Systematics of Neotropical Spiny Mice, Genus *Neacomys* Thomas, 1900 (Rodentia: Cricetidae), from Southeastern Amazonia, with Descriptions of Three New Species

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ABSTRACT

Species of *Neacomys* are small cricetid rodents that occur in forested habitats of Central and South America, from eastern Panama to central Bolivia and central/western Brazil. In order to assess species diversity of this poorly known genus, we obtained cytochrome *b* gene sequences from the most comprehensive taxonomic and geographic sampling analyzed to date. We also conducted morphological analyses on a large series of specimens housed in 15 museums, including types of 10 out of 14 nominal taxa. Our analyses of the genetic data recovered 17

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lineages clustered in four distinct clades. Among these lineages, 11 correspond to species currently recognized as valid, and the remaining six are putative new species. In southeastern Amazonia—the geographical scope of this report—four undescribed species were discovered, three of which are named herein: Neacomys marajoara, sp. nov., from the Island of Marajó, Pará state; Neacomys vossi, sp. nov., restricted to the Tapajós center of endemism (between the Tapajós and Xingu rivers); and Neacomys xingu, sp. nov., restricted to the Xingu center of endemism (between the Xingu and Araguaia/Tocantins rivers). The new species can be discriminated from other Neacomys species by the morphology of the nasal bones, zygomatic plate, interorbital region, subsquamosal fenestra, paraoccipital process, incisive foramina, auditory bullae, antercone and anteroloph of the first upper molar, carotid circulation pattern, and karyotype. Our results substantially improve our understanding of the genus Neacomys by providing morphological, morphometric, and novel molecular insights about these poorly known rodents and demonstrate that the diversity of small Amazonian mammals is still poorly known, even in the relatively accessible southeastern part of the biome.

INTRODUCTION

Species of Neacomys Thomas, 1900, are small (<42 g) Neotropical rodents belonging to the tribe Oryzomyini in the cricetid subfamily Sigmodontinae. Commonly known as spiny mice or bristly mice, they occur in forested habitats of Central and South America, from eastern Panama to central Bolivia and central/western Brazil (Weksler and Bonvicino, 2015). Fourteen nominal taxa are referred to the genus, of which 12 are currently recognized as valid: N. amoenus Thomas, 1903; N. dubosti Voss et al., 2001; N. guianae Thomas, 1905; N. macedoruizi Sánchez-Vendizú et al., 2018; N. minutus Patton et al., 2000; N. musseri Patton et al., 2000; N. paracou Voss et al., 2001; N. pictus Goldman, 1912; N. rosalindae Sánchez-Vendizú et al., 2018; N. spinosus (Thomas, 1882); N. tenuipes Thomas, 1900; and N. vargaslosai Hurtado and Pacheco, 2017. The nominal taxon pusillus Allen, 1912, has been considered a junior synonym of N. tenuipes (see Weksler and Bonvicino, 2015), and the nominal taxon careleni Hershkovitz, 1940, is currently considered to be a valid subspecies of N. amoenus (see Hurtado and Pacheco, 2017).

In their monographic study of the small mammals from the Juruá River, Brazil, a right-bank tributary of the Amazon River, Patton et al. (2000) estimated the phylogenetic affinities of local populations of Neacomys and assessed their taxonomic status. Based on sequence data from one mitochondrial gene (cytochrome b), linear body measurements, and discrete morphological data, these authors revealed the existence of several previously unrecognized clades within the genus. In addition to providing the first gene tree for the group, these authors documented high levels of genetic differentiation among several morphologically diagnosable lineages. Based on these results, Patton et al. (2000) described two new species from western Amazonia and suggested the existence of an undescribed taxon from eastern Amazonia, which they referred to as “Neacomys sp. clade 7.”

In a monograph on the mammals of Paracou, French Guiana, Voss et al. (2001) assessed the taxonomic status of local samples of Neacomys, provided an emended morphological diagnosis for the genus, and described two new sympatric species for the Guiana Region. More
recently, three new species have been described from western Amazonia (eastern Peru) based on molecular, morphological, and karyotypic data (Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018).

Cytogenetic studies have also indicated the existence of undescribed species of *Neacomys* in the eastern Amazon of Brazil. Silva et al. (2015) reported new karyotypes for specimens from Marajó Island and from Marabá, both in eastern Pará state, and Oliveira da Silva et al. (2017) described two additional new karyotypes associated with specimens from the right and left banks of the Tapajós River. By using comparative chromosome painting analyses, Oliveira da Silva et al. (2019) described yet another new karyotype for specimens from Santa Bárbara (in eastern Pará) and suggested that this and the other cytotypes previously reported by Silva et al. (2015) and Oliveira da Silva et al. (2017) could represent new species.

In view of the seven new species described in the past 20 years (Patton et al., 2000; Voss et al., 2001; Hurtado and Pacheco, 2017; and Sánchez-Vendizú et al., 2018), and the possible existence of undescribed taxa as suggested by molecular and cytogenetic studies (e.g., Patton et al., 2000; Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018; Oliveira da Silva et al., 2019), it is clear that *Neacomys* is much more diverse than had been assumed by mid-20th century authors (e.g., Cabrera, 1961). However, despite the geographically restricted studies mentioned earlier, no comprehensive taxonomic revision has ever been undertaken for the genus. As a result, the systematics of *Neacomys* remains a work in progress, and little is yet known about the geographic limits of the species currently recognized as valid; additionally, phylogenetic relationships, especially of the unnamed forms in the eastern Amazon, remain obscure. In fact, the need for a critical taxonomic reevaluation of the genus is widely recognized (Woodman et al., 1991; Voss et al., 2001; Musser and Carleton, 2005; Catzeflis and Tilak, 2009; Weksler and Bonvicino, 2015; Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018).

In this report, we review the alpha taxonomy of *Neacomys* from southeastern Amazonia and provide preliminary hypotheses about their phylogenetic relationships. Based on phylogenetic analyses of the mitochondrial cytochrome *b* gene, together with external and craniodental characters, we define the species limits of the populations occurring in the southeastern parts of Brazilian Amazonia. In total, we recognize four species of *Neacomys* in southeastern Amazonia, three of them herein described as new. Our work represents a first step toward a thorough systematic review, offering novel data to enlighten future biogeographic, taxonomic, and evolutionary studies of this neglected group of rodents.

**Materials and Methods**

**Source of Material:** We analyzed a total of 174 specimens (skulls, skins, and entire fluid-preserved specimens), including name-bearing types and other important material from most of the distributional range of *Neacomys* (table 1; appendix 1). This examined material, as well as unexamined vouchers for specimens with analyzed molecular sequences, is deposited in the following collections (abbreviations in parentheses): American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Carnegie Museum,
| Taxon            | Voucher | GenBank | Locality         | Source                                      |
|------------------|---------|---------|------------------|---------------------------------------------|
| amoenus amoenus  | UFMT 1669* | MT462078 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1659* | MT462079 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1367* | MT462080 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1374* | MT462081 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1373* | MT462082 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1370* | MT462083 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | MAS NB 46 * | MT462084 | Brazil: Rondonia  | This study                                  |
| amoenus amoenus  | INPA 3059* | MT462015 | Brazil: Acre      | This study                                  |
| amoenus amoenus  | INPA 3064* | MT462016 | Brazil: Amazonas  | This study                                  |
| amoenus amoenus  | INPA 3063* | MT462017 | Brazil: Amazonas  | This study                                  |
| amoenus amoenus  | UFMT 3382* | MT462086 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 3380* | MT462087 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | MVZ 155015* | KXX92049 | Peru: Amazonas    | Hurtado and Pacheco, 2017                  |
| amoenus amoenus  | MVZ 190634* | MT462019 | Brazil: Amazonas  | Patton et al., 2000                        |
| amoenus amoenus  | MVZ 190635* | MT462020 | Brazil: Amazonas  | Patton et al., 2000                        |
| amoenus amoenus  | INPA 3057* | MT462021 | Brazil: Amazonas  | This study                                  |
| amoenus amoenus  | MVZ 190372* | KXX92040 | Brazil: Amazonas  | Patton et al., 2000                        |
| amoenus amoenus  | USNM 588096 | KXX92042 | Perú: Cusco       | Hurtado and Pacheco, 2017                  |
| amoenus amoenus  | USNM 588051 | KXX92041 | Perú: Cusco       | Hurtado and Pacheco, 2017                  |
| amoenus amoenus  | USNM 584543 | KXX92022 | Bolivia: Santa Cruz | Patton et al., 2000                        |
| amoenus amoenus  | USNM 584544 | MT462022 | Bolivia: Santa Cruz | Patton et al., 2000                        |
| amoenus amoenus  | INPA 3058* | KYY895734 | Brazil: Acre      | Sánchez-Vendizú et al., 2018               |
| amoenus amoenus  | INPA 3060* | KXX92032 | Brazil: Acre      | Hurtado and Pacheco, 2017                  |
| amoenus amoenus  | INPA 3062* | KXX92033 | Brazil: Acre      | Hurtado and Pacheco, 2017                  |
| amoenus amoenus  | UFMT 1763* | MT462076 | Brazil: Mato Grosso | This study                                  |
| amoenus amoenus  | UFMT 1757* | MT462077 | Brazil: Mato Grosso | This study                                  |
| amoenus carceleni | ROM 104474 | KXX92045 | Ecuador: Napo     | Hurtado and Pacheco, 2017                  |
| amoenus carceleni | ROM 105278 | KXX92046 | Ecuador: Napo     | Hurtado and Pacheco, 2017                  |
| amoenus carceleni | ROM 105282 | KY859738 | Ecuador: Napo     | Sánchez-Vendizú et al., 2018               |
| amoenus carceleni | ROM 105290 | KXX92047 | Ecuador: Napo     | Hurtado and Pacheco, 2017                  |
| amoenus carceleni | ROM 105264 | MT462018 | Ecuador: Napo     | Patton et al., 2000                        |
| amoenus carceleni | USNM 574567 | KXX92048 | Ecuador: Pastaza  | Hurtado and Pacheco, 2017                  |
| dubosti          | CN 240 * | MT462036 | Brazil: Pará      | This study                                  |
| dubosti          | CM 76846 a | FM210781 | Suriname: Nickerie | Catzeflis et al., 2009                     |
| dubosti          | V-1134   | FM210773 | France: French Guiana | Catzeflis et al., 2009                   |
| guianae          | CM 76847* | FM210778 | Suriname: Nickeri | Catzeflis et al., 2009                     |
| Taxon       | Voucher   | GenBank  | Locality            | Source                        |
|------------|-----------|----------|---------------------|-------------------------------|
| *guianae*  | INPA 7102* | MT462037 | Brazil: Amazonas    | This study                    |
| *guianae*  | INPA 7100* | MT462038 | Brazil: Amazonas    | This study                    |
| *macedoruizi* | MUSM 45054b | KY859731 | Peru: Huánuco       | Sánchez-Vendizú et al., 2018 |
| *macedoruizi* | MUSM 45053c | KY859732 | Peru: Huánuco       | Sánchez-Vendizú et al., 2018 |
| *marajoara* | MPEG40440  | KX752075 | Brazil: Pará        | Oliveira da Silva et al., 2017|
| *marajoara* | MPEG 40443 | KX752072 | Brazil: Pará        | Oliveira da Silva et al., 2017|
| *marajoara* | MPEG 40441 | MT462067 | Brazil: Pará        | This study                    |
| *marajoara* | MPEG 40446 | KX752080 | Brazil: Pará        | Oliveira da Silva et al., 2017|
| *marajoara* | MPEG 40435 | MT462069 | Brazil: Pará        | This study                    |
| *marajoara* | MPEG 40434 | MT462069 | Brazil: Pará        | This study                    |
| *marajoara* | MPEG 40432d | MT462070| Brazil: Pará        | This study                    |
| *marajoara* | MPEG 40431 | MT462071 | Brazil: Pará        | This study                    |
| *marajoara* | MPEG 40429 | MT462072 | Brazil: Pará        | This study                    |
| *minutus* "downriver" | SISPUR 159* | MT462039 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | SISPUR 151* | MT462040 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | INPA 5392* | MT462023 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | INPA 5387* | MT462007 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | INPA 3048* | MT462008 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | INPA 3049* | MT462009 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | EE 110*    | MT462041 | Brazil: Amazonas    | This study                    |
| *minutus* "downriver" | MVZ 190360 | KX792069 | Brazil: Amazonas    | Patton et al., 2000          |
| *minutus* "downriver" | MVZ 190361 | KX792069 | Brazil: Amazonas    | Patton et al., 2000          |
| *minutus* "downriver" | MVZ 191209 | KX792072 | Brazil: Amazonas    | Patton et al., 2000          |
| *minutus* "downriver" | MVZ 190359 | KX792068 | Brazil: Amazonas    | Patton et al., 2000          |
| *minutus* "downriver" | MVZ 190363 | KX792071 | Brazil: Amazonas    | Patton et al., 2000          |
| *minutus* "downriver" | INPA 3051* | KX792065 | Brazil: Amazonas    | Hurtado and Pacheco, 2017    |
| *minutus* "downriver" | INPA 3047* | KX792063 | Brazil: Amazonas    | Hurtado and Pacheco, 2017    |
| *minutus* "downriver" | INPA 2689* | MT462010 | Brazil: Amazonas    | This study                    |
| *minutus* "upriver" | INPA 3055* | MT462011 | Brazil: Amazonas    | This study                    |
| *minutus* "upriver" | INPA 3053* | MT462012 | Brazil: Amazonas    | This study                    |
| *minutus* "upriver" | MVZ 190358 | U58392   | Brazil: Amazonas    | Sánchez-Vendizú et al., 2018  |
| *minutus* "upriver" | INPA 3050* | KX792064 | Brazil: Amazonas    | Sánchez-Vendizú et al., 2018  |
| *minutus* "upriver" | MVZ 190362 | KX792070 | Brazil: Amazonas    | Sánchez-Vendizú et al., 2018  |
| *minutus* "upriver" | INPA 3891* | KX792066 | Brazil: Amazonas    | Sánchez-Vendizú et al., 2018  |
| *musseri*  | MVZ 171487 | KX792074 | Peru: Cusco         | Hurtado and Pacheco, 2017    |
| *musseri*  | MVZ 171488 | KX859742 | Peru: Cusco         | Patton et al., 2000          |
| *musseri*  | INPA 3046* | U58392   | Brazil: Acre        | Hurtado and Pacheco, 2017    |
| Taxon               | Voucher | GenBank     | Locality         | Source              |
|---------------------|---------|-------------|------------------|---------------------|
| *paracou*           | CN 279* | MT462042    | Brazil: Pará     | This study          |
| *paracou*           | CN 263* | MT462043    | Brazil: Pará     | This study          |
| *paracou*           | MPEG 40080* | MT462044 | Brazil: Pará     | This study          |
| *paracou*           | MPEG 40078* | MT462045 | Brazil: Pará     | This study          |
| *paracou*           | CN 129 * | MT462046    | Brazil: Pará     | This study          |
| *paracou*           | MPEG 40000* | MT462047 | Brazil: Pará     | This study          |
| *paracou*           | INPA 7089 * | MT462049 | Brazil: Amazonas | This study          |
| *paracou*           | INPA 7138 * | MT462050 | Brazil: Amazonas | This study          |
| *paracou*           | ROM 114325* | FM210782   | Surinam: Brokopondo | Catzeflis et al., 2009 |
| *paracou*           | ROM 114315* | FM210767   | Surinam: Brokopondo | Catzeflis et al., 2009 |
| *rosalindae*        | ROM 104560  | KX792050   | Ecuador: Napo    | Hurtado and Pacheco, 2017 |
| *rosalindae*        | ROM 105265  | KX792051   | Ecuador: Napo    | Hurtado and Pacheco, 2017 |
| *rosalindae*        | ROM 105314  | KX792052   | Ecuador: Napo    | Hurtado and Pacheco, 2017 |
| *rosalindae*        | ROM 105315  | KX792053   | Ecuador: Napo    | Hurtado and Pacheco, 2017 |
| *rosalindae*        | MVZ 153530  | KX792054   | Peru: Amazonas   | Hurtado and Pacheco, 2017 |
| *rosalindae*        | MVZ 155299  | KY859730   | Peru: Amazonas   | Sánchez-Vendízú et al., 2018 |
| *rosalindae*        | KU 158172   | KX792055   | Peru: Loreto     | Hurtado and Pacheco, 2017 |
| species 1           | INPA 4190   | KX792061   | Brazil: Amazonas | Hurtado and Pacheco, 2017 |
| species 1           | INPA 4191   | KX792062   | Brazil: Amazonas | Hurtado and Pacheco, 2017 |
| species 1           | INPA 4189   | KX792059   | Brazil: Amazonas | Hurtado and Pacheco, 2017 |
| species 1           | INPA 4192   | KX792060   | Brazil: Amazonas | Hurtado and Pacheco, 2017 |
| species 1           | MPEG 45483  | MT462051   | Brazil: Amazonas | This study          |
| species 2           | MPEG 42838  | MT462052   | Brazil: Pará     | This study          |
| species 2           | JUR 82      | MT462053   | Brazil: Pará     | This study          |
| species 2           | JUR 19      | MT462054   | Brazil: Pará     | This study          |
| species 2           | UFPA 1227   | MT462034   | Brazil: Pará     | This study          |
| species 2           | UFPA 1530   | MT462035   | Brazil: Pará     | This study          |
| species 2           | UFPA 1413   | MT462055   | Brazil: Pará     | This study          |
| species 2           | JUR 042     | MT462056   | Brazil: Pará     | This study          |
| species 2           | MPEG 42901  | MT462057   | Brazil: Pará     | This study          |
| *spinosis*          | MUSM 36924  | KX258228   | Peru: Amazonas   | Hurtado and Pacheco, 2017 |
| *tenuipes*          | BMNH 3999.10.3.34*+ | KX792081    | Colombia: Cundinamarca | Patton et al., 2000 |
| *vargasllosai*      | MVZ 172650  | KX792082   | Peru: Puno       | Hurtado and Pacheco, 2017 |
| *vargasllosai*      | MVZ 172654  | MT462013   | Peru: Puno       | Patton et al., 2000 1 |
| *vargasllosai*      | MVZ 172655  | MT462014   | Peru: Puno       | Patton et al., 2000 1 |
| *vossi*             | UFPA 1277   | MT462024   | Brazil: Pará     | This study          |
| *vossi*             | UFPA 1284   | MT462025   | Brazil: Pará     | This study          |
| Taxon | Voucher | GenBank | Locality         | Source                |
|-------|---------|---------|------------------|-----------------------|
| vossi | UFPA 1647 | MT462026 | Brazil: Pará    | This study            |
| vossi | UFPA 1467 | MT462027 | Brazil: Pará    | This study            |
| vossi | UFPA 1583 | MT462028 | Brazil: Pará    | This study            |
| vossi | UFPA 1736 | MT462073 | Brazil: Pará    | This study            |
| vossi | UFPA 1577 | MT462029 | Brazil: Pará    | This study            |
| vossi | UFPA 1691 | MT462030 | Brazil: Pará    | This study            |
| vossi | UFPA 1520 | MT462031 | Brazil: Pará    | This study            |
| vossi | UFPA 1444 | MT462074 | Brazil: Pará    | This study            |
| vossi | UFPA 1391 | MT462075 | Brazil: Pará    | This study            |
| vossi | UFPA 1654 | MT462032 | Brazil: Pará    | This study            |
| vossi | UFPA 1487 | MT462033 | Brazil: Pará    | This study            |
| xingu | UFMT 1275 | MT462058 | Brazil: Pará    | This study            |
| xingu | UFMT 1273 | MT462059 | Brazil: Pará    | This study            |
| xingu | UFMT 1268 | MT462060 | Brazil: Pará    | This study            |
| xingu | MPEG 41805 | MT462061 | Brazil: Pará    | This study            |
| xingu | MPEG 42019 | MT462062 | Brazil: Pará    | This study            |
| xingu | MPEG 41804 | MT462063 | Brazil: Pará    | This study            |
| xingu | MPEG 41996 | MT462064 | Brazil: Pará    | This study            |
| xingu | PSA 69    | MT462065 | Brazil: Pará    | This study            |
| xingu | PSA 46    | MT462066 | Brazil: Pará    | This study            |
| xingu | USNM 549553 | KX792080 | Brazil: Pará    | Hurtado and Pacheco, 2017 |

* Paratype of *Neacomys dubosti*.

b Paratype of *Neacomys macedoruizi*.

c Holotype of *Neacomys macedoruizi*.

d Holotype of *Neacomys marajoara*.

e Holotype of *Neacomys minutus*.

f Holotype of *Neacomys musseri*.

g Holotype of *Neacomys tenipises*.

h Holotype of *Neacomys vossi*.

i Holotype of *Neacomys xingu*.

j *Neacomys “clade 7”* of Patton et al., 2000.

k Unpublished data from Patton et al., 2000.
Pittsburgh (CM); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte (MCN-M); University of Kansas Biodiversity Research Center, Lawrence (KU); Muséum d’Histoire Naturelle de la Ville de Genève, Geneva (MHNG), Muséum National d’Histoire Naturelle, Paris (MNHN); Museu Paraense Emílio Goeldi, Belém (MPEG); Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Royal Ontario Museum, Toronto (ROM); Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá (UFMT); Universidade Federal do Pará, Belém (UFPA); and National Museum of Natural History, Smithsonian Institution, Washington (USNM). Specimens with field numbers prefixed by CN, JUR, and PSA are currently held at the MPEG and by MAS NB, MSA FM, EE, and SISPUR are currently held at INPA. Those specimens will be deposited in the aforementioned collections.

Collecting Localities: Geographic data for collection localities were obtained from specimen tags. For specimens unaccompanied by geographic coordinates, we referred to Paynter and Traylor (1991), Paynter (1993), Prado and Percequillo (2013), Gardner (2008), and Patton et al. (2015) to obtain this information.

Molecular Analyses

Taxon Sampling: We obtained partial sequences (801 bp) of the mitochondrial cytochrome b gene (Cytb) from 75 Amazonian specimens of *Neacomys*. These new sequences are deposited in GenBank with accession numbers MT462007–MT462087. In addition, we downloaded 54 ingroup (*Neacomys*) sequences from GenBank and another six unpublished sequences from Patton et al.’s (2000) dataset (table 1). In total, our ingroup dataset includes all currently recognized species in the genus, with the sole exception of *N. pictus* (for which no sequence data are available). Among other nomenclaturally important sequences, we analyzed Cytb data from the holotypes of *N. minutus* (INPA 2689) and *N. tenuipes* (BMMH 1899.10.3.34), a paratype of *N. musseri* (INPA 3046), and the holotype (MUSM 45053) and a paratype (MUSM 45054) of *N. macedoruizi*.

We obtained sequences of the following outgroup taxa from Genbank (accession numbers in parentheses): *Thomasomys baeops* (DQ914654), *Hylaeamys megacephalus* (KF815441), *Oligoryzomys microtis* (OMU58381), *Scolomys ucyalensis* (EU579518), *Oreoryzomys balneator* (EU579510), and *Microryzomys minutus* (AF108698). The *T. baeops* sequence was used to root the trees in our phylogenetic analyses. Outgroup taxa were chosen based on the phylogenies of Weksler (2003), Weksler (2006), and Percequillo et al. (2011).

Laboratory Procedures: We extracted genomic DNA from ethanol-preserved tissues using the salt-extraction method (Aljanabi and Martinez, 1997). The Cytb gene was PCR-amplified using primers developed by Smith and Patton (1993): MVZ05 (5’-CGAAGCTTGATAT-GAAAAACCATCGTTG-3’) and MVZ16 (5’AAATAGGAARTATCAYTCTGGTTTRAT-3’). Each PCR reaction contained 2.5 μL of 10x buffer, 1.0 μL of MgCl₂ (50 mM), 1.25 μL of dNTP mix (1.25 mM for each nucleotide), 1 μL of each primer (10 mM), 0.2 μL of Ludwig Biotechnology Taq DNA Polymerase (5 μ/μL), 1 μL of DNA template, and water to a final volume of...
25 μL. For some difficult templates, concentrations of reagents were adjusted to increase PCR success. PCR conditions used a preheating step of initial denaturation at 94°C for 3–5 min, followed by 35 cycles at 94°C for 30 sec, 49°C for 45 sec, and 72°C for 1 min and 45 sec, and a final extension at 72°C for 5–7 min. PCR products were cleaned using Exonuclease I and shrimp alkaline phosphatase (Fermentas), and sequenced using an ABI 3130xl Genetic Analyzer (Life Technologies).

**Molecular Data Analyses:** We aligned sequences with Clustal W (Thompson et al., 1994) using default parameters. Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI). We coded all missing bases as unknown (“?”) prior to phylogenetic analyses. PartitionFinder ver. 2.1.1 (Lanfear et al., 2017)—which heavily relies on PhyML (Guindon et al., 2010)—was employed to select both the most suitable partition scheme and the best-fit model of nucleotide substitution for each data subset. The Akaike Information Criterion (AIC) was used to select the best-fit models; only models that could be applied in MrBayes were considered, and the “greedy” algorithm was implemented.

In order to find the best topology according to the ML optimality criterion, we conducted an analysis with 50 independent searches in GARLI 2.01 (Zwickl, 2006) using default settings. Maximum-likelihood bootstrap analysis was also carried out in GARLI 2.01 and implemented in the CIPRES Science Gateway (Miller et al., 2010) using 100 pseudoreplicated data matrices with 10 searches performed on each. The Bayesian analysis was conducted using the Markov Chain Monte Carlo (MCMC) sampling approach in MrBayes v. 3.2.3 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003; Altekar et al., 2004; Ronquist et al., 2012) and was also implemented through the CIPRES Science Gateway. The search started with a random tree and consisted of one cold chain and three heated chains. The Markov chains were run for 100,000,000 generations, and trees were sampled every 1000 generations. Default values were kept for the “relburnin” and “burninfrac” options in MrBayes; hence, the first 25,000,000 generations (i.e., 250,000 trees or 25%) were discarded as burn-in, and posterior probability estimates of all model parameters were based on the remaining (750,000) trees.

We calculated average pairwise genetic distances within and between groups using the uncorrected (p-distance) option in MEGA 6 (Tamura et al., 2011). Uncorrected distances were chosen to allow comparison with divergence estimates reported in previous studies of *Neacomys* (e.g., by Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018).

**Morphological and Morphometric Analyses**

**Morphology:** We examined the following external and craniodental characters for taxonomic variation: dorsal and ventral pelage color, tail color, morphology of the palate, carotid circulation type, features of the auditory bullae, and dental morphology. We made comparisons predominantly among specimens of the same age class to avoid conflating ontogenetic variation with taxonomic differences. Nomenclature for external and craniodental morphology follows Voss (1988), Patton et al. (2000), Voss et al. (2001), Weksler (2006), Hurtado and Pacheco (2017), and Sánchez-Vendizú et al. (2018).
**Age Criteria:** In order to distinguish ontogenetic from taxonomic variation, we grouped specimens into age classes based on patterns of molar eruption and degree of tooth wear (fig. 1), using the criteria defined by Voss (1991):

Age class 1  M3 incompletely erupted or unworn;
Age class 2  M3 fully erupted and exhibiting slight to moderate wear (some dentine exposed), but the occlusal surface still tubercular (the paracone raised and prominent), not flat;
Age class 3  M3 well worn, the occlusal surface flat or concave; M1–2 tubercular (the major cusps all separate and prominent); anteroloph of M2 distinct, not fused with paracone;
Age class 4  M3 flat or concave; M1–2 with cusps worn almost or quite flat but not below widest part of crown; anteroloph of M2 obliterated, fused with paracone;
Age class 5  M1–3 all worn flat or concave, below widest part of crowns; most details of occlusal topography obliterated.

Hereafter, we refer to specimens in age class 1 as “juveniles,” specimens in age classes 2–4 as “adults,” and specimens in age class 5 as “old adults.”

**Measurements:** We obtained 21 craniodental measurements (in millimeters, mm) that have been previously used in taxonomic studies of Neotropical cricetids (Voss, 1988; Patton et al., 2000; Voss et al., 2001; Flores et al., 2010). The following dimensions were measured with digital calipers to the nearest 0.01 mm while skulls were examined at low magnification under a stereomicroscope:

- **BH** Braincase height, measured in the midline from the basisphenoid-basioccipital suture on the ventral surface of the skull to the frontal-parietal suture on the dorsal surface;
- **BI** Breadth of incisive foramen, the greatest transverse dimension across both incisive foramina;
- **BM1** Breadth of M1, greatest crown breadth of the first upper molar (M1);
- **BPR** Breadth of palate at rostrum, measured between most posterior lower edges of the left and right infraorbital foramina on the ventral side of skull;
- **BZP** Breadth of zygomatic plate, least distance between the anterior and posterior edges of the zygomatic plate;
- **BB** Bullar breadth, distance between anterior opening of carotid foramen to ectotimpanic dorsal process;
- **CIL** Condylo-incisive length, from the greater curvature of one upper incisor to the articular surface of the condyle on the same side;
- **LCIB** Least condyloid-incisor breadth, greatest distance from the lower incisor base to the posterior margin of the condylar process on the same side of the mandible;
- **LIB** Least interorbital breadth, least distance across the frontal bones between the orbital fossae;
- **LD** Length of diastema, from the crown of M1 to the lesser curvature of the incisor on the same side;
- **LIF** Length of incisive foramen, greatest anterior-posterior dimension of one incisive foramen;
LLD  Length of lower diastema, from the crown of m1 to the lesser curvature of the incisor on the same side of the mandible;
LLM  Length of lower molars, crown length from m1 to m3;
LM   Length of molars, crown length from M1 to M3;
LN   Length of nasals, greatest anterior-posterior dimension of one nasal bone;
LPB  Length of palatal bridge, from the posterior margin of the upper incisors to the anterior margin of the mesopterygoid fossa;
MB   Mastoid breadth, distance across the cranium at the mastoid processes;
OL   Orbital length, internal distance between the anterior and posterior margins of the right or the left orbit;
RB   Rostral breadth, distance across the outside margins of the left and right nasolacrimal capsule;
RL   Rostral length, diagonal measurement taken from the anterior margin of the orbit to the anterior margin of the nasal bone on the same side;
ZB   Zygomatic breadth, greatest transverse dimension across the squamosal zygomatic processes.

In addition to these craniodental measurements, we transcribed five external measurements (in mm) taken in the field by collectors and recorded on specimen labels: total length (TL); length of head and body (HBL); length of tail (LT); length of hind foot (HF); and length of ear (Ear). We also transcribed weight (in grams, g) as recorded by collectors.

Statistical Analyses: We calculated standard descriptive univariate statistics for all external and craniodental measurements. In order to minimize potentially confounding ontogenetic variation, we included only adult and old adult specimens (age classes 2–5) in these analyses.
Principal component analyses (PCA) were conducted to assess whether morphometric data are congruent with results from the molecular analyses, qualitative morphological comparisons, and previously published karyotypic studies. For PCA, measurements were log-transformed and principal components were extracted from the variance-covariance matrix. Statistical analyses were performed using SPSS 22.0 for Windows.

RESULTS

Molecular Analyses

The Cytb gene fragment we sequenced was 801 base pairs long and included 470 conserved sites, 331 variable sites, and 287 parsimony-informative sites. Monophyly of Neacomys was recovered with strong support from our Bayesian analysis (Bayesian posterior probability [BPP] = 0.97); whereas our ML analysis provided only marginal support (bootstrap support [BS] = 51%) for generic monophyly (fig. 2A–C).

The gene trees obtained from our Bayesian and ML analyses both recovered 17 distinct lineages of Neacomys, 11 of which could be associated with taxa that are currently recognized as valid species: N. dubosti, N. guianae, N. minutus, N. musseri, N. paracou, N. spinosus, N. rosalindae, N. macedoruizi, N. amoenus, N. vargaslosai, and N. tenuipes. Among the remaining six lineages, three are formally described in this report (N. vossi, N. xingu, and N. marajoara) and three others are referred to by informal nomenclature: N. minutus “upriver” and N. minutus “downriver” (after Patton et al., 2000), Neacomys “sp. 1,” and Neacomys “sp. 2.” All these lineages received BPP support values ≥ 0.96, except for N. minutus “downriver” (BPP = 0.82). All undescribed lineages also had bootstrap values ≥ 94%, except for N. xingu and N. marajoara (with bootstrap values of 58% and 62%, respectively; fig. 2B). Mean interspecific genetic distances ranged from 3.9% (between N. marajoara and N. xingu) to 15.58% (between N. paracou and N. musseri; table 2), whereas intragroup divergences ranged from 0% in N. macedoruizi (two sequences from one locality) and N. vargaslosai (three sequences from one locality) to 1.88% in N. amoenus (34 sequences from 16 localities).

The only relationship that differs between our BI and ML topologies is the position of N. tenuipes, which is sister to a negligibly supported clade containing N. minutus, N. macedoruizi, N. rosalindae, N. musseri, Neacomys sp. 1, and N. guianae in the BI tree. By contrast, N. tenuipes is sister to a negligibly supported clade containing N. dubosti, N. marajoara, Neacomys sp. 2, N. vossi, and N. xingu in the ML tree (appendix 2).

Based on the BI topology, and for the purposes of this report, we recognize four groups of species within Neacomys. Two of these groups correspond to the Paracou and Spinosus groups (fig. 2C) of Hurtado and Pacheco (2017), whereas the Tenuipes Group (fig. 2A) of Hurtado and Pacheco (2017) was recovered as two monophyletic groups in our analysis. Herein we restrict the Tenuipes Group to N. tenuipes, N. guianae, Neacomys sp. 1, N. musseri, N. rosalindae, N. macedoruizi, and N. minutus; additionally, we recognize a Dubosti Group for N. dubosti, Neacomys sp. 2, and the three new species described in this report (N. marajoara, N. xingu, and N. vossi).
TABLE 2. Uncorrected average pairwise genetic distances (percent sequence divergence) within and among species of *Neacomys*.

|       | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11   | 12   | 13   | 14   | 15   | 16   | 17   |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 2     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 3     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 4     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 5     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 6     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 7     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 8     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 9     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 10    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 11    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 12    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 13    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 14    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 15    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 16    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| 17    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |

1. tenueipes —
2. rosalindae 8.4 1.3
3. guianae 8.0 11.3 **0.9**
4. species 1 8.8 10.6 7.5 **0.6**
5. minutus “upriver” 10.3 10.6 12.3 12.5 **0.4**
6. macedoruizi 9.0 10.2 12.3 12.1 4.7 —
7. minutus “downriver” 12.0 11.4 12.4 12.2 7.2 5.4 **1.7**
8. musseri 9.8 10.8 13.8 13.0 12.3 12.2 11.2 **1.5**
9. dubosti 13.9 11.5 13.1 12.0 14.9 12.8 12.9 **13.5** **0.7**
10. species 2 15.6 12.9 14.1 11.3 13.7 13.3 12.1 13.8 10.7 **0.4**
11. vossi 12.3 12.5 13.5 11.3 13.0 13.0 13.4 14.2 10.2 7.5 **0.5**
12. xingu 13.2 12.4 13.3 12.2 11.9 11.4 12.4 13.3 10.1 6.9 5.1 **0.3**
13. marajoara 11.7 12.3 13.1 12.0 12.7 12.4 13.0 13.9 9.3 8.7 5.4 3.9 **0.4**
14. amoenus 11.7 13.8 14.3 14.1 14.7 13.4 13.6 14.0 12.3 12.6 12.4 12.7 12.2 **1.9**
15. vargasilosai 8.5 12.1 13.5 12.3 13.0 12.7 12.4 11.8 13.0 12.9 12.2 12.6 12.8 **8.3** —
16. spinosus 12.8 12.6 15.1 13.3 14.0 13.7 13.8 13.5 13.8 13.9 13.6 14.4 13.9 **8.1** 8.3 —
17. paracou 12.6 14.2 15.0 13.5 15.1 14.3 14.4 15.6 15.0 15.1 14.6 14.4 13.5 14.7 13.2 14.0 **1.2**
Neacomys paracou (comprising the monotypic Paracou Group) was recovered as sister to the remaining species of Neacomys with strong Bayesian support, whereas the Spinosus Group was recovered as sister to the Dubosti and Tenuipes groups with strong Bayesian support. The sister-group relationship between the Dubosti and Tenuipes groups also received strong Bayesian support. Within the Spinosus Group, N. vargasloasi was recovered as sister to N. spinosus + N. amoenus with consistently strong support. Within the Dubosti Group, the sister-group relationship of N. dubosti to other group members in the nested clades (N. marajoara (N. xingu (Neacomys sp. 2 + N. vossi))) is also strongly supported. Lastly, with negligible support values, the Tenuipes Group includes N. tenuipes as sister to ((N. guianae + Neacomys sp. 1) ((N. musseri + N. rosalindae) ((N. macedoruizi + N. minutus “upriver”) N. minutus “downriver”))). In general, Cytb provided satisfactory resolution of supraspecific phylogenetic relationships. However, among the new species described herein, the relationships of N. xingu and N. vossi had negligible support values.

Morphometric Analyses

Descriptive statistics for adult and old adult specimens of Neacomys dubosti and three new species from southeastern Amazonia are shown in table 3. In general, our results document univariate and multivariate morphometric overlap among all species in the Dubosti Group. In all pairwise multivariate analyses herein provided, the first principal components comprise only positive coefficient values, indicating that they are predominantly related to variation in skull size. Comparing N. dubosti with N. marajoara, the plot of first (PC1) and second principal components (PC2) shows that specimens of N. dubosti group at the higher extremity of the size axis (fig. 3A, appendix 3). The PC1 corresponds to 46.98% of the total variation and is strongly related to CIL and ZB while the PC2 corresponds to 12.62% of the total variation and is strongly related to LIF and LM. Similarly, N. dubosti tended to occupy the higher extremity of the size axis when compared to N. vossi (fig. 3B, appendix 3). In this analysis, PC1 corresponds to 47.22% of the total variation and is strongly related to CIL and ZB, while the PC2 corresponds to 11.31% of the total variation. The latter species appeared at the higher extremity of the size axis, and the measurements with highest loadings were BZP, CIL, LN, RL, and ZB.

When N. marajoara was compared with N. vossi (fig. 3D, appendix 3), the PC1 explained 28.97% of the total variation, while the PC2 explained 15.48%. The specimens largely overlapped on both axes, and the measurements that most contributed for the variation were CIL, LIF, LN, RL, and ZB. By comparing N. marajoara and N. xingu (fig. 3E, appendix 3), the PC1 explained 41.20% of the total variance, while the PC2 explained 12.35%. The latter species appeared at the higher extremity of the size axis, and the variables that better contributed for variation were CIL, LM, LN, RL, and ZB.

In the PCA including N. vossi and N. xingu (fig. 3F, appendix 3), the PC1 explained 41.13% of the total variance, while the PC2 explained 10.94%. The latter species appeared at the higher extremity of the size axis, and the variables that better contributed for variation were CIL, LM, LN, RL, and ZB.
FIG. 2 A–C (above and following two pages). Bayesian phylogeny of *Neacomys* based on cytochrome *b* sequence data. Numbers represent Bayesian posterior probabilities (above) and ML bootstrap support (below) at nodes recovered by both analyses (bootstrap support for nodes only recovered by our ML analysis are shown in appendix 2). Only ML bootstrap support >50% is shown. Branch tips are labeled with geographic identifiers and voucher codes listed in table 1. Specimens marked with asterisks (*) indicate holotypes.
TABLE 3. Descriptive statistics for external and craniodental dimensions (in mm) and mass (in g) of species in the Dubosti Group of *Neacomys*.

|        | *dubosti* | *marajoara* | *xingu* | *vossi* |
|--------|-----------|-------------|---------|---------|
| TL     | 157 ± 7   | 144 ± 10    | 146 ± 5 | 140 ± 13|
|        | 148–167 (9)| 128–153 (9) | 138–156 (7) | 110–156 (14) |
| HBL    | 79 ± 4    | 72 ± 4      | 71 ± 2  | 68 ± 10 |
|        | 74–88 (9) | 62–77 (9)   | 68–75 (7) | 65–77 (14) |
| LT     | 77 ± 4    | 72 ± 8      | 74 ± 5  | 72 ± 6  |
|        | 71–83 (9) | 55–79 (9)   | 68–85 (7) | 60–84 (14) |
| HF     | 21 ± 1    | 17 ± 2      | 20 ± 3  | 16 ± 3  |
|        | 20–23 (9) | 13–19 (9)   | 14–26 (7) | 10–20 (14) |
| Ear    | 14 ± 1    | 12 ± 1      | 12 ± 1  | 12 ± 3  |
|        | 12–15 (9) | 11–14 (9)   | 11.5–14.5 (6) | 8–19 (14) |
| Mass   | 15 ± 3    | 12 ± 2      | 14 ± 3  | 12 ± 2  |
|        | 12–20 (9) | 9–16.5 (9)  | 11.5–18.5 (7) | 9–15.5 (14) |
| BH     | 7.14 ± 0.27 | 6.7 ± 0.32 | 6.77 ± 0.2 | 6.71 ± 0.38 |
|        | 6.61–7.48 (12) | 6.33–7.08 (7) | 6.4–7 (13) | 6.02–7.24 (8) |
| BIF    | 1.51 ± 0.1 | 1.40 ± 0.08 | 1.41 ± 0.11 | 1.44 ± 0.09 |
|        | 1.39–1.68 (12) | 1.30–1.55 (7) | 1.21–1.58 (13) | 1.31–1.56 (8) |
| BM1    | 0.90 ± 0.04 | 0.85 ± 0.03 | 0.87 ± 0.04 | 0.85 ± 0.08 |
|        | 0.82–0.98 (12) | 0.81–0.88 (7) | 0.80–1.01 (13) | 0.75–0.97 (8) |
| BPR    | 4.02 ± 0.18 | 3.76 ± 0.27 | 4.09 ± 0.20 | 3.92 ± 0.27 |
|        | 3.73–4.32 (12) | 3.37–4.06 (7) | 3.70–4.47 (13) | 3.50–4.34 (8) |
| BZP    | 2.06 ± 0.19 | 1.84 ± 0.11 | 1.99 ± 0.23 | 1.88 ± 0.07 |
|        | 1.86–2.58 (12) | 1.67–1.97 (7) | 1.73–2.62 (13) | 1.80–2.01 (8) |
| BB     | 3.66 ± 0.18 | 3.46 ± 0.22 | 3.63 ± 0.17 | 3.51 ± 0.11 |
|        | 3.38–3.93 (12) | 3.17–3.8 (7) | 3.39–3.92 (13) | 3.43–3.75 (8) |
| CIL    | 18.57 ± 0.59 | 17.51 ± 0.36 | 18.06 ± 0.58 | 17.37 ± 0.48 |
|        | 17.38–19.43 (12) | 16.92–18.06 (7) | 17.44–19.28 (13) | 16.75–18.3 (8) |
| LCIB   | 8.13 ± 0.97 | 7.71 ± 0.3 | 8.17 ± 0.53 | 7.93 ± 0.27 |
|        | 5.33–8.96 (12) | 7.13–7.97 (7) | 7.34–9.36 (13) | 7.58–8.34 (8) |
| LIB    | 4.65 ± 0.12 | 4.47 ± 0.2 | 4.56 ± 0.26 | 4.46 ± 0.18 |
|        | 4.47–4.87 (12) | 4.23–4.74 (7) | 4.11–4.93 (13) | 4.25–4.77 (8) |
| LD     | 5.36 ± 0.25 | 5.01 ± 0.2 | 5.06 ± 0.15 | 4.92 ± 0.14 |
|        | 4.94–5.69 (12) | 4.69–5.28 (7) | 4.74–5.37 (13) | 4.80–5.20 (8) |
| LIF    | 2.98 ± 0.26 | 2.99 ± 0.10 | 2.98 ± 0.23 | 2.91 ± 0.30 |
|        | 2.64–3.47 (12) | 2.83–3.16 (7) | 2.48–3.26 (13) | 2.53–3.57 (8) |
| LLD    | 3.0 ± 0.30 | 2.89 ± 0.23 | 2.87 ± 0.18 | 3.34 ± 0.99 |
|        | 2.24–3.3 (12) | 2.47–3.14 (7) | 2.43–3.08 (13) | 2.64–4.96 (8) |
| LLM    | 2.97 ± 0.13 | 2.77 ± 0.04 | 2.92 ± 0.08 | 2.77 ± 0.08 |
|        | 2.56–3.06 (12) | 2.71–2.82 (7) | 2.8–3.13 (13) | 2.64–2.87 (8) |
| LM     | 2.75 ± 0.07 | 2.53 ± 0.06 | 2.75 ± 0.09 | 2.58 ± 0.08 |
|        | 2.63–2.84 (12) | 2.42–2.61 (7) | 2.60–2.90 (13) | 2.45–2.65 (8) |
| LN     | 7.81 ± 0.35 | 7.45 ± 0.45 | 7.89 ± 0.46 | 7.24 ± 0.39 |
|        | 7.23–8.51 (12) | 6.62–7.90 (7) | 7.02–8.90 (13) | 6.56–7.84 (8) |
Our molecular analyses revealed the existence of 17 lineages of *Neacomys* with high levels of genetic divergence; of these, four occur in southeastern Amazonia (south of the Amazon River and east of the Rio Madeira). Although not strongly morphometrically differentiated, these previously unnamed southeastern lineages can be recognized as species based on our molecular analyses (which provide evidence of mtDNA divergence), by the karyotypic traits previously reported in the literature (which suggest they are reproductively isolated), and by qualitative morphological characters (which provide evidence of nuclear-gene divergence). Three of these species are described below, whereas the fourth (*Neacomys* “sp. 2”) will be described in another report with different authorship. Because all the new species belong to the Dubosti Group, our comparisons are restricted to members of that clade. Relevant summaries of morphometric variation and diagnostic traits are provided in tables 3 and 4, respectively.

**Neacomys marajoara**, new species

Marajoara Spiny Mouse

Figures 4, 7

**Holotype**: The holotype (MPEG 40432) is an adult male (age class 3), collected on 19 January 2009, by R.V. Rossi (field number MAJ 23; fig. 4) in a pitfall trap. The specimen consists of a stuffed skin (missing the tip of the tail), skull, and skeleton; a tissue sample of this specimen is preserved in ethanol, and a partial cytochrome *b* sequence that we obtained from it has been deposited in Genbank with accession number MT462070.

**Type Locality**: Tauari Farm, municipality of Chaves, Marajó Island, state of Pará, Brazil (0°39′S, 50°11′W, figs. 5, 6).

**Diagnosis**: *Neacomys marajoara* is a small species (table 3) that differs from congeneric taxa by the following combination of craniodental traits: skull delicate; interorbital region rela-
FIG. 3. Scatter plots of PC1 (horizontal axis) and PC2 (vertical axis) for pairwise analyses of craniodental measurement data for species in the Dubosti Group of Neacomys. In each plot, species are represented by minimum convex polygons that enclose all points in the plane of PC1 and PC2. A, *N. dubosti* (dub) versus *N. marajoara* (mar); B, *N. dubosti* versus *N. vossi* (vos); C, *N. dubosti* versus *N. xingu* (xin); D, *N. marajoara* versus *N. vossi*; E, *N. marajoara* versus *N. xingu*; F, *N. vossi* versus *N. xingu.*
Morphological Description: Dorsal pelage dark brown finely sprinkled with orange (fig. 4); ventral pelage varying from pure white to yellowish white, separated from the dorsal pelage by a very thin orange lateral line. Superciliary, genal, and mystacial vibrissae blackish and long (extending behind ears when laid back alongside the head); submental vibrissae absent; interramal vibrissae short and white. Ears small and rounded; postauricular hairs gray based with orange tips, forming an orange tuft behind each pinna. Ungual tufts white, longer than claws in most specimens examined (except MPEG 40435 and MPEG 40446, in which ungual tufts are as long as the claws); fore- and hind feet covered dorsally with buffy-cream hairs; hind feet narrow and elongate with small interdigital membranes present. Tail about the same length as head and body, bicolored, and covered by short, spiny, and clearly visible hairs; white hairs present on ventral caudal surface from base to midlength; tail tip with very short
(1 mm) terminal tuft; caudal scales small, arranged in annular series; each caudal scale with three subequal hairs inserted along its posterior margin.

Skull small and delicate in dorsal view (fig. 7), with straight anterior nasal margins, notably broad rostrum, and shallow zygomatic notches; posterior nasal terminus usually slightly pointed, extending beyond maxillary-frontal suture; premaxillaries terminating anterior to nasals; lacrimal bone small and visible in dorsal view, usually in broad contact with frontal bones; supraorbital margins slightly convergent anteriorly; interorbital region relatively broad; supraorbital beads developed as projecting shelves; lateral expansion of the parietal restricted to the dorsal cranial surface. Incisive foramina small and usually teardrop shaped, not extending posteriorly to level of M1s; maxillary portion of incisive septum (dividing the left and right foramina) narrow. Zygomatic plate narrow. Palate with two posterolateral pits on each side. Auditory bullae small and globular, with short and narrow eustachian tubes; periotic bone extends anteriorly to internal carotid canal (except MPEG 40435, MPEG 40443, and MPEG 40439, in which the periotic does not reach the internal carotid canal), but does not enter the canal. Subsquamosal fenestra large (almost half the size of the postglenoid foramen); hamular process of the squamosal long. Paraoccipital process narrow and small and separated from the auditory bullae. Sphenopalatine foramen large; alisphenoid strut absent; carotid circulation...
pattern usually derived\textsuperscript{7} (pattern 2, as identified by the presence of a large stapedial foramen and a large posterior opening of the alisphenoid canal, and by the absence of a squamosalalisphenoid groove and a sphenofrontal foramen; Voss, 1988).

First upper molar (M1) usually with broad, flat, and undivided anterocone; anteroloph usually fused with anterolabial conule (such that the anteroflexus is not distinguishable); M3 small; labial cusps (paracone and metacone) usually smaller than lingual cusps (protocone and hypocone); m1 anterocone undivided.

Mandible with mental foramen opening laterally; capsular process of lower incisor alveolus present, but indistinct (reduced to a slight rounded elevation), approximately at same height as coronoid process.

**Karyotypes:** Karyotypes of specimens from the type locality were obtained by Silva et al. (2015), and karyotypes from specimens collected elsewhere on Marajó Island were obtained

\textsuperscript{7} Most specimens of *Neacomys marajoara* (seven out of nine) exhibit carotid circulation pattern 2, but one specimen (MPEG 40446) exhibits circulatory pattern 1, and another (MPEG 40431) exhibits both patterns (on opposite sides of the skull).
by Oliveira da Silva et al. (2019), who described a chromosomal complement of $2n = 58$ and a fundamental number (FN) = 70 (table 5).

**Taxonomic Comparisons:** *Neacomys marajoara* differs from *N. dubosti* in dorsal pelage color (dark brown finely sprinkled with orange versus light to dark brown finely sprinkled with orange in *N. dubosti*), and by its bicolored tail (the tail is usually unicolored in *N. dubosti*), narrower interorbital region, teardrop-shaped incisive foramina (the lateral margins of the incisive foramina are usually subparallel in *N. dubosti*), globular auditory bullae (the bullae are usually flask-shaped in *N. dubosti*), and carotid circulation usually pattern 2 (versus pattern 1 in *N. dubosti*).
Neacomys marajoara differs from N. xingu in dorsal pelage color (dark brown finely sprinkled with orange versus orange-brown sprinkled with black in N. xingu), and by its bicolored tail (the tail is usually unicolored in N. xingu), anteriorly straight (versus anteriorly expanded) nasal bones, broader interorbital region, narrower maxillary septum of the incisive foramina, larger subsquamosal fenestrae, and carotid circulation usually pattern 2 (versus usually pattern 1).

|                          | dubosti           | xingu            | marajoara         | vossi             |
|--------------------------|-------------------|------------------|-------------------|-------------------|
| **Distribution**         | NE Amazonia       | SE Amazonia      | SE Amazonia       | SE Amazonia       |
| **Dorsal pelage**        | light to dark brown finely sprinkled with orange | orange-brown sprinkled with black | dark brown finely sprinkled with orange | brown sprinkled with orange and/or black |
| **Ventral pelage**       | pure white to buffy white | pure white to buffy white | pure white to yellowish white | pure white to buffy white |
| **Tail**                 | usually unicolored | usually unicolored | bicolored         | usually slightly bicolored |
| **Nasal bones**          | –                 | expanded anteriorly | straight anteriorly | expanded anteriorly |
| **Interorbital region**  | broad             | narrow           | relatively broad  | narrow            |
| **Paraoccipital process**| –                 | usually separated from auditory bullae | separated from auditory bullae | close to the auditory bullae |
| **Subsquamosal fenestrae**| –                | small            | large             | usually small     |
| **Sphenopalatine fora- men** | –               | small            | large             | large             |
| **Lateral expansion of parietal** | restricted | slightly expanded to restricted | restricted | slightly expanded to restricted |
| **Carotid circulation**  | pattern 1         | usually pattern 1\(^a\) | usually pattern 2\(^b\) | pattern 1         |
| **Incisive foramina**    | small and usually subparallel | small and subparallel | small and usually teardrop shaped | small and subparallel |
| **Maxillary septum of incisive foramina** | –           | wide             | narrow            | usually wide     |
| **Zygomatic plate**      | narrow            | narrow to broad  | narrow            | narrow            |
| **Auditory bullae**      | usually flask-shaped | usually broad    | globular          | globular          |
| **M1 anteroloph**        | –                 | fused            | fused or distinct | usually distinct |

\(^a\) We found variation in this character, please see Neacomys xingu description.  
\(^b\) We found variation in this character, please see Neacomys marajoara description.
**Neacomys marajoara** differs from *N. vossi* in dorsal pelage color (dark brown finely sprinkled with orange versus brown sprinkled with orange and/or black in *N. vossi*), and by its anteriorly straight (versus anteriorly expanded) nasal bones, broader interorbital region, paroccipital processes separated from the auditory bullae (versus processes close to the auditory bullae), larger subsquamosal fenestrae, carotid circulation usually pattern 2 (versus pattern 1), and narrower maxillary septum of the incisive foramina.

Karyotypically, *Neacomys marajoara* differs from other species in the Dubosti Group by having a diploid chromosomal complement of 58 (versus $2n = 64$ in *N. dubosti*; table 5), a uniquely large FN of 70 autosomal arms (versus FN = 64–68 in other group members), and submetacentric sex chromosomes (at least one of the sex chromosomes is acrocentric in *N. dubosti* and “species 2”).

**Distribution:** *Neacomys marajoara* has been recorded only on Marajó Island, state of Pará, Brazil (fig. 5).

**Etymology:** The specific epithet *marajoara* is to be treated as a noun in apposition. It is derived from Tupi Guarani (a language family that comprises many different indigenous Amazonian dialects) and denotes a native of Marajó Island (the type locality).

**Field Notes:** Of the nine specimens for which trapping information is available, eight were captured in pitfall traps and one was taken in a Sherman trap placed on the ground. One paratype (MPEG 40435) was pregnant with three fetuses.

**Remarks:** *Neacomys marajoara* was previously reported in the literature as “*Neacomys sp.*” (in part) by Silva at al. (2015) and as “*Neacomys sp. D*” by Oliveira da Silva et al. (2019).

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**Neacomys vossi**, new species

Voss’s Spiny Mouse

**Figures 8, 9**

**Holotype:** The holotype (UFPA 1583) is an adult female (age class 2) collected on 2 April 2013, by Ana Cristina Mendes Oliveira (original field number JB 031). The specimen consists of a stuffed skin, skull, and skeleton, all in good condition; additionally, a tissue sample is preserved in ethanol, and a partial cytochrome *b* sequence that we obtained from it has been deposited in Genbank with accession number MT462028.

**Type Locality:** Boca do Rato, on the right bank of the Rio Tapajós, Itaituba municipality, state of Pará, Brazil (5°14′S, 56°56′W, fig. 5).

**Diagnosis:** *Neacomys vossi* is a small species (table 3) that differs from congeneric taxa by the following combination of craniodental traits: skull delicate; interorbital region narrow; nasal bones expanded anteriorly; supraorbital margins convergent anteriorly; subsquamosal fenestra usually small (about ¼ the size of the postglenoid foramen on each side of the skull); paroccipital processes close to the auditory bullae; sphenopalatine foramen large; carotid circulation pattern 1 (sensu Voss, 1988); maxillary part of incisive septum (between the incisive foramina) usually wide; M1 usually with slightly flat, narrow, and undivided anterocone; and M1 anteroloph usually distinct (not fused with the anterolabial conule).
Morphological Description: Dorsal pelage brown sprinkled with orange and/or black (fig. 8); ventral pelage varying from pure white to buffy white; very thin orange lateral line. Superciliary, genal, and mystacial vibrissae blackish and long (extending behind ears when laid back alongside the head); submental vibrissae absent; interramal vibrissae short and white. Ears small and rounded; post-auricular hairs gray-based with orange tips, forming an orange tuft behind each pinna. Ungual tufts white, longer than claws; fore- and hind feet covered dorsally with buffy-cream hairs; hind feet narrow and elongate with small interdigital membranes. Tail about the same length as head and body, usually slightly bicolored (except in UFPA 1277, 1417, 1444, 1654, and 1736 which have unicolored tail) and covered by spiny and clearly visible hairs; tail tip of the tail with very short (approximately 1.4 mm long) terminal tuft; caudal scales small, arranged in annular series; each caudal scale with three subequal hairs inserted along its posterior margin.

Skull small and delicate in dorsal view (fig. 9); with expanded anterior nasal margins; notably broad rostrum and shallow zygomatic notches; posterior nasal terminus usually flat, extending beyond the maxillary-frontal suture; premaxillaries terminating slightly anterior to nasals; lacrimal bone small and visible in dorsal view, equally contacting maxillary and frontal bones; supraorbital margins convergent anteriorly; interorbital region narrow; supraorbital beads developed as projecting shelves; lateral expansion of the parietal restricted to the dorsal surface (except in UFPA 1227 and UFPA 1577, in which the parietal is slightly expanded ventrally near the squamosal root of the zygomatic arch). Incisive foramina small with subparallel lateral margins, not extending posteriorly to the level of M1s; maxillary portion of incisive septum (dividing the left and right foramina) usually wide. Zygomatic plate narrow. Palate with two posterolateral pits on each side of the palate. Auditory bullae small and globular, with short and narrow eustachian tubes; periotic bone extending anteriorly to internal carotid canal, but usually not entering into it (except in UFPA 1227, 1417, 1530, 1654, 1417, and 1736, in which the periotic does enter the internal carotid canal). Subsquamosal fenestra usually small (about ¼ the size of the postglenoid foramen); hamular process of the squamosal long. Paraoccipital process narrow, small, and close to the auditory bullae (Sánchez-Vendizú et al., 2018: fig. 3C). Sphenopalatine foramen large; alisphenoid strut absent; carotid circulation primitive (pattern 1, as identified by retaining a well-developed squamosal-alisphenoid groove and sphenofrontal foramen, both indicative of the presence of the supraorbital branch of the stapedial artery; Voss et al., 1988).

First upper molar (M1) usually with slightly flat and undivided anterocone; anteroloph usually distinct (not fused with the anterolabial conule); M3 small; labial cusps (paracone, metacone) usually taller than lingual cusps (protocone, hypocone); m1 anteroconid undivided.

Mandible with mental foramen opening laterally; capsular process of lower incisor alveolus present, but indistinct (reduced as a slight, rounded elevation), approximately at same height as coronid process.

Taxonomic Comparisons: *Neacomys vossi* differs from *N. dubosti* in dorsal pelage color (brown sprinkled with orange and/or black versus dark brown finely sprinkled with orange in
FIG. 8. Dorsal and ventral views of the skin of *Neacomys vossi* (UFPA 1583, holotype).
FIG. 9. Dorsal, ventral, lateral cranial views and lateral view of mandible of Neacomys vossi (UFPA 1583, holotype).
Neacomys vossi differs from Neacomys xingu in dorsal pelage color (brown sprinkled with orange and/or black versus orange-brown sprinkled with black in Neacomys xingu), larger sphenopalatine foramen, and an M1 anteroloph that is usually distinct (versus fused in Neacomys xingu).

Karyotypically, Neacomys vossi differs from other species in the Dubosti Group by having a diploid chromosome complement of 58 (versus $2n = 64$ in Neacomys dubosti and $2n = 64$ in “species 2”), an FN of 68 autosomal arms (versus FN = 70 in Neacomys marajoara, FN = 64 in Neacomys xingu, and FN = 66 in “species 2”), and submetacentric sex chromosomes (at least one of the sex chromosomes is acrocentric in Neacomys dubosti and “species 2”).

Distribution: Neacomys vossi has been collected on the right bank of the upper and middle Tapajós River and on the left bank of lower Xingu (fig. 5). According to our records, the species appears to be endemic to the Tapajós center of endemism (Silva et al., 2005).

Etymology: Named in honor of Robert S. Voss (fig. 10), curator of mammals at the American Museum of Natural History, New York, for his extensive contributions to our knowledge of Neotropical mammals, especially the taxonomy of Neacomys in northeastern Amazonia.

Field Notes: Among the specimens we examined for which trapping information is available, all 17 were captured in pitfall traps, two (UFPA 1277 and 1284) in upland (terra firme) forests and three (UFPA 1444, 1487, and 1583) in primary forest of unknown character.

Remarks: Neacomys vossi was previously reported in the literature as “Neacomys sp. A” by Oliveira da Silva et al. (2017, 2019).

Neacomys xingu, new species
Xingu Spiny Mouse
Figures 11, 12

Holotype: The holotype (UFMT 1268) is an adult female (age class 5), collected on 28 August 2009 by Cleuton Lima Miranda (original field number PSA 242) in a pitfall trap. The specimen is preserved as a skin, skull, and skeleton in good condition; additionally, a tissue is
preserved in alcohol, and a partial cytochrome \textit{b} sequence that we obtained from it has been deposited in Genbank with accession number MT462060.

Type Locality: Flona Tapirapé-Aquiri, Marabá, state of Pará, Brazil (5°46′S, 50°32′W, fig. 5).

Diagnosis: \textit{Neacomys xingu} is a small species (table 3) that differs from congeneric taxa by the following combination of craniodental traits: skull delicate; interorbital region narrow; nasal bones expanded anteriorly; supraorbital margins convergent anteriorly; subsquamosal fenestra small (about \(\frac{1}{4}\) the size of the postglenoid foramen on each side of the skull); paraoccipital process separated from the auditory bullae; sphenopalatine foramen small; carotid circulation usually pattern 1 (sensu Voss, 1988); maxillary part of incisive septum (between the incisive foramina) wide; M1 usually with flat and undivided anterocone; and M1 anteroloph fused with the anterolabial conule.

Morphological Description: Dorsal pelage orange-brown, sprinkled with black (fig. 11); ventral pelage varying from pure white to buffy white and separated from the dorsal pelage by a thin orange lateral line. Superciliary, genal, and mystacial vibrissae blackish and long (extending behind ears when laid back alongside the head); submental vibrissae absent; interramal vibrissae short and white; Ears small and rounded; postauricular hairs gray based with orange tips, forming an orange tuft behind each pinna. Ungual tufts white, longer than claws in length; fore- and hind feet covered dorsally with buffy-cream hairs; hind feet narrow and elongate with small interdigital membranes present. Tail about the same length as head and body, usually unicolored (except in PSA 069, MPEG 39901, and MPEG 42019, in which the tail is dark above and paler below), and covered by short, spiny, and clearly visible hairs; tail tip with very short (1–2 mm) terminal tuft; caudal scales small, arranged in annular series; each caudal scale with three subequal hairs inserted along its posterior margin.

Skull small and delicate in dorsal view (fig. 12); with anteriorly expanded nasal margins; notably broad rostrum and shallow zygomatic notches; posterior nasal terminus slightly pointed, extending beyond the maxillary-frontal suture; premaxillaries terminating slightly anterior to nasals; lacrimal bone small and visible in dorsal view, equally contacting the maxillary and frontal bones; supraorbital margins convergent anteriorly; interorbital region narrow; supraorbital beads developed as projecting shelves; lateral expansion of the parietal restricted to the dorsal cranial surface (except in MCN-M 1404 and MPEG 39901, in which the parietal is slightly expanded ventrally near the squamosal root of the zygomatic arch). Incisive foramina small with subparallel lateral margins, not extending posteriorly to level of M1s; maxillary portion of incisive septum (dividing the left and right foramina) usually wide. Zygomatic plate varying from broad to narrow. Palate with two posterolateral pits on each side. Auditory bullae small and usually globular, with short and narrow eustachian tubes; periotic bone extends anteriorly to the internal carotid canal but does not enter it (except in MPEG 42715 and MCN-M 1404, in which the periotic does not reach the internal carotid canal). Subsquamosal fenestra small (about \(\frac{1}{4}\) the size of the postglenoid foramen); hamular process of the squamosal long. Paraoccipital process narrow and small and usually separated from the auditory bullae (Sánchez-Vendizú et al., 2018: fig. 3C). Sphenopalatine foramen small (except in MPEG 41991,
FIG. 11. Dorsal and ventral views of the skin of *Neacomys xingu* (UFMT 1268, holotype).
whose sphenopalatine foramen is large); alisphenoid strut absent; carotid circulation pattern usually primitive\(^8\) (pattern 1, as identified by retaining a well-developed squamosal-alisphenoid groove and sphenofrontal foramen, both indicative of the presence of the supraorbital branch of the stapedial artery; Voss, 1988: fig. 18A, B).

First upper molar (M1) usually with slightly flat and undivided anterocone; anteroloph usually fused with the anterolabial conule (such that the anteroflexus is not distinguishable); M3 small; labial cusps (paracone, metacone) usually taller than lingual cusps (protocone, hypocone); m1 anteroconid undivided.

Mandible with mental foramen opening laterally; capsular process of lower incisor alveolus present, but indistinct (reduced to a slight rounded elevation), approximately at same height of coronoid process.

**Taxonomic Comparisons:** *Neacomys xingu* differs from *N. dubosti* in dorsal pelage color (orange-brown sprinkled with black versus light to dark brown finely sprinkled with orange), and by its narrower interorbital region, globular auditory bullae (the bullae are usually flask shaped in *N. dubosti*), and carotid circulation usually pattern 1 (versus always pattern 1 in *N. dubosti*).

Karyotypically, *Neacomys xingu* differs from all other members of the Dubosti Group by having a diploid chromosomal complement of 58 (versus \(2n = 64\) in *N. dubosti* and \(2n = 54\) in “species 2”), a uniquely small FN of 64 autosomal arms (versus FN = 66–60 in other species), and submetacentric sex chromosomes (at least one sex chromosome is acrocentric in *N. dubosti* and “species 2”).

**Distribution:** *Neacomys xingu* has been collected on the right bank of the lower Xingu River and in the region of Serra de Carajás, in southeastern Pará state (fig. 5). According to cytogenetic data (Di-Nizo et al., 2017; Oliveira da Silva et al., 2019), the species also ranges southward into Vila Rica in northeastern Mato Grosso state. These records suggest that the species is restricted to the Xingu center of endemism (Silva et al., 2005).  

**Etymology:** The specific epithet *xingu* is to be treated as a noun in apposition. The species name refers to the Xingu center of endemism, delimited by the Xingu and Tapajós rivers, where the species occurs.

**Remarks:** *Neacomys xingu* was previously reported in the literature as “*Neacomys clade 7*” by Patton et al. (2000), “*Neacomys sp.*” (in part) by Silva at al. (2015), “*Neacomys sp.*” by Di-Nizo et al. (2017) and Brandão et al. (2019), and “*Neacomys sp. C*” by Oliveira da Silva et al. (2019).

**DISCUSSION**

This study includes the largest mitochondrial DNA dataset yet assembled for *Neacomys*, the results of which support generic monophyly, as have all previous analyses of *Cytb* sequence data (Catzflies and Tilak, 2009; Silva et al., 2015; Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018). Our analyses additionally reveal the existence of 17 distinct

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\(^8\) Most specimens of *Neacomys xingu* have carotid circulation pattern 1, whereas four specimens had circulatory pattern 2 (MPEG 40446, MPEG 39901, MCN-M 1403, and MCN-M 1404).
lineages clustered in four main groups. Two of these groups correspond to the Paracou and Spinosus groups of Hurtado and Pacheco (2017) and Sánchez-Vendizú et al. (2018), but the inclusion of new sequence data from southeastern Amazonia in our analyses make it expedient to restrict the membership of their Tenuipes Group and to recognize a fourth clade, which we refer to as the Dubosti Group.

The three new species herein described—*N. marajoara*, *N. xingu*, and *N. vossi*—belong to the Dubosti Group. These species, together with an unnamed member species (“species 2”), have genetic divergences varying from 3.9% to 9.4%, comparable to distances previously reported for recently described species such as *N. vargasillosai* and *N. spinosus* (7.8%; Hurtado

FIG. 12. Dorsal, ventral, lateral cranial views and lateral view of mandible of *Neacomys xingu* (UFMT 1268, holotype).
and Pacheco, 2017), and \textit{N. macedoruizi} and the “upriver” clade of \textit{N. minutus} (4.9%; Sánchez-Vendizú et al., 2018). Although \textit{N. marajoara} and \textit{N. xingu} have the lowest genetic divergence value (3.9%) reported for any pair of \textit{Neacomys} species, this value is within the known range of interspecific mammalian distances (Baker and Bradley (2006). Additionally, cytogenetic studies have revealed karyotypic differences among these lineages (Silva et al., 2015; Oliveira da Silva et al., 2017, 2019). These, along with qualitative-morphological data reported in our study, provide evidence of reproductive isolation and nuclear-gene divergence, respectively.

Carotid circulation patterns have long been considered a reliable character for diagnosing sigmodontine species (Voss, 1988; Carleton and Musser, 1989; Voss and Carleton, 1993; Steppan, 1995; Carleton and Olson, 1999; Weksler, 2006; Hurtado and Pacheco, 2017; and Sánchez-Vendizú et al., 2018). However, intraspecific polymorphism in this character was reported by Voss (1991), and our observations provide additional evidence that oryzomyine species can be polymorphic for carotid circulatory traits. Carotid polymorphisms in \textit{N. marajoara} and \textit{N. xingu} may be related to the recency of speciation events from which these lineages arose, as evidenced by their minimal genetic divergence. Because these are not the only congeneric species that exhibit carotid polymorphisms (T.B.F.S., unpublished), observations of sample differences in carotid traits should be interpreted cautiously unless accompanied by other evidence of taxonomic divergence.

The discovery of new species of \textit{Neacomys} in southeastern Amazonia is not unexpected, in view of similar recent discoveries in western and northeastern Amazonia (Patton et al., 2000; Voss et al., 2001; Hurtado and Pacheco, 2017; and Sanchez-Vendizú et al., 2018) and previous reports of karyotypic variation and genetic divergence among southeastern forms (Patton et al., 2000; Catzeflis and Tilak, 2009; Silva et al., 2015; Oliveira da Silva et al., 2017; Hurtado and Pacheco, 2017; and Sanchez-Vendizú et al., 2018). Although southeastern Amazonia has long been accessible to collectors, our study underscores the fact that faunal inventories and taxonomic studies are still needed in this region, which is among the most extensively deforested and environmentally threatened parts of the Amazonian biome, due to industrial agriculture, road construction, mining, and hydroelectric dams (Fearnside, 1989, 2005; Gascon et al., 2001).

| TABLE 5. Karyotypes $^a$ of \textit{Neacomys} species in the Dubosti Group. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                  | $2n$ | FN  | gA  | gB  | gC  | gD  | X   | Y   | Source                      |
| dubosti          | 64   | 68  | —   | 6   | —   | 56  | SM  | A   | Silva et al., 2015          |
| marajoara        | 58   | 70  | —   | 14/8| —   | 42/48| SM  | SM  | Silva et al., 2015          |
| vossi            | 58   | 68  | —   | 12  | —   | 44  | SM  | SM  | Oliveira da Silva et al., 2017 |
| xingu            | 58   | 64  | —   | 8   | —   | 48  | SM  | SM  | Silva et al., 2015          |
| species 2        | 54   | 66  | 8   | 6   | —   | 38  | A   | A   | Oliveira da Silva et al., 2017 |

$^a$ Diploid number ($2n$); fundamental number (FN); group A (gA) = large metacentric and submetacentric autosomes; group B (gB) = medium and small metacentric or submetacentric autosomes; group C (gC) = medium and small subtelocentric autosomes; group D (gD) = large, medium, and small acrocentric autosomes. Abbreviations for sex chromosome (X and Y) morphology: M = metacentric, SM = submetacentric, ST = subtelocentric, A = acrocentric.
ACKNOWLEDGMENTS

We are grateful to the following curators and collection managers for permitting access to specimens under their care: Robert Voss and Eileen Westwig (at AMNH), Kris Helgen and Darrin Lunde (USNM), Burton Lim (ROM), Priscilla Tucker and Cody Thompson (UMMZ), Roberto Portella (BMNH), John R. Wible and Susan B. McLaren (CM), Manuel Ruedi (MHNG), Fernando Pacheco (UNB), Suely Marques-Aguiar (MPEG), Manoel Santos Filho (UNEMAT), Cláudia Costa (PUC-MG). This study was supported by the Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT/PRONEM #477017/2011 to R.V.R). I.P.F. was supported by the Project CNPq/SISBIOTA-BioPHAM 563348/2010. T.B.F.S. was partially supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior–Brasil (CAPES), Finance Code 001; by an Ernst Mayr Grant from the Museum of Comparative Zoology at Harvard University, Cambridge, MA; by small grants from the American Museum of Natural History (New York) and the Muséum d'Histoire Naturelle (Geneva); by the Programa de Pós-Graduação em Zoologia da Universidade Federal de Mato Grosso (PPGZOO/UFMT); and by scholarships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Ministério da Ciência, Tecnologia, Inovações e Comunicações (MCTIC) (300617/2020-8).

T.B.F.S. is additionally grateful to Marinez I. Marques (head of the PPGZOO, 2014-2016) who provided financial support to this study, and to Karl-L. Schuchmann. We thank Luan Silva for helping with the layout of figure 5; Silvia Pavan for kindly providing sequence data from MPEG 45483; Cleuton L. Miranda for reading a previous version of the manuscript; and Guilherme Garbino, Robert Voss, and Pablo Teta who made several helpful suggestions for its improvement. T.B.F.S. wants to express his gratitude and love for his father, Antonio F. Semedo Fernandes, who passed away during the completion of this study.

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APPENDIX 1

Specimens Examined

The localities of specimens from the Dubosti Group that we examined and from which we analyzed sequence data are listed below. The largest administrative units within each country (state, department, or province) are italicized. Verbatim locality names are placed in quotes, but others have been emended for brevity and to conform with current geographic usage. For each locality we provide geographic coordinates and the collection number of the voucher specimens examined. Numbers identify locality symbols plotted on map (fig. 5). The paratypes of our new species are designated here.

BRAZIL

1. Amapá, Serra do Navio km 190 efa. (00°59’S, 52°03’W; USNM 461589; N. dubosti).
2. Amapá, Rio Amapari (00°59’S, 52°03’W; USNM 461573, 461587; N. dubosti).
3. Pará, Almeirim Municipality, Reserva Biológica Maicuru (00°50’N, 53°56’W; CN 240; N. dubosti).
4. Pará, Chaves municipality, Marajó Island, Tauari Farm (00°39’S, 50°11’W; MPEG 40429, 40431, 40434, 40435, 40439–40441, 40443, 40446 [paratypes]; MPEG 40432 [holotype]; N. marajoara).
5. Pará, Mangabal community on right bank of Rio Tapajós, Itaituba (5°35’S, 57°7’W; UFPA 1736 [paratype]; N. vossi).
6. Pará, Itaituba Municipality, Boca do Rato on right bank of Rio Tapajós (6°7’S, 57°36’W; UFPA 1391, 1520, 1577 [paratypes]; UFPA 1583 [holotype]; N. vossi).
7. Pará, Itaituba, Mamãe-anã (Canta-galo) on right bank of Rio Tapajós (5°48’S, 57°24’W; UFPA 1277, 1284, 1487, 1647, 1654 [paratypes]; N. vossi).
8. Pará, Itaituba (5°40’S, 57°00’W; UFPA 1467, JB 27; N. vossi).
9. Pará, Itaituba, São Martins on right bank of Rio Tapajós (6°07’S, 57°36’W; UFPA 1691 [paratype]; N. vossi).
10. Pará, Itaituba, Jacaré on right bank of Rio Tapajós (5°41’S, 57°14’W; UFPA 1444 [paratype]; N. vossi).
11. Pará, 18 km south and 19 km west of Altamira- Agrovila da União (03°22’S, 52°23’W; USNM 521468, 521539; N. vossi).
12. Pará, Itaituba, Br 230, Itaituba-Jacareacanga Km 212 on Transamazonica Highway (5°40’S, 56°45’W; USNM 545957–545959, 545960–545964; N. vossi).
13. Pará, Marabá Municipality, Flona Tapirapé-Aquiri (5°51’S, 50°31’W; UFMT 1273, 1275 [paratypes]; MPEG 39901, 41804, 41805, 41991, 41996, 42019; MPEG-PSA 46, 69 [paratypes]; UFMT 1268: [holotype]; N. xingu).
14. Pará, East bank Rio Xingu 52 km SSW Altamira (3°39’S, 52°22’W; USNM 549553; N. xingu).
15. Pará, 54 km south and 150 km west of Altamira (3°41’S, 51°45’W; USNM 519180, 521464–521467; N. xingu).
16. Pará, Flona Carajás, Parauapebas (6˚3’S, 50˚35’W; MCN-M 1401–1404, 1443 [paratypes]; Neacomys sp. 2).
17. Pará, left bank of Rio Tapajós (5˚17’S, 57˚8’W; MPEG 42838, 42901; Neacomys sp. 2).
18. Pará, Juruti (2˚09’S, 56˚5’W; JUR 19, 42, 82; Neacomys sp. 2).
19. Pará, Penedo on left bank of Rio Tapajós (5˚30’S, 57˚6’W; UFPA 1227, 1413, 1417, 1530; Neacomys sp. 2).
20. Pará, Reserva Biológica Maicuru. 00˚50’N. 53˚56’W (CN 240: Neacomys dubosti).

FRENCH GUIANA
21. Paracou near Sinnamary (05˚17’N. 52˚55’W; AMNH 267569 [holotype]; N. dubosti)
22. Cacao, Roura, Cayenne (04˚34’N, 52˚27’W; MHNG 1963.025: N. dubosti).
23. Route de Kaw, Cayenne (04˚36’N, 52˚15’W; MHNG 1894.013: N. dubosti).

SURINAM
24. Nickerie District, Sipaliwini Airstrip (02˚02’N, 56˚07’W; CM 76846: N. dubosti).
25. Sipaliwini, Werehpai Camp (02˚23’N, 56˚42’W; ROM 120726: N. dubosti).
26. Sipaliwini, Iconja Landing on Sipaliwini River (01˚59’N, 56˚05’W: ROM 120288: N. dubosti).
27. Marowijne, Oelemarie (03˚06’N, 54˚31’W; CM 76835–76837, 76839, 76840, 76842–76844; N. dubosti).
APPENDIX 2

Phylogenetic Relationships of Neacomys Based on Maximum-Likelihood Analysis

(For simplicity, clades shared with our Bayesian results [in fig. 2A–C] are cartooned. Branch support values are bootstrap frequencies.)
### APPENDIX 3

**Results of Principal Components Analyses of Species in the Dubosti Group of Neacomys**

|                 | PC1  | PC2  | PC1  | PC2  | PC1  | PC2  | PC1  | PC2  | PC1  | PC2  | PC1  | PC2  |
|-----------------|------|------|------|------|------|------|------|------|------|------|------|------|
| **BH**          | 0.54 | 0.47 | 0.80 | 0.23 | 0.59 | 0.57 | 0.30 | -0.79| 0.04 | -0.65| 0.38 | 0.27 |
| **BIF**         | 0.65 | -0.09| 0.41 | 0.15 | 0.68 | -0.03| 0.09 | 0.63 | 0.52 | 0.40 | 0.21 | -0.02|
| **BM1**         | 0.73 | 0.37 | 0.62 | 0.30 | 0.83 | 0.14 | 0.38 | 0.33 | 0.70 | -0.24| 0.49 | 0.50 |
| **BPR**         | 0.52 | 0.36 | 0.70 | -0.03| 0.85 | -0.07| 0.76 | 0.22 | 0.66 | 0.05 | 0.57 | 0.30 |
| **BZP**         | 0.71 | 0.26 | 0.64 | 0.31 | 0.71 | 0.23 | -0.09| 0.25 | 0.77 | -0.14| 0.66 | 0.34 |
| **BB**          | 0.29 | -0.49| 0.70 | -0.37| 0.55 | -0.21| 0.20 | 0.14 | 0.28 | -0.14| 0.44 | -0.28|
| **CIL**         | 0.87 | -0.37| 0.93 | -0.19| 0.92 | -0.19| 0.88 | -0.12| 0.90 | 0.11 | 0.90 | -0.18|
| **LCIB**        | 0.25 | 0.35 | 0.13 | 0.60 | 0.19 | 0.63 | 0.32 | -0.67| 0.69 | -0.17| 0.73 | -0.23|
| **LIB**         | 0.47 | 0.13 | 0.53 | 0.44 | 0.64 | 0.20 | 0.06 | 0.26 | 0.42 | 0.53 | 0.32 | -0.17|
| **LD**          | 0.69 | -0.40| 0.88 | -0.26| 0.87 | -0.33| 0.75 | 0.22 | 0.58 | 0.60 | 0.68 | -0.49|
| **LIF**         | 0.23 | -0.68| 0.48 | -0.69| 0.22 | -0.56| 0.82 | -0.20| 0.15 | 0.57 | 0.45 | -0.65|
| **LLD**         | 0.50 | 0.25 | 0.40 | 0.38 | 0.43 | 0.07 | 0.05 | 0.33 | 0.26 | 0.18 | 0.22 | 0.17 |
| **LLM**         | 0.40 | 0.26 | 0.71 | 0.16 | 0.68 | 0.39 | 0.49 | -0.04| 0.66 | -0.53| 0.70 | 0.23 |
| **LM**          | 0.48 | 0.54 | 0.78 | 0.28 | 0.73 | 0.47 | 0.28 | -0.54| 0.68 | -0.43| 0.76 | 0.40 |
| **LN**          | 0.53 | -0.48| 0.77 | -0.46| 0.67 | -0.57| 0.81 | 0.28 | 0.86 | 0.05 | 0.89 | -0.14|
| **LPB**         | 0.48 | 0.24 | 0.51 | 0.26 | 0.67 | 0.05 | 0.23 | 0.10 | 0.69 | -0.21| 0.49 | 0.49 |
| **MB**          | 0.79 | 0.02 | 0.86 | 0.20 | 0.83 | 0.27 | 0.21 | -0.71| 0.71 | -0.31| 0.75 | 0.07 |
| **OL**          | 0.75 | -0.43| 0.80 | -0.25| 0.72 | -0.42| 0.51 | 0.12 | 0.68 | 0.34 | 0.75 | -0.39|
| **RB**          | 0.45 | 0.20 | 0.36 | 0.07 | 0.34 | -0.28| 0.68 | 0.40 | 0.59 | -0.08| 0.58 | 0.39 |
| **RL**          | 0.66 | -0.33| 0.74 | -0.38| 0.70 | -0.44| 0.78 | 0.23 | 0.83 | 0.30 | 0.79 | -0.17|
| **ZB**          | 0.85 | 0.00 | 0.92 | 0.07 | 0.87 | 0.12 | 0.79 | -0.28| 0.81 | -0.05| 0.88 | -0.07|
| **% Variance**  | 46.98| 12.62| 47.22| 11.31| 35.58| 13.33| 28.97| 15.48| 41.20| 12.35| 41.13| 10.94|

Variation explained by PC1 and PC2 for each pairwise comparison.
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