of the Tapajós and Juruena Rivers (localities 1, 2, 3, 4, 24; Figs. 1 and 2) nested in a separate clade from the rest of the species. Similarly, specimens of *O*. *roberti* from the Tapajós River basin (except for one individual from locality 15) grouped with a sample from the Pantanal (HM594597). Finally, the *O*. *tapajinus* clade included samples from the Tapajós River basin and the Araguaia–Tocantins Rivers basin.

We recorded *O*. *bicolor*, *O*. *paricola* and *O*. *tapajinus* in sympatry on the east bank of the Tapajós River, whereas only *O*. *cleberi* specimens were recorded on the west bank. In the middle east Teles Pires River, we recorded *O*. *bicolor*, *O*. *paricola* and *O*. *roberti*. In the low east Teles Pires River we recorded *Oecomys* aff. *catherinae*, *O*. *paricola* and *O*. *roberti*. In the Teles Pires–Juruena interfluve, we recorded *Oecomys* aff. *catherinae*, *O*. *cleberi*, *O*. *paricola* and *O*. *roberti*. Finally, on the west bank of the Juruena River we recored *Oecomys* aff. *catherinae*, *O*. *catherinae* and *O*. *cleberi* (Fig. 1; Supplementary Material, Table 1).

Population structure of O. bicolor, O. cleberi and O. paricola from the Tapajós River basin

The AMOVA of the *O*. *bicolor*/*O*. *cleberi* complex indicated greater variation between these groups (56.26%), followed by the variation between populations within groups (26.73%) and the variation within the populations (17.01%; Table 1), supporting the differentiation between these two species that appeared separated by 25 mutational steps in the haplotypes network.

The species *O*. *cleberi* presented two haplogroups in the Teles Pires–Juruena interfluve (haplogroups B and D, Fig. 4), separated by 19 mutational steps. Individuals from the west bank of the Juruena River were separated into two haplogroups (A and C, Fig. 4), with one individual from this region grouped with the west bank of the Tapajós River (haplogroups C, Fig. 4), indicating the presence of gene flow between populations on the west bank of the Juruena and Tapajós Rivers. Despite the haplogroups B and D occur in the same region, the former is closer to the haplogroups A and C, from which it differs by 11 and seven mutational steps respectively, evidencing the absence of geographic structure in the species. We found no evidence of haplotype sharing across the Juruena River opposite banks.

Although one haplotype from the west bank of the Juruena River nests with haplotypes of the west bank of the Tapajós River forming the haplogroup C, the greatest genetic differentiation (Fst value of 0.62; Supplementary Material, Table 4) was found between the populations on the west bank of the Tapajós and Juruena Rivers. The Mantel test was not significant (r= 0.124 p= 0.09), indicating the absence of isolation by distance in populations of the species.

The species *O*. *bicolor* was represented by two haplogroups separeted by nine mutational steps (haplogroups E and F, Fig. 4), which presented Fst equal to 0.84 (Supplementary Material, Table 4). The Mantel test showed high correlation between genetic and geographical distance in populations of the species (r= 0.585 p= 0.0009).

The haplotypes network of *O*. *paricola* did not reveal geographic structure (Fig. 5), with haplotypes shared between individuals from opposite banks of the Teles Pires River. According to the AMOVA, high genetic variation (62.65%) occurs within the populations (Table 1), with the highest Fst (0.65) recovered between the populations from the middle and low Teles Pires River, and the lowest value (0.25) found between the populations from the middle Tapajós River and low Teles Pires

River (Supplementary Material, Table 4). We also did not find significant values in the genetic isolation test for geographical distance (r= 0.092 p= 0.09).

Populations of the three analyzed species showed irregular and multimodal mismatch distribution (Fig. 6) (*O*. *bicolor*: r= 0.06, p= 0.06; *O*. *cleberi*: r= 0.005, p= 0.94; *O*. *paricola*: r= 0.009, p= 0.86). Among the neutrality tests herein performed, only the Fs showed significant results for *O*. *cleberi* and *O*. *paricola*. The haplotype diversity was high and nucleotide diversity was low for the three species (Table 2).

Discussion

Diversity of Oecomys in the Tapajós River basin

Our analyses confirmed the occurence of seven species of *Oecomys* in the Tapajós River basin. Among these species, two comprise specimens that have been previously associated to the *O*. *catherinae* complex (Suárez-Villota et al., 2018). In our analyses with cytb data, one species grouped with the lineage that represents *O*. *catherinae* stricto sensu from eastern Brazil and, for that reason, it is herein called *O*. *catherinae*. The other species forms a tritomy with *O*. *catherinae* and *O*. *rex* (Fig. 2). Due to its morphological similarity and close relationship with *O*. *catherinae* pointed out by Suárez-Villota et al. (2018), the species is herein referred as *Oecomys* aff. *catherinae*. This species presented 8.94% of mean genetic divergence from *O*. *catherinae* (Supplementary Material, Table 2), which is similar to the 7.2-8.87% of mean genetic divenge values reported by Suárez-Villota et al. (2018) between the *O*. *catherinae* western clade (= ours *Oecomys* aff. *catherinae*) and the other lineages within the *O*. *catherinae* complex of the authors. In addition, the species was recovered as the sister species of a clade composed of *O*. *bicolor*, *O*. *catherinae*, *O*. *cleberi*, *O*. *franciscorum*, *O*. *paricola*, *O*. *roberti*, and *O*. *tapajinus* in our BI and MV analyses with concatenated data (Fig. 3). Therefore, the relationship of *Oecomys* aff. *catherinae* with other congeners needs further clarification.

Oecomys paricola has recently been revealed as a species complex by Rosa et al. (2012), who found karyotypic differences and high intraspecific genetic distance (3.9%) within the species. In turn, Suárez-Villota et al. (2018) recognized three distinct lineages in *O*. *paricola* (northern, eastern, and western lineages of authors), with genetic divergences varying from 2.9 to 6.2% among them. Our specimens grouped with the *O*. *paricola* western clade of the authors, evidencing that this

lineage extends to the right bank of the Tapajós River (Fig. 1). The species presented 1.83% of intraspecific genetic divergence, notably lower than the 3.6% and 4.1% internal divergences found by Rocha et al. (2011) and Rocha et al. (2012), respectively.

Based on the cytb marker and 11 specimens, Rocha et al. (2012) recovered *O*. *bicolor* and *O*. *cleberi* as reciprocal monophyletic groups with high support values and 6.8% of mean genetic distance. Despite of Rocha´s et al. (2012) promising results, Suarez-Villota et al. (2018) were not able to separate these species employing cytb and two nuclear markers of 24 specimens. Therefore, the latter authors included both species in a single species complex, in which they recognized two lineages associated to *O*. *cleberi* and six lineages associated to *O*. *bicolor*, with genetic distances varying from 3.3% to 6.9% among them. Our cytb analyses did not recover *O*. *bicolor* and *O*. *cleberi* as reciprocal monophyletic groups either (Fig. 2). By contrast, our BI analysis with concatenated data recovered both species as monophyletic, with high support and 4.84% of mean genetic divergence. Interestingly, specimens of *O*. *bicolor* central and western clades of Suarez-Villota et al. (2018) nested within our *O*. *cleberi* clade (Fig. 3). These results were also obtained by our populational analyses, discussed below. Therefore, based on our BI and populational analyses, we recognize the presence of both *O*. *bicolor* and *O*. *cleberi* in the Tapajós River basin. These analyses also showed that *O*. *cleberi* geographic distribution, currently restricted to south-central Brazil and sothern Amazonia (Pardiñas et al., 2017; Suárez-Villota et al., 2018), extends to the west bank of the Tapajós River (Fig. 1).

Oecomys roberti has recently been recognized as a species complex by Suarez-Villota et al. (2018), composed of three distinct lineages called eastern, central, and western clades by the authors, with genetic distances varying from 5.2% to 9.1% among them. Our samples of *O*. *roberti* grouped with the authors´ central clade, while our samples of *O*. *tapajinus* grouped with the author´s eastern clade. In this sense, this latter clade of Suarez-Villota et al. (2018) corresponds to *O*. *tapajinus*, a species revalidated by Rocha et al. (2018). Additionally, *O*. *tapajinus* was recovered as sister to *O*. *roberti* in our BI and MV analyses with concatenated data and our BI analysis with cytb data, supporting the close relation between these species previously reported in the literature (Rocha et al., 2012; Rocha et al., 2018; Suarez-Villota et al., 2018).

Despite Carleton and Musser (2015) report of *O*. *trinitatis* in Humboldt Laboratory, Aripuanã, state of Mato Grosso, and even southward in Maracaju, state of Mato Grosso do Sul, we did not find individuals of this species in our samples. According to the authors, *O*. *trinitatis* exhibits dorsal fur soft and dense (10–13 mm over middle rump), ventral fur that ranges from dark grayish white to rich ochraceous gray, and robust skull, with narrow interorbit and distinct supraorbital ridges or shelves that strongly diverge caudally to join prominent temporal ridges. All these characters also apply to specimens of the *O*. *catherinae* complex, which Carleton and Musser (2015) discriminate from *O*. *trinitatis* on the basis of a supposed smaller size exhibited by the latter species. Considering that (i) we were not able to confidently associate any of our specimens to *O*. *trinitatis*, (ii) there are no molecular studies reporting this species to the state of Mato Grosso or farthest south, and (iii) the diagnostic characters provided by Carleton and Musser (2015) cannot confidently discriminate *O*. *trinitatis* from *O*. *catherinae*, we argue that the presence of the former species in the Tapajós River basin still needs to be confirmed.

Species of *Oecomys* traditionally not recognized to occur in the Tapajós River basin, such as *O*. *auyantepui*, *O*. *concolor*, *O*. *franciscorum*, *O*. *mamorae*, *O*. *rex*, *O*. *rutilus*, *O*. *superans*, and *O*. *sydandersoni* were not identified in our samples. Also, we were not able to associate any of our specimens to the three unnamed lineages (*Oecomys* sp.1, *Oecomys* sp.2 e *Oecomys* sp.3) recognized by Suárez-Villota et al. (2018).

Our results show the occurrence of up to four sympatric species in the Tapajós River basin. Four to five *Oecomys* species in sympatry have already been reported by Patton et al. (2000) in Colocação Vira-Volta, left bank the Juruá River, Amazonas state, Brazil (four species); by Voss et al. (2001) in Kartabo, Guyana (five species), in Arataye, French Guiana (four species), and in 52 km SSW Altamira, right bank of the Xingu River, Brazil (four species); by Silva et al. (2013) in Cachoeira Santo Antônio, Amapá state, Brazil; and by Suárez-Villota et al. (2018) in Cláudia, state of Mato Grosso, Brazil.

According to Carleton and Musser (2015), species of *Oecomys* may be classified as small-sized (head and body length 84–105 mm), medium-sized (head and body length 109–125 mm) and large-sized (head and body length 125–150 mm). In the Juruena–Teles Pires interfluve, we observed sympatry among *Oecomys*

356 species of the three body size classes, namely *O*. *cleberi* (small), *O*. *paricola* and *O*.
357 *roberti* (medium), and *Oecomys* aff. *catherinae* (large).
358 The sympatry among different-sized species of *Oecomys* were already
359 mentioned by Patton et al. (2000) and Suárez-Villota et al. (2018). As already
360 discussed by the latter authors, although there is no study of niche occupancy for
361 *Oecomys*, it is reasonable to infer that species with different body sizes explore
362 distintic resources, allowing their coexistence. Similarly, arboreality might be related
363 to the different ways species of *Oecomys* use the forest strata, favoring sympatry. In
364 a compilation of ecological studies on small nonvolant mammals from the Cerrado
365 biome, Alho (2015) pointed out that more than 80% of the captures of a small-sized
366 *Oecomys* species (identified by him as *O*. *bicolor*) occured in the superior stratum,
367 while a medium-sized species (identified by him as *O*. *concolor*) were more
368 frequently captured in the inferior stratum, close to the groud.
369 Simpatry among *Oecomys* species with similar body size has also been
370 reported in the literature. Patton et al. (2000), for exemple, recorded two small-bodied
371 species (*O*. *bicolor* and *Oecomys* sp.2 of the authors) in Colocação Vira-Volta, left
372 bank the Juruá River. However, this sympatry has been more frequently recorded for
373 medium-sized species, such as *O*. *roberti* and *O*. *tapajinus* in localities of the mid-
374 Araguaia River basin (Rocha et al., 2014, 2018), *O*. *paricola* and *O*. *roberti* in both
375 banks of the Teles Pires River, and *O*. *paricola* and *O*. *tapajinus* in the east bank of
376 the Tapajós River (this study). Despite these recurrent records, the real causes for
377 the high level of sympatry found in *Oecomys*, which is a rare phenomenon for the
378 Sigmodontinae rodents, will only be unveiled if studies are carried out to investigate
379 the use of resources by its species.

380 **Population structure of Oecomys from the Tapajós River basin**

381 The geographic distributions of *O*. *bicolor* and *O*. *cleberi* appear to be shaped
382 by the Tapajós and Teles Pires Rivers, with the former species occurring on the east
383 bank and the latter species on the west bank of both rivers. Moreover, *O*. *cleberi* was
384 the only *Oecomys* species to be recorded on the west bank of the Tapajós River.
385 This pattern supports Oliveira´s et al. (2017) argument that the major Amazonian
386 rivers coincides with breaks in species composition, acting as dispersal barriers for
387 some species. In particular, the Tapajós River have also been pointed out as a

388 barrier for some species of birds (Harvey and Brumfield, 2014, Ribas et al., 2012),
389 amphibians and squamates (Moraes et al., 2016).
390 Our results of populational analyses indicate the presence of gene flow
391 between populations of *O*. *cleberi* on the west bank of the Juruena and Tapajós
392 Rivers, and absence of gene flow between populations of *O*. *bicolor* on the east bank
393 of the Teles Pires and Tapajós Rivers. These results may be related to the great
394 geographical distance between the two populations of *O*. *bicolor* herein analyzed,
395 namely East Tapajós and Middle East Teles Pires (Fig. 4). Similar results were
396 obtained by Rocha et al. (2014), who studied the populational structure of *Oecomys*
397 aff. *roberti* (= *O*. *tapajinus*) along the mid-Araguaia river basin. However, by analysing
398 a greater number of populations, Rocha et al. (2018) refuted the scenario of isolation
399 by distance for this species.
400 One implication of the riverside hypothesis is the existence of unique
401 haplotypes in monophyletic clades and on opposite river banks (Antonelli et al., 2010;
402 Patton et al., 2000). The Araguaia River has already been considered a barrier for
403 rodents of the genus *Rhipidomys* (Rocha et al., 2011) and small marsupials with
404 specialized habits, like *Gracilinanus* (Rocha et al., 2015). On the other hand, this
405 river does not constitute a barrier for large-sized marsupials with generalist habits,
406 such as *Didelphis* (Rocha et al., 2015), nor for the rodents *Hylaeamys*
407 *megacephalus* (Rocha et al., 2014). For *O*. *tapajinus*, Rocha et al. (2014)
408 demonstrated shared haplotypes in populations from opposite banks of the Araguaia
409 River, rejecting this hypothesis for the diversification of the species. Similarly, we
410 found that individuals of *O*. *paricola* from opposite banks of the Teles Pires River
411 share the same haplotype, indicating that this river does not act as a barrier for this
412 species.
413 According to Haffer (2008), the number of species delimited by Amazonian
414 rivers is proportional to the width of the rivers, that is, narrower rivers may not act as
415 barriers for certain groups. Bates et al. (2004) emphasized that the Teles Pires River
416 is a narrow tributary (100-300 m wide) that can be easily crossed, rejecting the
417 hypothesis that this river acts as a barrier for birds. The absence of structure of the
418 populations of *O*. *paricola* herein analyzed support this idea.
419 The distribution of *Oecomys* species might also be associated with
420 evolutionary factors, such as species population expansion, which was not confirmed
421 by the mismatch analysis. Nevertheless, the existence of population expansion

cannot be completely discarded, since Fu´s Fs were significant for *O*. *cleberi* and *O*. *paricola*. A scenario of population expansion have already been proposed for *O*. *tapajinus* by Rocha et al. (2018), who suggested that this scenario may be linked to ecological characteristics of *Oecomys* that are subjected to the expansion and retraction of forests during glacial cycles, such as the arboreal habits and forest speciality.

In short, our results show high diversity of *Oecomys* species in the Tapajós River basin, consisting of at least seven species. Our results also refute the hypothesis that the Teles Pires River is a barrier to gene flow for *O*. *paricola* and indicate that the Tapajós River shape the geographical distribution of *Oecomys* species in this region.

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Figures

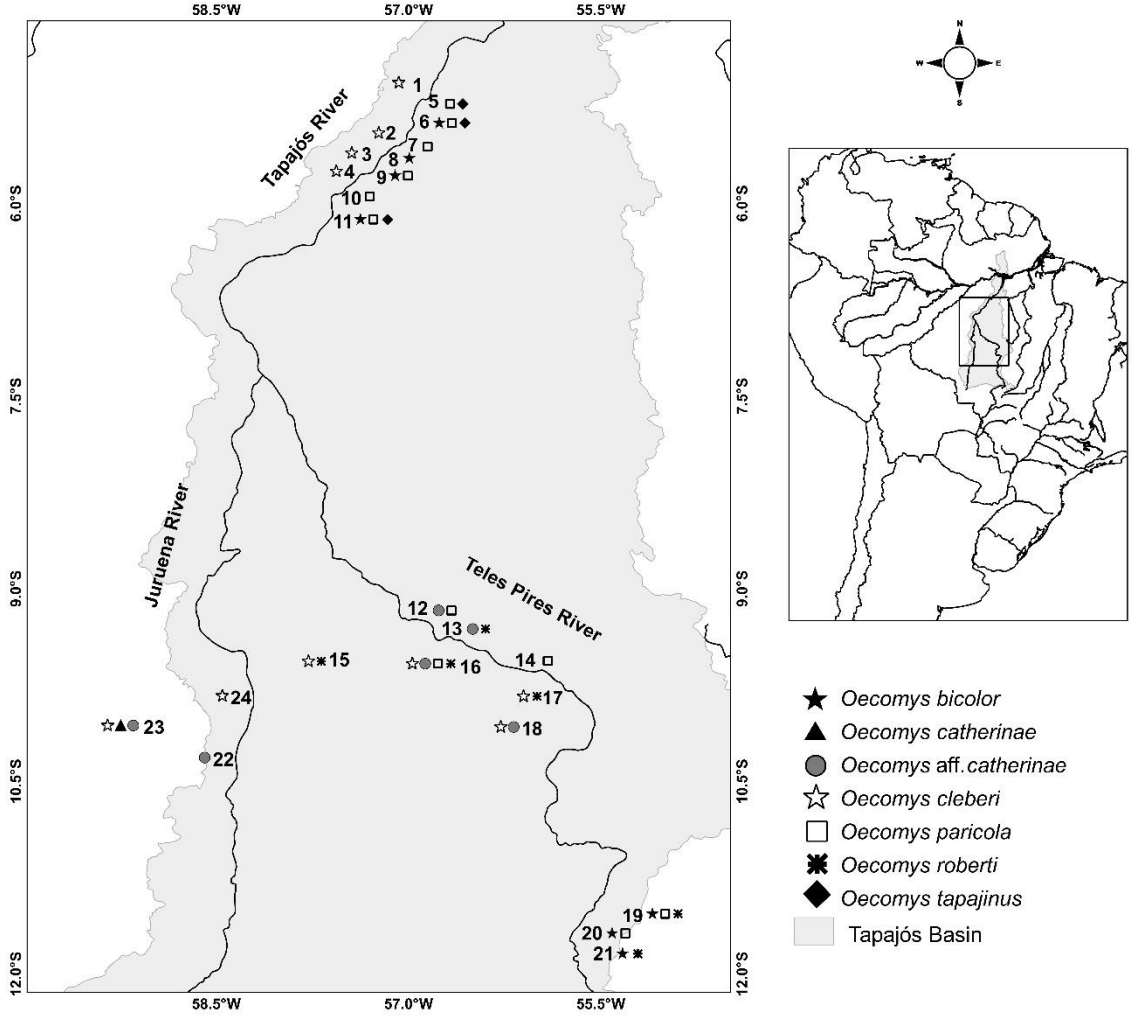
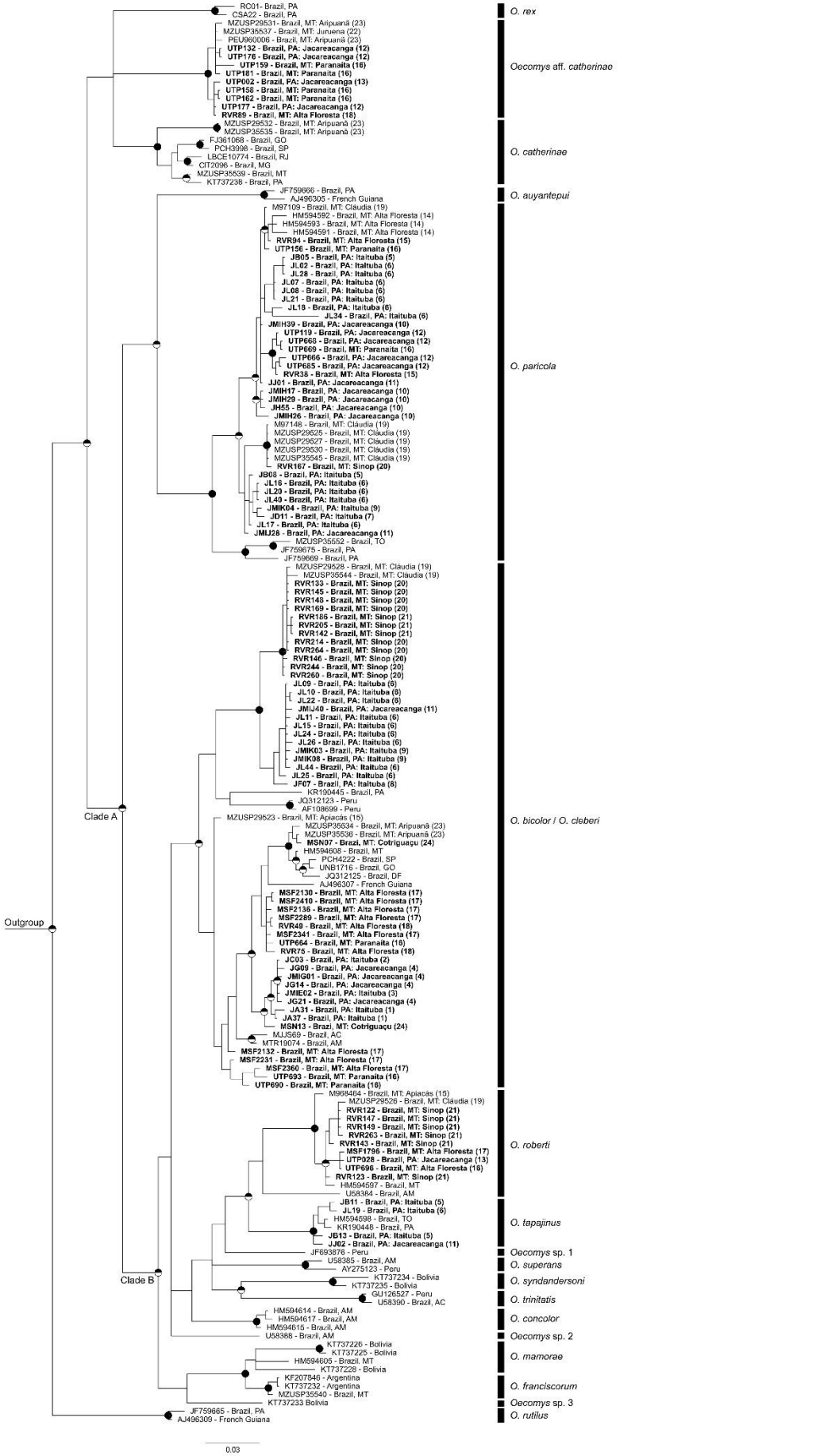


Fig. 1. Map indicating the main rivers in the Tapajós River basin and sampled localities. Numbers indicate the collection points and the symbols indicate the species collected at these points. Coordinates and number of locations are listed in Supplementary Material, Table 1.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CSA22 - Brazil, PA
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MZUSP35537 - Brazil, MT: Juruena (22)
PEU960006 - Brazil, MT: Aripuanã (23)
UTP132 - Brazil, PA: Jacareacanga (12)
UTP176 - Brazil, PA: Jacareacanga (12)
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UTP181 - Brazil, MT: Paranaita (16)
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UTP162 - Brazil, MT: Paranaita (16)
UTP177 - Brazil, PA: Jacareacanga (12)
RVR89 - Brazil, MT: Alta Floresta (18)
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MZUSP35535 - Brazil, MT: Aripuanã (23)
FJ361068 - Brazil, GO
PCH3998 - Brazil, SP
LBCE10774 - Brazil, RJ
CIT2096 - Brazil, MG
MZUSP35539 - Brazil, MT
KT737238 - Brazil, PA
JF759666 - Brazil, PA
AJ496305 - French Guiana
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JL07 - Brazil, PA: Itaituba (6)
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JL21 - Brazil, PA: Itaituba (6)
JL19 - Brazil, PA: Itaituba (6)
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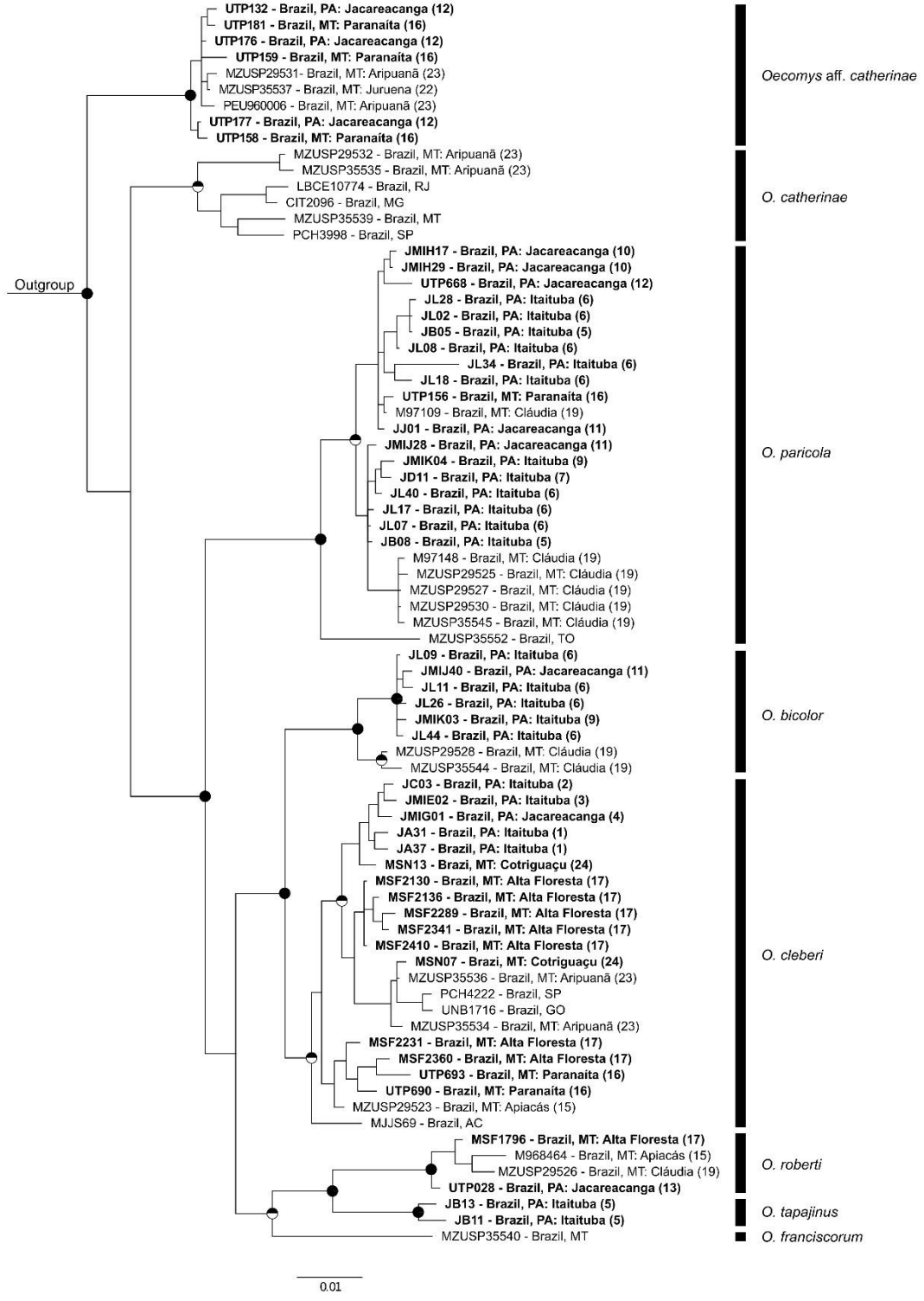
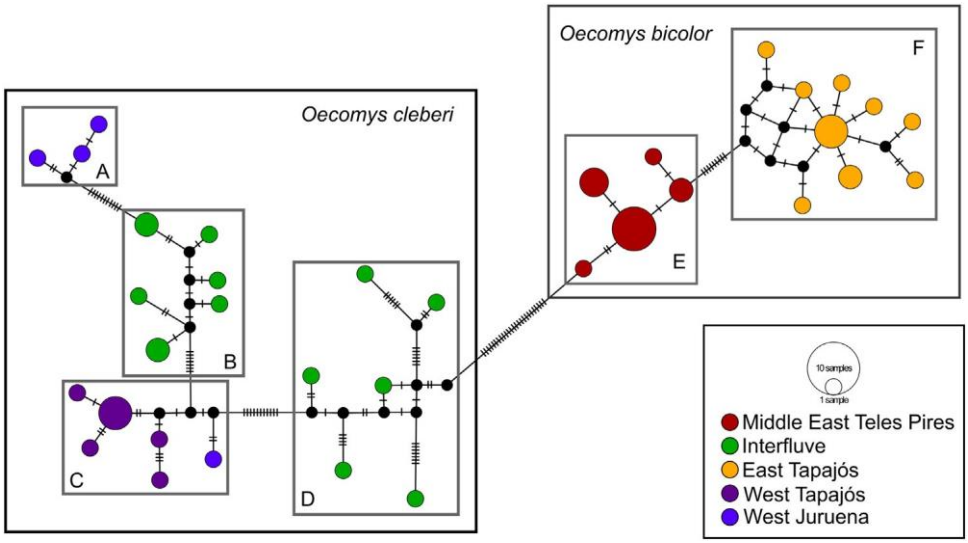
HM594614 - Brazil, AM
HM594617 - Brazil, AM
HM594615 - Brazil, AM
U58388 - Brazil, AM
KT737226 - Bolivia
KT737225 - Bolivia
HM594605 - Brazil, MT
KT737228 - Bolivia
KF207648 - Argentina
KT737232 - Argentina
MZUSP35540 - Brazil, MT
KT737233 Bolivia
JF759665 - Brazil, PA
AJ496309 - French Guiana
Outgroup
Clade A
Clade B
0.03
O. rex
Oecomys aff. catherinae
O. catherinae
O. auyantepui
O. paricola
O. bicolor / O. cleberi
O. roberti
O. tapajinus
Oecomys sp. 1
O. superans
O. syndandersoni
O. trinitatis
O. concolor
Oecomys sp. 2
O. mamorae
O. franciscorum
Oecomys sp. 3
O. rutilus

Fig. 2. Bayesian Inference topology based on *Oecomys* cytochrome b gene data. Rigid circles indicate posterior probability greater than 0.95 and maximum likelihood bootstrap of more than 80%. Half black circles indicate posterior probability above 0.95. Numbers in parentheses refer to the localities from the Tapajós River basin indicated in Fig. 1. Boldfaced samples indicate sequences obtained in this study. Identification of samples and their locations are listed in Supplementary Material, Table 1.

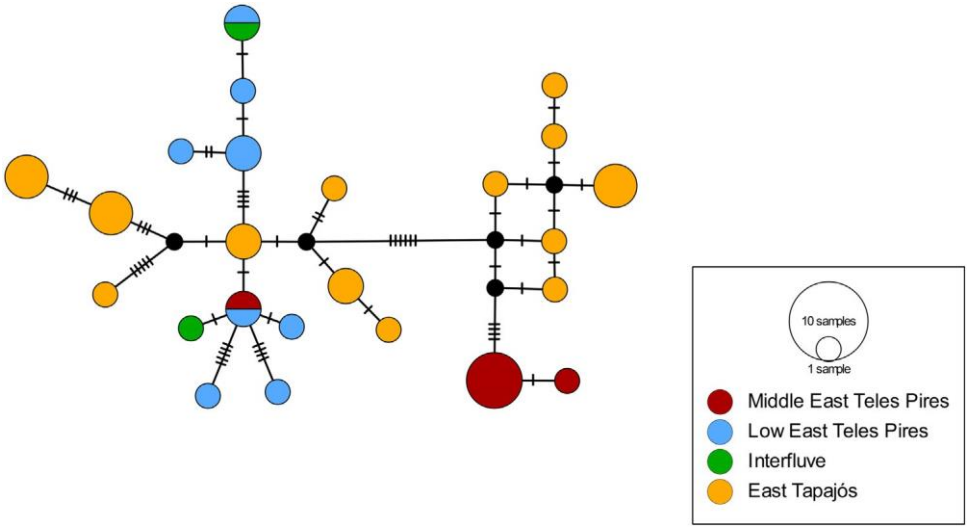


588 **Fig. 3**. Bayesian Inference topology based on concatenated data from cytochrome b
589 gene and nuclear marker intron 7 β-fibrinogen gene of *Oecomys*. Circles indicate
590 posterior probability greater than 0.95 and maximum likelihood bootstrap greater than
591 80%. Half black circles indicate posterior probability above 0.95. Numbers in
592 parentheses refer to the localities from the Tapajós River basin indicated in Fig. 1.
593 Boldfaced samples indicate sequences obtained in this study. Identification of
594 samples and their locations are listed in Supplementary Material, Table 1.



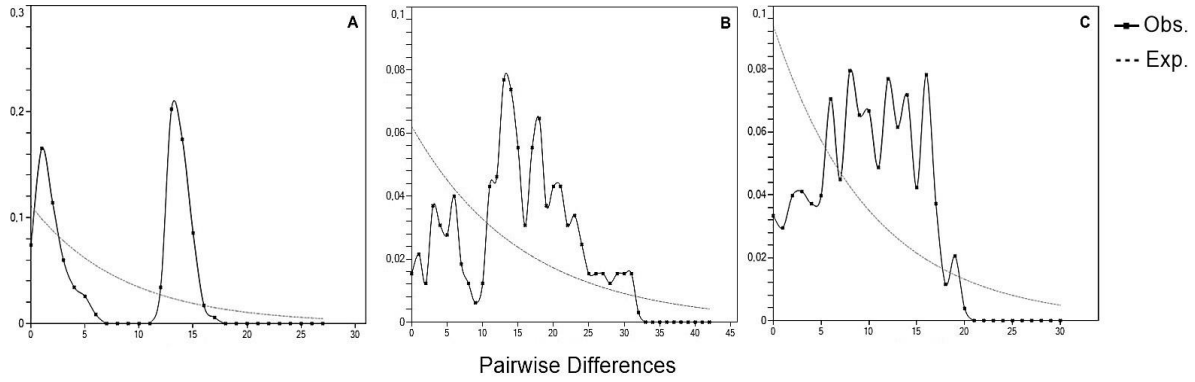
595

596 **Fig. 4.** Median-joining haplotype network based on cytochrome b gene data,
597 representing the relationships in the *Oecomys bicolor*/*Oecomys cleberi* species
598 complex. The size of the circle is proportional to the frequency of the haplotypes and
599 the colors correspond to the localities. The mutational steps are indicated on the
600 branches.



601

602 **Fig. 5.** Median-joining haplotype network based on data from the cytochrome b gene
603 of *Oecomys paricola*. The size of the circle is proportional to the frequency of the
604 haplotypes and the colors correspond to the localities. The mutational steps are
605 indicated on the branches.



606

607 **Fig. 6.** Mismatch distribution graphs based on cytochrome b data from *Oecomys*
608 *bicolor* (A), *Oecomys cleberi* (B) and *Oecomys paricola* (C). Dotted gray line
609 indicates the expected distribution and solid black line indicates the frequency of
610 distribution observed.

611 **Tables**

612 **Table 1**. Percentage of variation and fixation index of Analysis of Molecular Variance
613 (AMOVA) based on cytochrome b data of the *Oecomys bicolor*/*Oecomys cleberi*
614 complex (2 groups) and *O*. *paricola*. *Significant values (p<0.05).

615

	O. *bicolor*/*O*. *cleberi*		*O*. *paricola*	
	% Variation	Fixation index	% Variation	Fixation index
Among groups	56.26*	Φ_{CT} 0.56*		
Among populations	26.73*	Φ_{ST} 0.83*	37.35*	Φ_{ST} 0.37*
Within populations	17.01*	Φ_{SC} 061*	62.65*	

616

617 **Table 2**. Genetic diversity indices and demographic expansion of *Oecomys bicolor*,
618 *O*. *cleberi* and *O*. *paricola* based on cytochrome b data. N: Sample number; H:
619 number of haplotypes; h: haplotype diversity, π: nucleotide diversity. *Significant
620 values (p<0.05).

621

	N	H	h* ± DP	π* ± DP	D (Tajima)	p	Fs (Fu)	p
Oecomys bicolor	27	17	0.954 ± 0.022	0.011 ± 0.006	0.46	0.72	-2.71	0.13
Oecomys cleberi	26	17	0.991 ± 0.015	0.021 ± 0.010	-0.20	0.52	-8.71	0.007 *
Oecomys paricola	39	29	0.975 ± 0.013	0.014 ± 0.007	0.68	0.26	-10.28	0.001 *

622

Supplementary Material

Table 1. Field number, voucher number, GenBank accession number, geographical coordinates, region and locality of specimens included in this study. Localities are indicated in Figure 1 (map). MT: Mato Grosso; PA: Pará; BR: Brazil.

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys cleberi	JA31	UFPAM1560	MK874374	MK874455	-5,062	-56,879	1	West Tapajós River	PA: Itaituba	This study
Oecomys cleberi	JA37	UFPAM1566	MK874375	MK874456	-5,062	-56,879	1	West Tapajós River	PA: Itaituba	This study
Oecomys cleberi	JC03	UFPAM1407	MK874376	MK874457	-5,453	-57,085	2	West Tapajós River	PA: Itaituba	This study
Oecomys cleberi	JMIE02	UFPAM1163	MK874380	MK874458	-5,610	-57,296	3	West Tapajós River	PA: Itaituba	This study
Oecomys cleberi	JG09	UFPAM1459	MK874377	-	-5,722	-57,366	4	West Tapajós River	PA: Jacareacanga	This study
Oecomys cleberi	JG14	-	MK874378	-	-5,722	-57,366	4	West Tapajós River	PA: Jacareacanga	This study
Oecomys cleberi	JG21	UFPAM1627	MK874379	-	-5,722	-57,366	4	West Tapajós River	PA: Jacareacanga	This study
Oecomys cleberi	JMIG01	UFPAM1177	MK874381	MK874459	-5,722	-57,366	4	West Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JB05	UFPAM1390	MK874397	MK874471	-5,227	-56,929	5	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JB08	UFPAM1393	MK874398	MK874472	-5,227	-56,929	5	East Tapajós River	PA: Itaituba	This study
Oecomys tapajinus	JB11	UFPAM1396	MK874439	MK874491	-5,227	-56,929	5	East Tapajós River	PA: Itaituba	This study
Oecomys tapajinus	JB13	UFPAM1398	MK874440	MK874492	-5,227	-56,929	5	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL09	UFPAM1526	MK874341	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL10	UFPAM1527	MK874342	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL11	UFPAM1528	MK874343	MK874444	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL15	UFPAM1531	MK874344	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL22	UFPAM1538	MK874345	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL24	UFPAM1540	MK874346	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL25	UFPAM1541	MK874347	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL26	UFPAM1542	MK874348	MK874445	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JL44	UFPAM1708	MK874349	MK874446	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL02	UFPAM1519	MK874402	MK874475	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL07	UFPAM1524	MK874403	MK874476	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL08	UFPAM1525	MK874404	MK874477	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL16	UFPAM1532	MK874405	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys paricola	JL17	UFPAM1533	MK874406	MK874478	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL18	UFPAM1534	MK874407	MK874479	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL20	UFPAM1536	MK874408	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL21	UFPAM1537	MK874409	-	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL28	UFPAM1544	MK874410	MK874480	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL34	UFPAM1698	MK874411	MK874481	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JL40	UFPAM1704	MK874412	MK874482	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys tapajinus	JL19	UFPAM1535	MK874442	MK874493	-5,376	-56,923	6	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JD11	UFPAM1734	MK874399	MK874473	-5,580	-57,123	7	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JF07	UFPAM1446	MK874340	-	-5,661	-57,247	8	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JMIK03	UFPAM1164	MK874351	MK874448	-5,766	-57,277	9	East Tapajós River	PA: Itaituba	This study
Oecomys bicolor	JMIK08	UFPAM1165	MK874352	-	-5,766	-57,277	9	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JMIK04	UFPAM1166	MK874418	MK874486	-5,766	-57,277	9	East Tapajós River	PA: Itaituba	This study
Oecomys paricola	JH55	UFPAM1662	MK874400	-	-5,817	-57,395	10	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JMIH17	UFPAM1171	MK874413	MK874483	-5,817	-57,395	10	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JMIH26	UFPAM1168	MK874414	-	-5,817	-57,395	10	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JMIH29	UFPAM1173	MK874415	MK874484	-5,817	-57,395	10	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JMIH39	UFPAM1167	MK874416	-	-5,817	-57,395	10	East Tapajós River	PA: Jacareacanga	This study
Oecomys bicolor	JMIJ40	UFPAM1162	MK874350	MK874447	-6,127	-57,588	11	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JJ01	UFPAM1504	MK874401	MK874474	-6,127	-57,588	11	East Tapajós River	PA: Jacareacanga	This study
Oecomys paricola	JMIJ28	UFPAM1172	MK874417	MK874485	-6,127	-57,588	11	East Tapajós River	PA: Jacareacanga	This study
Oecomys tapajinus	JJ02	UFPAM1505	MK874441	-	-6,127	-57,588	11	East Tapajós River	PA: Jacareacanga	This study
Oecomys aff. *catherinae*	UTP132	UFMT1686	MK874367	MK874449	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys aff. *catherinae*	UTP176	UFMT1775	MK874371	MK874452	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys aff. *catherinae*	UTP177	UFMT1776	MK874372	MK874453	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys paricola	UTP685	UFMT1780	MK874427	-	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys paricola	UTP119	UFMT1685	MK874422	-	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys paricola	UTP666	UFMT1778	MK874424	-	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys paricola	UTP668	UFMT1779	MK874425	MK874488	-9,311	-56,768	12	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys aff. *catherinae*	UTP002	UFMT1680	MK874366	-	-9,385	-56,732	13	Low East Teles Pires River	PA: Jacareacanga	This study

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys roberti	UTP028	UFMT1682	MK874437	MK874490	-9,385	-56,732	13	Low East Teles Pires River	PA: Jacareacanga	This study
Oecomys paricola	LPC559	MVZ197507	HM594592	-	-9,583	-55,917	14	Low East Teles Pires River	MT: Alta Floresta	Rocha et al. (2011)
Oecomys paricola	LPC570	MVZ197507	HM594593	-	-9,583	-55,917	14	Low East Teles Pires River	MT: Alta Floresta	Rocha et al. (2011)
Oecomys paricola	LPC525	UFMG2841	HM594591	-	-9,583	-55,917	14	Low East Teles Pires River	MT: Alta Floresta	Rocha et al. (2011)
Oecomys paricola	RVR 38	UFMT4116	MK874419	-	-9,604	-56,090	14	Low East Teles Pires River	MT: Alta Floresta	This study
Oecomys cleberi	M968410	MZUSP29523	MG323750	MG323834	-9,567	-57,383	15	Interfluve (Teles Pires - Juruena)	MT: Apiacás	Suárez-Villota et al. (2018)
Oecomys paricola	RVR 94	UFMT4112	MK874420	-	-9,604	-56,090	15	Low East Teles Pires River	MT: Alta Floresta	This study
Oecomys roberti	M968464	-	MG323719	MG323806	-9,567	-57,383	15	Interfluve (Teles Pires - Juruena)	MT: Apiacás	Suárez-Villota et al. (2018)
Oecomys aff. *catherinae*	UTP158	UFMT1772	MK874368	MK874450	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys aff. *catherinae*	UTP159	UFMT1773	MK874369	MK874451	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys aff. *catherinae*	UTP162	UFMT1774	MK874370	-	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys aff. *catherinae*	UTP181	UFMT1806	MK874373	MK874454	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys cleberi	UTP664	UFMT1777	MK874394	-	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys cleberi	UTP690	UFMT1781	MK874395	MK874469	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys cleberi	UTP693	UFMT1782	MK874396	MK874470	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys paricola	UTP669	UFMT1848	MK874426	-	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys paricola	UTP156	UFMT1771	MK874423	MK874487	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Paranaíta	This study
Oecomys roberti	UTP696	UFMT1783	MK874438	-	-9,485	-56,472	16	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2130	-	MK874382	MK874460	-9,757	-55,972	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2136	-	MK874384	MK874461	-9,757	-55,972	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2410	-	MK874389	MK874466	-9,798	-55,926	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2289	-	MK874386	MK874463	-9,824	-55,893	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2341	-	MK874387	MK874464	-9,824	-55,893	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2132	-	MK874383	-	-9,757	-55,972	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2231	-	MK874385	MK874462	-9,867	-55,900	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	MSF2360	-	MK874388	MK874465	-9,867	-55,900	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys roberti	MSF1796	-	MK874430	MK874489	-9,840	-56,005	17	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys aff. *catherinae*	RVR 89	UFMT4118	MK874365	-	-10,007	-56,038	18	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys cleberi	RVR 49	UFMT4111	MK874392	-	-9,978	-56,083	18	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys cleberi	RVR 75	UFMT4117	MK874393	-	-9,978	-56,083	18	Interfluve (Teles Pires - Juruena)	MT: Alta Floresta	This study
Oecomys bicolor	M97074	MZUSP29528	MG323726	MG323812	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys bicolor	M97107	MZUSP35544	MG323725	MG323785	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M97023	MZUSP29525	MG323713	MG323802	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M97073	MZUSP29527	MG323711	MG323800	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M97109	-	MG323708	MG323798	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M97141	MZUSP29530	MG323709	MG323799	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M97148	-	MG323710	MG323776	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys paricola	M976296	MZUSP35545	MG323712	MG323801	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys roberti	M97060	MZUSP29526	MG323720	MG323807	-11,583	-55,167	19	Middle East Teles Pires River	MT: Cláudia	Suárez-Villota et al. (2018)
Oecomys bicolor	RVR133	UFMT4313	MK874353	-	-11,677	-55,333	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR145	UFMT4316	MK874355	-	-11,677	-55,333	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR146	UFMT4333	MK874356	-	-11,697	-55,277	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR148	UFMT4318	MK874357	-	-11,677	-55,333	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR169	UFMT4321	MK874358	-	-11,666	-55,280	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR214	UFMT4639	MK874361	-	-11,671	-55,525	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR244	UFMT4642	MK874362	-	-11,697	-55,277	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR260	UFMT4646	MK874363	-	-11,697	-55,277	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR264	UFMT4647	MK874364	-	-11,697	-55,277	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys paricola	RVR167	UFMT4320	MK874421	-	-11,665	-55,511	20	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR142	UFMT4314	MK874354	-	-11,733	-55,360	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR186	UFMT4636	MK874359	-	-11,733	-55,360	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys bicolor	RVR205	UFMT4638	MK874360	-	-11,714	-55,402	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys roberti	RVR122	UFMT4311	MK874431	-	-11,817	-55,411	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys roberti	RVR123	UFMT4312	MK874432	-	-11,742	-55,229	21	Middle East Teles Pires River	MT: Sinop	This study

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys roberti	RVR143	UFMT4315	MK874433	-	-11,677	-55,333	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys roberti	RVR147	UFMT4317	MK874434	-	-11,733	-55,360	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys roberti	RVR149	UFMT4319	MK874435	-	-11,794	-55,413	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys roberti	RVR263	UFMT4651	MK874436	-	-11,697	-55,277	21	Middle East Teles Pires River	MT: Sinop	This study
Oecomys aff. *catherinae*	APC145	MZUSP35537	MG323757	MG323779	-10,317	-58,483	22	West Juruena River	MT: Juruena	Suárez-Villota et al. (2018)
Oecomys aff. *catherinae*	APC244	MZUSP29531	MG323756	MG323777	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys aff. *catherinae*	PEU960006	-	MG323755	MG323839	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys catherinae	APC243	MZUSP35535	MG323759	MG323841	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys catherinae	APC249	MZUSP29532	MG323758	MG323840	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys cleberi	APC210	MZUSP35534	MG323745	MG323829	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys cleberi	PEU960047	MZUSP35536	MG323744	MG323828	-10,167	-59,450	23	West Juruena River	MT: Aripuanã	Suárez-Villota et al. (2018)
Oecomys cleberi	MSN07	UFMT1363	MK874390	MK874467	-9,836	-58,253	24	West Juruena River	MT: Cotriguaçu	This study
Oecomys cleberi	MSN13	UFMT1366	MK874391	MK874468	-9,836	-58,253	24	West Juruena River	MT: Cotriguaçu	This study
Oecomys auyantepui	-	CN120	JF759666	-	1,167	-55,650	-	-	Pará, BR	Rosa et al. (2012)
Oecomys auyantepui	-	V-1001	AJ496305	-	4,083	-52,683	-	-	French Guiana	Mauffrey et al. (unpubl.)
Oecomys bicolor	FSF34r	-	KR190445	-	-9,630	-50,144	-	-	Pará, BR	Rocha et al. (2015)
Oecomys bicolor	-	MVZ154990	JQ312123	-	-5,517	-79,817	-	-	Peru	Rocha et al. (2012)
Oecomys bicolor	-	MVZ154999	AF108699	-	-5,517	-79,817	-	-	Peru	Smith and Patton (1999)
Oecomys catherinae	-	MN36747	FJ361068	-	-13,517	-48,217	-	-	Goiás, BR	Miranda et al. (unpubl.)
Oecomys catherinae	PCH3998	-	MG323764	MG323846	-20,483	-47,850	-	-	São Paulo, BR	Suárez-Villota et al. (2018)
Oecomys catherinae	CIT2096	-	MG323772	MG323774	-19,533	-42,533	-	-	Minas Gerais, BR	Suárez-Villota et al. (2018)
Oecomys catherinae	-	LBCE10774	MG323771	MG323852	-23,217	-44,717	-	-	Rio de Janeiro, BR	Suárez-Villota et al. (2018)
Oecomys catherinae	APC289	MZUSP35539	MG323766	MG323848	-10,017	-51,117	-	-	Mato Grosso, BR	Suárez-Villota et al. (2018)

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys catherinae	-	USNM549530	KT737238	-	-3,650	-52,367	-	-	Pará, BR	Pardiñas et al. (2016)
Oecomys cleberi	-	AMNH269823	AJ496307	-	-4,083	-52,683	-	-	French Guiana	Mauffrey et al. (unpubl.)
Oecomys cleberi	MJJS69	-	MG323749	MG323833	-9,333	-68,317	-	-	Acre, BR	Suárez-Villota et al. (2018)
Oecomys cleberi	MTR19074	-	MG323752	MG323836	-4,717	-62,117	-	-	Amazonas, BR	Suárez-Villota et al. (2018)
Oecomys cleberi	-	MN24131	JQ312125	-	-15,950	-47,933	-	-	Distrito Federal, BR	Rocha et al. (2012)
Oecomys cleberi	APC553	UNB1716	MG323734	MG323818	-18,100	-52,917	-	-	Goiás, BR	Suárez-Villota et al. (2018)
Oecomys cleberi	-	UFMG2802	HM594608	-	-15,633	-52,350	-	-	Mato Grosso, BR	Rocha et al. (2011)
Oecomys cleberi	PCH4222	-	MG323741	MG323825	-20,500	-47,833	-	-	São Paulo, BR	Suárez-Villota et al. (2018)
Oecomys concolor	JLP16728	-	HM594614	-	-2,217	-62,383	-	-	Amazonas, BR	Rocha et al. (2011)
Oecomys concolor	JLP16729	-	HM594617	-	-2,217	-62,383	-	-	Amazonas, BR	Rocha et al. (2011)
Oecomys concolor	JLP16806	-	HM594615	-	-2,217	-62,383	-	-	Amazonas, BR	Rocha et al. (2011)
Oecomys franciscorum	roe224	-	KF207846	-	-25,917	-58,933	-	-	Argentina	Orozco et al. (2014)
Oecomys franciscorum	-	MACN26663	KT737232	-	-25,967	-58,167	-	-	Argentina	Pardiñas et al. (2016)
Oecomys franciscorum	PNPA300	MZUSP35540	MG323716	MG323786	-17,650	-57,433	-	-	Mato Grosso, BR	Suárez-Villota et al. (2018)
Oecomys mamorae	PZ94	-	KT737226	-	-14,150	-67,917	-	-	Bolivia	Pardiñas et al. (2016)
Oecomys mamorae	PZ316	-	KT737225	-	-15,283	-68,383	-	-	Bolivia	Pardiñas et al. (2016)
Oecomys mamorae	-	MVZ197505	HM594605	-	-17,120	-56,946	-	-	Mato Grosso, BR	Rocha et al. (2011)
Oecomys mamorae	-	MSB63354	KT737228	-	-19,550	-64,133	-	-	Bolivia	Pardiñas et al. (2016)
Oecomys paricola	BAR013	-	JF759675	-	-1,500	-48,667	-	-	Pará, BR	Rosa et al. (2012)
Oecomys paricola	APC1240	MZUSP35552	MG323702	MG323794	-11,233	-46,850	-	-	Tocantins, BR	Suárez-Villota et al. (2018)
Oecomys paricola	-	MPEG40843	JF759669	-	-0,650	-50,183	-	-	Pará, BR	Rosa et al. (2012)
Oecomys rex	RC01	-	MK874429	-	-	-	-	-	Pará, BR	This study
Oecomys rex	CSA22	-	MK874428	-			-	-	Pará, BR	This study
Oecomys roberti	-	UFMG2845	HM594597	-	-17,120	-56,946	-	-	Mato Grosso, BR	Rocha et al. (2011)

Species	Field number	Voucher number	GenBank Cyt*b*	GenBank iBF7	Coordinates		Map	Region	Locality	Reference
Oecomys roberti	JLP15241	MVZ200947	U58384	-	-6,833	-70,750	-	-	Amazonas, BR	Patton and Da Silva (1995)
Oecomys rutilus	CN123	-	JF759665	-	-1,167	-55,650	-	-	Pará, BR	Rosa et al. (2012)
Oecomys rutilus	-	MNHN1995.3236	AJ496309	-	-	-	-	-	French Guiana	Mauffrey et al. (unpubl.)
Oecomys superans	-	MVZ200944	U58385	-	-6,833	-70,750	-	-	Amazonas, BR	Patton and Da Silva (1995)
Oecomys superans	-	MVZ155006	AY275123	-	-5,517	-79,817	-	-	Peru	D'Elía (2003)
Oecomys sydandersoni	-	USNM584557	KT737234	-	-15,250	-61,017	-	-	Bolivia	Pardiñas et al. (2016)
Oecomys sydandersoni	-	USNM588189	KT737235	-	-14,767	-61,033	-	-	Bolivia	Pardiñas et al. (2016)
Oecomys tapajinus	FSF53r	-	KR190448	-	-9,630	-50,144	-	-	Pará, BR	Rocha et al. (2015)
Oecomys tapajinus	-	UFES1354	HM594598	-	-9,970	-50,069	-	-	Tocantins - BR	Rocha et al. (2011)
Oecomys trinitatis	-	MUSM13320	GU126527	-	-5,200	-72,883	-	-	Peru	Percequillo et al. (2011)
Oecomys trinitatis	-	MVZ200948	OTU58390	-	-8,667	-72,783	-	-	Acre, BR	Patton and Da Silva (1995)
Oecomys sp. 1	-	MVZ155005	JF693876	-	-5,517	-79,817	-	-	Peru	Pine et al. (2012)
Oecomys sp. 2	JUR354	MVZ200905	U58388	-	-3,317	-66,017	-	-	Amazonas, BR	Patton and Da Silva (1995)
Oecomys sp. 3	-	MSB68480	KT737233	-	-15,117	-68,867	-	-	Bolivia	Pardiñas et al. (2016)
Euryoryzomys macconnelli	LGV151	-	MK874443	-	-	-	-	-	Pará, BR	This study
Handleyomys intectus	-	CADV088	EU579490	-	-	-	-	-	Colombia	Hanson and Bradley (unpub.)
Handleyomys melanotis	-	ASNHC3419	KF658409	KF658415	-	-	-	-	México	Almendra et al. (2014)
Oligoryzomys utiaritensis	-	MN75625	JQ013752	JQ282893	-	-	-	-	Mato Grosso, BR	Agrellos et al. (2012)

626

627 **Table 2.** Kimura 2 parameters genetic distance among and within (bold numbers) *Oecomys* clades based on cytochrome b. Values in
628 percentage. Standard deviation values are shown above boldfaced numbers.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	*O. auyantepui*	**1.00**	1.70	2.26	1.83	1.80	1.96	1.81	1.83	1.81	1.83	2.26	1.96	2.11	1.95	1.95	1.88	1.87	1.77
2	*O. bicolor* / *O. cleberi*	10.62	**3.15**	1.77	1.51	1.13	1.57	1.40	1.50	1.72	1.26	1.53	1.19	1.33	1.08	1.32	1.74	1.12	1.57
3	*O.* aff. *catherinae*	14.19	10.91	**0.70**	1.55	2.00	1.96	2.05	1.76	1.74	1.85	2.12	2.19	2.39	2.06	1.83	2.29	1.84	1.83
4	*O. catherinae*	11.54	9.66	8.94	**3.51**	1.27	1.76	1.62	1.62	1.39	1.73	1.74	1.74	1.63	1.66	1.81	1.83	1.68	1.81
5	*O. concolor*	9.85	5.60	10.66	6.89	**0.00**	1.37	1.32	1.52	1.60	1.31	1.69	1.50	1.34	1.37	1.65	1.69	1.37	1.44
6	*O. franciscorum*	11.57	9.12	11.54	10.48	6.64	**0.33**	0.87	1.59	1.91	1.67	2.02	1.80	1.49	1.46	1.84	1.64	1.68	1.57
7	*O. mamorae*	11.17	8.89	12.62	10.64	7.20	4.21	**3.71**	1.49	1.79	1.47	1.86	1.57	1.46	1.35	1.71	1.59	1.53	1.48
8	*O. paricola*	11.09	9.44	10.44	10.12	8.17	8.76	9.18	**1.83**	1.80	1.45	2.15	1.74	1.71	1.72	1.62	1.69	1.58	1.43
9	*O. rex*	10.24	10.17	9.49	8.23	8.14	11.12	11.23	10.56	**0.74**	1.80	1.97	1.97	1.89	1.90	1.69	2.22	1.94	1.76
10	*O. roberti*	10.13	7.02	10.54	10.41	5.99	8.59	8.20	7.87	9.70	**0.61**	1.88	1.30	1.76	1.68	1.36	1.79	1.16	1.48
11	*O. rutilus*	14.09	8.88	12.13	10.64	8.56	12.02	11.42	13.24	11.65	10.30	**0.25**	2.05	1.99	1.56	1.87	2.19	1.70	2.04
12	*Oecomys* sp.1	11.22	6.16	12.75	10.39	7.09	9.55	9.00	9.87	10.73	5.97	11.48	**n/c**	1.75	1.69	1.57	1.61	1.31	1.70
13	*Oecomys* sp.2	12.25	6.68	13.33	8.84	5.64	7.07	8.01	9.46	10.09	9.30	10.55	8.65	**n/c**	1.57	1.76	1.78	1.59	1.55
14	*Oecomys* sp.3	12.16	5.71	12.19	10.19	6.46	7.33	7.65	10.00	10.36	8.75	7.78	8.54	7.09	**n/c**	1.58	1.89	1.50	1.86
15	*O. superans*	11.90	7.51	10.58	11.44	8.58	11.04	10.80	9.83	8.94	7.05	10.23	8.02	9.37	8.26	**2.29**	1.93	1.62	1.51
16	*O. sydandersoni*	11.38	10.78	14.32	11.60	8.91	8.88	9.61	9.82	13.18	9.74	13.48	8.45	9.80	10.57	11.58	**2.28**	1.70	1.57
17	*O. tapajinus*	11.22	6.37	10.36	10.32	6.54	9.12	8.96	8.78	11.25	5.64	9.54	6.15	8.02	7.86	9.34	9.56	**0.95**	1.58
18	*O. trinitatis*	10.37	9.03	9.86	11.16	6.69	8.15	8.67	7.69	9.51	7.44	12.04	8.80	7.86	10.79	8.36	8.77	8.17	**0.25**

629

630 **Table 3.** Kimura 2 parameters genetic distance among and within (boldfaced numbers) *Oecomys* clades based on cytochrome b of samples
631 used in concatenated analyzes. Values in percentage. Standard deviation values are shown above boldfaced numbers.

		1	2	3	4	5	6	7	8
1	*O. bicolor*	**1.12**	1.55	1.45	0.76	1.30	1.43	1.26	1.15
2	*O.* aff *catherinae*	11.43	**0.60**	1.18	1.37	1.51	1.48	1.54	1.39
3	*O. catherinae*	11.65	8.38	**3.36**	1.15	1.43	1.30	1.35	1.48
4	*O. cleberi*	4.84	9.98	9.20	**2.12**	1.03	1.11	1.17	1.09
5	*O. franciscorum*	9.08	10.91	11.47	7.52	**n/c**	1.31	1.36	1.39
6	*O. paricola*	11.08	11.68	10.87	8.97	10.16	**1.78**	1.22	1.36
7	*O. roberti*	9.18	10.71	10.61	8.56	10.05	9.31	**1.00**	1.09
8	*O. tapajinus*	7.31	9.73	11.47	7.29	9.63	9.81	6.99	**1.20**

632
633 **Table 4.** Fst values based on cytochrome b sequences of *Oecomys bicolor*, *O. cleberi* and *O. paricola* from the Tapajós River basin.

	O. bicolor	*O. cleberi*		*O. paricola*	
	Middle Teles Pires	West Juruena	Interfluve	Middle Teles Pires	Low Teles Pires
East Tapajós	0.83895	0.62055	0.42155	0.40981	0.25431
West Juruena	-	-	0.27168	-	-
Low Teles Pires	-	-	-	0.65305	-

634

CAPÍTULO II

Integrative analysis supports a new species of the *Oecomys catherinae* complex (Rodentia, Cricetidae) from Amazonia

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Running Header: A new Amazonian *Oecomys* species

Integrative analysis supports a new species of the *Oecomys catherinae* complex (Rodentia, Cricetidae) from Amazonia

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The sigmodontine rodent *Oecomys catherinae* has been recognized as a species complex that includes five different lineages distributed throughout Brazil south of the Amazon river, named in literature according to their geographic position (central, eastern, northern, western, and westernmost). The western lineage has also been referred as *Oecomys* aff. *catherinae* in literature, because it may represent a distinct species. Herein, we used molecular and morphological data to investigate the possible species distinctiveness within the *O. catherinae* complex. From molecular analyses, we recovered the western lineage as a monophyletic

group with high genetic divergence from the other lineages of the complex. This lineage can be differentiated from other lineages of the *O. catherinae* complex and other congeners through a combination of morphometric and morphological characters that includes: smaller size; posterior margin of nasals usually surpassing the maxillary-frontal suture; supraorbital crest moderately developed, similar to the temporal crest; parietal slightly expanded laterally; subsquamosal fenestra present; alisphenoid strut absent; and anterior cingulum of M1 present. The western lineage occurs in the southern Amazonia, in sympatry with the westernmost lineage and other species of *Oecomys*. Herein we describe this lineage as a new species, increasing to 19 the number of species within *Oecomys*.

Key words: Sigmodontinae, Oryzomyini, Species delimitation, Taxonomy.

O roedor sigmodontíneo *Oecomys catherinae* foi reconhecido como um complexo de espécies que inclui cinco linhagens distintas distribuídas ao sul do rio Amazonas, referidas na literatura de acordo com sua posição geográfica (central, leste, norte, oeste e extremo oeste). A linhagem oeste também já foi referida na literatura como *Oecomys* aff. *catherinae*, uma vez que pode representar uma espécie distinta. Neste estudo, utilizamos dados moleculares e morfológicos para investigar a possível distinção de espécies dentro do complexo *O. catherinae*. Nas análises moleculares recuperamos a linhagem oeste como um grupo monofilético, com alta divergência genética das demais linhagens do complexo. Esta linhagem pode ser diferenciada dos demais clados dentro do complexo *O. catherinae* e de outros congêneres a partir de uma combinação de caracteres morfométricos e morfológicos, que inclui: tamanho menor; margem posterior dos nasais geralmente ultrapassando a sutura maxilar-frontal; crista supraorbital levemente desenvolvida, similar à crista temporal; parietal com pequena expansão lateral; fenestra subesquamosal presente; barra do alisfenóide ausente;

e cíngulo anterior do M1 presente. A linhagem oeste ocorre na Amazônia meridional, em simpatria com a linhagem extremo oeste e outras espécies do gênero *Oecomys*. Aqui nós descrevemos esta linhagem como uma nova espécie, elevando para 19 o número de espécies em *Oecomys*.

Palavras–chave: Delimitação de espécies, Oryzomyini, Sigmodontinae, Taxonomia.

In a recent literature review on rodent systematics, D'Elía et al. (2019) showed that integrative taxonomy with molecular, karyotypes, and morphological, data provides a better understanding of the diversification of this group, including aspects of morphological evolution. In a similar way, Rocha et al. (2018) stated that analyses of morphological and molecular variation through space are essential in the identification of cryptic species, such as those belonging to the genus *Oecomys*.

Since Musser and Carleton (1993, 2005) consolidated *Oecomys* as a genus with 15 valid species, *O. sydandersoni* and *O. franciscorum* were described, and *O. tapajinus* was revalidated, the latter two based on molecular, morphological, and morphometric, data (Carleton et al. 2009; Pardiñas et al. 2016; Rocha et al. 2018, respectively). Thus, the genus *Oecomys* currently is one of the most diverse in the tribe Oryzomyini, with 18 recognized species (Pardiñas et al. 2017; Rocha et al. 2018), most of which are distributed in the Amazon Basin (Carleton and Musser 2015; Pardiñas et al. 2017).

Based on a systematic study of *Oecomys* integrating morphological, karyotypic, and molecular data, Suárez-Villota et al. (2018) recognized seven valid species, three undescribed species, and five species complexes, which altogether account 15 species. One of these species complexes is *O. catherinae* (hereafter referred to as the *O. catherinae* complex *sensu lato* in this report), consisting of five lineages according to the authors. Despite great

morphological similarity, these lineages exhibit substantial molecular divergences (*Cytb* K2P: 1.6 – 8.7%), and different karyotypes (2n = 54 – 62) and distributions. Suárez-Villota et al. (2018) treated these lineages as western, westernmost, northern, central, and eastern, clades. The first two clades include specimens from the northern part of Mato Grosso state; the third occurs in northwestern Mato Grosso and southeastern Pará states; the fourth lineage includes specimens from the central region of Brazil; and the fifth lineage includes specimens from the south and southeast of Brazil. The geographic distribution of the latter clade comprises the type locality of *O. catherinae*, which is Joinville, Santa Catarina state (Thomas 1909). Another available name for this species complex is *bahiensis* Hershkovitz, 1960, currently recognized as a junior synonym of *O. catherinae* fide Carleton and Musser (2015). As a nominal taxon also described from the Brazilian Atlantic Forest—particularly for Fazenda Almada, Ilhéus, state of Bahia—*Oryzomys concolor bahiensis* probably applies to the eastern clade of Suárez-Villota et al. (2018).

Populations of *O. catherinae* complex *s. l.* corresponding to the northern and eastern clades already have been identified by Malcher et al. (2017) based on chromosomal differences, but without consistent morphological and molecular differentiation, suggesting that these populations may represent cryptic species. In addition, the western clade has been suggested to represent a distinct taxonomic entity by Saldanha et al. (2019), based on its high genetic divergence from the other clades within the complex.

During the morphological examination of samples from the western clade of Suárez-Villota et al. (2018; = *Oecomys* aff. *catherinae* sequenced by Saldanha et al. 2019), we realized that this form can consistently be distinguished from the other lineages within *O. catherinae* complex *s. l.* and from other congeneric species. To investigate the molecular and morphological distinctiveness within the *O. catherinae* complex *s. l.* and to evaluate whether *Oecomys* aff. *catherinae* (sensu Saldanha et al. 2019) represents a new species, we analyzed

DNA sequences, and external and craniodental morphology of the largest sample from this complex gathered to date, including the holotype of *O. catherinae*.

MATERIALS AND METHODS

Phylogenetic Analysis.—We used nucleotide sequences of the mitochondrial marker Cytochrome *b* (*Cytb*) available from GenBank (http://www.ncbi.nlm.nih.gov/genbank). The data matrix contains 71 specimens of the *O. catherinae* complex *s. l.*, including 14 individuals referred as *Oecomys* aff. *catherinae* by Saldanha et al. (2019). In addition, we included four sequences of *O. rex*, and two from each of the other species recognized in the genus with available sequences, totaling 26 specimens. Sequences of *Euryoryzomys macconnelli*, *E. nitidus*, *Handleyomys intectus*, and *Hylaeamys megacephalus*, were used as an external group (Supplementary Data S1).

We also used nucleotide sequences from the nuclear marker intron 7 β-fibrinogen (*i7-fgb*) available from GenBank and obtained sequence from the specimen UFMT 4118, following the extraction, amplification and sequencing protocols described by Saldanha et al. (2019). This sequence is available at Genbank under number MT978188. This data matrix contains 28 specimens from the *O. catherinae* complex *s. l.*, including 12 individuals of *Oecomys* aff. *catherinae*. We also included sequences of the other species from the genus with available sequences. Sequences of *i7-fgb* and *Cytb* were concatenated into a single data matrix based on the same *i7-fgb* matrix specimens. Sequences of *Oligoryzomys utiaritensis*, "*Handleyomys" melanotis*, *Euryoryzomys nitidus*, and *Hylaeamys megacephalus*, were used as an external group in the analyses of *i7-fgb* and concatenated data (Supplementary Data SD1).

The three data sets of sequences (*Cytb*, *i7-fgb*, and concatenated data) were aligned in the program BioEdit 7.0.5.3 (Hall 1999) with the ClustalW tool. Subsequently, the JModeltest 2.1.6 program (Darriba et al. 2012) was used to define the evolutionary model of each data

matrix in the CIPRES platform (Miller et al. 2010). The data matrix composed of 106 sequences with 801 *Cytb* base pairs was best represented by the GTR + I + G evolutionary model. The data matrix composed of 46 sequences with 736 *i7-fgb* base pairs was best represented by the HKY + G evolutionary model. The *Cytb* + *i7-fgb* concatenated data matrix, consisting of 46 sequences with 1,537 base pairs, was best represented by the GTR + I + G and HKY + G evolutionary models, respectively.

We carried out the Bayesian Inference (BI) analysis using the MrBayes 3.2.6 program (Ronquist et al. 2012) on the CIPRES platform (Miller et al. 2010), enabling four chains, 50 million generations, sampling every 1000 generation, with 25% burnin. Maximum likelihood analysis (ML) was obtained using the Garli program 2.0 (Zwickl 2006), with bootstrap of 1000 replicates and a majority consensus tree summarized in the SumTrees program (Sukumaran and Holder 2010).

The resulting trees were visualized and edited in the FigTree program v1.4.3 (Rambaut 2016). Branch supports were evaluated by Bayesian Posterior Probability (BPP) values in BI and bootstrap values in ML. The genetic distances within and among the clades were calculated in the MEGA7 (Kumar et al. 2016) by uncorrected *p*-method.

To estimate putative species, we used *Cytb* sequences for Bayesian implementation of Poisson Tree Processes (bPTP) analysis (Zhang et al. 2013) and Generalized Mixed Yule Coalescent (GMYC) analysis (Fujisawa and Barraclough 2013). The bPTP method also was used to delimit species with concatenated (*Cytb* + *i7-fgb*) data.

For the bPTP analysis, we used the concatenated tree and *Cytb* tree obtained by BI, exported in Newick tree format. These trees were submitted as input file for the bPTP analysis on the online platform https://species.h-its.org/ptp/.

For GMYC analysis, we used an ultrametric tree obtained from 84 sequences (duplicates were removed) from the *Cytb* marker. From these sequences we generated an .xml

file in BEAUti v. 2.4.8 (Bouckaert et al. 2014) with the evolutionary model GTR + I + G, uncorrelated lognormal Relaxed Clock, 20 million MCMC generations and a priori model of Yule. The ultrametric tree was estimated in BEAST 2.4.8 (Bouckaert et al. 2014) on the CIPRES platform (Miller et al. 2010) with three independent runs, subsequently combined into a single run with 25% burnin. Tracer v1.6 (Rambaut et al. 2014) was used to check the values and effective size of the samples (ESS) generated in BEAST. Trees were summarized into a summary tree using TreeAnnotator v.1.8 (Drummond et al. 2012), visualized in FigTree v1.4.3 (Rambaut 2016) and finally exported in Newick format for GMYC analysis on the online platform https://species.h–its.org/gmyc/ with the Single Threshold model.

Morphological Analysis.—We examined 116 specimens from the *O. catherinae* complex *s. l.* and eight specimens of *O. rex*. This latter species was included in the examined material for comparison purposes, because of the morphological similarity and putative sister-species position with the *O. catherinae* complex *s. l.* previously reported in the literature. The specimens, preserved as skins, skulls, and fluid, are deposited in the following institutions: Museu Nacional da Universidade Federal do Rio de Janeiro (MN); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Paraense Emílio Goeldi (MPEG); Universidade do Estado de Mato Grosso (Unemat); and Universidade Federal de Mato Grosso (UFMT). We also examined the holotypes of *O. catherinae* (MNH 1909.11.19.24) and *O. rex* (MNH 1910.9.29.17), deposited in the Natural History Museum, London. Collection locations and geographic coordinates were obtained from the labels of the specimens and inserted in the QGIS 2.18 program (https://www.qgis.org) to produce maps of collecting localities of vouchers and tissue samples included in this report (Fig. 1).

Some of the specimens of the *O. catherinae* complex *s. l.* included in this study were collected by RVR in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011). They were measured and weighed in the field and prepared

as skins and skeletons. Vouchers were deposited in the Coleção Zoológica da Universidade Federal de Mato Grosso (UFMT).

In the specimens examined, we observed patterns of dorsal and ventral pelage coloration, tail coloration, pattern of distribution of the caudal scales, and number and size of caudal scale hairs. We observed aspects of cranial morphology such as bone shape, presence and position of foramina, fenestrae, and sutures, development and morphology of crests, and morphology of the auditory region and teeth. The nomenclature used to describe the skull and its structures follows Voss et al. (2001) and Weksler (2006). Molar nomenclature follows Reig (1977) and Pires et al. (2016).

Morphometric Analysis.—For the morphometric analyses, specimens were grouped into five different age classes following Voss (1991). Only specimens considered adults (with third upper molar completed erupted) were used. External measurements were obtained directly from specimen label and include head and body length (HBL), length of tail (TL), length of hindfoot with claw (HFL), length of ear (Ear), and mass (Weight). In the absence of HBL, this measurement was calculated by subtracting the length of tail from the total length.

Thirty-one craniodental measurements were obtained using a 0.01 mm precision caliper while specimens were being examined under a stereomicroscope. Thirteen of these measurements were defined by Voss (1988), as follows: breadth across the exoccipital condyles (BOC); breadth across the incisive foramina (BIF); breadth of incisor (BI); breadth of M1 (BM1); breadth of nasals (BN); breadth of the zygomatic plate (BZP); condylo-incisive length (CIL); coronal length of upper molars (CLM); greatest zygomatic breadth (ZB); least interorbital breadth (LIB); length of incisive foramen (LIF); length of nasals (LN); and length of upper diastema (LD). Four measurements followed Carleton and Musser (1995): bullar breadth (BB); length of palatal bridge (LPB); length of rostrum (LR); and occipitonasal length (ONL). The remaining 14 measurements were based on unpublished dissertations

(Percequillo 1988; Flores 2010). These measurements and their respective descriptions are: braincase height (BH), measured from the basisphenoid-basioccipital suture to the frontal-parietal suture on midline; breadth of interparietal (BIP), the greatest breadth of interparietal bone; breadth of m1 (Bm1), the greatest crown breadth of the first lower molar; breadth of rostrum at palate (BRP), measured between most posterior lower edges of infraorbital foramina on ventral side of skull; breadth of rostrum (BR), the distance between the inside margins of nasolachrymal capsule; condylo-zygomatic length (CZL), measured from the most anterior point in anterior edge of zygomatic plate to the articular surface of the condyle on the same side; coronal length of lower molars (CLLM), the crown length from m1 to m3; least condyloid-Incisor breadth (LCIB), measured from the crown of the first cheektooth to the less curvature of the incisor on the same side; length of interparietal (LIP), the greatest length of interparietal bone; length of lower diastema (LLD), measured from the crown of the first cheektooth to the less curvature; mandible height (MH), the distance across cranium at mastoid processes; mastoid breadth (MB), measured from the angular process to the condyloid process on the same side; orbital length (OL), the internal distance between anterior and posterior margins of the orbit; and zygomatic length (ZL), the greatest transverse dimension across the squamosal zygomatic process.

External and craniodental measurements were summarized as basic descriptive statistics. Craniodental dimensions were used in uni- and multivariate statistical analyses. Initially, we carried out a Kolmogorov-Smirnov test to assess the normal distribution of the variables (Sokal and Rohlf 1981). Since most variables displayed a normal distribution, we used the Student's *t*-test to evaluate sexual dimorphism from the total studied sample. This was discarded for the tested variables, except BH and LPB. Subsequent analyses therefore were carried out with males and females together.

Measurements were transformed into a base 10 logarithms to be used in Principal Component Analysis (PCA) and Discriminant Analysis (DA), to investigate which variables respond to most of the data variation and which have the greatest discrimination power among the species, respectively. Scatter plots were provided to visualize how specimens behave in the multivariable space. All statistical tests were carried out using SPSS 22.00 (IBM Corp., Armonk, New York) with a significance level of $\alpha = 0.05$.

RESULTS

Phylogenetic Analysis.—Each of the five clades of the *O. catherinae* complex *s. l.* was recovered with strong support by the *Cytb* gene dataset, as well as the complex itself, supporting a sister relationship between the western clade and remaining clades of the complex. The remaining four clades of the *O. catherinae* complex *s. l.* were recovered as a strongly supported monophyletic group, with the westernmost clade as the most external lineage (Fig. 2).

The *O. catherinae* complex *s. l.* had no statistical support based on the *i7-fgb* gene dataset. The topology differed from that obtained with the mitochondrial marker, with the western clade sister to the eastern clade, followed by westernmost, central, and northern, clades, with no resolution among internal branches (Supplementary Data S2).

With the concatenated data, the five clades of the *O. catherinae* complex *s. l.* were recovered, each with strong support. However, the *O. catherinae* complex *s. l.* itself was not supported, because the western clade was recovered outside the complex, as sister to the other four clades of the complex plus all remaining species of *Oecomys* included in the analysis. The westernmost, central, northern, and eastern, clades formed a strongly supported distinct monophyletic group, with the western clade as the most external branch. A group comprising the central and northern clades also had strong support in this analysis (Fig. 3).

In the *O. catherinae* complex *s. l.*, the western clade presented the highest genetic divergence in *Cytb*, ranging from 6.97% to the eastern clade, to 8.75% with respect to the westernmost clade. Regarding the other *Oecomys* species, divergence of the western clade ranged from 7.36% to *O. concolor*, to 10.29% to *O. rutilus*. Among the other clades in the *O. catherinae* complex *s. l.*, the lowest genetic divergence was 1.38% between the eastern and northern clades, and the highest was 4.66% between the westernmost and northern clades (Table 1).

The species delimitation analysis of bPTP from the *Cytb* tree indicated 21 evolutionary lineages, of which 12 corresponded to species recognized in the literature, as well as two independent lineages within the *O. superans* clade and two within the *O. sydandersoni* clade (Fig. 2). The other five evolutionary lineages recognized by bPTP corresponded to the five clades of *O. catherinae* complex *s. l.* (Figure 2). The GMYC analysis of species delimitation based on the *Cytb* indicated the presence of 20 evolutionary lineages, of which 14 corresponded to species recognized in the literature and six to the *O. catherinae* complex *s. l.* (Fig. 2). The analysis recognized two independent lineages of individuals from the Atlantic forest. One of these lineages comprises specimens from the states of Rio de Janeiro, São Paulo, and southern Minas Gerais, while the other comprises specimens from the states of Espírito Santo and northern Minas Gerais. Although there is some geographical structure in this arrangement, with the former lineage at north and the latter at south, the low support values (BPP = 0.89) and uncorrected p-distance (1.0%) between them led us to provisionally recognize a single lineage (named eastern clade; Fig. 2). The bPTP analysis from the *Cytb* + *i7-fgb* concatenated tree presented 14 evolutionary lineages, of which seven corresponded to species recognized in the literature, as well as two independent lineages within the *O. cleberi* clade. The remaining five lineages corresponded to the five clades of *O. catherinae* complex

s. l. (Figure 3). Based on these results, we treated these five clades of the *O. catherinae* complex *s. l.* as independent lineages in our morphological and morphometric analyses.

Morphological and Morphometric Analyses.—Descriptive statistics of the lineages morphometrically analyzed herein are provided in Table 2. In the Principal Component Analysis (PCA), the first component (PC1) accounted for 54.9% of the total data variation and PC2 for only 8.5% of the variation. The coefficients of all variables showed positive sign in PC1, indicating that this component represents overall size variation. The variables that most contributed to this component were related to the length of the skull (ONL, CIL, and ZL), length of diastema (LD), and height of mandible (MH). With both positive and negative coefficients, PC2 can be associated with skull shape. The variables that contributed most to this component were related to the breadth of first molars (BM1 and Bm1, positive values), length of toothrow (CLM and CLLM, positive values), and bullar breadth (BB, negative value; Supplementary Data S3). The scatter plot of PC1 and PC2 shows specimens of the western lineage overlapping with those of northern and eastern lineages, and slightly overlapping with those of central and westernmost lineages (Fig. 4).

The discriminant analysis indicated that the first canonical variate (CV1) is responsible for 62.1% of the total data variation while the second (CV2) is responsible for 20.9% of the total variation. Craniodental measurements that most contributed to CV1 are related to the skull length (LR, negative value), zygomatic breadth (ZB, negative value), orbital and diastema length (OL and LD, positive values), and interorbital length (LIB, positive value). In CV2, the most important measurements are related to skull and mandible lengths (CIL positive value; OL and LCBI, negative values), and to the bullar and zygomatic breadth (BB and ZB, positive values; Supplementary Data S3).

The scatter plot of CV1 and CV2 shows that the western lineage does not overlap the other four lineages in morphospace (Fig. 4). The discriminant functions generated correctly

classified 95.1% of the analyzed specimens (Supplementary Data S3). The western, central, and westernmost, lineages' specimens were correctly classified in 100% of cases, whereas the eastern and northern lineages specimens were correctly classified in 96.3% and 87.5% of cases, respectively.

In summary, both morphometric and morphological analyses (as described below) allowed us to discriminate the western clade from all remaining clades of the *O. catherinae* complex *s. l.* This is concordant with the molecular analyses, which revealed high genetic divergence between the western clade and the remaining four clades of the *O. catherinae* complex *s. l.* These results in combination provide sufficient evidence to recognize the western clade as a new species of *Oecomys*, which we describe below, and to restrict the *O. catherinae* complex to the eastern, central, northern, and westernmost clades, hereafter referred as *O. catherinae* complex *sensu stricto*.

TAXONOMY

Family Cricetidae Fischer, 1817

Subfamily Sigmodontinae Wagner, 1843

Tribe Oryzomyini Vorontsov, 1959

Genus *Oecomys* Thomas, 1906

***Oecomys* sp. nov.**

Figures 5 – 8; Tables 2 and 3

Oecomys sp. 1: Di-Nizo et al. 2017:843

Oecomys catherinae western clade: Suárez-Villota et al. 2018:190.

Oecomys aff. *catherinae*: Saldanha et al. 2019:44.

Oecomys catherinae western clade: Brandão et al. 2019:266

Holotype.—UFMT 4118, Adult, male, preserved in dry skin, skull and complete postcranial skeleton. Collected by Rogério Vieira Rossi (Field number RVR 89) on 12 May 2014. Hologenotypes *Cytb* and *i7-fgb* are deposited in GenBank (accession number MK874365 and MT978188, respectively).

Measurements (in mm) and body mass of the holotype.—TL= 226, HBL= 106, T= 120, E= 17, HFL= 26, ONL= 28.90, CIL= 25.86, BH= 8.36, CZL= 20.51 ZL= 13.35, LD= 6.71, BZP= 2.96, BN= 3.74, LN= 11.15, LR= 9.08, BR= 4.44, LIB= 5.20, OL= 10.39, ZB= 14.98, LIP= 3.81, BIP= 9.58, BIF= 2.12, LIF= 3.94, BRP= 4.58, LPB= 5.95, MB= 10.32, BOC= 5.99, BB= 4.38, BI= 1.51, BM1= 1.32, CLM= 4.77, Bm1= 1.22, CLLM= 4.97, LLD= 2.89, LCIB= 14.64, MH= 6.67, body mass 33 g.

Paratypes.—UFMT 1773, adult, female, preserved as skin and skull. Collected by T. S. Santos-Júnior on 29 October 2009 (Field number UTP 159) from the Teles Pires Hydroelectric Power Plant, Paranaíta municipality, Mato Grosso state, coordinates: 9º29'06"S, 56º28'19"W, left bank of the Teles Pires River, tributary of the Tapajós River. Measurements: HBL= 105,82 mm, T= 122,05 mm, E= 15,72 mm, HFL= 25,52 mm, weight 34 g. UFMT 1680, adult, male, preserved in skin and skull. Collected by T. S. Santos-Júnior on 18 April 2009 (Field number UTP 02) at the Teles Pires Hydroelectric Power Plant, Paranaíta municipality, Mato Grosso state, coordinates: 9º29'10"S, 56º28'19"W, left bank of the Teles Pires River, tributary of the Tapajós River. Measurements: HBL= 125 mm, T= 132 mm, E= 17 mm, HFL= 24 mm, weight 22 g.

Type locality.—Estância Santa Clara, Alta Floresta municipality, left bank of the Teles Pires River, tributary of the Tapajós River, Mato Grosso state, coordinates: 10º00'25"S, 56º02'17"W (GPS coordinates taken at the trap site).

Additional material.—Twenty specimens from Mato Grosso State, Brazil: skin of MSF1878, female (9°46'12."S, 56°10'15.6"W, Alta Floresta); skin and skull of MZUSP29531, female (10º10'01"S, 59º27'W, Aripuanã); skins of MSF1406, female; MSF1407, 1411, males (11º34'58"S, 55º10'01"W, Cáceres); skin and skull of MZUSP35543, male (11º34'58"S, 55º10'01"W, Cláudia); skin and skull of MZUSP29516, female (13º04'58"S, 53º16'58"W, Gaúcha do Norte); skin and skull of MZUSP35537, female (10º19'01"S, 58º28'58"W, Juruena); skin and skull of UFMT931, female (12°51'S, 58°56'W, Juruena); skins and skulls of UFMT1772, 1774, 1806, females (9º29'06"S, 56º28'19"W, Paranaíta); skins and skulls of AC207, 230, males; AC255, 266, females (15º04'45.9"S, 56º33'15.7"W, Rosário Oeste); skins of RFO013, female; RFO027, 029, 040, males (15°10'33.6"S, 59°59'38.4"W, Vila Bela da Santíssima Trindade). Four specimens from Pará state, Brazil: skins and skulls of UFMT1775, 1776, males, UFMT1686, UFMT1690, females (9º18'40"S, 56º46'05"W, Jacareacanga). One specimen from Rondônia state, Brazil: skin and skull of MPEG34224 (12º43'S, 60º7'W, Vilhena).

Diagnosis.—Soft, long dark reddish-brown dorsal fur (length: 7 – 11 mm); ventral fur dark cream, composed of gray-based hairs throughout the venter and self-dark cream hairs on areas of the throat, neck, forelimbs, and genitalia; caudal tuft absent, but hairs exceed tail tip (< 1 mm). Rostrum narrow and moderately long; posterior margin of the nasals V- or U-shaped, surpassing or aligned to the posterior portion of the maxillary-frontal suture, and premaxillaries terminating anterior to the nasals; supraorbital crest moderately developed, similar to the temporal crest; parietal slightly expanded below the lateral edges of the dorsum of the braincase; hamular process narrow; subsquamosal fenestra present; alisphenoid strut usually absent; complete stapedial circulation (pattern 1, Voss 1988); and anterior cingulum present on the first upper molar.

371 *Morphological description*.—*Oecomys* sp. nov. is characterized by medium size
372 (HBL: 85–135 mm), tail longer (TL: 106–160 mm) than combined head and body (i.e. tail
373 from 104–148% of HBL). Soft and abundant pelage, with hairs varying from 7 – 11 mm in
374 length. Dorsal hairs gray-based with terminal tips dark reddish-brown, mixed with some gray-
375 based and dark brown-tipped hairs (Figure 5A). Flanks lighter than the dorsum, with poorly
376 marked lateral/ventral transition. Venter dark cream with gray-based hairs throughout the
377 belly, except on the throat, neck, forelimbs, and genitalia, where the hairs are self-dark cream
378 (Figure 5A). Hairs shortest and lightest in the rostrum. Mystacial vibrissae abundant and dark
379 brown, with the longest surpassing the posterior edge of the pinnae. Ears light brown at the
380 base and dark brown at the end, with orange and some brown hairs on the outer and inner
381 pinnae surfaces. Manus and pes dorsally covered with white hairs, mixed with brown hairs in
382 the median portion; on the manus, the brown fur covers the arms towards the body. Ungual
383 hairs white, abundant and long, surpassing the claws, except for digit I. Distal end of digit I
384 surpasses the 2nd interdigital pad. Plantar surface with small scales between pads, four
385 developed interdigital pads equal in size and closely positioned, a hypothenar pad smaller
386 than the interdigital pads, and a developed and long thenar pad that extends proximally. Tail
387 completely brown, but slightly bicolor on the proximal portion. Caudal scales with three hairs,
388 with the longest hair exceeding two scale rows in length. Caudal tuft absent, but hairs exceed
389 tail tip about 1 mm in length. Four mammary pairs distributed as follows: one pectoral, one
390 postaxial, one abdominal, and one inguinal (Voss and Carleton, 1993).
391 Skull small when compared to the other lineages of the *O. catherinae* complex *s. s.*
392 (Table 2), and medium compared to other congeners. Rostrum narrow and moderately long.
393 Anterior margins of the nasal bones rounded, surpassing the anterior portion of premaxillary
394 bones; posterior nasal margins V- or U-shaped, aligned or extending beyond the posterior
395 portion of the maxillary-frontal sutures (Figs. 6, 7A), and premaxillaries terminating anterior

to the nasals. Poorly developed zygomatic notch, but dorsally visible. Lacrimal in contact with maxillary and frontal bones. Interorbital region convergent anteriorly, with narrow median region; supraorbital ridges moderately developed, as well as the temporal ridges (Figures 6, 7C). Rounded cranial vault. Interparietal wider than posterior border of frontals, but not contacting the squamosal. Exoccipital crests absent or poorly developed in dorsal view (Fig. 6).

Zygomatic plate broad, slightly projected anteriorly to the maxillary root of the zygomatic, and posterior margin positioned anteriorly to M1. Jugals small, their maxillary and squamosal processes not overlapping. Squamosal root of the zygomatic arch expanded laterally. Parietal slightly expanded below the lateral edges of the dorsum of the braincase (greater expansion in UFMT 1680; Fig. 7E). Hamular process narrow; subsquamosal fenestra small or medium, never larger than the postglenoid foramen (Figure 7E). Lambdoidal crests poorly developed. Mastoid with small fenestra that does not contact the edge of the exoccipital, or with a larger fenestra that reaches the exoccipital edge.

Incisive foramina small, drop or oval shaped, with posterior margin not reaching the first molars. Palate long and wide (sensu Hershkovitz, 1962) with conspicuous posterolateral palatal pits located in deep palatal depressions. Mesopterygoid fossa U-shaped, aligned with the posterior margin of the maxillary; roof of mesopterygoid fossa fully ossified or with small perforations. Parapterygoid fossa dorsally excavated, but not reaching the mesopterygoid level. Alisphenoid strut absent (except in MPEG 34224 and UNEMAT - AC 266). Primitive pattern of stapedial circulation (pattern 1 of Voss [1988]), with stapedial foramen and posterior opening of the alisphenoid canal developed, and presence of squamosal-alisphenoid groove and sphenofrontal foramen. Tegmen tympani not contacting the squamosal, or contacting the squamosal punctually. Small ectotympanic bulla; periotic slightly exposed and

usually reaching the carotid canal. Eustachian tube narrow and short, with edge parallel to the basioccipital suture (Fig. 6).

Mandible robust, with mental foramina dorsally located in the diastema, anterior to m1. Upper and lower masseteric ridges converge and fuse only in the anterior portion, below the anterior portion of m1. Capsular process lower incisor small and conspicuous. Coronoid process small and pointed. Angular process short. Condyloid process elongated (Fig. 6).

Upper incisors opisthodont ungrooved, with yellow-orange anterior enamel surfaces; upper molar rows parallel arranged in opposite labial-lingual pairs. Molars are pentalophodont and brachyodont. Upper first molar (M1): anterior cingulum (i.e. stylar shelf on the anterior border of the procingulum, positioned anteriorly to the anterocone) present (refer to Pires et al. 2016 for description and comments on this structure); procingulum with a central fossete; anterocone not divided by anteromedian flexus (anteromedian flexus present in UFMT 1773, dividing the procingulum into anterolabial and anterolingual conules); anteroloph present and connected to the anterocone and paracone by parastyle; paracone connected to protocone by median mure, with long paraflex; protocone connected to the anterior mure and separated from the anterocone by protoflexus; paralophule present in paracone and connected to the mesoloph; posteroloph fused to metacone, with presence of fossetus derived from the posteroflexus; labial and lingual accessory roots absent; labial and lingual cingula absent (Fig. 8). Upper second molar (M2): Anteroloph present; anterolingual cingulum present, but poorly developed in the anterior portion of the protocone; lingual cingulum present; paralophule connecting paracone to mesoloph; posteroloph present (Fig. 8). Upper third molar (M3): smaller than the half of M1 and larger than half of M2; mesoloph and short posteroloph present; hypocone slightly reduced with respect to protocone and separated from the protocone by hypoflexus; reduced metacone (Fig. 8).

Lower first molar (m1): anteromedian flexid present, dividing procingulum into anterolabial and anterolingual conulids; procingulum with anteromedian fossetid well-developed. Anterolabial cingulum connected to a well-developed protostylid; ectolophid present; metaconid with metalophulid connected to mesolophid that is fused in its distal portion to the entoconid; posterolophid long and fused by wear to the entoconid; hypolophulid present (Fig. 8). Lower second molar (m2): anterolabial cingulum present and well-developed; entoconid small; small ectolophid and ectostylid present; posterolophid connected to the entoconid (Fig. 8). Lower third molar (m3): smaller than half of m1 and same length as m2; anterolabial cingulum present; small ectolophid and ectostylid present; posterolophid probably present and connected to the entoconid, that is reduced (Fig. 8).

Karyotype.—Specimens of the western clade exhibited 2n=54, FN=54, with a small submetacentric pair (pair 1) and all the other autosomes acrocentric (pairs 2−26). The X-chromosome is large and submetacentric, with a short heterochromatic arm, and the Y-chromosome is medium sized, metacentric and entirely heterochromatic (see Suárez-Villota et al. 2018).

Etymology.—The specific name is a geographical reference to the Brazilian state of Mato Grosso, where the holotype was collected and where most of the species distribution is located.

Distribution and sympatry.—*Oecomys* sp. nov. occurs in southern Amazonia; the species' distributional area extends from Jacareacanga (on the right bank of the Teles Pires river in the extreme southwest of Pará state) southward to Cáceres (in the extreme southwest of Mato Grosso state), and from Vilhena (Rondônia state) and Aripuanã (between the Juruena and Aripuanã rivers, in Mato Grosso state) eastward to Gaúcha do Norte (on the left bank of the Xingu River, Mato Grosso state).The species occurs in sympatry with *O. cleberi* and the

westernmost lineage of *O. catherinae* complex *s. s.* on the west margin of the Juruena River, Mato Grosso state; and with *O. bicolor*, *O. paricola*, and *O. roberti*, in the municipality of Cláudia, Mato Grosso state (Suárez-Villota et al. 2018; Saldanha et al. 2019).

Habitat information.—*Oecomys* sp. nov. was collected in forested habitats from the southern Amazonia, particularly from the Amazonia-Cerrado transition zones, and the edge of the Pantanal biome. Also, two collecting points are located in the Cerrado biome (Localities 6 and 9; Fig. 1), but habitat information was not available on the vouchers' labels.

Comparisons.—*Oecomys* sp. nov. is distinguished from *O. catherinae* complex *s. s.* lineages by exhibiting smaller body size (Tables 2 and 3; Fig. 5) and short dorsal pelage (7 – 11 mm) with dark reddish-brown coloration, versus long dorsal pelage (9 – 15 mm) with reddish-brown color. In addition, the new species has a darker cream ventral pelage when compared to the central and eastern lineages (Fig. 5; Table 3).

The skull is smaller in *Oecomys* sp. nov. than in *O. catherinae* complex *s. s.* lineages (Table 2). The rostrum is narrow and moderately long in the new species, but is wide and long in eastern and westernmost lineages of *O. catherinae* complex *s. s.*, wide and short in the central lineage, and narrow and short in northern lineage (Table 3). The posterior margin of the nasals extends beyond the posterior portion of the maxillary-frontal suture in *Oecomys* sp. nov. (Fig. 7A), contrasting with the *O. catherinae* complex *s. s.* lineages, whose posterior margin of the nasals does not reach or is aligned to the posterior part of the maxillary-frontal suture (Fig. 7B). In *Oecomys* sp. nov., the interorbital region is narrower compared to the eastern, westernmost, and northern, lineages of *O. catherinae* complex *s. s.* Moreover, the supraorbital and temporal crests are moderately developed in the new species (Fig. 7C), whereas the supraorbital crest is dorsolaterally and distinctly more developed than the temporal crest in the *O. catherinae* complex *s. s.* lineages (Fig. 7D). The subsquamosal

fenestra always is present in *Oecomys* sp. nov. (Fig. 7E), while it is reduced in the eastern and westernmost lineages of *O. catherinae* complex *s. s*., and fully ossified in the central and northern lineages (Fig. 7F). The parietal is slightly expanded below the lateral edges of the dorsum of the braincase in *Oecomys* sp. nov. (Fig. 7E), while it is deeply expanded onto the lateral surface of the braincase in the *O. catherinae* complex *s. s*. lineages (Fig. 7F).

Because *O. catherinae* is externally similar to *O. rex* in pelage color and texture, we provide comparisons of *Oecomys* sp. nov. with the latter species. Externally, the new species differs from *O. rex* by exhibiting shorter dorsal fur (7 – 11 mm versus 9 – 14 mm in *O. rex*) and lacking a caudal tuft (versus a small tuft present in *O. rex*). Cranially, the skull is smaller in *Oecomys* sp. nov. (mean 28.9 mm) than in *O. rex* (mean 31.05 ± 3.10 mm; $n = 8$); the supraorbital and temporal crests are moderately developed in the former species (versus strongly developed supraorbital crests, joining in a prominent temporal crest in *O. rex*); and the subsquamosal fenestra always is open in *Oecomys* sp. nov., while it is reduced or absent in *O. rex*.

Oecomys sp. nov. can be distinguished from other congeneric sympatric species, such as *O. bicolor*, *O. cleberi*, *O. roberti*, and *O. paricola*, by exhibiting medium body and cranial size (versus smaller body and cranial size in *O. bicolor* and *O. cleberi*); dark reddish-brown dorsal coloration (versus orangish-brown in *O. bicolor* and *O. cleberi*; reddish to orangish-brown in *O. roberti*; and reddish-brown in *O. paricola*); dark cream ventral coloration (versus totally white or cream venter in *O. bicolor* and *O. cleberi*; fully white or a white ventral midline with gray-based lateral bands in *O. roberti*); and absence of caudal tuft (versus presence of caudal tuft in *O. bicolor*, *O. cleberi*, and *O. paricola*). Detailed descriptions of the mentioned species can be found in Rocha et al. (2012), Carleton and Musser (2015), and Rocha et al. (2018).

DISCUSSION

Although *O. catherinae* was recognized as monotypic by Carleton and Musser (2015) and Pardiñas et al. (2017), the species exhibits great genetic diversity and was reported as a species complex by Malcher et al. (2017) and Suárez-Villota et al. (2018). In this study, we analyzed the five clades of the *O. catherinae* complex *s. l.* currently recognized as possible distinct lineages (Suárez-Villota et al. 2018) and found a body of evidence that allowed us to positively recognize the western clade of previous studies as a new species.

As noted by Carstens et al. (2013), the appropriate way to conduct a species delimitation is to analyze data with a wide variety of methods and delimit lineages that are consistent across the results. In this report, the western lineage of the *O. catherinae* complex *s. l.* was recovered as monophyletic, with strong support in all the phylogenetic and species delimitation analyses employed herein. In addition, the western lineage was discriminated from remaining lineages of the complex in multivariate space, exhibited several qualitative characters that distinguish it from these latter lineages, and presented the highest interlineage genetic distance values within the complex. Indeed, the genetic distance between *Oecomys* sp. nov. and the westernmost lineage, with which it is sympatric, is high (8.75%) when compared to the distances recorded between the new species and the other *O. catherinae* complex *s. s.* lineages (6.97 – 7.38%). These are higher values compared to those reported for closely related *Oecomys* species in the literature, such as *O. franciscorum* and *O. mamorae* (7.0%; Pardiñas et al. 2016), and *O. tapajinus* and *O. roberti* (5.8%; Rocha et al. 2018).

The western lineage also presents an exclusive karyotype within the complex. According to Suárez-Villota et al. (2018), it has a diploid number 2n = 54 and fundamental number FN = 54. In contrast, other lineages of the *O. catherinae* complex *s. l.* present distinct karyotypes, with 2n = 60 in the central, eastern, and westernmost, lineages, and 2n = 62 in the northern lineage (Langguth et al. 2005; Di-Nizo et al. 2017; Malcher et al. 2017; Suárez-

Villota et al. 2018). Altogether, these results give us strong support to recognize the western lineage as an independent species, herein described as *Oecomys sp. nov.*

On the other hand, the remaining four clades of the *O. catherinae* complex *s. l.* (eastern, central, northern, and westernmost) showed low genetic distances among themselves, no exclusive combination of morphological characters, and greatly overlapped in the multivariate space. Moreover, the GMYC analysis recognized two different evolutionary lineages in the central clade, the westernmost clade was not recovered with adequate support, and the central clade was not recovered as a monophyletic group in the BI with *i7-fgb* data (Supplementary Data S2). These results prevent us for now to recognize these four lineages as different species, instead retaining them in the *O. catherinae* complex *s. s*. In this sense, we again follow Carstens et al. (2013), who stated that species delimitation studies should be conservative and, in most contexts, it is better to fail to delimit species than it is to falsely delimit entities that do not represent actual evolutionary lineages.

Our phylogenies showed mitonuclear discordance, with the mitochondrial marker recovering the new species as sister to the *O. catherinae* complex *s. s*., and the nuclear marker recovering *Oecomys* sp. nov. as sister to the eastern lineage of this complex. According to Després (2019), mitonuclear discordance can result from several factors, such as incomplete lineage sorting, asymmetrical introgression, or natural selection. Mitochondrial and nuclear DNA also respond differently to demographic fluctuations, such as during glacial periods, for which mitochondrial DNA will diverge while nuclear genome will retain variability (Després 2019). The phylogenies presented by Suárez-Villota et al (2018) also showed mitonuclear discordance for the *O. catherinae* complex *s. l.* clades. The authors discarded the introgressive hybridization hypothesis, because the samples of the eastern clade exhibit 2n = 60 rather than 2n = 57 or 58, which would be expected in hybrids between the western (= *Oecomys* sp. nov. ; 2n = 54) and the other lineages of the *O. catherinae* complex *s. l.* (2n = 60 and 62).

566 The new species is distributed in southern Amazonia and the Amazonia – Cerrado
567 transition areas, where it occurs in sympatry with the westernmost lineage of the *O.*
568 *catherinae* complex *s. s*. and other four species of the genus (*O. bicolor*, *O. cleberi*, *O.*
569 *paricola*, and *O. roberti*). Sympatry among *Oecomys* species in the Amazonian region has
570 been reported by several authors (e.g., Voss and Emmons, 1996; Patton et al. 2000; Voss et al.
571 2001; Rocha et al. 2011; Suárez-Villota et al. 2018; Saldanha et al. 2019). In contrast,
572 sympatry between two different lineages of the same *Oecomys* species complex only has been
573 reported recently by Suárez-Villota et al. (2018), who recorded sympatry for lineages both of
574 the *O. roberti* complex and the *O. catherinae* complex (= *O. catherinae* complex *s. l.* in this
575 report). By using morphological and molecular markers, Rocha et al. (2018) showed that one
576 of the *O. roberti* complex lineages pointed out by Suárez-Villota et al. (2018) actually
577 represents a distinct species, for which the name *O. tapajinus* was available. Similarly, our
578 results based on several kinds of evidences gave us enough support to recognize Suárez-
579 Villota et al.'s (2018) western lineage of the *O. catherinae* complex as *Oecomys* sp. nov. .
580 The description of *Oecomys* sp. nov. in this report increases the richness within the
581 genus from 18 (Pardiñas et al. 2017; Rocha et al. 2018) to 19 species in *Oecomys*. This, allied
582 with the restriction of the *O. catherinae* complex to the eastern, central, northern, and
583 westernmost, lineages, partially reduces the taxonomic intricacies of this complex. Regarding
584 the four lineages of the *O. catherinae* complex *s. s*., our results showed that they are
585 morphologically similar, and data from the literature show they present low diploid number
586 variation (2n = 60 and 62). Among them, the westernmost lineage is that with highest genetic
587 divergence (from 3.99 – 4.66%). Similar results were found by Suárez-Villota et al. (2018) in
588 their analyses using *Cytb* only and a concatenated dataset of *Cytb* and two nuclear markers.
589 Specimens of westernmost lineage are rare in collections (we have examined only
590 eight, some of which are young), and collecting more individuals is important for better

591 evaluating whether this lineage merits consideration as a species. Finally, the relationships
592 among the eastern, central, and northern, lineages still are inconclusive based on our results,
593 corroborating the findings of Suárez-Villota et al. (2018). Further phylogenetic studies with a
594 greater number of genetic markers are required to determine how diversification of these
595 lineages took place.

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608 ## SUPPLEMENTARY DATA

609 **Supplementary Data SD1**.—List of specimens of *Oecomys* analyzed in the present study.
610 **Supplementary Data SD2**.—Bayesian inference topology based on the nuclear intron 7 β-
611 fibrinogen dataset.
612 **Supplementary Data SD3**.—Quantitative morphological analyses of the *Oecomys*
613 *catherinae* complex *lato sensu*.

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FIGURES

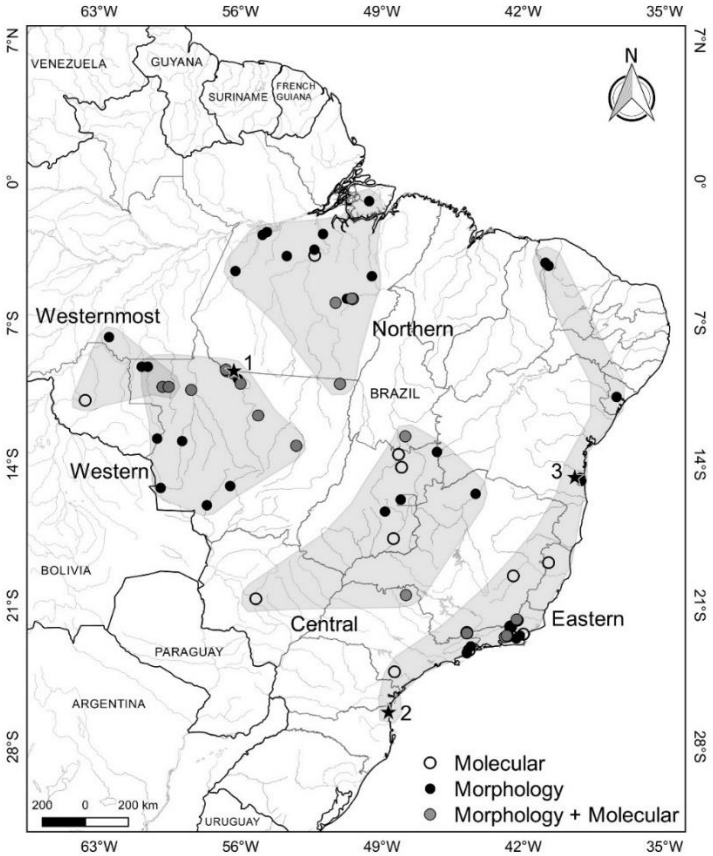


Fig. 1.—Map of samples of the *Oecomys catherinae* complex *s. l.* included in this study, with discrimination of the lineages recognized for the complex. Stars indicate the type localities of *Oecomys* sp. nov. (1; western lineage), *Oecomys catherinae* (51), and *Oryzomys concolor bahiensis* (39).

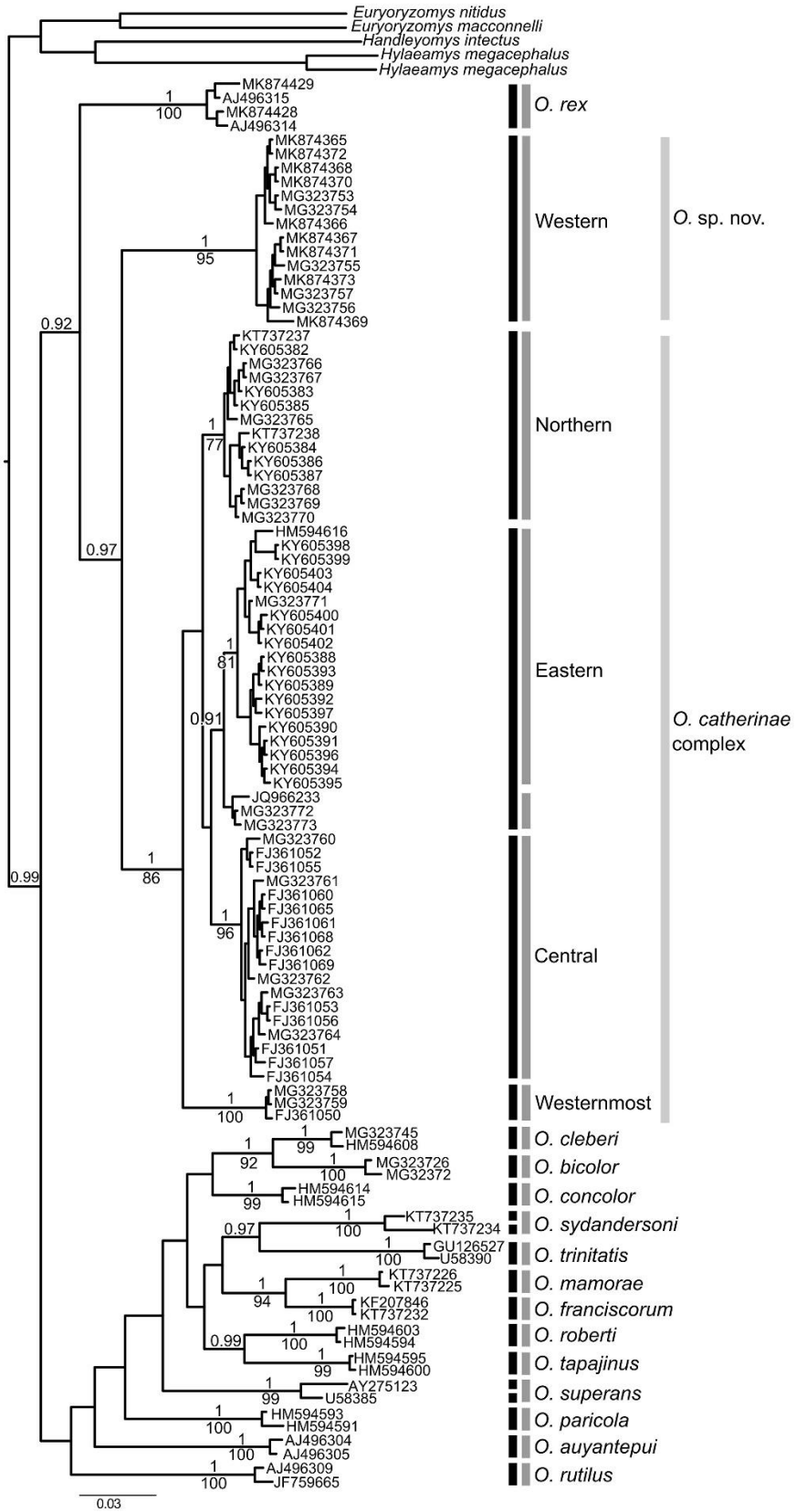


Fig. 2.—Bayesian Inference topology based on mitochondrial Cytochrome b gene. Numbers above the branches indicate bayesian posterior probabilities and below the branches indicate

maximum likelihood bootstrap values. Side bars indicate evolutionary lineages recognized in bPTP (black) and GMYC (medium gray) analyses. The light gray side bars indicate *Oecomys* sp. nov. and the *Oecomys catherinae* complex *s.s.* recognized in this study. The sample data are presented in Supplementary Data S1.

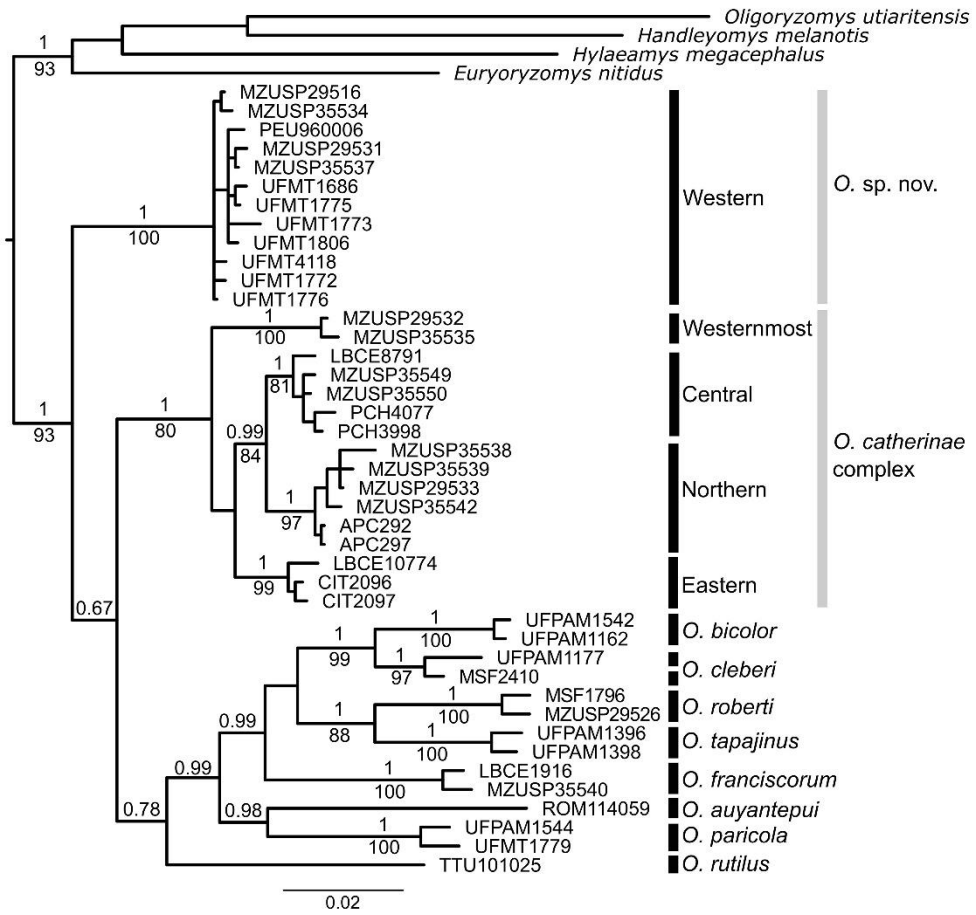
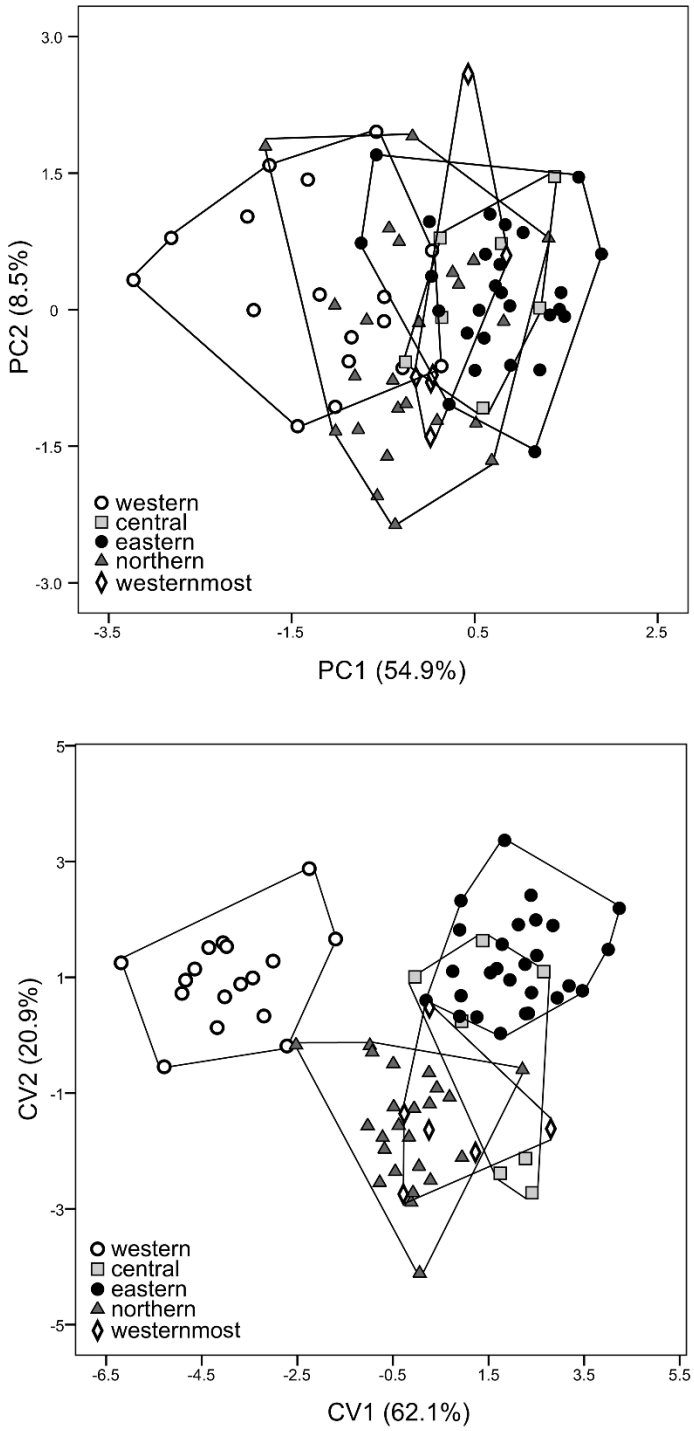


Fig. 3.—Bayesian Inference topology based on the mitochondrial Cytochrome b gene and nuclear intron 7 β-fibrinogen concatenated. Numbers above the branches indicate bayesian posterior probabilities and below the branches indicate maximum likelihood bootstrap values. The black side bars indicate evolutionary lineages recognized in the analysis of bPTP and the light gray bars indicate *Oecomys* sp. nov. and the *Oecomys catherinae* complex recognized in this study. Sample data is provided in Supplementary Data S1.



783

784 **Fig. 4**.—Scatterplot of principal components 1 and 2 of Principal Component Analysis (top)

785 and of canonical variate 1 and 2 of Discriminant Analysis (bottom) of 31 craniodental

786 measurements of the *Oecomys catherinae* complex *s. l.* The western lineage corresponds to

787 *Oecomys* sp. nov. described in this study.

788

789 **Fig. 5**.—Dorsal view (above) and ventral view (below) of: A) the holotype of *Oecomys* sp.

790 nov. (UFMT 4118), and specimens of the *Oecomys catherinae* complex lineages: B) eastern

791 (MN 10748), C) central (PCH 4077), D) westernmost (APC 292), and E) northern (MZUSP

792 35535 above, and MZUSP 29532 below).

Fig. 6.—Dorsal, ventral and lateral views of skull and lateral view of mandible of the holotype (UFMT 4118) of *Oecomys* sp. nov. from Estância Santa Clara, Alta Floresta, Mato Grosso state, Brazil. Scale: 5 mm.

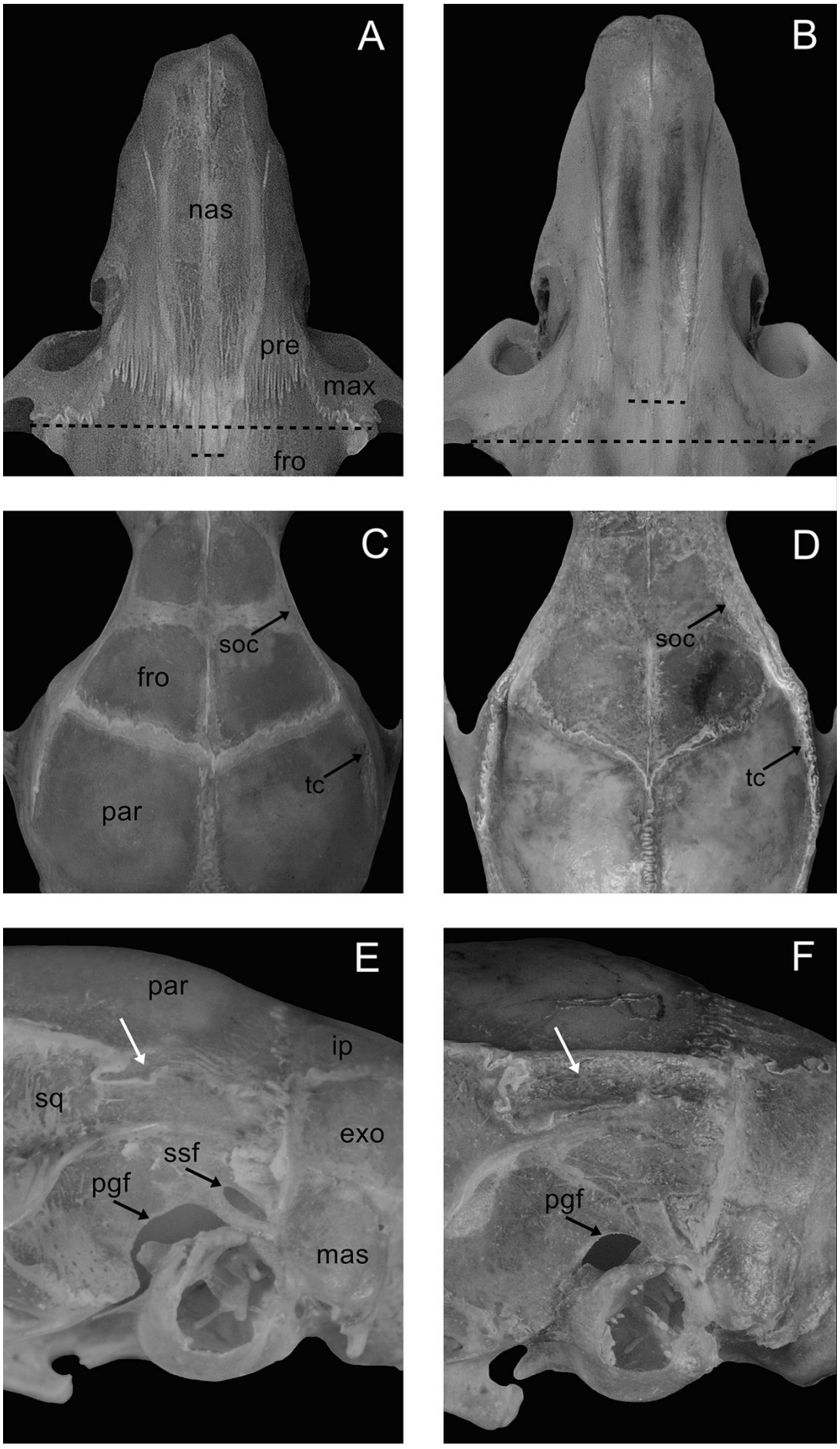

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Fig. 7.—Anatomical traits that differentiate *Oecomys* sp. nov. (UFMT 4118) from the *O. catherinae* complex lineages: A) posterior nasal terminus (shorter dashed line) surpassing the maxillary-frontal suture (longer dashed line) and the premaxillaries terminating anterior to the nasal in *Oecomys* sp. nov. ; B) posterior nasal terminus (shorter dashed line) anterior to the maxillary-frontal suture (longer dashed line) and the premaxillaries aligned to the posterior margin of the nasals in *O. catherinae* (BNMH 9.11.19.24); C) supraorbital and temporal crests poorly developed in *Oecomys* sp. nov. ; D) supraorbital crest dorsolaterally expanded in *O. catherinae* northern lineage (MPEG 39899), being more developed than temporal crest; E) subsquamosal fenestra present, always smaller than postglenoid foramen, and parietal slightly expanded below the lateral edges of the dorsum of the braincase (white arrow) in *Oecomys* sp. nov. ; F) subsquamosal fenestra ossified and parietal deeply expanded onto the lateral surface of the braincase (white arrow) in *O. catherinae* northern lineage (MPEG 39899). Abbreviations: exo, exoccipital; fro, frontal; ip, interparietal; mas, mastoid; max, maxillary; nas, nasal; par, parietal; pgf, postglenoid foramen; pre, premaxillary; soc, supraorbital crest; sq, squamosal; ssf, subsquamosal fenestra; tc, temporal crest.

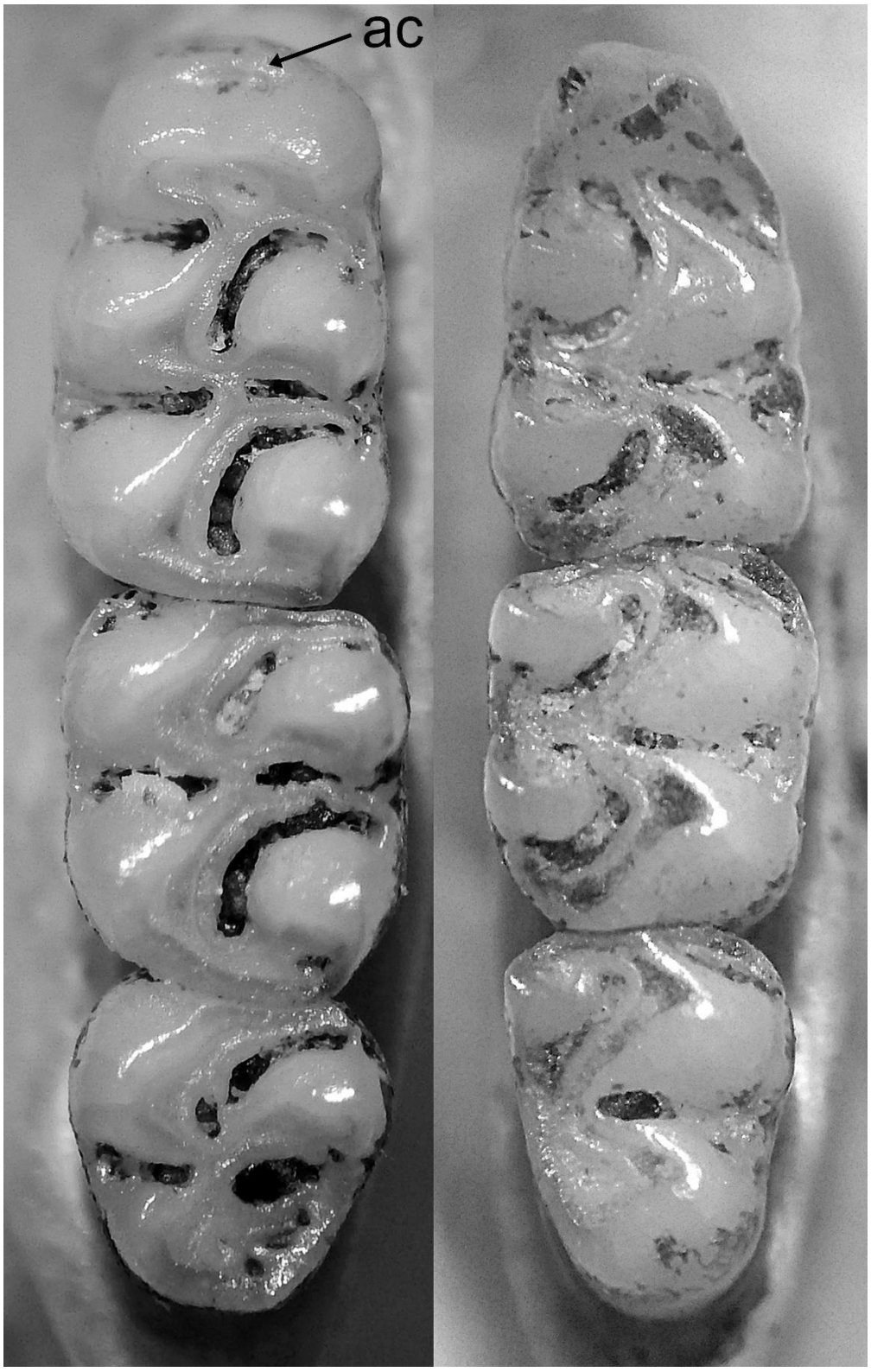

Fig. 8.—Paratype of *Oecomys* sp. nov. from Teles Pires Hydroelectric Power Plant, Paranaíta municipality, Mato Grosso state, Brazil (UFMT 1680): upper molar series (left) and lower molar series (right). Abbreviation: ac, anterior cingulum.

TABLES

Table 1.—Uncorrected p-distances of the Cytochrome b within and among *Oecomys* species. Eastern, central, northern, western, and westernmost, correspond to lineages in the *Oecomys catherinae* complex *sensu lato*. Values above diagonal correspond to standard deviation and bold numbers to genetic distance within clades. Values in percentage.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Western*	**0.77**	1.27	1.22	1.25	1.47	1.46	1.42	1.34	1.29	1.38	1.50	1.48	1.43	1.50	1.34	1.41	1.38	1.38	1.41
2	Central	7.38	**0.24**	0.57	0.66	1.04	1.42	1.41	1.48	1.45	1.58	1.64	1.53	1.55	1.58	1.47	1.53	1.52	1.51	1.42
3	Eastern	6.97	1.76	**0.88**	0.49	1.05	1.34	1.37	1.43	1.39	1.51	1.55	1.51	1.49	1.53	1.43	1.46	1.48	1.47	1.34
4	Northern	7.16	1.85	1.38	**0.34**	1.15	1.36	1.41	1.47	1.44	1.56	1.56	1.52	1.56	1.60	1.48	1.49	1.54	1.51	1.38
5	Westernmost	8.75	3.99	4.14	4.66	**0**	1.42	1.67	1.57	1.58	1.66	1.68	1.67	1.56	1.50	1.62	1.55	1.70	1.64	1.39
6	*O. auyantepui*	9.37	8.48	7.59	7.87	8.08	**0.6**	1.51	1.46	1.42	1.49	1.49	1.47	1.43	1.55	1.46	1.54	1.59	1.54	1.36
7	*O. bicolor*	8.30	8.97	8.83	8.92	11.53	9.43	**0.3**	1.01	1.35	1.36	1.34	1.53	1.48	1.52	1.34	1.60	1.32	1.33	1.60
8	*O. cleberi*	7.89	9.41	9.00	9.37	10.18	8.08	4.34	**0.6**	1.28	1.29	1.44	1.50	1.35	1.52	1.27	1.57	1.27	1.42	1.60
9	*O. concolor*	7.36	8.53	8.11	8.19	9.43	7.93	6.89	6.44	**0.3**	1.15	1.41	1.43	1.24	1.53	1.34	1.38	1.39	1.35	1.51
10	*O. franciscorum*	8.08	10.31	9.62	9.75	10.78	9.88	7.34	6.89	5.24	**0**	1.26	1.43	1.35	1.57	1.41	1.40	1.40	1.51	1.61
11	*O. mamorae*	9.56	11.44	10.41	10.35	11.98	9.88	7.63	8.68	7.63	5.69	**0**	1.56	1.45	1.55	1.38	1.53	1.51	1.47	1.63
12	*O. paricola*	9.64	9.71	9.77	9.67	11.08	8.98	9.43	8.68	8.83	8.08	10.48	**1.2**	1.41	1.66	1.32	1.38	1.49	1.52	1.62
13	*O. roberti*	8.79	9.12	9.09	9.24	9.28	8.23	8.53	7.56	5.99	6.74	8.23	7.78	**0.3**	1.45	1.41	1.36	1.36	1.39	1.63
14	*O. rutilus*	10.29	10.84	10.45	10.86	9.58	9.88	9.43	9.13	9.88	10.78	11.08	11.38	9.13	**1.2**	1.50	1.62	1.61	1.69	1.55
15	*O. superans*	8.02	9.55	9.32	9.39	10.93	9.13	8.08	7.49	7.78	8.23	8.08	7.19	7.49	9.88	**1.5**	1.45	1.38	1.31	1.43
16	*O. sydandersoni*	8.90	9.86	9.35	9.39	10.03	9.43	9.88	9.73	7.49	6.74	9.13	7.86	7.04	11.83	8.68	**0.3**	1.54	1.46	1.67
17	*O. tapajinus*	7.78	9.68	9.59	9.75	11.98	10.78	6.74	6.89	7.34	6.89	8.38	9.43	6.74	11.38	7.78	8.83	**0**	1.48	1.63
18	*O. trinitatis*	7.87	8.98	9.09	9.24	10.48	9.58	7.34	8.38	7.34	9.58	8.98	9.43	7.49	12.28	7.34	8.83	8.98	**0**	1.66
19	*O.rex*	8.19	7.55	7.23	7.06	7.63	7.63	10.63	10.18	8.38	10.63	11.08	10.33	9.58	9.96	8.23	11.08	10.48	10.03	**0.5**
20	Outgroup	12.45	14.17	13.60	13.67	14.13	12.66	13.62	13.14	13.14	13.53	13.23	14.31	12.66	14.55	13.98	13.98	13.29	14.19	14.07

* Referred as *Oecomys* aff. *catherinae* by Saldanha et al. (2019). Named as *Oecomys* sp. nov. in this report.

822 **Table 2**.—External, cranial and dental measurements (in mm) and weight (in grams) of adult specimens of *Oecomys* sp. nov. and lineages of the

823 *Oecomys catherinae* complex *stricto sensu*. See "Material and Methods" section for abbreviations.

	Oecomys sp. nov.	*Oecomys catherinae* complex *stricto sensu*				*Oecomys catherinae*
		Eastern	Central	Northern	Westernmost	
	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Holotype[a]
HBL	111.46 ± 14.84 85–135 (23)	131.69 ± 11.16 105–151 (26)	129 ± 13.65 112– 150 (6)	123.64 ± 12.08 103–146 (18)	126.43 ± 6.9 120–140 (7)	132
TL	130.27 ± 15.68 106–160 (23)	157.08 ± 10.73 138–180 (25)	144.67 ± 8.36 131–155 (6)	138.89 ± 10.36 121–154 (18)	141.57 ± 16.45 115–161 (7)	166
HFL	25.19 ± 1.52 21–27.04 (23)	28.46 ± 3.61 23–38 (25)	26.33 ± 3.78 20–31 (6)	26.47 ± 1.72 22–30 (18)	27.86 ± 1.21 26–29 (7)	30
Ear	16.64 ± 2.32 12–21 (23)	18.29 ± 2.89 12–24 (26)	16.67 ± 3.39 11–20 (6)	17.65 ± 1.5 15–20 (17)	18.36 ± 1.55 15–19.5 (7)	20
Weight	40.37 ± 12.37 22–63 (23)	73.63 ± 19.55 33–110.7 (23)	51.67 ± 2.89 50–55 (3)	58.69 ± 14.11 35–90 (16)	72.2 ± 13.79 54–90 (5)	-
BB	4.69 ± 0.25 4.35–5.05 (15)	5.26 ± 0.29 4.52–5.68 (27)	5.20 ± 0.20 4.96–5.46 (7)	4.98 ± 0.30 4.33–5.62 (24)	4.93 ± 0.15 4.70–5.18 (6)	4.52
BH	8.44 ± 0.53 7.62–9.61 (15)	9.07 ± 0.37 8.53–9.89 (28)	9.33 ± 0.32 8.89–9.81 (7)	8.71 ± 0.34 7.97–9.49 (24)	8.86 ± 0.17 8.60–9.10 (7)	8.84
BI	1.59 ± 0.16 1.30–1.86 (16)	1.91 ± 0.21 1.63–2.74 (27)	1.83 ± 0.15 1.62–2.07 (7)	1.80 ± 0.17 1.47–2.28 (24)	1.81 ± 0.09 1.72–1.98 (7)	2.74
BIF	2.30 ± 0.26 1.94–2.70 (16)	2.54 ± 0.20 2.04–2.94 (28)	2.47 ± 0.16 2.19–2.65 (7)	2.27 ± 0.21 1.74–2.77 (24)	2.46 ± 0.17 2.34–2.83 (7)	2.65
BIP	9.45 ± 0.59 8.08–10.17 (16)	10.11 ± 0.52 8.62–10.89 (27)	10.03 ± 0.36 9.47–10.56 (7)	9.79 ± 0.35 9.27–10.42 (24)	9.98 ± 0.63 9.20–10.92 (7)	8.62

	Oecomys sp. nov.	*Oecomys catherinae* complex *stricto sensu*				*Oecomys catherinae*
		Eastern	Central	Northern	Westernmost	
	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Holotype[a]
BM1	1.44 ± 0.14 1.32–1.76 (16)	1.47 ± 0.06 1.36–1.61 (28)	1.46 ± 0.10 1.34–1.61 (7)	1.43 ± 0.11 1.21–1.72 (24)	1.45 ± 0.11 1.32–1.66 (7)	1.46
Bm1	1.27 ± 0.07 1.18–1.42 (16)	1.35 ± 0.08 1.12–1.52 (28)	1.37 ± 0.09 1.24–1.53 (7)	1.27 ± 0.08 1.12–1.40 (24)	1.32 ± 0.08 1.23–1.46 (7)	1.28
BN	3.63 ± 0.33 2.83–4.32 (16)	4.02 ± 0.31 3.42–4.61 (27)	3.96 ± 0.23 3.60–4.26 (7)	3.74 ± 0.25 3.36–4.29 (24)	3.80 ± 0.22 3.50–4.02 (7)	-
BOC	6.46 ± 0.24 5.99–6.97 (15)	7.12 ± 0.28 6.47–7.58 (28)	7.13 ± 0.21 6.70–7.40 (7)	6.89 ± 0.23 6.50–7.31 (23)	6.89 ± 0.28 6.50–7.25 (7)	7.43
BRP	4.79 ± 0.29 4.40–5.52 (16)	5.46 ± 0.41 4.61–6.19 (28)	5.00 ± 0.38 4.30–5.50 (7)	5.16 ± 0.28 4.72–5.67 (24)	5.34 ± 0.30 4.95–5.83 (7)	6.13
BR	4.70 ± 0.25 4.18–5.00 (16)	5.07 ± 0.40 4.00–5.67 (28)	5.13 ± 0.32 4.65–5.47 (7)	4.93 ± 0.30 4.20–5.54 (24)	5.25 ± 0.32 4.93–5.85 (7)	5.18
BZP	3.07 ± 0.36 2.45–3.70 (16)	3.66 ± 0.23 3.21–4.21 (27)	3.64 ± 0.20 3.37–3.87 (7)	3.42 ± 0.27 2.85–3.93 (24)	3.40 ± 0.51 2.80–4.35 (7)	3.95
CIL	26.82 ± 1.76 23.49–29.74 (15)	30.19 ± 1.42 27.07–32.62 (28)	29.94 ± 0.97 28.80–31.09 (7)	28.54 ± 1.46 25.73–32.16 (24)	28.94 ± 0.98 27.35–30.55 (7)	31.04
CLM	4.94 ± 0.25 4.68–5.46 (16)	5.17 ± 0.17 4.86–5.57 (28)	5.14 ± 0.16 4.90–5.33 (7)	4.95 ± 0.21 4.64–5.34 (24)	5.04 ± 0.31 4.73–5.62 (7)	5.26
CLLM	5.04 ± 0.18 4.78–5.50 (16)	5.24 ± 0.14 4.98–5.52 (28)	5.20 ± 0.19 5.04–5.48 (7)	5.02 ± 0.19 4.64–5.37 (24)	5.12 ± 0.38 4.75–5.91 (7)	5.46
CZL	21.18 ± 1.46 18.18–23.40 (15)	23.92 ± 1.04 21.86–25.57 (27)	23.81 ± 0.78 22.90–24.96 (7)	23.09 ± 2.24 20.50–32.28 (24)	22.87 ± 0.81 21.72–24.32 (7)	25.14
LCIB	15.32 ± 1.06 13.31–17.08 (16)	16.77 ± 1.15 12.85–18.27 (28)	16.98 ± 0.35 16.35–17.47 (7)	16.39 ± 0.87 14.68–18.55 (24)	16.57 ± 0.62 15.35–17.25 (7)	12.85

	Oecomys sp. nov.	*Oecomys catherinae* complex *stricto sensu*				*Oecomys catherinae*
		Eastern	Central	Northern	Westernmost	
	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Holotype[a]
LD	7.25 ± 0.59 6.24–8.23 (16)	8.21 ± 0.54 7.00–8.92 (28)	8.13 ± 0.42 7.48–8.56 (7)	7.73 ± 0.49 6.58–8.95 (24)	7.95 ± 0.36 7.44–8.47 (7)	8.50
LIB	5.14 ± 0.18 4.64–5.34 (16)	5.90 ± 0.34 5.23–6.52 (28)	5.80 ± 0.38 5.37–6.35 (7)	5.54 ± 0.38 5.07–6.54 (24)	5.56 ± 0.44 4.90–6.04 (7)	6.16
LIF	4.83 ± 0.445 3.94–5.54 (16)	5.45 ± 0.44 3.96–6.14 (28)	5.68 ± 0.34 5.11–6.03 (7)	5.07 ± 0.34 4.47–5.71 (24)	5.22 ± 0.22 4.79–5.50 (7)	5.54
LIP	4.13 ± 0.41 3.54–4.72 (16)	4.77 ± 0.39 3.78–5.34 (28)	4.71 ± 0.40 4.26–5.18 (7)	4.30 ± 0.37 3.45–5.06 (24)	4.36 ± 0.42 3.97–5.24 (7)	3.78
LLD	3.36 ± 0.25 2.89–3.70 (16)	3.75 ± 0.37 3.03–4.43 (27)	3.65 ± 0.28 3.24–4.03 (7)	3.67 ± 0.36 2.81–4.36 (24)	3.58 ± 0.20 3.27–3.80 (7)	4.43
LN	10.67 ± 1.06 8.29–12.41 (16)	11.39 ± 0.68 9.93–12.66 (28)	11.21 ± 0.43 10.51–11.80 (7)	11.23 ± 0.81 9.41–13.39 (24)	11.47 ± 0.63 10.60–12.20 (7)	10.91
LPB	6.22 ± 0.37 5.29–6.83 (16)	6.78 ± 0.50 5.94–8.01 (28)	6.39 ± 0.35 5.94–6.89 (7)	6.42 ± 0.45 5.59–7.81 (24)	6.50 ± 0.19 6.30–6.88 (7)	7.18
LR	9.46 ± 0.79 7.77–10.58 (16)	10.32 ± 0.66 8.54–11.62 (28)	10.39 ± 0.57 9.68–11.12 (7)	9.90 ± 0.48 8.74–10.52 (24)	10.16 ± 0.34 9.86–10.87 (7)	10.80
MB	10.50 ± 0.41 9.91–11.50 (15)	11.22 ± 0.37 10.44–11.88 (27)	11.27 ± 0.38 10.83–11.74 (7)	10.85 ± 0.39 10.12–11.79 (24)	10.85 ± 0.22 10.45–11.05 (6)	11.30
MH	7.40 ± 0.68 6.40–8.60 (16)	8.63 ± 0.59 7.38–10.06 (28)	8.57 ± 0.55 7.55–9.34 (7)	8.16 ± 0.64 6.89–9.53 (24)	8.07 ± 0.38 7.60–8.74 (7)	8.35
OL	10.54 ± 0.61 9.50–11.47 (16)	11.61 ± 0.54 10.00–12.32 (28)	11.63 ± 0.20 11.42–11.90 (7)	11.31 ± 0.48 10.32–12.34 (24)	11.45 ± 0.39 10.82–12.02 (7)	11.66
ONL	29.89 ± 1.88 26.06–32.21 (15)	33.30 ± 1.36 30.21–35.77 (27)	33.33 ± 1.00 32.25–34.67 (7)	31.77 ± 1.41 28.47–34.90 (24)	32.17 ± 1.06 30.74–34.22 (7)	-

	Oecomys sp. nov.	*Oecomys catherinae* complex *stricto sensu*				*Oecomys*
		Eastern	Central	Northern	Westernmost	*catherinae*
	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Mean ± *SD* Min.–Max. (N)	Holotype[a]
ZB	15.48 ± 0.96 13.70–16.80 (16)	16.94 ± 0.84 14.93–18.61 (28)	16.79 ± 0.81 15.85–18.10 (7)	15.97 ± 1.07 14.29–18.05 (24)	16.34 ± 0.39 15.84–16.83 (7)	16.41
ZL	13.36 ± 0.86 11.47–14.59 (16)	15.06 ± 0.63 13.67–15.88 (27)	15.01 ± 0.40 14.60–15.60 (7)	14.52 ± 0.74 12.85–15.77 (24)	14.45 ± 0.74 13.34–15.46 (7)	-

[a] External measurements were transcribed from original skin labels.

825 **Table 3**.—External and craniodental character comparisons among *Oecomys* sp. nov. and lineages of the *Oecomys catherinae* complex *stricto*
826 *sensu* (central, eastern, northern, and westernmost). HBL, head and body length; M1, upper first molar; TL, tail length. See the "Comparisons"
827 section for comparisons of *Oecomys* sp. nov. with other congeneric species.

	Oecomys sp. nov.	*O. catherinae* eastern	*O. catherinae* central	*O. catherinae* westernmost	*O. catherinae* northern
TL in relation to HBL	118.28% 103.8–147.62 (23)	119.69% 101.33–132.74 (25)	113.08% 96.67–131.25 (6)	112.21% 88.46–128.8 (7)	113.08% 84.93–136.36 (18)
Dorsal fur color	Gray-based, terminal tips dark reddish-brown, mixed with dark brown	Gray-based, terminal tips reddish-brown, mixed with dark brown	Gray-based, terminal tips reddish-brown, mixed with dark brown	Gray-based, terminal tips reddish-brown, mixed with dark brown	Gray-based, terminal tips reddish-brown, mixed with dark brown
Dorsal body fur length	7–11 mm	12–15 mm	12–14 mm	9–12 mm	9–12 mm
Ventral fur color	Dark cream, gray-based except on throat, neck, forelimbs, and genitalia (self-dark cream)	Cream, gray-based except on ventral midline, throat, neck, and genitalia (self-cream)	Cream, gray-based except ventral midline, throat, neck, and genitalia (self-cream)	Dark cream, inconspicuously gray-based except on throat and neck (self- dark cream)	Dark cream, gray-based except on throat and neck (self-dark cream)
Tail color	Brown, slightly bicolored at the base	Brown	Brown, bicolored at the base	Brown	Brown, slightly bicolored at the base
Tail apical tuft	Absent or poorly developed (< 1 mm)	Poorly developed (< 1 mm)	Absent or poorly developed (< 1 mm)	Absent or poorly developed (< 1 mm)	Poorly developed (< 1 mm)
Rostrum	Narrow and moderately long	Wide and long	Wide and short	Wide and long	Narrow and short

	Oecomys sp. nov.	*O. catherinae* eastern	*O. catherinae* central	*O. catherinae* westernmost	*O. catherinae* northern
Posterior margin of nasals	Surpassing or aligned to the maxillary-frontal suture	Aligned to the maxillary-frontal suture	Aligned to the maxillary-frontal suture	Aligned to the maxillary-frontal suture	Aligned to the maxillary-frontal suture
Zygomatic plate	Slightly projected previously to the maxillary root	Projected previously to the maxillary root	Projected previously or the same level to the maxillary root	Projected previously to the maxillary root	Projected previously to the maxillary root
Interorbital region	Narrow, anteriorly convergent	Moderate, anteriorly convergent	Narrow, anteriorly convergent	Moderate, anteriorly convergent	Moderate, anteriorly convergent
Supraorbital and temporal crests	Both present and moderately developed	Supraorbital crests dorsolaterally expanded, more developed than temporal crests	Supraorbital crests dorsolaterally expanded, more developed than temporal crests	Supraorbital crests dorsolaterally expanded, more developed than temporal crests	Supraorbital crests dorsolaterally expanded, more developed than temporal crests
Lateral expansion of parietals	Slightly expanded bellow the lateral edges of the dorsum of the braincase	Deeply expanded onto the lateral surface of the braincase	Deeply expanded onto the lateral surface of the braincase	Deeply expanded onto the lateral surface of the braincase	Deeply expanded onto the lateral surface of the braincase
Alisphenoid strut	Usually absent	Usually absent	Absent	Usually absent	Usually absent
Subsquamosal fenestra	Present, smaller than postglenoid foramen	Reduced	Ossified	Reduced	Ossified
Incisive foramina	Oval or drop shaped	Anteriorly convergent	Oval or drop shaped	Parallel or anteriorly convergent	Anteriorly convergent

	Oecomys sp. nov.	*O. catherinae* eastern	*O. catherinae* central	*O. catherinae* westernmost	*O. catherinae* northern
Posterolateral palatal pits	Conspicuous perforations in deeply depression	Small perforations	Large, in palatal depression	Large, in small palatal depression	Large, in palatal depression
Anterior cingulum of M1	Present	Usually absent	Present	Absent	Absent
Diploid chromosome number (2n) *	54	60	60	60	62

828 * (Suaréz-Villota et al. 2018).

APPENDIX I: Specimens examined

Specimens examined are deposited in the following institutions: Museu Nacional (MN), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Museu Paraense Emílio Goeldi (MPEG), Belém; Universidade do Estado de Mato Grosso (Unemat), Cáceres; Universidade Federal de Mato Grosso (UFMT), Cuiabá; and The Natural Natural History Museum (BNMH), London. The material examined also includes uncatalogued specimens, such as those collected by Manoel dos Santos Filho (MSF), Robson Oliveira (RFO), and A. Casagrande (AC), which will be deposited at Unemat. Specimens collected by Ana Paula Carmignoto (APC) and by several biologists in the Pequena central Hidrelétrica de São Joaquim da Barra (PCH) will be deposited at MZUSP. Finally, specimens collected by the Serviço Nacional da Peste (IP) will be deposited at the MN.

Oecomys sp. nov. (n = 28): Brazil: Mato Grosso: Alta Floresta (1): UFMT 4118 (10º00'25"S, 56º02'17"W); Unemat–MSF 1878 (9°54'12"S, 56°10'15.6"W), Aripuanã (12): MZUSP 29531 (10º10'01"S, 59º27'W); Cáceres (7): Unemat–MSF 1406, 1407, 1411 (16°01'55"S 57°42'24"W); Campos de Julho (9): UFMT 931 (12°51'00"S, 58°56'00"W); Cláudia (4): MZUSP 35543 (11º34'58"S, 55º10'01"W); Gaúcha do Norte (5): MZUSP 29516 (13º04'58"S, 53º16'58"W); Juruena (11): MZUSP 35537 (10º19'01"S, 58º28'58"W); Paranaíta (2): UFMT 1772, 1773, 1774, 1806 (9º29'06"S, 56º28'19"W); Rosário Oeste (6): Unemat–AC 207, 230, 255, 266 (15º04'45.9"S, 56º33'15.7"W); Vila Bela da Santíssima Trindade (8): Unemat–RFO 013, 027, 029, 040 (15°10'33.6"S, 59°59'38.4"W). Pará: Jacareacanga (3): UFMT 1680 (9º29'06"S, 56º28'19"W), UFMT 1775, 1776, 1686, 1690 (9º18'40"S, 56º46'05"W). Rondônia: Vilhena (10): MPEG 34224 (12º43'S, 60º7'W).

Oecomys catherinae complex *s.s.* (n = 89): Central lineage (n = 11): Brazil: Distrito Federal: Brasília (31): MN 21996, 22013 (15°45'21"S, 48°06'28"W); Goiás: Anápolis (32): MN4346, 4348 (16°20'37"S 48°53'08"W); São Domingos (28): MZUSP 4012, 4020, MPEG 10901

(13°23'36"S 46°18'55"W); São Paulo: São Joaquim da Barra (34): MZUSP-PCH 3998, 4077 (20º28'58"S, 47º51'W); Tocantins: Paranã (27): MZUSP 35549, 35550 (12º37'01"S, 47º52'58"W). Eastern lineage (n = 41): Brazil: Bahia: Ilhéus (39): MN 9340, 10648, 10691, 10724, 10748, 10761, 10792, 10812, 10854, 10882, 10940, 10951, 11212, 11561 (14°40'15"S, 39°12'46"W); Ceará: Guaraciaba do norte (37): MN-IP 738 (4°10'04"S, 40°46'58"W); São Benedito (36): MN-IP 804, 806, 820, 831 (4°01'19"S, 40°56'31"W); Minas Gerais: Pirapitinga (42): MN 72737 (21º41'28"S, 42º22'05"W); Rio de Janeiro: Cachoeira de Macacu (46): MN 74364, MN 74367 (22º31'S, 42º48'W), MN 74370, 74374 (22º30'S, 42º45'W), MN 74371 (22º28'58"S, 42º51'W); Casimiro de Abreu (44): MN 44805 (22°29'32"S, 42°12'43"W); Guapimirim (47): MN 74359 (22º34'58"S, 42º57'W), MN 74360 (22°33'00"S 42°57'00"W), MN 74369 (22º34'S, 42º54'W); Paraty (48): MN 75261 (23°01'30"S, 44°38'13"W); Silva Jardim (45): MN 66137 (22°38'09"S, 42°23'13"W); Sumidouro (43): MN 53616 (22°03'14"S, 42°40'04"W); Santa Catarina: Joinville (51): BMNH 9.11.19.24; Sergipe: Areia Branca (38): MPEG 24553, 24554, 24561, 24562, 24563 (10º40'S, 37º25'W); São Paulo: Ubatuba (49): MN 74375, 74376, 74378 (23º19'58"S, 44º49'58"W). Northern lineage (n = 29): Brazil: Mato Grosso: Vila Rica (16): MZUSP-APC 292, 297, MZUSP 29533, 35538, 35539, 35542 (10º01'01"S, 51º07'01"W); Pará: Altamira (23): MPEG 10913 (3º22'01"S, 52º22'58"W), Altamira (24): MPEG 10251, 10911, 10912 (3º41'S, 53º45'W); Belterra: MPEG 15293, 15294 (2º38'S, 54º57'W); Ilha de Marajó (21): MN 2000 (0º57'58"S, 49º40'16"W); Itaituba (26): MN 2001 (4°25.5'S, 56°17.5'W); Marabá (17): MPEG 38898, 38976 (6ºS, 51º19'58"W), Marabá (18): UFMT 1294 (5°47'51.8"S 50°46'15.3"W), Marabá (19) MPEG 39899, 39900 (5º49'01"S, 50º28'58"W), MPEG 39901, 39903, 39909 (5º46'58"S, 50º31'58"W); Novo Repartimento (20): MPEG 10924 (4º41'S, 49º32'W); Santarém (25): MPEG 8229, 15094, 15099, 15120, 15121 (2°29'34"S, 54°44'06"W); Senador José Porfírio (22): MPEG 42454 (2°35'59"S, 51°56'42"W).

879 Westernmost lineage (n = 8): Brazil: Amazonas (15): Humaitá: MPEG 13171 (7º41'53"S,
880 62º33'11"W); Mato Grosso: Aripuanã (12): MZUSP 29532, 35535 (10º10'01"S, 59º27'W);
881 Colniza (13): MPEG 12652, 12654, 12691, 13172, 13173 (9º10'S, 60º38'W).

882 *Oecomys rex* (n = 09): Brazil: Amazonas: Manaus: MN 19617, 19618 (2º57'32"S,
883 59º56'49"W); Amapá: rio Amapari: MN 20646 (1°05'42.3"N 52°11'49.1"W); rio Maracá: MN
884 20688 (0°11'00.4"S 51°43'56.0"W); Serra do Navio: MZUSP 20517, 20518 (1º04'58"N,
885 52º14'10"W); Vila Velha do Cassiporé: MPEG 8044, 8047 (3º13'N, 51º13'W); Guiana:
886 BMNH 1910.9.29.17 (6º58'58"N, 58º31'01"W).

SUPPLEMENTARY DATA SD1

Supplementary Data S1.—Field number, voucher, Genbank accession number (Cytochrome b and intron 7 β-fibrinogen), specimen includes in morphological analyses (Morphology), country, division/state, locality and coordinates of samples analyzed in the present study. Lineages of the *Oecomys catherinae* complex: eastern, central, western, westernmost, and northern.

Species/Lineage	Field number	Voucher number	GenBank *Cytb*	GenBank *i7-fgb*	Morphology	Country: Division	Locality	Map	Lat.	Long.	Source
Western *	RVR 89	UFMT4118	MK874365	MT978188	Skin/skull	Brazil: Mato Grosso	Alta Floresta	1	-10.007	-56.038	1
Western *	UTP02	UFMT1680	MK874366	-	Skin/skull	Brazil: Mato Grosso	Paranaíta	2	-9.485	-56.472	1
Western *	UTP132	UFMT1686	MK874367	MK874449	Skin/skull	Brazil: Pará	Jacareacanga	3	-9.311	-56.768	1
Western *	UTP158	UFMT1772	MK874368	MK874450	Skin/skull	Brazil: Mato Grosso	Paranaíta	2	-9.485	-56.472	1
Western *	UTP159	UFMT1773	MK874369	MK874451	Skin/skull	Brazil: Mato Grosso	Paranaíta	2	-9.485	-56.472	1
Western *	UTP162	UFMT1774	MK874370	-	Skin/skull	Brazil: Mato Grosso	Paranaíta	2	-9.485	-56.472	1
Western *	UTP176	UFMT1775	MK874371	MK874452	Skin/skull	Brazil: Pará	Jacareacanga	3	-9.311	-56.768	1
Western *	UTP177	UFMT1776	MK874372	MK874453	Skin/skull	Brazil: Pará	Jacareacanga	3	-9.311	-56.768	1
Western *	UTP181	UFMT1806	MK874373	MK874454	Skin/skull	Brazil: Mato Grosso	Paranaíta	2	-9.485	-56.472	1
Western *	M000029	MZUSP29516	MG323753	MG323837	Skin/skull	Brazil: Mato Grosso	Gaúcha do Norte	5	-13.083	-53.283	2
Western *	M97055	MZUSP35543	MG323754	MG323838	Skin/skull	Brazil: Mato Grosso	Cláudia	4	-11.583	-55.167	2
Western *	PEU960006	-	MG323755	MG323839	-	Brazil: Mato Grosso	Aripuanã	12	-10.167	-59.450	2
Western *	APC244	MZUSP29531	MG323756	MG323777	Skin/skull	Brazil: Mato Grosso	Aripuanã	12	-10.167	-59.450	2
Western *	APC145	MZUSP35537	MG323757	MG323779	Skin/skull	Brazil: Mato Grosso	Juruena	11	-10.317	-58.483	2
Eastern	CIT2096	CIT2096	MG323772	MG323774	-	Brazil: Minas Gerais	Parque Estadual rio Doce	41	-19.533	-42.533	2
Eastern	CIT2097	CIT2097	MG323773	MG323775	-	Brazil: Minas Gerais	Parque Estadual rio Doce	41	-19.533	-42.533	2
Eastern	-	LBCE10774	MG323771	MG323852	-	Brazil: Rio de Janeiro	Paraty	48	-23.217	-44.717	2
Eastern	FS4-1	MN74359	KY605388	-	Skin/skull	Brazil: Rio de Janeiro	Guapimirim	47	-22.583	-42.950	3
Eastern	FS4-35	MN74360	KY605389	-	Skin/skull	Brazil: Rio de Janeiro	Guapimirim	47	-22.550	-42.950	3
Eastern	FS4-38	MN74361	KY605390	-	-	Brazil: Rio de Janeiro	Guapimirim	47	-22.550	-42.950	3
Eastern	FS08-21	MN74366	KY605391	-	-	Brazil: Rio de Janeiro	Guapimirim	47	-22.517	-42.800	3

Eastern	FS08-55	MN74368	KY605392	-	-	Brazil: Rio de Janeiro	Guapimirim	47	-22.517	-42.800	3
Eastern	FS14-20	MN74371	KY605393	-	Skin/skull	Brazil: Rio de Janeiro	Cachoeiras de Macacu	46	-22.492	-42.860	3
Eastern	FS14-35	NM74372	KY605394	-	-	Brazil: Rio de Janeiro	Cachoeiras de Macacu	46	-22.446	-42.686	3
Eastern	FU16	-	KY605396	-	-	Brazil: Rio de Janeiro	Casimiro de Abreu	44	-22.475	-42.210	3
Eastern	FU17	-	KY605397	-	-	Brazil: Rio de Janeiro	Casimiro de Abreu	44	-22.475	-42.210	3
Eastern	ITA30	MN72737	KY605398	-	Skin/skull	Brazil: Minas Gerais	Pirapitinga	42	-21.691	-42.368	3
Eastern	ITA31	MN72738	KY605399	-	-	Brazil: Minas Gerais	Pirapitinga	42	-21.691	-42.368	3
Eastern	PSP12	MN74377	KY605400	-	-	Brazil: São Paulo	Ubatuba	49	-23.333	-44.833	3
Eastern	PSP19	MN74378	KY605401	-	Skin/skull	Brazil: São Paulo	Ubatuba	49	-23.333	-44.833	3
Eastern	PSP38	MN74379	KY605402	-	-	Brazil: São Paulo	Ubatuba	49	-23.333	-44.833	3
Eastern	SU63	-	KY605403	-	-	Brazil: Rio de Janeiro	Sumidouro	43	-22.054	-42.668	3
Eastern	SU86	-	KY605404	-	-	Brazil: Rio de Janeiro	Sumidouro	43	-22.054	-42.668	3
Eastern	FS14-40	MN74373	KY605395	-	-	Brazil: Rio de Janeiro	Cachoeiras de Macacu	46	-22.492	-42.860	3
Eastern	-	MVZ200982	HM594616	-	-	Brazil: São Paulo	Capão Bonito	51	-24.283	-48.417	4
Eastern	-	UFES247	JQ966233	-	-	Brazil: Espírito Santo	Águia Branca	40	-18.875	-40.786	5
Central	-	MN36231	FJ361060	-	-	Brazil: Goiás	Colinas do Sul	30	-14.150	-48.067	14
Central	-	MN36273	FJ361061	-	-	Brazil: Goiás	Colinas do Sul	30	-14.150	-48.067	14
Central	-	MN36301	FJ361062	-	-	Brazil: Goiás	Colinas do Sul	30	-14.150	-48.067	14
Central	-	MN36350	FJ361065	-	-	Brazil: Goiás	Colinas do Sul	30	-14.150	-48.067	14
Central	-	MN36747	FJ361068	-	-	Brazil: Goiás	Minaçu	29	-13.517	-48.217	14
Central	-	MN36791	FJ361069	-	-	Brazil: Goiás	Minaçu	29	-13.517	-48.217	14
Central	-	MN37763	FJ361051	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37764	FJ361052	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37765	FJ361053	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37766	FJ361054	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37767	FJ361055	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37768	FJ361056	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	MN37769	FJ361057	-	-	Brazil: Goiás	Caldas Novas	33	-17.683	-48.467	14
Central	-	LBCE8791	MG323760	MG323842	-	Brazil: Mato Grosso do Sul	Dois Irmãos de Buriti	35	-20.667	-55.283	2
Central	MRT3875	MZUSP35549	MG323761	MG323843	Skin/skull	Brazil: Tocantins	Paranã	27	-12.617	-47.883	2
Central	MRT3897	MZUSP35550	MG323762	MG323844	Skin/skull	Brazil: Tocantins	Paranã	27	-12.617	-47.883	2

Central	PCH4077	-	MG323763	MG323845	Skin	Brazil: São Paulo	São Joaquim da Barra	34	-20.483	-47.850	2
Central	PCH3998	-	MG323764	MG323846	Skin/skull	Brazil: São Paulo	São Joaquim da Barra	34	-20.483	-47.850	2
Westernmost	-	MN37776	FJ361050	-	-	Brazil: Rondônia	Guajará-Mirim	15	-10.833	-63.733	14
Westernmost	APC249	MZUSP29532	MG323758	MG323840	Skin/skull	Brazil: Mato Grosso	Aripuanã	12	-10.167	-59.450	2
Westernmost	APC243	MZUSP35535	MG323759	MG323841	Skin/skull	Brazil: Mato Grosso	Aripuanã	12	-10.167	-59.450	2
Northern	APC288	MZUSP35538	MG323765	MG323847	Skin/skull	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	APC289	MZUSP35539	MG323766	MG323848	Skin/skull	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	APC304	MZUSP29533	MG323767	MG323849	Skin	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	-	MZUSP29533	KY605382	-	Skin/skull	Brazil: Mato Grosso	Vila Rica	-	-	-	3
Northern	APC292	-	MG323768	MG323850	Skin/skull	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	APC297	-	MG323769	MG323784	Skin	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	APC310	MZUSP35542	MG323770	MG323851	Skin/skull	Brazil: Mato Grosso	Vila Rica	16	-10.017	-51.117	2
Northern	CS26	-	KT737237	-	-	Brazil: Pará	Flona Tapirape-Aquiri	19	-5.800	-50.500	6
Northern	-	USNM549530	KT737238	-	-	Brazil: Pará	East bank rio Xingu	23	-3.650	-52.367	6
Northern	IAVRD330	MPEG38898	KY605383	-	Skin/skull	Brazil: Pará	Marabá	17	-6.000	-51.333	3
Northern	PSA128	MPEG39899	KY605384	-	Skin/skull	Brazil: Pará	Marabá	19	-5.817	-50.483	3
Northern	PSA139	MPEG39900	KY605385	-	Skin/skull	Brazil: Pará	Marabá	19	-5.817	-50.483	3
Northern	PSA164	MPEG39901	KY605386	-	Skin/skull	Brazil: Pará	Marabá	19	-5.783	-50.533	3
Northern	PSA176	MPEG39903	KY605387	-	Skin/skull	Brazil: Pará	Marabá	19	-5.783	-50.533	3
O. rex	CSA22	IEPA2410	MK874428	-	-	Brazil: Amapá	Laranjal do Jari, Iratapuru	-	0.1472	-52.520	1
O. rex	RC01	IEPA2038	MK874429	-	-	Brazil: Amapá	Laranjal do Jari, Reserva extrativista do rio Cajari	-	-0.7261	-52.008	1
O. rex	V-1102	-	AJ496314	-	-	French Guiana	Sauel	-	-3.617	-53.200	14
O. rex	V-1099	-	AJ496315	-	-	French Guiana	Sauel	-	-3.617	-53.200	14
O. auyantepui	V-971	-	AJ496304	-	-	French Guiana	Les Nouragues	-	4.083	-52.683	14
O. auyantepui	V-1001	-	AJ496305	-	-	French Guiana	Les Nouragues	-	4.083	-52.683	14
O. auyantepui	ROM114059	-	KP778302	KP778670	-	Suriname: Brokopondo	Brownsberg Nature Park	-	-	-	14
O. bicolor	M97074	MZUSP29528	MG323726	-	-	Brazil: Mato Grosso	Cláudia	-	-11.583	-55.167	2
O. bicolor	M97107	MZUSP35544	MG323725	-	-	Brazil: Mato Grosso	Cláudia	-	-11.583	-55.167	2
O. bicolor	JL26	UFPAM1542	MK874348	MK874445	-	Brazil: Pará	Itaituba	-	-5.376	-56.923	1
O. bicolor	JMIJ40	UFPAM1162	MK874350	MK874447	-	Brazil: Pará	Jacareacanga	-	-6.127	-57.588	1
O. cleberi	APC210	MZUSP35534	MG323745	-	-	Brazil: Mato Grosso	Aripuanã	-	-10.167	-59.450	1

O. cleberi	-	UFMG2802	HM594608	-	-	Brazil: Mato Grosso	Barra do Garças	-	-15.633	-52.350	4
O. cleberi	JMIG01	UFPAM1177	MK874381	MK874459	-	Brazil: Pará	Jacareacanga	-	-5.722	-57.366	1
O. cleberi	MSF2410	-	MK874389	MK874466	-	Brazil: Mato Grosso	Alta Floresta	-	-9.798	-55.926	1
O. concolor	JLP16728	-	HM594614	-	-	Brazil: Amazonas	rio Jau	-	-2.217	-62.383	4
O. concolor	JLP16806	-	HM594615	-	-	Brazil: Amazonas	rio Jau	-	-2.217	-62.383	4
O. franciscorum	roe224	-	KF207846	-	-	Argentina: Chaco	Pampa del Indio	-	-25.917	-58.933	7
O. franciscorum	-	MACN26663	KT737232	-	-	Argentina: Formosa	Estacion Guaycolec	-	-25.967	-58.167	6
O. franciscorum	LBCE1916	-	MG323715	MG323804	-	Brazil: Mato Grosso do Sul	Corumbá	-	-19.000	-57.650	2
O. franciscorum	PNPA300	MZUSP35540	MG323716	MG323786	-	Brazil: Mato Grosso	Parque Nacional do Pantanal	-	-17.000	-57.433	2
O. mamorae	PZ94	-	KT737226	-	-	Bolivia: La Paz	Tumupasa	-	-14.150	-67.917	6
O. mamorae	PZ316	-	KT737225	-	-	Bolivia: La Paz	Buena Vista	-	-15.283	-68.383	6
O. paricola	LPC570	MVZ197507	HM594593	-	-	Brazil: Mato Grosso	Alta Floresta	-	-9.583	-55.917	4
O. paricola	LPC525	UFMG2841	HM594591	-	-	Brazil: Mato Grosso	Alta Floresta	-	-9.583	-55.917	4
O. paricola	JL28	UFPAM1544	MK874410	MK874480	-	Brazil: Pará	Itaituba	-	-5.376	-56.923	1
O. paricola	UTP668	UFMT1779	MK874425	MK874488	-	Brazil: Pará	Jacareacanga	-	-9.311	-56.768	1
O. roberti	-	UFES1370	HM594603	-	-	Brazil: Pará	Santana do Araguaia	-	-9.630	-50.144	4
O. roberti	-	MVZ197619	HM594594	-	-	Brazil: Mato Grosso	Chapada dos Guimarães	-	-15.194	-55.950	4
O. roberti	MSF1796	-	MK874430	MK874489	-	Brazil: Mato Grosso	Alta Floresta	-	-9.840	-56.005	1
O. roberti	M97060	MZUSP29526	MG323720	MG323807	-	Brazil: Mato Grosso	Cláudia	-	-11.583	-55.166	2
O. rutilus	CN123	-	JF759665	-	-	Brazil: Pará	Floresta Trombetas	-	-1.167	-55.650	8
O. rutilus	-	MNHN1995.3236	AJ496309	-	-	Frech Guiana	Saint-Eugene	-	-	-	14
O. rutilus	TTU101025	-	KP778344	KP778659	-	Peru: Loreto	Maynas	-	-	-	14
O. superans	JLP15517	MVZ200944	U58385	-	-	Brazil: Amazonas	Right bank rio Juruá	-	-6.833	-70.750	9
O. superans	-	MVZ155006	AY275123	-	-	Peru: Amazonas	Huampami, rio Cenepa	-	-5.517	-79.817	10
O. sydandersoni	-	USNM584557	KT737234	-	-	Bolívia: Santa Cruz	Parque Kempff mercado	-	-15.250	-61.017	6
O. sydandersoni	-	USNM588189	KT737235	-	-	Bolívia: Santa Cruz	rio Paraguay	-	-14.767	-61.033	6
O. tapajinus	-	MVZ197511	HM594595	-	-	Brazil: Tocantins	Peixe, rio Santa tereza	-	-11.833	-48.633	4
O. tapajinus	-	UFES1359	HM594600	-	-	Brazil: Tocantins	Lagoa da Confusão	-	-10.861	-49.713	4
O. tapajinus	JB11	UFPAM1396	MK874439	MK874491	-	Brazil: Pará	Itaituba	-	-5.227	-56.929	1
O. tapajinus	JB13	UFPAM1398	MK874440	MK874492	-	Brazil: Pará	Itaituba	-	-5.227	-56.929	1
O. trinitatis	-	MUSM13320	GU126527	-	-	Peru: Loreto	rio Galvez	-	-5.200	-72.883	11

O. trinitatis	-	MVZ200948	U58390	-	-	Brazil: Acre	-	-	-8.667	-72.783	9
Euryoryzomys nitidus	-	MZUSP29524	MG323695	MG323787	-	Brazil: Mato Grosso	Apiacás	-	-	-	2
Hylaeamys megacephalus	-	M968452	MG323696	MG323788	-	Brazil: Mato Grosso	Apiacás	-	-	-	2
Euryoryzomys macconnelli	-	AMNH272669	GU126538	-	-	Peru: Loreto	rio Galvez	-	-	-	11
Hylaeamys megacephalus	GD463	-	AY275124	-	-	-	-	-	-	-	10
Handleyomys intectus	-	CADV088	EU579490	-	-	Colombia: Antioquia	4 km S El Tetiro	-	-	-	14
Oligoryzomys utiaritensis	-	MN75625	JQ013752	JQ282893	-	Brazil: Mato Grosso	Campo Novo do Parecis	-	-	-	12
Handleyomys melanotis	-	ASNHC3419	KF658409	KF658415	-	Mexico: Nayarit	8 KM E of San Blas	-	-	-	13

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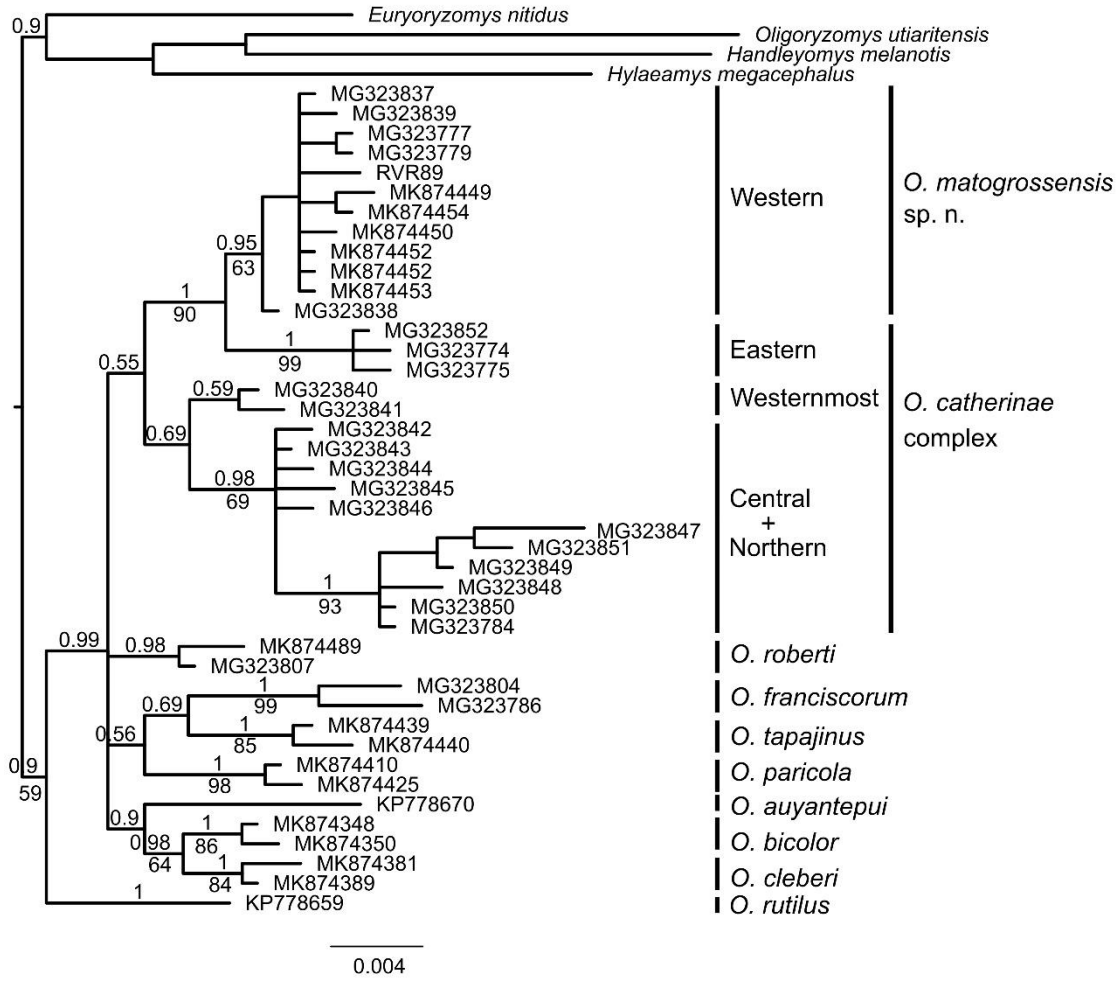
SUPPLEMENTARY DATA S2



Supplementary Data S2.—Bayesian Inference topology of *Oecomys*, based on the nuclear intron 7 β-fibrinogen dataset. Numbers above branches indicate Bayesian posterior probabilities and below branches indicate maximum likelihood bootstrap values. The black side bars indicate lineages and species recognized in this study.

SUPPLEMENTARY DATA S3

Table S3.1.—Results of the Principal Component Analysis of adult specimens of *Oecomys* sp. nov. and lineages of the *Oecomys catherinae* complex *stricto sensu* based on 31 craniodental variables. See "Materials and Methods" section for abbreviations. PC = principal component. Bold numbers correspond to the five most contributive variables for each PC.

Variables	PC1	PC2	PC3
ONL	**0.959**	-0.064	-0.071
CIL	**0.964**	-0.025	-0.097
BH	0.736	-0.136	0.156
CZL	0.845	0.032	-0.064
ZL	**0.922**	-0.001	-0.104
LD	**0.901**	-0.213	-0.159
BZP	0.785	0.007	-0.068
BN	0.791	0.145	-0.012
LN	0.675	-0.215	-0.214
LR	0.844	-0.056	-0.070
BR	0.421	-0.077	**0.576**
LIB	0.800	0.084	-0.043
OL	0.883	-0.083	-0.096
ZB	0.889	0.002	-0.136
LIP	0.567	0.221	**0.541**
BIP	0.532	-0.026	**0.431**
BIF	0.611	-0.202	0.056
LIF	0.788	-0.088	-0.040
BRP	0.744	-0.084	-0.055
LPB	0.734	0.103	-0.223
MB	0.820	-0.008	0.021
BOC	0.743	-0.127	0.226
BB	0.589	**-0.283**	**0.551**
BI	0.775	-0.068	-0.233
BM1	0.277	**0.759**	-0.023
CLM	0.550	**0.696**	0.056
Bm1	0.382	**0.698**	0.042
CLLM	0.462	**0.789**	-0.036
LLD	0.591	-0.198	**-0.298**
LCIB	0.820	-0.205	0.086
MH	**0.910**	-0.097	0.026
% Variance	54.9	8.5	5.0

Table S3.2.—Results of the Discriminant Function Analysis of adult specimens of *Oecomys* sp. nov. and lineages of the *Oecomys catherinae* complex *stricto sensu* based on 31 craniodental variables. See "Materials and Methods" section for abbreviations. CV = canonical variate. Bold numbers correspond to the five most contributive variables for each CV.

Variables	CV1	CV2	CV3
ONL	0.579	0.086	-0.139
CIL	0.066	**1.102**	-0.512
BH	-0.073	-0.511	**0.761**
CZL	-0.484	-0.675	0.083
ZL	0.063	0.168	0.292
LD	**0.755**	-0.296	0.117
BZP	0.394	0.316	0.214
BN	-0.533	0.516	0.168
LN	0.403	-0.322	-0.445
LR	**-1.413**	0.259	**0.861**
BR	0.134	-0.743	0.409
LIB	**0.701**	-0.085	-0.175
OL	**0.871**	**-1.143**	-0.069
ZB	**-0.799**	**0.965**	-0.043
LIP	0.521	0.341	-0.288
BIP	0.214	0.043	-0.395
BIF	0.090	0.924	-0.077
LIF	-0.374	0.085	**0.721**
BRP	-0.001	0.071	**-0.764**
LPB	-0.516	0.523	**-0.529**
MB	0.083	-0.239	0.338
BOC	0.423	-0.172	0.016
BB	0.233	**0.943**	-0.212
BI	0.312	-0.187	-0.391
BM1	-0.265	-0.062	0.007
CLM	0.465	-0.059	0.187
Bm1	0.535	0.101	0.310
CLLM	-0.154	0.066	-0.152
LLD	0.203	-0.371	-0.125
LCIB	-0.352	**-1.164**	0.090
MH	-0.023	-0.313	-0.167
Eigenvalue	5.226	1.761	0.868
% Variance	62.1	20.9	10.3

943 **Table S3.3.—**Classification matrix determined by the Discriminant Function Analysis of
944 *Oecomys* sp. nov. and the *Oecomys catherinae* complex *stricto sensu* lineages (central,
945 eastern, northern and westernmost).

Group	Group classification					Total	% correct classification
	Oecomys sp. nov.	Central	Eastern	Northern	Westernmost		
Oecomys sp. nov.	17	0	0	0	0	17	100
Central	0	7	0	0	0	7	100
Eastern	0	1	26	0	0	27	96.3
Northern	1	1	0	21	1	24	87.5
Westernmost	0	0	0	0	6	6	100
Total							95.1

946

CAPÍTULO III

Diversificação do complexo *Oecomys catherinae* Thomas, 1909 (Rodentia, Sigmodontinae): quantas espécies existem?

RESUMO

A espécie *Oecomys catherinae* foi apontada como um complexo de espécies em vários estudos, com linhagens amplamente distribuídas em território brasileiro. Destas linhagens, apenas uma foi reconhecida como distinta do complexo e descrita como uma nova espécie, enquanto as demais linhagens apresentam relações de parentesco e diversificação ainda confusas, principalmente em relação as possíveis linhagens da Mata Atlântica. Neste estudo, investigamos a diversificação e relações entre as linhagens de *O. catherinae* e da nova espécie. Para isso, realizamos analises moleculares com Citocromo b, uma representação do genoma (ddRADeseq) e análises morfométricas, de representantes de todas as linhagens mencionadas na literatura. Nossas análises moleculares indicaram a ocorrência de outra possível linhagem com ocorrência no nordeste do Brasil. Recuperamos o monofiletismo com a linhagem extremo oeste como irmã das demais, seguida da linhagem norte, central, nordeste e leste, esta última com dois subclados, denominados leste A e leste B. Apesar disso, apenas três grupos biológicos foram recuperados, sendo um com a linhagem extremo oeste, outro com a linhagem norte e o terceiro grupo com central, nordeste e leste juntos. Estimamos os eventos de diversificação do complexo para o Pleistoceno em concordância com os refúgios da Amazônia e as glaciações na Mata Atlântica. Em contrapartida das diferenciações moleculares, as análises morfométricas indicam ampla sobreposição entre as linhagens, principalmente as do Cerrado e Mata Atlântica. Com isso, consideramos como espécies distintas apenas as linhagens extremo oeste e norte. Consideramos as linhagens central, leste e nordeste como espécies crípticas, visto que ainda é necessária uma ampla amostragem das lacunas de distribuição da Mata Atlântica para confirmar se estas linhagens estão evoluindo separadamente.
Palavras-chave: Espécies crípticas, ddRADeseq, Mata Atlântica, Pleistoceno.

ABSTRACT

Oecomys catherinae was indicated as a species complex in several studies, with lineages widely distributed in Brazilian territory. With five lineages in the complex, only one was recognized as distinct and described as a new species, while the other lineages relationship and diversification still uncertain. In this study, we investigate the divergence and relationships between the *O. catherinae* lineages and the new species. For this, we used molecular analysis with Cytochrome b, a genome representation (ddRADeseq), and morphometric analysis, of all the lineages mentioned on literature. Our molecular analyses recovered another probable lineage with occurrence in the northeastern of Brazil, and the group monophyly, with the westernmost lineage as sister of the others, followed by the northern, central, northeastern and eastern lineage, the last one with two subclades (eastern A and eastern B). However, only three biological groups were recovered, one with the westernmost lineage, the second with the northern lineage and the third group with the central, northeastern and eastern together. The diversification events of the complex were estimated to the Pleistocene in agreement with the refuges on Amazonia and glaciation periods in the Atlantic Forest. Besides the molecular differentiations, the morphometric analyses indicate a wide overlap between the lineages. With this, we consider as distinct species only the westernmost and northern lineages. We consider the central, eastern and northeastern as cryptic species, since a large number of samples of the Atlantic Forest gaps distribution are necessary to confirm if these lineages are evolving separately.

Keywords: Crytptic species, ddRADeseq, Atlantic Forest, Pleistocene.

1. INTRODUÇÃO

Quando descrita, a espécie *Oecomys catherinae* Thomas, 1909 apresentava distribuição conhecida ao sul da Mata Atlântica, com localidade tipo no município de Joinville, Santa Catarina, Brasil. Outros dois nomes provenientes do estado da Bahia foram associados a *O. catherinae*. O primeiro foi *Mus cinnamomeus* Pictet & Pictet, 1844, porém este estava pré-ocupado por *Mus cinnamomeus* Lichtenstein, 1830, associado a um *Proechimys*. Outro nome foi *Oryzomys concolor bahiensis* Hershkovitz 1960 descrita em substituição a *Mus cinnamomeus*, com localidade tipo Ilhéus, Bahia. Atualmente, ambos são considerados sinônimos de *O. catherinae*, cuja distribuição estende-se até o sul do estado da Bahia (Carleton & Musser 2015; Musser & Carleton 2005). Mais recentemente, em análises de registros de ocorrência de *O. catherinae*, Asfora et al. (2011) confirmaram a presença de representantes da espécie no estado da Paraíba, Brasil, estendendo mais ao norte os limites da distribuição geográfica da espécie. Além disso, os autores apontaram a existência de duas populações aparentemente disjuntas: uma abrangendo as regiões sul, sudeste e central do Brasil e outra restrita à região nordeste ao norte do rio São Francisco.

Além da ocorrência *O. catherinae* confirmada ao norte da Mata Atlântica e em florestas de galeria do Cerrado (Asfora et al. 2011, Carleton & Musser 2015), recentes estudos comprovaram a ocorrência desta espécie também na Amazônia (Malcher et al. 2017; Suárez-Villota et al. 2018; Saldanha et al. 2019, Saldanha & Rossi, no prelo). Segundo Asfora et al. (2011), estes relatos de ocorrência disjunta da espécie podem ser artefatos de amostragem ou indicam que *O. catherinae*, como atualmente reconhecido, pode ser composto por mais de uma espécie.

O primeiro indício da existência de espécies crípticas em *O. catherinae* foi indicada por Malcher et al. (2017), que revelaram ausência de diferenciação molecular (marcador Citocromo b) e morfológica significativa entre populações de *O. catherinae* da Mata Atlântica e Amazônia, porém indicaram a presença de variações cromossômicas entre estas duas populações. Na última revisão sistemática do gênero *Oecomys*, Suárez-Villota et al. (2018), usando dados moleculares (marcador mitocondrial Citocromo b e marcadores nucleares proteína ligante do fotoreceptor retinóide e íntron 7 Beta-fibrinogênio), afirmam que este grupo é, de fato, um complexo de espécies amplamente distribuído, composto por cinco linhagens. Além disso, os autores afirmam que o nome *O. catherinae* estaria restrito a indivíduos distribuídos na Mata Atlântica (leste do território brasileiro) e que as demais

linhagens representam supostas novas espécies dentro do complexo, distribuídas na região central, norte, oeste e extremo oeste do território brasileiro.

Recentemente, a linhagem oeste do complexo *O. catherinae* (senso Suárez-Villota et al. 2018), com ocorrência na Amazônia, foi descrita como uma nova espécie – *Oecomys* sp. nov. – por Saldanha & Rossi (no prelo) com base em dados morfológicos, moleculares e citogenéticos. Com isso, devido as semelhanças morfológicas, baixa distância genética e escassa divergência no número diploide, os autores restringiram o complexo *O. catherinae* às linhagens leste, central, norte e extremo oeste de Suárez-Villota et al. (2018).

Saldanha & Rossi (no prelo) também indicaram a existência de dois grupos de *O. catherinae* na Mata Atlântica, um ao norte e outro ao sul, mas devido ao baixo suporte filogenético e baixas distâncias genéticas, os autores consideraram uma única linhagem para esta região (linhagem leste). A ocorrência de linhagens distintas ao norte e sul da Mata Atlântica já foi mencionada para outros grupos, cuja origem é geralmente associada às mudanças climáticas do Pleistoceno e mudanças vegetacionais a elas associadas (Costa & Leite 2012). Na Mata Atlântica, também existem registros de ocorrência da espécie *O. catherinae* ao norte do rio São Francisco (Asfora et al. 2011), porém, amostras desta região não foram incluídas em estudos filogenéticos anteriores, sendo os registros de quebras filogenéticas para este complexo apenas ao sul deste rio (Saldanha & Rossi, no prelo).

Os recentes estudos com o complexo *O. catherinae* indicaram discordância nas topologias entre hipóteses filogenéticas obtidas a partir do marcador mitocondrial Citocromo b e de marcadores nucleares, principalmente relacionadas às relações de parentesco entre as linhagens (Suárez-Villota et al. 2018; Saldanha & Rossi, no prelo). Com essas descobertas sobre a problemática do complexo *O. catherinae* quanto aos baixos suportes nos nós nas relações de parentesco, diversificação e evolução entre as linhagens que constituem o grupo, o presente estudo tem como objetivo esclarecer estas relações filogenéticas e inferir sobre a diversificação de linhagens evolutivas dentro do complexo *O. catherinae*. Assim como investigar as possíveis origens da diversificação entre as linhagens, principalmente na problemática da Mata Atlântica, incluindo o norte do rio São Francisco, onde são registradas populações disjuntas para o complexo. Para isso, além do marcador mitocondrial (Citb), utilizamos novas abordagens com fragmentos de DNA associados a sítios de restrição produzidos pela técnica de ddRADseq, e dados morfométricos, a fim de verificar a congruência entre as inferências filogenéticas e inferir a diversidade e diversificação de linhagens e espécies do complexo.

2. MATERIAL E MÉTODOS

Dados moleculares

Empregamos análises moleculares com o gene mitocondrial Citocromo b (Citb) e com fragmentos de DNA associados a sítios de restrição (*double digest restriction site-associated DNA sequencing* - ddRADseq), obtidos com sequenciamento de nova geração. Para isso, utilizamos alíquotas de tecidos de exemplares do acervo de mamíferos (Anexo 02) da Universidade Federal de Mato Grosso, do laboratóRio de Ecologia e Evolução do Instituto Butantan, do laboratóRio de Mastozoologia da Universidade do Estado do Rio de Janeiro e do acervo de mamíferos da universidade Federal de Pernambuco, permitindo a reunião de amostras de representantes de todas as linhagens mencionadas na literatura.

Os procedimentos laboratoriais de extração do DNA total foram realizados no LaboratóRio de Citogenética e Genética Animal (LabGen) da Universidade Federal de Mato Grosso (UFMT), campus Cuiabá, Mato Grosso, através dos protocolos de extração salina de Aljanabi & Martinez (1997) e no LaboratóRio de Evolução e Genética Animal (LEGAL) na Universidade Federal do Amazonas (UFAM), campus Manaus, Amazonas, através dos protocolos de extração CTAB 2% (Doyle & Doyle 1987).

Obtenção de dados mitocondriais

A amplificação do gene citocromo b (Citb) do DNA mitocondrial (mtDNA) foi obtida através da reação em cadeia da polimerase (PCR) para dez amostras sem sequências disponíveis no GenBank (Anexo 01, Tabela 1). As reações de amplificação, purificação e sequenciamento foram realizadas no LEGAL/UFAM. A amplificação foi obtida com os *primers forward* L14725 (5'-CGAAGCTTGATATGAAAAACCATCGTTG-3') (Kocher et al. 1989) e *reverse* MVZ16 (5'-AAATAGGAARTATCAYTCTGGTTTRAT-3') (Smith & Patton 1993).

A PCR foi realizada com volume final de 15 µL contendo 6,8 µL de H2O, 1,5 µL de tampão 10X, 1,5 µL do primer L14725 (2 pmol), 1,5 µL do primer MVZ16 (2 pmol), 1,2 µL de dNTPs (2 mM), 1,2 µl MgCl2 (25 mM), 0,3 µl da taq (0,02 U) e 1 µL de DNA. A PCR foi realizada em termociclador, com um ciclo inicial a 94º C por 2 minutos, seguido por 35 ciclos de desnaturação a 94º C por 15 segundos, anelamento a 55º C por 35 segundos e extensão a 68º C por 1 minuto e 30 segundos, seguido de um ciclo de extensão final de 68º C por 5 minutos.

As amostras de PCR foram purificadas com ExoSap-IT® e posteriormente sequenciadas utilizando-se os mesmos primers da PCR, em uma reação com 4,5 µl de H2O, 1,45 µl de tampão de sequenciamento 5X, 2 µl do *primer forward* ou *reverse*, 0,3 µl de BigDye Terminator v 3.1 (Applied Biosystems®) e 2 µl do PCR purificado. As reações de sequenciamento seguiram as recomendações indicadas pelo fabricante. Posteriormente, os produtos foram purificados com a adição de 2,5 µL de Acetato e 30 µL de álcool 70% e então ressuspendidos em 10 µl de formamida e injetado em sequenciador automático ABI 3500 (Applied Biosystems®). As sequências obtidas foram visualizadas e alinhadas para montagem da fita consenso no programa Geneious®.

Análise de dados mitocondriais

Além das 10 sequências obtidas neste estudo, utilizamos mais 63 sequências de Citb das linhagens do complexo *O. catherinae*, 15 sequências de *Oecomys* sp. nov., espécie irmã do complexo e até recentemente incluída nele (= linhagem oeste de Suarez-Villota et al. 2018), e mais 23 sequências do grupo externo depositadas no Genbank, que inclui as espécies *Oecomys auyantepui*, *O. bicolor*, *O. concolor*, *O. franciscorum*, *O. mamorae*, *O. paricola*, *O. rex*, *O. roberti*, *O. rutilus*, *O. superans*, *O. sydandersoni*, *O. tapajinus*, *O. trinitatis*, *Holoclilus brasiliensis*, *H. chacarius*, *H. sciureus*, *Hylaeamys megacephalus*, *Oligoryzomys destructor*, *O. flavescens*, *O. fulvencens*, *O. microtis* e *O. nigripes* (Anexo 01: tabela 1). Posteriormente, todas as sequências foram editadas e alinhadas no programa BioEdit 7.0.5.2 (Hall 1999).

Para a análise filogenética utilizamos os métodos de Inferência Bayesiana (IB), realizada no programa MrBayes 3.2.7a (Ronquist et al. 2012), com quatro cadeias, 50 milhões de gerações e uma amostragem de árvore a cada 1.000 gerações. O modelo evolutivo que melhor representa a matriz de dados foi o *Transition model* com proporção de sítios invariáveis e distribuição gama (TIM2 + I + G) gerado através do programa JModeltest2 (Darriba et al. 2012). As árvores obtidas foram visualizadas e editadas no programa Figtree 1.4.3 (Rambaut 2016). As relações entre os haplótipos foi avaliada através da rede haplotípica com o método *Median-Joining* (Bandelt et al. 1999) no programa PopArt (http://popart.otago.ac.nz).

Obtenção de dados genômicos

Para a representação parcial do genoma utilizamos a técnica de ddRADseq de Peterson et al. (2012), com modificações para a plataforma *Ion Torrent*. A técnica

ddRADseq foi aplicada em 43 amostras, sendo 21 espécimes da linhagem leste, quatro da linhagem central, seis da linhagem norte, duas da linhagem extremo oeste, uma amostra do nordeste e nove amostras da espécie *Oecomys* sp. nov. (= linhagem oeste de Suarez-Villota et al. 2018; Anexo 01: tabela 1). Além destes, utilizamos a biblioteca genômica de indivíduos de *O. auyantepui*, *O. bicolor*, *O. paricola*, *Hylaeamys megacephalus* e *Sooretamys angouya* como grupo externo.

A integridade e concentração do DNA foram checadas em Nanodrop 2000 (Thermo Scientific, USA) para posterior diluição e obtenção da concentração de 50 ng/ul. Para a digestão do DNA de cada amostra utilizamos a enzima de restrição de corte frequente SdaI e a enzima de corte raro Csp6I. Essas enzimas cortam as moléculas de DNA, criando pontas livres em ambas as extremidades para a ligação dos adaptadores. Utilizamos dois adaptadores, sendo o adaptador P1 comum a todas as amostras, que se liga à ponta gerada pela enzima SdaI, e o adaptador AY, no qual o Y representa um barcode único para cada amostra e se liga à ponta gerada pela enzima Csp6I. O processo de digestão e ligação ocorre de forma simultânea.

A reação de digestão/ligação foi realizada com volume final de 50 µL, sendo 4,0 µL de DNA (200 ng), 0,1 µL (1 U) da enzima SdaI, 0,1 µL (1 U) da enzima Csp6I, 2,0 µl (0,1 µM) do adaptador P1, 2,0 µl (5 uM) do adaptador AY (individual), 0,5 µl (5 U) da enzima T4 ligase, 0,5 µl de ATP (5 mmol) e 5 µl Tampão Tango 10X. A reação ocorreu em termociclador com um ciclo de 37º C durante 3 horas para a digestão do DNA pelas enzimas e ligação dos adaptadores, seguido de um ciclo de 68º C durante 15 minutos para desnaturação das enzimas.

Em seguida, realizamos uma PCR teste para a verificação da reação de digestão, com volume final de 15 µL contendo 4,25 µL de H2O, 1,5 µL de tampão 10X, 1,5 µL do primer P1 (2 mM), 1,5 µL do primer AY-individual (2 mM), 1,5 µL de BSA, 1,2 µL dNTPs (10 mM), 1,2 µl MgCl2 (25 mM), 0,35 µl da taq (1 U) e 2 µL de DNA digerido. A PCR foi realizada com um ciclo inicial a 94º C por 2 minutos, seguido por 35 ciclos de 94º C por 15 segundos, 55º C por 35 segundos e 68º C por 1 minuto e 30 segundos, seguido de um ciclo de final de 68º C por 1 minutos e 30 segundos. As amplificações testes foram checadas via eletroforese em gel de agarose a 1%.

Posteriormente, realizamos a etapa de enriquecimento com quatro réplicas de PCR para cada amostra, para aumentar o número dos fragmentos de DNA que realizaram a ligação com os adaptadores P1 e AY. Cada uma das quatro PCR de cada amostra ocorreram em volume final de 25 µL, sendo 11,45 µL de H2O, 2,0 µL MgCl2 (25 mM), 2,0 µL dNTPs

(10 mM), 2,5 μL de tampão 10X, 2,5 μL de primer P1 (2 mM), 2,5 μL de primer AY-individual (2 mM), 0,05 μL de Taq (Klentaq) e 2 μL do DNA digerido. As PCR foram realizadas em termociclador, com um ciclo inicial de 68º C por 1 minuto seguido por 18 ciclos de 93º C por 10 segundos, 52º C por 35 segundos, 68º C por 1 min e 30 segundos e um ciclo final de 68º C por 7 minutos. Em seguida, as cinco PCR foram agrupadas em um único tubo por amostra, totalizando um volume final de 100 μL.

As amplificações foram quantificadas no Qubit 2.0 (Thermo Fisher Scientific), seguindo o protocolo do fabricante. Estas amostras foram unidas em um único tudo, de maneira equimolar (200 ng/ul de cada amostra), e posteriormente foram concentradas em Speedvac até atingir aproximadamente 100 ul. Em seguida, realizamos a purificação com AMPure Beads (Beckman Coulter Inc), seguindo o protocolo dos fabricantes.

Após a purificação, selecionados fragmentos variando entre 350 – 450 pb através do Pippin Prep em gel de agarose 2 % Pippin Prep (Sage Science). Após a construção da biblioteca, realizamos o sequenciamento no sequenciador Ion Torrent (PGM, Life Technologies) com a utilização do kit de sequenciamento 318 Ion PGM chip de 400 pb, seguindo as recomendações dos fabricantes.

Análise de dados genômicos

As leituras da biblioteca genômica obtidas no Ion Torrent foram processadas no programa pyRAD 3.0.66 (Eaton 2014), onde separamos as sequências de cada indivíduo por barcode (AY-individual) e posteriormente os barcodes e adaptadores foram removidos. Em seguida, foi realizado o alinhamento destas sequências com a ferramenta Vsearch (Rognes et. al. 2016) com similaridade de 88% e os alinhamentos finais foram obtidos com a ferramenta MUSCLE. Os arquivos de saída (output) foram gerados a partir de uma matriz de dados para análises populacionais, somente com o complexo *O. catherinae* e a espécie *Oecomys* sp. nov., e uma matriz de dados para análises filogenéticas com a inclusão do grupo externo (*O. auyantepui*, *O. bicolor*, *O. paricola*, *Hylaeamys megacephalus* e *Sooretamys angouya*).

As árvores filogenéticas foram estimadas através do método de Máxima verossimilhança (MV) no programa RAxML versão 8 (Stamatakis 2014) e do método de Inferência Bayesiana (IB) no programa MrBayes 3.2.7a (Ronquist et al. 2012). Para a análise de MV, utilizamos o modelo GTR+GAMMA com 1.000 réplicas de bootstrap. Para a IB, utilizamos 50 milhões de gerações amostradas a cada 1.000 gerações e 25% de *burnin*.

Para a inferência da árvore de espécies, utilizamos a matriz de SNP (*Single Nucleotide Polimorphism*) não ligados, convertida pelo pacote Phrynomics do R. A ferramenta utilizada para gerar a árvore de espécies foi o pacote SNAPP 1.3.0 implementado no Beauti e Beast 2.4.7 (Bouckaert et al. 2014), com as taxas de mutação U e V = 1 e lambda *prior* com distribuição gamma estimada pelo programa. A cadeia de MCMC teve o comprimento de um milhão de gerações, amostrados a cada 1.000 e 10% de *burnin*. A convergência entre as cadeias foi observada através dos valores de ESS no programa Tracer 1.6 (Rambaut et al. 2014).

Para a delimitação das linhagens do complexo *O. catherinae*, obtidos com os resultados das análises de MV e IB dos ddRADseq, utilizamos o *Bayes factor delimitation* (BFD*). Testamos seis modelos com distintos números e arranjos de linhagens, cada um deles com *path sampling* de 48 *steps*, com 1.000 gerações por *step*, 10% de *burnin* e alpha de 0,3. A avaliação dos modelos com delimitações de linhagens alternativas foi realizada com o ranqueamento conforme o marginal *likelihood*, seguindo o *Bayes Factor* de Kass & Raftery (1995) para comparação de modelos.

Para estimar o tempo de divergência entre as linhagens, utilizamos como ponto de calibração a diversificação estimada entre *Oecomys* e *Hylaeamys* em 3,5 M.a (Leite et al. 2014), com desvio padrão de 0,5 M.a. Além disso, utilizamos a taxa de mutação estimada com base em Kimura (1980). Considerando a distância genética média (*p-distance*) de 4,289% entre *Oecomys* e *Hyaleamys* para o conjunto de dados com 612854 loci e o tempo de divergência entre as duas espécies, estimada em 3,5 M.a., a taxa de mutação foi de 0,0062 substituições por sítio por milhão de ano. A análise foi realizada no programa Beast 1.8.0 através do Relógio Relaxado Lognormal não Correlacionado e Yule Process como prior, com 50 milhões de gerações, uma amostragem de árvore a cada 1.000 gerações, e *burnin* de 10%. Posteriormente, as árvores foram sumarizadas no programa TreeAnnotator 1.7.1 (Drummond et al. 2012) e visualizadas no FigTree 1.4.3 (Rambaut 2016).

A verificação da estrutura populacional e grupos biológicos foi realizada através do programa FastSTRUCTURE (Raj et al. 2014), com os agrupamentos estimados com o *prior simple*. Realizamos interações com K= 1-10, sendo o modelo K que melhor explica a estrutura do conjunto de dados estimado pela ferramenta chooseK.py. Posteriormente, utilizamos o distruct.py para visualização gráfica dos agrupamentos do melhor K.

Dados morfométricos

Para as análises morfométricas, utilizamos as informações de linhagens obtidas nas análises genéticas. Ademais, como não foi possível distinguir morfologicamente os exemplares pertencentes aos subclados leste A e leste B através de caracteres morfológicos qualitativos, alocamos exemplares sem dados moleculares a estes subclados com base na distribuição geográfica. Assim, exemplares entre o sul do rio Jequitinhonha e norte do rio Paraíba do Sul foram alocados ao subclado leste B, e os exemplares ao sul deste último rio, ao subclado leste A (Figura 2). A linhagem nordeste, localizada ao norte do rio São Francisco, está representada em nossas amostras apenas por um exemplar, sem dados morfométricos, não sendo possível inclui-la nas análises morfométricas. Com isso, restringimos a análise morfométrica a cinco supostas linhagens/subclados de *O. catherinae* (extremo oeste, norte, central, leste A e leste B) e à espécie *Oecomys* sp. nov. .

Examinamos o crânio de 77 exemplares do complexo *O. catherinae* e 14 exemplares da espécie *Oecomys* sp. nov. (Anexo 02), estes adicionados na análise devido a estreita relação desta espécie com o complexo, visto que foi recentemente descrita como distinta de *O. catherinae*. Extraímos 17 medidas craniodentárias utilizando paquímetro digital com precisão de duas casas decimais enquanto os espécimes eram examinados em estereomicroscópio. Seguimos Voss (1988) para 13 dimensões craniodentárias: largura entre os côndilos occipitais (LCO), largura através do forame incisivo (LFI), largura do dente incisivo (LI), largura do primeiro molar superior (LM1), largura do nasal (LNA), largura da placa zigomática (LZP), comprimento côndilo–incisivo (CCI), comprimento coronal dos molares superiores (CCM), largura do zigomático (LZI), menor largura interorbital (LIO), comprimento do forame incisivo (CFI), comprimento do nasal (CN) e comprimento do diastema superior (CDI). Além destas, seguimos Carleton & Musser (1995) para as dimensões craniodentárias largura da bula auditiva (LBU), comprimento da ponte palatina (CPP), comprimento do rostro (CR) e comprimento occipto-nasal (CON).

Os exemplares foram agrupados em classes etárias de acordo com a eclosão e desgaste dos dentes seguindo Reig (1977). Utilizamos somente dados morfométricos de exemplares adultos como variáveis nos testes estatísticos. O dimorfismo sexual foi testado através do teste t de Student aplicado a exemplares pertencentes a uma mesma linhagem. Os dados foram transformados em logaritmos na base 10 para a realização de Análise de Componentes Principais (CP) e Análise Discriminante (AD), com o intuito de testar possíveis diferenças morfométricas para os agrupamentos identificados a partir das análises

moleculares. Todos os testes estatísticos foram realizados no programa SPSS 20 com nível de significância de 5%.

3. RESULTADOS

Dados mitocondriais

A análise de inferência Bayesiana com o banco de dados com o marcador mtDNA Citb recuperou a espécie *Oecomys* sp. nov. com alto suporte (PP = 1), irmã (PP = 0,9) do complexo *O. catherinae* (PP= 1), este último formado por cinco linhagens, cada uma com suporte ≥ 0,99 (o suporte para a linhagem nordeste, constituída por um único exemplar, não foi calculado). Com alto suporte, a linhagem extremo oeste (PP = 1), composta por exemplares da região oeste da Amazônia brasileira e Amazônia do Peru, aparece como irmã das demais. Também com alto suporte, as linhagens nordeste, com o exemplar da região ao norte da Mata Atlântica, linhagem norte, com exemplares do norte da Amazônia, linhagem central, com exemplares do cerrado (PP = 1) e linhagem leste com exemplares da Mata Atlântica (PP = 0,99) formam um grupo monofilético, porém as relações entre elas não estão bem resolvidas, sustentadas por baixo suporte (Figuras 1 e 2). Dentro da linhagem leste verificamos a ocorrência de dois subclados com alto suporte filogenético (PP≥ 0,99), aqui denominados subclados leste A e leste B (Figuras 1 e 2).

A rede de haplótipos obtida com os dados de Citb (Figura 3) apontou uma clara separação para a maioria das linhagens recuperadas na análise filogenética. O haplogrupo de Oecomys sp. nov. aparece mais distante, separado por 45 passos mutacionais do haplogrupo mais próximo (extremo oeste). O haplogrupo extremo oeste separa-se do haplogrupo nordeste por 34 passos mutacionais e dos demais haplogrupos por 21 (norte), 25 (leste) e 28 (central) passos mutacionais. No haplogrupo leste não recuperamos o compartilhamento de haplótipos entre os subclados A e B, mas o número de passos mutacionais que separa estes subclados é de apenas dois. O haplogrupo central separa-se dos haplogrupos norte e leste por 13 passos mutacionais, e o haplogrupo norte e leste estão separados por 10 passos mutacionais (Figura 3).

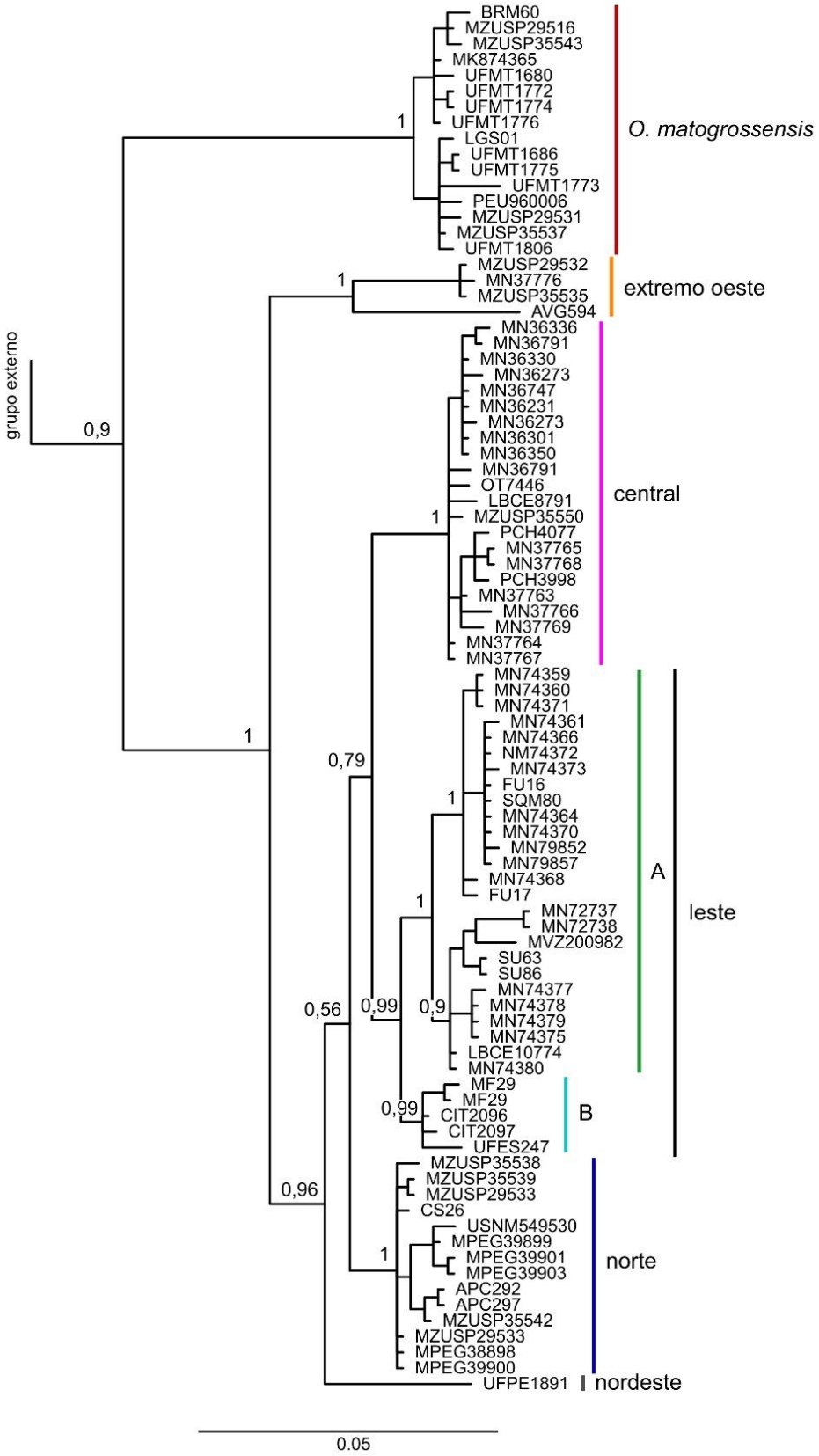


Figura 1. Topologia de inferência Bayesiana com o marcador mitocondrial Citocromo b de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo). Números próximos aos ramos indicam a probabilidade posterior (PP). Os dados das amostras e grupo externo utilizados são apresentados no Anexo 01: tabela 1.

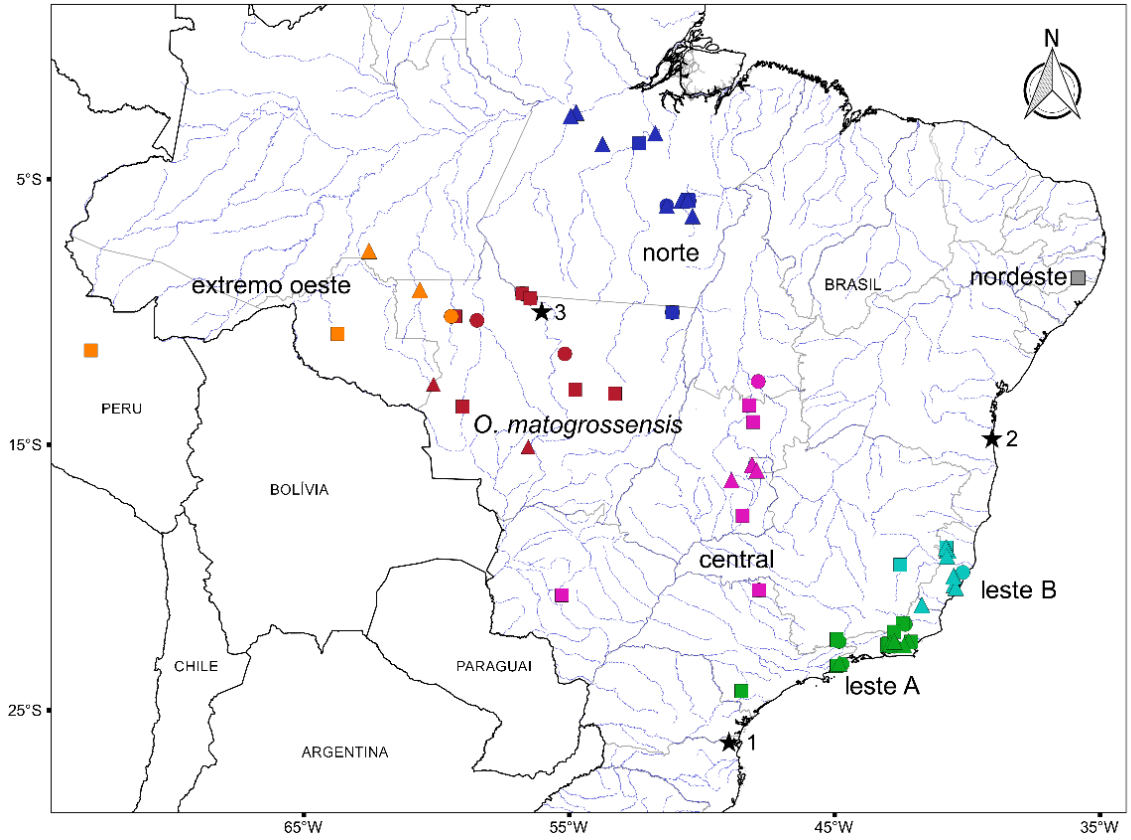


Figura 2. Mapa com as localidades das amostras de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo). As cores representam as espécies e linhagens obtidas nas análises filogenéticas. Triângulos representam exemplares com dados morfológicos, quadrados com dados moleculares, e círculos com ambos os dados. As estrelas pretas representam a localidade tipo de *O. catherinae* (1), *O. bahiensis* (2) e *Oecomys* sp. nov. (3).

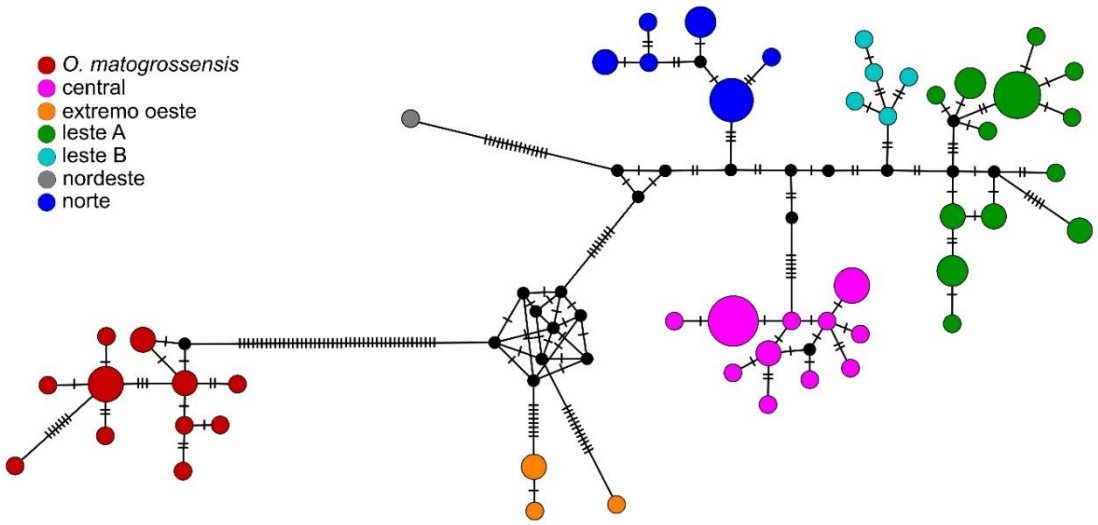


Figura 3. Rede haplotípica com o marcador mitocondrial Citocromo b de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo). As cores representam as espécies e linhagens obtidas nas análises filogenéticas, e o tamanho das amostras (círculos) representa o número de haplótipos. Círculos pretos representam haplótipos não amostrados e as barras representam eventos de passos mutacionais.

Dados genômicos

As análises moleculares com ddRADseq resultaram em hipóteses filogenéticas com alto suporte, confirmando o monofiletismo de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo), assim como a relação entre estes clados, sendo congruente com a maior parte dos resultados obtidos pelos dados de Citb, exceto pela posição da linhagem nordeste que aparece nitidamente relacionada à linhagem leste (Figura 4), porém, na filogenia com Citb a linhagem nordeste aparece agrupada com as linhagens norte, central e leste, com a posição dentro do grupo não definida (Figura 1).

No complexo *O. catherinae* recuperamos quatro linhagens com alto valor de suporte (PP = 1 e bootstrap = 100): norte, central, leste e extremo oeste. Dentro da linhagem leste recuperamos os subclados A e B com alto suporte (leste A: PP = 1 e bootstrap = 100; leste B: PP = 1 e bootstrap = 90), assim como a amostra do nordeste, esta última como irmã dos subclados leste A e B (Figura 4).

A estimativa de tempo de divergência molecular apontou que os eventos de diversificação relacionados a *Oecomys* sp. nov. e *O. catherinae* ocorreram durante o Pleistoceno. O surgimento do clado composto por *Oecomys* sp. nov. e as linhagens do complexo *O. catherinae* ocorreu há cerca de 2,35 M.a. (95% HPD = 2,02–2,77), e a diversificação entre estes dois grupos foi estimada para 1,53 M.a. (95% HPD = 1,29–1,8). Dentro do complexo, o ancestral da linhagem do extremo oeste diversificou há cerca de 1,05 M.a. (95% HPD = 0,89–1,23). O ancestral da linhagem norte diversificou há 0,85 M.a. (95% HPD = 0,73–1,01), e as linhagens central e leste se diversificaram há cerca de 0,58 M.a. (95% HPD = 0,5–0,68). Dentro da linhagem leste, a amostra do nordeste divergiu das demais há cerca de 0,47 M.a. (95% HPD = 0,41–0,54), e os subclados A e B divergiram entre si há cerca de 0,4 M.a. (95% HPD = 0,35–0,46) (Figura 5).

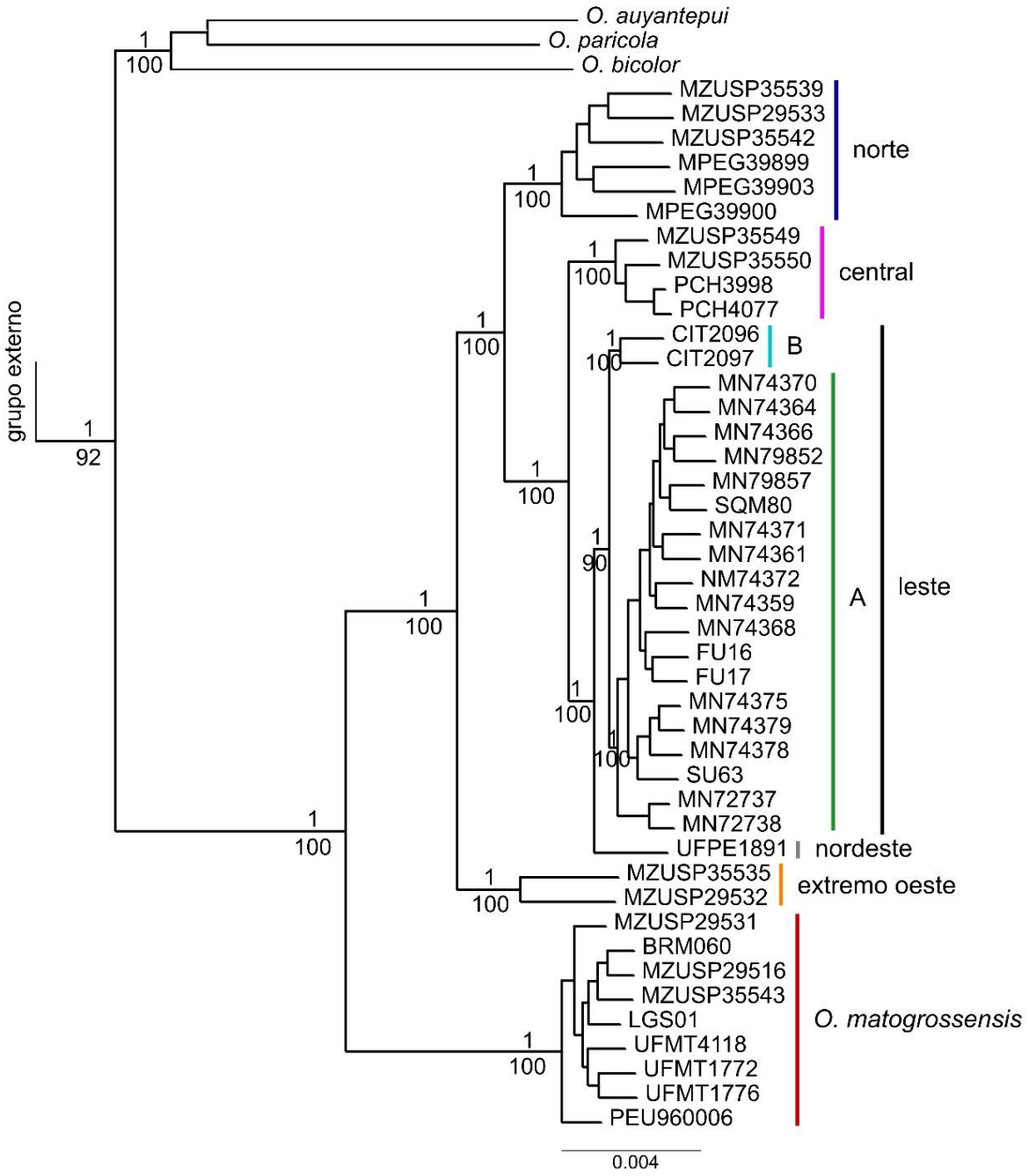


Figura 4. Topologia de inferência Bayesiana com matriz de dados de ddRADseq de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo). Valores acima dos ramos indicam a probabilidade posterior (PP) e, abaixo dos ramos, o valor de bootstrap. Os dados das amostras são apresentados no Anexo 01: tabela 1.

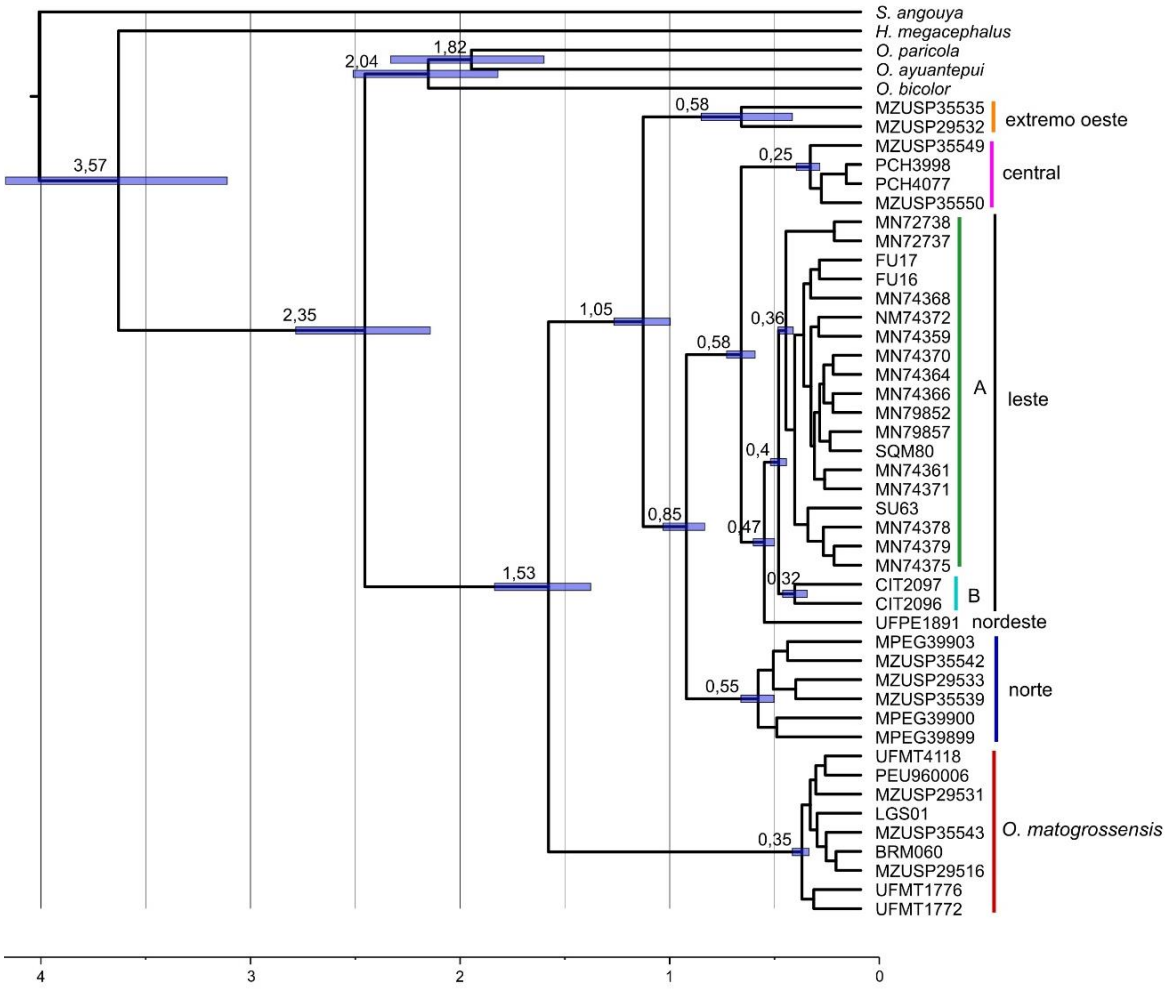


Figura 5. Árvore datada de *Oecomys* sp. nov. e do complexo *O. catherinae* (senso Saldanha & Rossi, no prelo). Os valores acima dos nós se referem às datas de divergência estimadas em milhões de anos pelo BEAST, e as barras correspondem aos intervalos de confiança de 95% das datas estimadas. Os dados das amostras são apresentados no Anexo 01: tabela 1.

Entre os seis modelos de delimitação das linhagens testadas, o BFD* selecionou como o melhor modelo a topologia com *Oecomys* sp. nov. irmão do complexo *O. catherinae*, este último composto por seis linhagens (Marginal Likelihood = -2976,7, Tabela 1). Estas linhagens são coincidentes com as encontradas nas análises de IB e MV com RADseq e também com aqueles presentes nas análises com Citb. O SNAPP recuperou alto suporte para a relação entre a maioria das linhagens (Figura 6), exceto para as relações entre leste A e B (0,5) e destas com a linhagem nordeste (0,81).

Tabela 1. Modelos de linhagens testadas pela *Bayes Factor Delimitation* (BFD*) para os dados se SNPs. ML: marginal likelihood, BF= Bayes Factor.

Modelo testado	linhagens	ML	BF	classificação
Oecomys sp. nov. / complexo *O. catherinae* (taxonomia atual)	2	-7306,8	-	-
Oecomys sp. nov. / extremo oeste / norte+central+leste	3	-6242,1	-2129,5	5
Oecomys sp. nov. / extremo oeste / norte / central / leste	5	-4836,1	-4941,4	4
Oecomys sp. nov. / extremo oeste / norte / central / leste A+B / nordeste	6	-3271,3	-8071,1	2
Oecomys sp. nov. / extremo oeste / norte / central / leste A / nordeste+leste B	6	-4603,6	-5406,4	3
Oecomys sp. nov. / extremo oeste / norte / central / leste A / leste B / nordeste	7	-2976,7	-11637,0	1

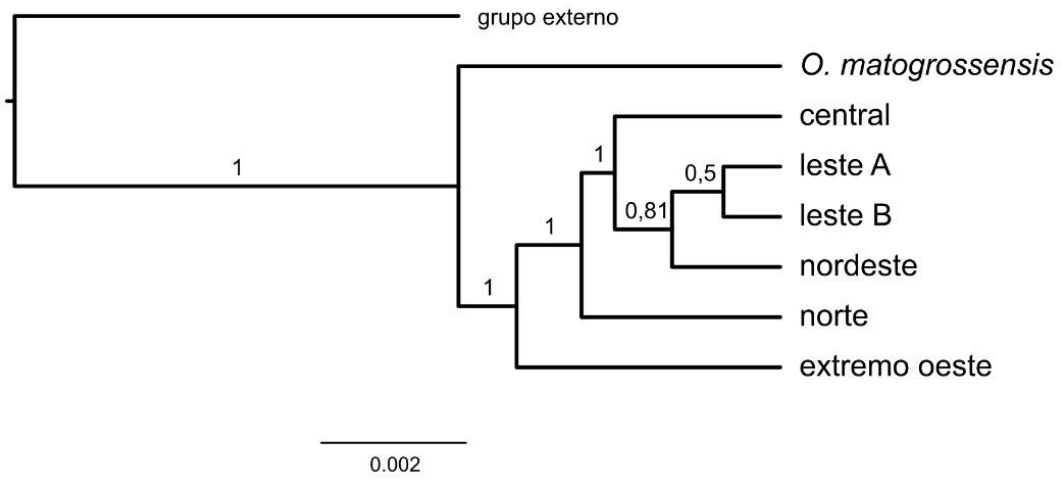


Figura 6. Árvore de espécie obtida no programa SNAPP para o modelo com *Oecomys* sp. nov. mais seis linhagens/subclados de *O. catherinae* (extremo oeste, norte, central, nordeste, leste A e leste B).

A análise realizada no FastSTRUCTURE apontou o K = 4 (Figura 7) como o mais provável para explicar a estrutura do banco de dados testado. Esta análise identificou agrupamentos biológicos com nenhum admixture e distintos daqueles apontados pelas analises filogenéticas de RADseq e mtDNA. Esses agrupamentos incluem na mesma população os subclados leste A, leste B, linhagens nordeste e central, as demais populações com linhagens isoladas (extremo oeste, norte e *Oecomys* sp. nov.).

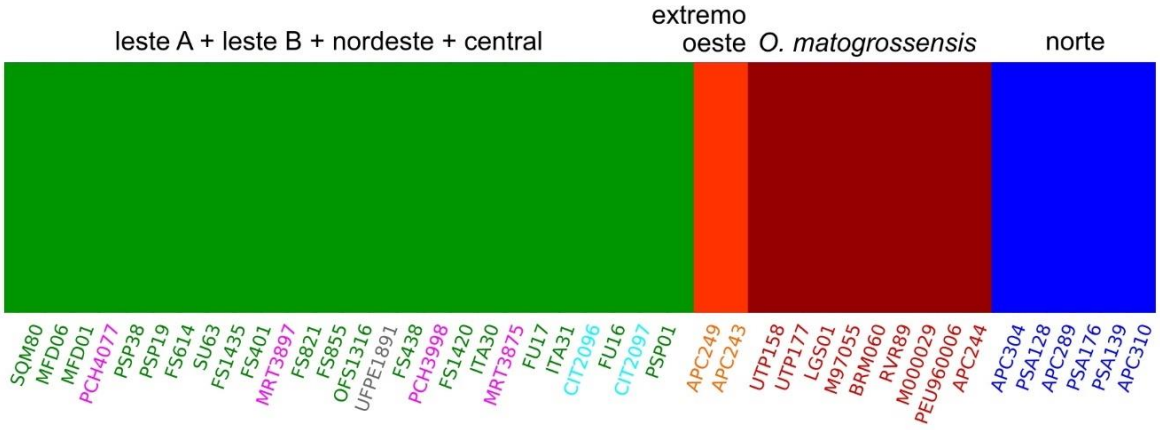


Figura 7. Grupos biológicos apontados pelo FastSTRUCTURE com K=4 para *Oecomys* sp. nov., e as linhagens do complexo *O. catherinae*. As cores aplicadas aos exemplares indicam as espécies e linhagens reconhecidas nas análises filogenéticas.

Dados morfométricos

A Análise de Componentes Principais indica que o primeiro componente principal (CP 1) explica 57,75% da variação total e o segundo componente principal (CP 2), 9,24% da variação total. As medidas que mais contribuíram para o CP 1 foram comprimento occipto-nasal (CON) e comprimento côndilo-incisivo (CCI). Já no CP 2, as principais medidas foram largura do primeiro molar superior (LM1) e comprimento coronal dos molares superiores (CCM; Tabela 2). O gráfico dos escores do primeiro e segundo componentes mostrou que exemplares de *Oecomys* sp. nov. separam-se completamente dos exemplares da linhagem central e leste A de *O. catherinae* ao longo do eixo do CP1 e tendem a se separar das demais linhagens do complexo ao longo deste mesmo eixo (Figura 8A), que expressa o tamanho geral dos exemplares uma vez que os coeficientes são todos positivos neste componente principal (Tabela 2). Ademais, a linhagem leste A sobrepõe parcialmente com a linhagem norte e extremo oeste ao longo do eixo da CP1, e há ampla sobreposição entre as linhagens leste A, leste B e central ao longo do mesmo eixo. Não há separação de nenhuma das amostras ao longo do eixo da CP2.

Tabela 2. Resultado da Análise de Componentes Principais de espécimes de *Oecomys* sp. nov. e linhagens do complexo *Oecomys catherinae* com base em 17 medidas crânio-dentárias. As descrições das medidas são apresentadas na seção Material e Métodos.

	Componente		
	1	2	3
CON	0,97	-0,04	-0,05
CCI	0,96	0,01	-0,02
CDI	0,92	-0,13	-0,12
LPZ	0,78	0,00	0,01
LNA	0,75	0,13	0,01
CN	0,65	-0,05	-0,63
CR	0,88	-0,04	-0,18
LIO	0,77	-0,01	0,38
LZI	0,88	0,08	-0,11
LFI	0,66	-0,15	-0,04
CFI	0,84	-0,10	0,15
CPP	0,70	0,24	-0,13
LCO	0,71	-0,27	0,50
LBU	0,54	-0,45	0,24
LI	0,80	-0,07	-0,06
LM1	0,25	0,83	0,24
CCM	0,49	0,69	0,04
% da variação	57,75	9,24	6,00

A Análise de Função Discriminante indica que a primeira função é responsável por 69,5% da variação, enquanto a segunda função responde por 18,8% da variação. As medidas que mais contribuíram para a função 1 foram o comprimento do rostro (CR, coeficiente negativo) e a largura do zigomático (LZI, coeficiente negativo). Para a função 2, as medidas que mais contribuíram foram a largura do incisivo (LI, coeficiente negativo) e forame incisivo (LFI, coeficiente positivo; Tabela 3).

O gráfico com as funções discriminantes 1 e 2 confirma a clara separação da espécie *Oecomys* sp. nov. em relação ao complexo *O. catherinae* ao longo do eixo da primeira função. No complexo *O. catherinae*, a linhagem extremo oeste não se sobrepõe às linhagens leste A e central, e a linhagem norte tende a se separar das demais linhagens ao longo do eixo da função 2. Em contrapartida, as linhagens central, leste A e leste B estão amplamente sobrepostas entre si (Figura 8B).

Tabela 3. Resultado da análise de Função Discriminante de espécimes de *Oecomys* sp. nov. e linhagens do complexo *Oecomys catherinae* com base em 17 medidas crânio-dentárias. As descrições das medidas são apresentadas na seção Material e Métodos.

	Função				
	1	2	3	4	5
CON	0,31	0,23	-2,18	-0,56	-0,48
CCI	0,42	-0,47	0,94	-0,24	-0,11
CDI	0,27	-0,67	0,62	0,31	0,52
LPZ	0,25	-0,24	0,16	-0,50	-0,08
LNA	-0,05	0,19	0,28	-0,05	-0,14
CN	0,12	-0,68	0,32	0,28	0,23
CR	-0,78	0,49	0,40	-0,15	0,37
LIO	0,38	-0,05	-0,28	0,50	0,05
LZI	-0,64	0,57	0,87	-0,42	-0,44
LFI	0,13	0,71	-0,13	0,34	0,35
CFI	0,10	0,67	-0,23	-0,22	0,03
CPP	-0,15	0,44	-0,24	1,05	-0,37
LCO	0,56	-0,12	-0,08	-0,04	0,25
LBU	0,41	0,03	0,44	0,01	-0,71
LI	0,08	-0,76	-0,34	0,30	0,23
LM1	-0,10	0,28	-0,34	-0,17	-0,29
CCM	0,16	-0,21	0,56	-0,08	0,73
% da variação	69,5	18,8	6,4	4,3	1,1
Autovalor	3,88	1,05	0,36	0,24	0,06

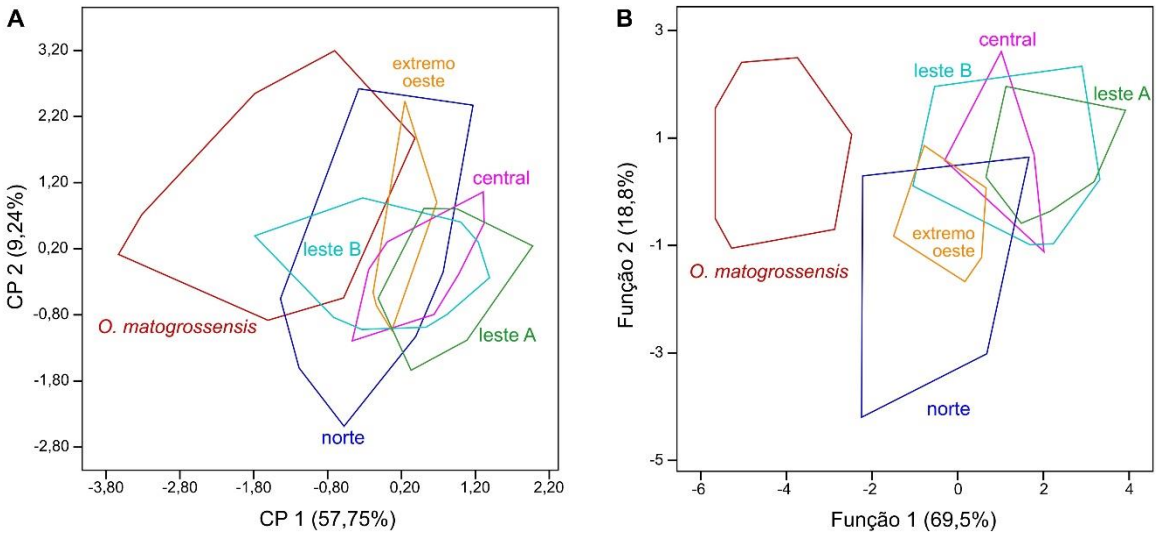


Figura 8. Gráfico de dispersão dos componentes principais 1 e 2 (A) e funções discriminantes 1 e 2 (B), de espécimes de *Oecomys* sp. nov. e linhagens do complexo *Oecomys catherinae* com base em 17 medidas crânio-dentárias.

4. DISCUSSÃO

Os recentes estudos envolvendo sistemática e diversidade genética do gênero *Oecomys* proporcionaram uma nova visão sobre *Oecomys catherinae*. Apontado como um complexo de espécies por diversos autores, o grupo apresenta ampla distribuição geográfica e considerável divergência genética, em contraste com a escassez ou ausência de variação morfológica (Suárez-Villota et al. 2018; Saldanha & Rossi, no prelo). Apenas uma das linhagens deste complexo pôde ser distinguida morfologicamente, descrita como uma nova espécie por Saldanha & Rossi (no prelo). Com os nossos dados, corroboramos a distinção de *Oecomys* sp. nov. do complexo *O. catherinae* em todas as análises realizadas com mtDNA e RADseq. Recuperamos a ocorrência de dois subclados na linhagem leste, como mencionado por Saldanha & Rossi (no prelo). Ademais, esclarecemos as relações entre as linhagens, recuperando a linhagem extremo oeste como irmã das demais, seguida da linhagem norte, central e leste, discordando da topologia apresentada por Suárez-Villota et al. (2018). Por fim, recuperamos outra possível linhagem para o complexo (aqui denominada linhagem nordeste), além das linhagens já citadas, localizada ao norte do rio São Francisco.

Na filogenia com mtDNA, evidenciamos a incerteza no posicionamento da linhagem nordeste, em contraste com resultados de RADseq onde a linhagem nordeste aparece nitidamente relacionada à linhagem leste (Figuras 1 e 4, respectivamente). Incongruências entre topologias de hipóteses filogenéticas em *Oecomys* já foram relatadas na literatura (Rocha et al. 2018; Suárez-Villota et al. 2018; Saldanha et al. 2019; Saldanha & Rossi, no prelo). Por isso, o uso de marcador mitocondrial como única ferramenta para estudos de delimitação de espécies e populações é amplamente questionada, pois pode limitar a compreensão da evolução e histórico populacional (Galtier et al. 2009).

Na abordagem multilocus com RADseq, o BFD* apontou como melhor modelo para o conjunto de dados o modelo com maior número de espécies (Tabela 1). Estudos com outros grupos também verificaram que o BFD tende a apontar como melhor modelo aquele com o maior número de espécies (ver Villamil et al. 2019). Além disso, este método não considera explicitamente o fluxo gênico, isolamento por distância, seleção ou vários outros processos biológicos importantes, e os resultados devem considerar outros aspectos como a geografia das possíveis espécies antes de concluir as delimitações (Leaché & Bouckaert 2018).

Em contraposição aos métodos filogenéticos, que buscam reconstruir o passado evolutivo das espécies, as análises de estrutura populacional visam detectar padrões de fluxo gênico atuais, que permitem a delimitação geográfica das populações (Cunha &

Solé-Cava 2012). Com isso, a relação de maior proximidade da linhagem nordeste com os subclados leste A e leste B fica evidente nas análises populacionais, corroborando a topologia obtida com matriz de dados de ddRADseq. Ademais, os agrupamentos biológicos obtidos indicam a ausência de compartilhamento de haplótipos entre as espécies e linhagens analisadas (Figura 3).

Assim, nossos resultados sugerem a ocorrência de dois grupos biológicos com populações distintas (linhagens norte e extremo oeste), sem fluxo gênico, na Amazônia, e um grupo biológico com populações nas regiões de Mata Atlântica (subclados leste A, leste B e linhagem nordeste) e Cerrado (linhagem central) (Figuras 2 e 7). A ocorrência de um único grupo biológico composto por linhagens do Cerrado e Mata Atlântica vai ao encontro ao proposto por Costa (2003), ao afirmar que a região central do Brasil não se comporta como uma região separada, mas sim complementar à Amazônia ou à Mata Atlântica, a depender do táxon em questão. Em particular, no caso do grupo denominado como *Oecomys trinitatis* por Costa (2003), a autora confirma a relação do Cerrado e Caatinga como áreas irmãs da Mata Atlântica, e não da Amazônia, assim como a linhagem central do complexo *O. catherinae*.

Com a árvore datada, nossos dados apontam a divergência estimada entre *Oecomys* e *Hylaeamys* para cerca de 3,57 M.a., durante o Plioceno, semelhante aos 4,4 M.a. propostos por Parada et al. (2013). Segundo os autores, a maioria das tribos de Sigmodontinae, incluindo Oryzomyini, diversificou-se no Mioceno Superior (7,72 M.a.), com distribuição do ancestral mais recente para a região sul-americana antes do fechamento do Istmo do Panamá. A divergência entre o complexo *O. catherinae* e a espécie *Oecomys* sp. nov. foi estimada para o Pleistoceno Calabriano (cerca de 1,53 M.a.), na região amazônica. Posteriormente, ainda na região amazônica, divergiu a extremo oeste seguida da linhagem norte ainda no pleistoceno.

A diversificação da espécie *Oecomys* sp. nov. das linhagens da Amazônia podem estar associados à hipótese dos refúgios (Haffer 1969), que relaciona mudanças climáticas durante o Pleistoceno com ciclos de fragmentação e reconexão de florestas, que formavam refúgios, isolando populações e promovendo a especiação. Apesar do número, tamanho e localização destes refúgios ainda serem incertos, a distribuição de *Oecomys* sp. nov. e da linhagem extremo oeste coincidem com possíveis refúgios nas florestas úmidas adjacentes do Planalto dos Parecís (Haffer 2008). Similarmente, a área de distribuição da linhagem norte pode ter surgido na Serra do Cachimbo, cujos arredores constituídos por

terras baixas foram cobertos por camadas de areia no Pleistoceno tardio (Haffer 2008; Haffer & Prance 2002), promovendo o isolamento de populações nas partes mais altas da Serra.

A linhagem central, que ocupa o Cerrado, divergiu das linhagens da Mata Atlântica no Pleistoceno médio (cerca de 0,58 M.a.), mesmo período estimado para a divergência das linhagens e clados dentro da Mata Atlântica (0,47 e 0,4 M.a). Costa et al. (2000), em análise parcimoniosa de endemismo, identificou a ocorrência de duas regiões (norte e sul) na Mata Atlântica e propôs que a Serra da Mantiqueira seria o local da divisão entre essas regiões. Outros estudos na Mata Atlântica também identificaram uma lacuna entre os táxons do norte e sul, que coincide com a Depressão do rio Paraíba do Sul, localizado entre duas principais montanhas do sudeste do Brasil, a Serra da Mantiqueira e a Serra do Mar (Silva & Straube 1996). Entretanto, para *O. catherinae*, as divergências entre as linhagens da Mata Atlântica não são compatíveis com a formação da Serra do Mar e Serra da Mantiqueira, estimadas durante o Plioceno-Pleistoceno (ver Silva & Straube 1996).

Na Mata Atlântica, a estrutura genética de alguns táxons coincide com a presença de sistemas fluviais, sendo a quebra filogeográfica mais profunda coincidente com o sistema do rio Doce (Costa & Leite 2012). Apesar disso, para os subclados A e B da linhagem leste, o rio Doce não atua como um divisor, visto que exemplares do subclado leste B estão presentes ao norte (UFES247) e ao sul (MF29) deste rio. Além disso, para o roedor *Akodon cursor*, o rio Doce não constitui uma barreira efetiva ao fluxo gênico entre populações (Colombi et al. 2010). Estudos sobre o papel dos rios da Mata Atlântica como barreiras ainda são negligentes, porém, entre as teorias mais citadas como possíveis explicações para a quebras populacionais da Mata Atlântica, estão as mudanças climáticas e vegetais que ocorreram no Plioceno e Quaternário (Costa & Leite 2012). Resultado semelhante foi encontrado por Nascimento et al. (2013), onde a diversificação de *Thrichomys* não foi associada ao rio São Francisco como barreira, devido à idade mais avançada do rio em relação à origem de *Thrichomys*. Segundo os autores é mais provável que o padrão de diversificação observado seja consequência de mudanças climáticas e períodos áridos.

Distintos componentes nas regiões norte e sul da Mata Atlântica foram relatados por Costa (2003). Para o roedor *Rhipidomys* e o marsupial *Micoureus*, por exemplo, os clados recuperados pela autora correspondem a espécies distintas; já para o marsupial *Metachirus nudicaudatus*, Costa (2003) recuperou dois clados estruturados geograficamente. Segundo a autora, essa quebra entre espécies e clados ao norte e sul da Mata Atlântica é coincidente e as flutuações climáticas são uma explicação plausível para

este padrão coincidente no espaço, mas não no tempo. Apesar disso, para a diversificação entre as linhagens nordeste, que ocorre ao norte do rio São Francisco, e entre os subclados leste A e leste B, entre distintas regiões do rio Paraíba do Sul, as divergências estimadas são compatíveis com as mudanças climáticas ocasionadas pela glaciação Mindel estimada em 0,45 M.a. (Nascimento et al. 2013).

Nossos resultados morfométricos indicam a sobreposição entre as linhagens analisadas, principalmente as procedentes da Mata Atlântica (consideramos as amostras ao sul do rio Paraíba do Sul como pertencentes ao subclado leste A e ao norte do subclado leste B) e Cerrado (Figura 8B). Apesar de todas as hipóteses filogenéticas apontarem a divergência molecular entre linhagens, os agentes evolutivos, como a seleção natural, não atuam diretamente sobre a diversidade genética, mas sim sobre os fenótipos (Shorrocks 1980). Por isso, linhagens que não podem ser reconhecidas como espécies distintas a partir da morfologia representam espécies crípticas, como é o caso dos subclados leste A, leste B e linhagem central. A definição mais recente do conceito de espécie unificada sugere que, para serem consideradas espécies, as linhagens não necessitam ser distinguíveis ou diagnosticáveis morfologicamente, monofiléticas, isolados reprodutivamente, ecologicamente divergentes ou outras definições (de Queiroz 2007). Segundo o autor, basta as linhagens evoluírem separadamente de outras linhagens. Entretanto, estas definições podem servir como critérios para avaliar se as espécies estão evoluindo separadamente (de Queiroz 2007).

Levando em consideração o conjunto de análises apresentados, nossos resultados apontam os subclados A e B da linhagem leste como possíveis linhagens alopátricas que, junto com as linhagens nordeste e central, representam um grupo biológico com indícios de especiação, dada a divergência evolutiva apontada pelas hipóteses filogenéticas. Já as linhagens extremo oeste e norte, apesar da ausência de caracteres diagnósticos (Saldanha & Rossi, no prelo) e leve sobreposição morfométrica, representam linhagens evolutivas distintas. O reconhecimento da linhagem norte como espécie distinta é corroborado por caracteres citogenéticos, com os representantes desta linhagem apresentando cariótipo com 2n = 62, distinto das demais linhagens, 2n = 60 (Suárez-Villota et al. 2018; Malcher et al. 2017; Saldanha & Rossi, no prelo).

Neste estudo, apresentamos a primeira abordagem para a inferência filogenética e diversificação do complexo *O. catherinae* com mtDNA, ddRADseq e morfometria combinados. Devido às semelhanças morfológicas entre as linhagens e variação individual de caracteres dentro das linhagens, as análises integrativas são essenciais para

auxiliar o entendimento da diversidade oculta deste complexo. Com nossos resultados, confirmamos *Oecomys* sp. nov. como espécie distinta do complexo, e a existência de três espécies no complexo *O. catherinae* que correspondem as linhagens extremo oeste (espécie 1), linhagem norte (espécie 2) e as linhagens leste A e B, nordeste e central (espécie 3 = *Oecomys catherinae*). Não pudemos confirmar se a evolução das linhagens da Mata atlântica e Cerrado possuem histórias evolutivas distintas, o que nos leva a considerar estas linhagens como uma única espécie. Para elucidar as relações evolutivas entre os subclados da Mata Atlântica, sugerimos um estudo mais amplo com amostras provenientes do estado da Bahia e demais pontos da porção mais norte da Mata Atlântica.

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ANEXO 01

Tabela 1. Número de campo, tombo, acesso do Genbank (Citocromo b), exemplares incluídos nas análises genômicas (ddRADseq) e localidades dos exemplares utilizados neste estudo. Linhagens do complexo *Oecomys catherinae*: central, extremo oeste, leste A, leste B, nordeste e norte.

Linhagem / espécie	Campo	Tombo	ddRAD	GenBank	Localidade
Central	MRT3875	MZUSP35549	ok	MG323761	Brasil: Tocantins, Paranã
Central	MRT3897	MZUSP35550	ok	MG323762	Brasil: Tocantins, Paranã
Central	PCH3998	-	ok	MG323764	Brasil: São Paulo, São Joaquim da Barra
Central	PCH4077	-	ok	MG323763	Brasil: São Paulo, São Joaquim da Barra
Central	-	MN37763	-	FJ361051	Brasil: Goiás, Caldas Novas
Central	-	MN37764	-	FJ361052	Brasil: Goiás, Caldas Novas
Central	-	MN37765	-	FJ361053	Brasil: Goiás, Caldas Novas
Central	-	MN37766	-	FJ361054	Brasil: Goiás, Caldas Novas
Central	-	MN37767	-	FJ361055	Brasil: Goiás, Caldas Novas
Central	-	MN37768	-	FJ361056	Brasil: Goiás, Caldas Novas
Central	-	MN37769	-	FJ361057	Brasil: Goiás, Caldas Novas
Central	OT7446	-	-	FJ361058	-
Central	OT7447	-	-	FJ361059	-
Central	-	MN36231	-	FJ361060	Brasil: Goiás, Colinas do Sul
Central	-	MN36273	-	FJ361061	Brasil: Goiás, Colinas do Sul
Central	-	MN36301	-	FJ361062	Brasil: Goiás, Colinas do Sul
Central	-	MN36330	-	FJ361063	-
Central	-	MN36336	-	FJ361064	-
Central	-	MN36350	-	FJ361065	Brasil: Goiás, Colinas do Sul
Central	-	MN36747	-	FJ361068	Brasil: Goiás, Minaçu

Linhagem / espécie	Campo	Tombo	ddRAD	GenBank	Localidade
Central	-	MN36791	-	FJ361069	Brasil: Goiás, Minaçu
Central	-	LBCE8791	-	MG323760	Brasil: Mato Grosso do Sul, Dois Irmãos de Buriti
Extremo Oeste	APC243	MZUSP35535	ok	MG323759	Brasil: Mato Grosso, Aripuanã
Extremo Oeste	APC249	MZUSP29532	ok	MG323758	Brasil: Mato Grosso, Aripuanã
Extremo Oeste	-	MN37776	-	FJ361050	Brasil: Rondônia, Guajará-Mirim
Extremo Oeste	-	AVG594	-	MG988098	Peru: Cusco, Laconvencio, Echarate, Camisea, Lote 88
Leste A	FS6-14	MN74364	ok	-	Brasil: Rio de Janeiro, Cachoeiras de Macacu, Fazenda "sem
Leste A	FS13-16	MN74370	ok	-	Brasil: Rio de Janeiro, Cachoeiras de Macacu, Fazendas Pica
Leste A	FS14-20	MN74371	ok	KY605393	Brasil: Rio de Janeiro, Cachoeiras de Macacu, Sítio
Leste A	FS14-35	NM74372	ok	KY605394	Brasil: Rio de Janeiro, Cachoeiras de Macacu, Sítio
Leste A	MFD 01	MN79852	ok	-	Brasil: Rio de Janeiro, Cachoeiras de Macacu, Estação
Leste A	MFD 06	MN79857	ok	-	Brasil: Rio de Janeiro, Cachoeiras de Macacu
Leste A	SQM80	-	ok	-	Brasil: Rio de Janeiro, Cachoeiras de Macacu
Leste A	FU16	-	ok	KY605396	Brasil: Rio de Janeiro, Cassemiro de Abreu, Reserva
Leste A	FU17	-	ok	KY605397	Brasil: Rio de Janeiro, Cassemiro de Abreu, Reserva
Leste A	FS4-1	MN74359	ok	KY605388	Brasil: Rio de Janeiro, Guapimirim, Fazenda Chorona
Leste A	FS4-38	MN74361	ok	KY605390	Brasil: Rio de Janeiro, Guapimirim, Fazenda Chorona
Leste A	FS8-21	MN74366	ok	KY605391	Brasil: Rio de Janeiro, Guapimirim, Fazenda Iguaçu
Leste A	FS8-55	MN74368	ok	KY605392	Brasil: Rio de Janeiro, Guapimirim, Fazendas Consorciadas
Leste A	ITA30	MN72737	ok	KY605398	Brasil: Minas Gerais, Pirapetinga
Leste A	ITA31	MN72738	ok	KY605399	Brasil: Minas Gerais, Pirapetinga
Leste A	SU63	-	ok	KY605403	Brasil: Rio de Janeiro, Sumidouro
Leste A	PSP01	MN74375	ok	-	Brasil: São Paulo, Ubatuba, Parque Estadual da Serra do Mar
Leste A	PSP19	MN74378	ok	KY605401	Brasil: São Paulo, Ubatuba, Parque Estadual da Serra do Mar

Linhagem / espécie	Campo	Tombo	ddRAD	GenBank	Localidade
Leste A	PSP38	MN74379	ok	KY605402	Brasil: São Paulo, Ubatuba, Parque Estadual da Serra do Mar
Leste A	-	MVZ200982	-	HM594616	Brasil: São Paulo, Capão Bonito
Leste A	FS4-35	MN74360	-	KY605389	Brasil: Rio de Janeiro, Guapimirim
Leste A	FS14-40	MN74373	-	KY605395	Brasil: Rio de Janeiro, Cachoeiras de Macacu
Leste A	PSP12	MN74377	-	KY605400	Brasil: São Paulo, Ubatuba
Leste A	SU86	-	-	KY605404	Brasil: Rio de Janeiro, Sumidouro
Leste A	-	LBCE10774	-	MG323771	Brasil: Rio de Janeiro, Paraty
Leste A	PSP42	MN74380	-	-	Brasil: São Paulo, Ubatuba, Parque Estadual da Serra do Mar
Leste B	MF29	-	-	EU579507	-
Leste B	-	UFES247	-	JQ966233	Brasil: Espírito Santo, Águia Branca
Leste B	MF29	-	-	GU126525	Brasil: Espirito Santo, rio Doce
Leste B	CIT2096	CIT2096	ok	MG323772	Brasil: Minas Gerais, Parque Estadual do rio Doce
Leste B	CIT2097	CIT2097	ok	MG323773	Brasil: Minas Gerais, Parque Estadual do rio Doce
Nordeste	PHA466	UFPE1891	ok	-	Brasil: Pernambuco, Jaqueira, Usina Colônia, RPPN Frei
Norte	PSA128	MPEG39899	ok	KY605384	Brasil: Pará, Parauapebas
Norte	PSA139	MPEG39900	ok	KY605385	Brasil: Pará, Parauapebas
Norte	PSA176	MPEG39903	ok	KY605387	Brasil: Pará, Parauapebas
Norte	APC289	MZUSP35539	ok	MG323766	Brasil: Mato Grosso, Vila Rica
Norte	APC304	MZUSP29533	ok	MG323767	Brasil: Mato Grosso, Vila Rica
Norte	APC310	MZUSP35542	ok	MG323770	Brasil: Mato Grosso, Vila Rica
Norte	CS26	-	-	KT737237	Brasil: Pará, Floresta Nacional Tapirape-Aquiri
Norte	-	USNM549530	-	KT737238	Brasil: Pará, East bank rio Xingu, 52 km SSW Altamira
Norte	-	MZUSP29533	-	KY605382	Brasil: Mato Grosso, Vila Rica
Norte	IAVRD330	MPEG38898	-	KY605383	Brasil: Pará, Marabá

Linhagem / espécie	Campo	Tombo	ddRAD	GenBank	Localidade
Norte	PSA164	MPEG39901	-	KY605386	Brasil: Pará, Parauapebas
Norte	APC288	MZUSP35538	-	MG323765	Brasil: Mato Grosso, Vila Rica
Norte	APC292	-	-	MG323768	Brasil: Mato Grosso, Vila Rica
Norte	APC297	-	-	MG323769	Brasil: Mato Grosso, Vila Rica
Oecomys sp. nov.	RVR 89	UFMT4118	ok	MK874365	Brasil: Mato Grosso, Alta Floresta
Oecomys sp. nov.	UTP177	UFMT1776	ok	MK874372	Brasil: Pará, Jacareacanga, margem direita rio Teles Pires
Oecomys sp. nov.	UTP158	UFMT1772	ok	MK874368	Brasil: Mato Grosso, Paranaíta, margem esquerda rio Teles
Oecomys sp. nov.	APC244	MZUSP29531	ok	MG323756	Brasil: Mato Grosso, Aripuanã
Oecomys sp. nov.	PEU960006	-	ok	MG323755	Brasil: Mato Grosso, Aripuanã
Oecomys sp. nov.	M97055	MZUSP35543	ok	MG323754	Brasil: Mato Grosso, Cláudia
Oecomys sp. nov.	M000029	MZUSP29516	ok	MG323753	Brasil: Mato Grosso, Gaúcha do Norte
Oecomys sp. nov.	BRM-060	-	ok	-	Brasil: Mato Grosso, Nova Ubiratã
Oecomys sp. nov.	LGS-01	-	ok	-	Brasil: Mato Grosso, Sapezal
Oecomys sp. nov.	APC145	MZUSP35537	-	MG323757	Brasil: Mato Grosso, Juruena
Oecomys sp. nov.	UTP02	UFMT1680	-	MK874366	Brasil: Mato Grosso, Paranaíta
Oecomys sp. nov.	UTP132	UFMT1686	-	MK874367	Brasil: Pará, Jacareacanga
Oecomys sp. nov.	UTP159	UFMT1773	-	MK874369	Brasil: Mato Grosso, Paranaíta
Oecomys sp. nov.	UTP162	UFMT1774	-	MK874370	Brasil: Mato Grosso, Paranaíta
Oecomys sp. nov.	UTP176	UFMT1775	-	MK874371	Brasil: Pará, Jacareacanga
Oecomys sp. nov.	UTP181	UFMT1806	-	MK874373	Brasil: Mato Grosso, Paranaíta
O. auyantepui	-	-	-	AJ496304	-
O. bicolor	RVR146	UFMT4333	ok	MK874356	Brazil: Mato Grosso, Sinop
O. concolor	JLP16806	-	-	HM594615	Brail: Amazonas, rio Jau
O. franciscorum	roe_224	-	-	KF207846	Argentina: Pampa del Indio, Chaco

Linhagem / espécie	Campo	Tombo	ddRAD	GenBank	Localidade
O. mamorae	PZ316	-	-	KT737225	Bolivia: La Paz, Buena Vista
O. paricola	UTP669	UFMT1848	ok	MK874426	Brazil: Mato Grosso, Paranaita
O. rex	CSA22	-	-	MK874428	Brazil: Para
O. roberti	-	UFES1370	-	HM594603	Para, Santana do Araguaia
O. rutilus	T-1896	MNHN1995.3236	-	AJ496309	French Guiana:Saint-Eugene
O. superans	-	MVZ155006	-	AY275123	-
O. sydandersoni	LHE1407	USNM:588189	-	KT737235	Bolivia: Santa Cruz, El Refugio
O. tapajinus	LPC710	MVZ197511	-	HM594595	Tocantins, Peixe
O. trinitatis	-	MUSM13320	-	GU126527	Peru: Loreto, rio Galvez
Oligoryzomys destructor	-	-	-	EU258544	-
Oligoryzomys flavescens	-	-	-	GU185919	-
Oligoryzomys fulvescens	-	-	-	DQ227457	-
Oligoryzomys microtis	-	-	-	AY439000	-
Oligoryzomys nigripes	-	-	-	GU185910	-
Holochilus brasiliensis	-	-	-	EU579496	-
Holochilus chacarius	-	-	-	DQ227455	-
Holochilus sciureus	-	-	-	EU579497	-
Hylaeamys megacephalus	-	-	-	MG323696	-
Hylaeamys megacephalus	-	-	-	AY275124	-

ANEXO 02

Os espécimes utilizados nas análises morfométricas estão depositados nas seguintes instituições: Museu Nacional (MN), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Museu Paraense Emílio Goeldi (MPEG), Belém; Universidade do Estado de Mato Grosso (Unemat), Cáceres; Universidade Federal de Mato Grosso (UFMT), Cuiabá. Universidade de Brasília (UnB), Brasília; e Universidade Federal do Espírito Santo (UFES), Vitória. O material examinado também inclui espécimes não catalogados, coletados por: A. Casagrande (AC), que serão depositados na Unemat. Coletados por Ana Paula Carmignoto (APC) e coletados na Pequena central Hidrelétrica de São Joaquim da Barra (PCH), serão depositados no MZUSP.

Oecomys sp. nov. (n = 14): Brasil: Mato Grosso: Alta Floresta (1): UFMT 4118 (10º00'25"S, 56º02'17"W); Aripuanã: MZUSP 29531 (10º10'01"S, 59º27'W); Cláudia: MZUSP 35543 (11º34'58"S, 55º10'01"W); Juruena: MZUSP 35537 (10º19'01"S, 58º28'58"W); Paranaíta: UFMT 1772, 1773, 1774 (9º29'06"S, 56º28'19"W); Rosário Oeste: Unemat–AC 207, 230, 266 (15º04'45.9"S, 56º33'15.7"W); Pará: Jacareacanga: UFMT 1680 (9º29'06"S, 56º28'19"W), UFMT 1776, 1686 (9º18'40"S, 56º46'05"W). Rondônia: Vilhena: MPEG 34224 (12º43'S, 60º7'W).

Complexo *Oecomys catherinae* (n = 77)

linhagem central (n = 9): Brasil: Distrito Federal: Brasília: MN 21996, 22013 (15°45'21"S, 48°06'28"W), UnB 3319, 3320 (15°56'55"S, 47°56'02"W); Goiás: Anápolis: MN 4348 (16°20'37"S 48°53'08"W); São Domingos: MPEG 10901 (13°23'36"S 46°18'55"W); São Paulo: São Joaquim da Barra (34): MZUSP-PCH 3998 (20º28'58"S, 47º51'W); Tocantins: Paranã: MZUSP 35549, 35550 (12º37'01"S, 47º52'58"W).

Linhagem extremo oeste (n = 6): Brasil: Amazonas: Humaitá: MPEG 13171 (7º41'53"S, 62º33'11"W); Mato Grosso: Aripuanã: MZUSP 29532, 35535 (10º10'01"S, 59º27'W); Colniza: MPEG 12654, 12691, 13173 (9º10'S, 60º38'W).

Linhagem leste A (n = 13): Brasil: Minas Gerais: Pirapitinga: MN 72373 (21º41'28"S, 42º22'05"W); Rio de Janeiro: Cachoeira de Macacu: MN 74364, MN 74367 (22º31'S, 42º48'W), MN 74370, 74374 (22º30'S, 42º45'W), MN 74371 (22º28'58"S, 42º51'W); Casimiro de Abreu: MN 44805 (22°29'32"S, 42°12'43"W); Guapimirim: MN 74359 (22º34'58"S, 42º57'W), MN 74360 (22°33'00"S 42°57'00"W, ,), MN 74369 (22º34'S,

42º54'W); Paraty: MN 75261 (23°01'30"S, 44°38'13"W); Silva Jardim: MN 66137 (22°38'09"S, 42°23'13"W); São Paulo: Ubatuba: MN 74375 (23º19'58"S, 44º49'58"W).

Linhagem leste B (n = 23): Brasil: Espírito Santo: Águia Branca: UFES 160, 272, 273, 274 (18°58'24"S, 40°45'46"W); UFES 275 (18°58'47"S, 40°43'11"W); UFES 276, 277 (18°52'29"S, 40°47'10"W); UFES 278 (18°53'23"S, 40°48'24"W); Aracruz: UFES-MF29 (19º48'46"S, 40º10'28"W); Cariacica: UFES 569, 570 (20°16'52"S, 40°30'41"W); Pancas: UFES 279 (19°12'16"S, 40°46'17"W); Santa Tereza: UFES 902, 903, 904 (19°57'10"S, 40°30'30"W); São José do Calçado: UFES 2312, 2313, 2314, 2315, 2316 (21°02'33"S, 41°43'09"W); Viana: UFES 810, 811, 812 (20°23'20"S, 40°26'19"W).

Linhagem norte (n = 26): Brasil: Mato Grosso: Vila Rica: MZUSP-APC 292, MZUSP 29533, 35538, 35539, 35542 (10º01'01"S, 51º07'01"W); Pará: Altamira: MPEG 10913 (3º22'01"S, 52º22'58"W), MPEG 10251, 10911, 10912 (3º41'S, 53º45'W); Belterra: MPEG 15293, 15294 (2º38'S, 54º57'W); Canaã dos Carajás: UFES 1567 (6°23'14"S, 50°21'37"W); Marabá: MPEG 38898, 38976 (6ºS, 51º19'58"W), UFMT 1294 (5°47'51.8"S 50°46'15.3"W), MPEG 39899, 39900 (5º49'01"S, 50º28'58"W), MPEG 39903, 39909 (5º46'58"S, 50º31'58"W); Novo Repartimento: MPEG 10924 (4º41'S, 49º32'W); Santarém: MPEG 8229, 15094, 15099, 15120, 15121 (2°29'34"S, 54°44'06"W); Vitória do Xingu: UFES 2924 (3°16'19"S, 51°45'26"W).

3. CONCLUSÃO FINAL

• Evidenciamos a existência de complexos de espécies com alta diversidade na bacia do rio Tapajós, algumas destas em simpatia e com distribuição moldada pelos rios Amazônicos;

• Uma das linhagens do complexo *O. catherinae* corresponde à uma nova espécie válida, a qual descrevemos com base em dados moleculares e morfológicos;

• As diversificações entre as linhagens do complexo *O. catherinae* ocorreram no pleistoceno, possivelmente moldada durante as mudanças climáticas do Pleistoceno e mudanças vegetacionais e refúgios a elas associadas durante os períodos de glaciação na Amazônia e Mata Atlântica.

• O complexo *O. catherinae* é composto por três espécies distintas.

• Duas das linhagens do complexo *O. catherinae*, extremo oeste e norte, correspondem a espécies distintas (espécie 1= extremo oeste, espécie 2= norte);

• As linhagens do complexo *O. catherinae* com ocorrência na Mata atlântica e cerrado constituem um único grupo biológico, a qual consideramos como uma única espécie (espécie 3) com históricos de evolução ainda obscuro.