A REVISION OF THE DIDELPHID MARSUPIAL
GENUS MARMOSA

PART 2. SPECIES OF THE RAPPOSA GROUP
(SUBGENUS MICOUREUS)

ROBERT S. VOSS, THOMAS C. GIALLA,
JUAN F. DÍAZ-NIETO, AND SHARON A. JANSA

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(SUBGENUS MICOUREUS)

ROBERT S. VOSS
Division of Vertebrate Zoology (Mammalogy),
American Museum of Natural History

THOMAS C. GIARLA
Department of Biology,
Siena College, Loudonville, NY

JUAN F. DÍAZ-NIETO
Departamento de Ciencias Biológicas and Grupo de Investigación BEC,
Universidad EAFIT, Medellín, Colombia

SHARON A. JANSA
Department of Ecology, Evolution, and Behavior; and
J.F. Bell Museum of Natural History,
University of Minnesota, St. Paul, MN

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ABSTRACT

In this report, the second of a revisionary series on mouse opossums (*Marmosa*), we analyze cytochrome *b* sequence data from 166 specimens of the subgenus *Micoureus* and delimit putative species using the multirate Poisson Tree Processes (mPTP) method. That analysis identifies 21 putative species, many of which can be matched with available names, including *alstoni*, *constantiae*, *demerarae*, *limae*, *germana*, *meridae*, *paraguayana*, *parada*, *perplexa*, *phaea*, *rapposa*, and *rutteri*. However, some of these nominal taxa are not morphologically diagnosable, and in the absence of other corroborating evidence, we do not recommend that they all be recognized as valid. Phylogenetic analyses of a multigene dataset suggest that putative species of *Micoureus* belong to several well-supported clades, one of which (the "Rapposa Group") is revised in this report. As defined herein, the Rapposa Group includes at least three valid species: *M. rapposa* Thomas, 1899 (including *budini* Thomas, 1920); *M. parada* Tate, 1931; and *M. rutteri* Thomas, 1924. Herein we document their ecoregographic distributions and diagnostic traits, comment on their taxonomic histories, and list the specimens we examined (including all relevant type material).

INTRODUCTION

The didelphid marsupials that Tate (1933) referred to the genus *Marmosa*, Gray, 1821, included many superficially similar small opossums—black-masked, prehensile-tailed, and pouchless—that are now referred to several genera. Of the species that remain in *Marmosa* (sensu Voss et al., 2014), the so-called woolly mouse opossums of the subgenus *Micoureus* have not been revised for many decades, and their taxonomy is correspondingly problematic. Twenty-one available names are currently referred to *Micoureus* (table 1), of which only six (*alstoni*, *constantiae*, *demerarae*, *paraguayana*, *phaea*, and *regina*) were recognized as valid species in the last synoptic treatment of this clade (Gardner and Creighton, 2008). However, recently published molecular and morphological analyses (Silva et al., 2019; Voss et al., 2019) support the recognition of additional valid species and suggest the need for a comprehensive taxonomic revision.

In fact, empirical support for several synonyms implied by current usage is nonexistent. The nominal taxa *germana*, *mapiriensis*, and *rapposa*, for example, were originally described as full species, and all were regarded as such by Tate (1933) and Cabrera (1958). Although no evidence to the contrary has ever been published, these three taxa are now treated as synonyms or subspecies of *Marmosa regina*. As currently understood, *M. regina* ranges from the Magdalena Valley of Colombia to eastern Bolivia (Gardner and Creighton, 2008: map 35). Because no other small nonvolant mammal is known to be similarly distributed—spanning such formidable barriers as the northern Andes and the upper Amazon—the hypothesis that all the nominal taxa currently synonymized with *M. regina* are conspecific is obviously suspect.

Although phylogenetic analyses of mitochondrial gene sequences have provided useful information about historical relationships among sampled populations of *Micoureus*, analytic results are often difficult to interpret taxonomically in the absence of supporting revisionary work. Patton et al. (2000), for example, discovered that two species with highly divergent cytochrome *b* sequences were broadly sympatric in western Brazil, but the names that properly applied to them were unclear, as the authors themselves acknowledged. A genetically divergent mtDNA haplogroup from southeastern Brazil was successively identified as *M. limae* by Patton et al. (2000), as *M. paraguayana* by Voss et al. (2001), and as *M. travassosi* by Patton and Costa (2003). Confusingly, cytochrome *b* sequences identified as *M. constantiae* have clustered with *M. demerarae* in some studies (e.g., Patton and Costa, 2003), but with *M. regina* in others (e.g., de la Sancha et al., 2012), a paradox that was only recently cleared up by Silva et al. (2019).
With this report, the second in a series on Marmosa (Rossi et al., 2010), we initiate a revision of the subgenus Micoureus based on analyses of mitochondrial and nuclear gene sequences, first-hand examination of morphological voucher material, and an extensive study of unsequenced specimens, including name-bearing types. Herein we provide a molecular-phylogenetic overview of the subgenus, define several multi-species clades, and formally revise the geographically widespread complex of species closely related to Marmosa rapposa, specimens of which have been consistently misidentified in published reports and museum collections for many years.

### Materials and Methods

Specimens examined: Specimens cited in our tables and text are preserved in the following collections (listed in order of their standard insti-
tutional abbreviations): AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); CBF, Colección Boliviana de Fauna (La Paz); CM, Carnegie Museum of Natural History (Pittsburgh); CTUA, Colección Teriológica de la Universidad de Antioquia (Medellín); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus); ISEM, Institut des Sciences de l’Evolution de Montpellier (Montpellier); KU, University of Kansas Biodiversity Research Center (Lawrence); LSUMZ, Louisiana State University Museum of Natural Science (Baton Rouge); MN, Museu Nacional (Rio de Janeiro); MNHN, Muséum National d’Histoire Naturelle (Paris); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); MSB, Museum of Southwestern Biology (University of New Mexico, Albuquerque); MVZ, Museum of Vertebrate Zoology (University of California, Berkeley); MZUSP, Museu de Zoolologia da Universidade de São Paulo (São Paulo); OMNH, Sam Noble Oklahoma Museum of Natural History (Norman); PUCMG, Pontifícia Universidade Católica de Minas Gerais (Belo Horizonte); ROM, Royal Ontario Museum (Toronto); TTU, Museum of Texas Tech University (Lubbock); UFES, Universidade Federal do Espírito Santo; UFMG, Universidade Federal de Minas Gerais (Belo Horizonte); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); and USNM, National Museum of Natural History (Washington, DC). Two specimens with field numbers prefixed by “LHE” have yet to be cataloged in any collection at the time of writing; they are currently held at the USNM.

**Taxon Sampling and Laboratory Methods:** The cytochrome *b* sequence data analyzed in this report represent most of the nominal taxa currently referred to the subgenus *Micoureus*, including sequences that we obtained from holotypes, paratypes, topotypes, and other geographically representative material (table 2, figs. 1–3). Additionally, we sequenced morphologically distinctive specimens that represent candidate new taxa, and we made a diligent effort to sequence material from sparsely sampled regions. In the latter respect we were not entirely successful, because the eastern slopes of the Andes, much of central Amazonia, southeastern Colombia, and northern Central America are conspicuous sampling gaps.

We also downloaded cytochrome *b* sequence data deposited in GenBank by previous researchers. Careful checking of these sequences for provenance revealed that several pairs of accessions are duplicates (sequences obtained from the same specimen: e.g., AJ606442 and HM106375, both obtained from RSV 2085), of which we retained only the longer sequence from each pair for analysis. We did not analyze the following GenBank accessions, all of which have ambiguous base calls that suggest sequencing problems: AJ606435 (from Steiner and Catzeflis, 2004); GU112916, GU112917, GU112919, GU112921, GU112923, and GU112924 (from Agrizzi et al., 2012); and JN887137 and JN887138 (from de la Sancha et al., 2012). Lastly, we omitted two problematic GenBank sequences (U34673, U34674) for which no satisfactory explanation seems to be available. Other cytochrome *b* sequences were kindly made available to us by the Patton lab at the University of California at Berkeley, of which we discarded four that have premature stop codons (JLP 16758, JLP 16769, JLP 16770, and JLP 16788).

We extracted DNA from preserved tissues or dried museum specimens using methods described in Voss and Jansa (2009) and Giarla et al. (2010). To minimize risk of contamination, all extractions from museum specimens were performed in an isolated laboratory where mamma-
| Haplogroup | Voucher<sup>a</sup> | Field #<sup>c</sup> | Locality<sup>d</sup> | bp<sup>e</sup> | GenBank | Source |
|-----------|---------------------|-------------------|----------------------|--------|--------|--------|
| *alstoni* | AMNH 139280*        | U 3712            | Costa Rica: Cartago (70) | 978    | MN978596 | This study |
| *alstoni* | KU 143495*          | CAL 2830          | Costa Rica: Puntarenas (71) | 275    | MN978597 | This study |
| *alstoni* | AMNH 131732*        | U 3168            | Costa Rica: San José (72) | 978    | MN978598 | This study |
| *alstoni* | UMMZ 76733*         | MJA 34            | Nicaragua: Zelaya (87) | 372    | MN978599 | This study |
| *alstoni* | USNM 449564*        | FMG 2281          | Panama: Bocas del Toro (88) | 1149   | MN978600 | This study |
| *alstoni* | USNM 449565*        | FMG 2293          | Panama: Bocas del Toro (88) | 1149   | MN978601 | This study |
| *alstoni* | AMNH 272942*        | ACC 40            | Panama: Colón (89) | 475    | MN978602 | This study |
| *alstoni* | AMNH 148757*        | U 3003            | Costa Rica: Alajuela (90) | 475    | MN978603 | This study |
| *constantiae* | AMNH 209158* | AX 2389           | Bolivia: Beni (1) | 475    | MN978605 | This study |
| *constantiae* | CBF 7540*    | EY 1913           | Bolivia: Cochabamba (6) | 1149   | MN978606 | This study |
| *constantiae* | USNM 584470* | LHE 1550          | Bolivia: Santa Cruz (13) | 1149   | MN978608 | This study |
| *constantiae* | [USNM?]    | JLS 173           | Bolivia: Santa Cruz (14) | 630    | JF281093 | Rocha et al. (2015) |
| *constantiae* | [INPA] | MNFS 185          | Brazil: Amazonas (18) | 1149   | MN992047 | Patton lab |
| *constantiae* | [INPA] | MNFS 187          | Brazil: Amazonas (18) | 1149   | MN992048 | Patton lab |
| *constantiae* | MVZ 190308 | JLP 15833         | Brazil: Amazonas (20) | 1149   | MN978609 | This study |
| *constantiae* | MVZ 190302 | JLP 15368         | Brazil: Amazonas (23) | 1149   | MN978610 | This study |
| *constantiae* | MVZ 190305 | JLP 15362         | Brazil: Amazonas (25) | 1149   | KJ868124 | Mitchell et al. (2014) |
| *constantiae* | AMNH 92874* | AO 3245           | Brazil: Amazonas (26) | 372    | MN978611 | This study |
| *constantiae* | OMNH 37209*       | MK 0374           | Brazil: Mato Grosso (36) | 475    | MN978612 | This study |
| *constantiae* | [UFMG?] | LPC 561           | Brazil: Mato Grosso (39) | 801    | JF281084 | Rocha et al. (2015) |
| *constantiae* | [UFMG?] | LPC 562           | Brazil: Mato Grosso (39) | 801    | JF281085 | Rocha et al. (2015) |
| *constantiae* | MVZ 197407 | LPC 497           | Brazil: Mato Grosso (39) | 1149   | MN978613 | This study |
| *constantiae* | MVZ 197410 | LPC 500           | Brazil: Mato Grosso (39) | 801    | JF281086 | Rocha et al. (2015) |
| *constantiae* | USNM 544465*      | A 1353            | Brazil: Pará (48) | 475    | MN978614 | This study |
| *constantiae* | USNM 544467*      | A 1383            | Brazil: Pará (48) | 475    | MN978615 | This study |
| *constantiae* | USNM 588015*      | LHE 1447          | Peru: Cusco (96) | 1149   | MN978616 | This study |
| *constantiae* | FMNH 174443*      | BDP 4076          | Peru: Cusco (97) | 1149   | MN978617 | This study |
| *constantiae* | USNM 588018*      | MRR 781           | Peru: Cusco (98) | 1149   | MN978618 | This study |
| *constantiae* | MUSM 15312       | DWF 568           | Peru: Loreto (105) | 802    | EF587309 | Dias et al. (2010) |
| *constantiae* | AMNH 272667*      | RSV 2029          | Peru: Loreto (105) | 1146   | HM106374 | Gutierrez et al. (2010) |
| *constantiae* | MUSM 13294*      | RSV 2085          | Peru: Loreto (105) | 1146   | HM106375 | Gutierrez et al. (2010) |
| *constantiae* | KU 144096*       | CAS 715           | Peru: Madre de Dios (108) | 1149 | MN978619 | This study |
| *constantiae* | FMNH 203510*     | BDP 4695          | Peru: San Martín (109) | 1149   | MN978620 | This study |
| *demerarae* | MN 69110        | CRB 2101          | Brazil: Amazonas (19) | 803    | EF587290 | Dias et al. (2010) |
| *demerarae* | MN 69126        | CRB 2178          | Brazil: Amazonas (24) | 803    | EF587291 | Dias et al. (2010) |
| Haplogroup | Voucher | Field | Locality | bp | GenBank | Source |
|-----------|---------|-------|----------|----|---------|--------|
| demerarae | ISEM V-1308 | T-2721 | French Guiana (77) | 800 | AJ606437 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-1320 | T-2733 | French Guiana (77) | 800 | AJ606447 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-966 | T-1998 | French Guiana (78) | 800 | AJ606446 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-973 | T-2005 | French Guiana (78) | 800 | AJ606444 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-972 | T-2006 | French Guiana (78) | 820 | AJ487005 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-884* | T-2083 | French Guiana (78) | 1149 | MN978621 | This study |
| demerarae | ISEM V-1040 | T-2287 | French Guiana (78) | 796 | AJ606440 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-1590 | T-3615 | French Guiana (79) | 799 | AJ606436 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-1183 | T-2468 | French Guiana (80) | 659 | AJ606439 | Steiner & Catzeflis (2004) |
| demerarae | ISEM V-1143 | T-2526 | French Guiana (81) | 787 | AJ606438 | Steiner & Catzeflis (2004) |
| demerarae | ROM 104708* | F 38299 | Guyana: Potaro-Siparuni (82) | 799 | AJ606434 | Steiner & Catzeflis (2004) |
| demerarae | KU 154874* | F 39096 | Guyana: Potaro-Siparuni (83) | 1149 | MN978622 | This study |
| demerarae | ROM 113431* | F 50411 | Guyana: U.Demerara-Berbice (84) | 1149 | MN978623 | This study |
| demerarae | ROM 106634* | F 38631 | Guyana: U.Takutu-U.Essequibo (85) | 1149 | MN978624 | This study |
| demerarae | ROM 98124 | FN 31126 | Guyana: U.Takutu-U.Essequibo (86) | 800 | AJ606441 | Steiner & Catzeflis (2004) |
| demerarae | USNM 560533 | ALG 14086 | Venezuela: Amazonas (110) | 801 | JF281070 | Rocha et al. (2015) |
| demerarae | USNM 560731* | ALG 14485 | Venezuela: Amazonas (111) | 1149 | U34674 | Patton et al. (1996) |
| demerarae | USNM 560741* | ALG 14656 | Venezuela: Amazonas (112) | 1149 | MN978625 | This study |
| demerarae | MVZ 160041* | JLP 9046 | Venezuela: Bolivar (114) | 726 | MN978626 | This study |
| germana A | ROM 105521* | F 37754 | Ecuador: Orellana (76) | 1149 | MN978627 | This study |
| germana A | TTU 98988* | TK 73900 | Peru: Loreto (103) | 1149 | MN978628 | This study |
| germana A | TTU 101236* | TK 75120 | Peru: Loreto (103) | 1149 | MN978629 | This study |
| germana A | KU 157972* | RMT 4053 | Peru: Loreto (106) | 1149 | MN978630 | This study |
| germana A | KU 157973* | NW 855 | Peru: Loreto (107) | 1149 | MN978631 | This study |
| germana B | LSUMZ 28018* | JMC 243 | Peru: Loreto (104) | 1149 | MN978632 | This study |
| limae A | [UFMG?] | LPC 446 | Brazil: Mato Grosso (37) | 801 | GU112918 | Agrizzi et al. (2012) |
| limae A | MVZ 197415 | LPC 748 | Brazil: Mato Grosso (38) | 1149 | MN978633 | This study |
| limae A | [MN?] | CRB 2791 | Brazil: Mato Grosso (40) | 803 | EF587295 | Dias et al. (2010) |
| limae A | USNM 549286* | MDC 598 | Brazil: Pará (47) | 1149 | MN978634 | This study |
### TABLE 2 continued

| Haplotype | Voucher | Field # | Locality | bp | GenBank | Source |
|-----------|---------|---------|----------|----|---------|--------|
| limae A   | USNM 549287* | MDC 602 | Brazil: Pará (47) | 1149 | MN978635 | This study |
| limae A   | BAC 313 | Brazil: Pará (49) | 801 | JF281079 | Rocha et al. (2015) |
| limae A   | BAC 352 | Brazil: Pará (49) | 801 | JF281073 | Rocha et al. (2015) |
| limae A   | [uncataloged]* | TL 17107 | Brazil: Pará (51) | 726 | MN978636 | This study |
| limae A   | RNL 88 | Brazil: Pará (52) | 801 | JF281090 | Rocha et al. (2015) |
| limae A   | RNL 89 | Brazil: Pará (52) | 801 | JF281076 | Rocha et al. (2015) |
| limae A   | RGR 357 | Brazil: Pará (53) | 801 | JF281075 | Rocha et al. (2015) |
| limae A   | RGR 32 | Brazil: Tocantins (57) | 801 | JF281078 | Rocha et al. (2015) |
| limae A   | RGR 34 | Brazil: Tocantins (57) | 801 | JF281077 | Rocha et al. (2015) |
| limae A   | RGR 360 | Brazil: Tocantins (57) | 801 | JF281072 | Rocha et al. (2015) |
| limae A   | RGR 360 | Brazil: Tocantins (57) | 801 | JF281072 | Rocha et al. (2015) |
| limae A   | RGR 360 | Brazil: Tocantins (57) | 801 | JF281072 | Rocha et al. (2015) |
| limae B 20.7.14.41* | BMNH | | Brazil: Ceará (34) | 498 | MN978637 | This study |
| limae B [MN?] | CRB 2304 | Brazil: Goiás (35) | 803 | EF587292 | Dias et al. (2010) |
| limae B MN 67083 | CRB 2320 | Brazil: Goiás (35) | 803 | EF587293 | Dias et al. (2010) |
| limae B [MN?] | CRB 2324 | Brazil: Goiás (35) | 803 | EF587294 | Dias et al. (2010) |
| limae B | RNL 100 | Brazil: Pará (50) | 801 | JF281088 | Rocha et al. (2015) |
| limae B | RNL 103 | Brazil: Pará (50) | 801 | JF281089 | Rocha et al. (2015) |
| limae C [UFES?] | LPC 898 | Brazil: Alagoas (17) | 801 | JF281091 | Rocha et al. (2015) |
| limae D [UFMG?] | LPC 106 | Brazil: Bahia (27) | 801 | JF281082 | Rocha et al. (2015) |
| limae D MVZ 197416* | LPC 198 | Brazil: Bahia (28) | 1149 | MN978636 | This study |
| limae D MVZ 197417* | LPC 199 | Brazil: Bahia (28) | 1149 | MN978639 | This study |
| limae D MVZ 197419* | LPC 209 | Brazil: Bahia (28) | 801 | GU112915 | Agriizzi et al. (2012) |
| limae D [UFMG?] | LPC 222 | Brazil: Bahia (28) | 801 | JF281080 | Rocha et al. (2015) |
| limae D [UFMG?] | LPC 229 | Brazil: Bahia (28) | 801 | JF281081 | Rocha et al. (2015) |
| limae D [UFMG?] | RM 108 | Brazil: Bahia (29) | 803 | EF587299 | Dias et al. (2010) |
| limae D [UFMG?] | RM 109 | Brazil: Bahia (29) | 803 | EF587297 | Dias et al. (2010) |
| limae D [UFMG?] | RM 198 | Brazil: Bahia (30) | 803 | EF587300 | Dias et al. (2010) |
| limae D SLF 13 | Brazil: Bahia (31) | 801 | JF281083 | Rocha et al. (2015) |
| limae D [UFMG?] | RM 219 | Brazil: Bahia (32) | 803 | EF587296 | Dias et al. (2010) |
| limae D [UFMG?] | RM 116 | Brazil: Bahia (33) | 803 | EF587298 | Dias et al. (2010) |
| meridae USNM 280895* | PH 1132 | Colombia: Cesar (65) | 1149 | MN978640 | This study |
| meridae USNM 280896* | PH 1180 | Colombia: Cesar (65) | 475 | MN978641 | This study |
| meridae AMNH 276581* | RPA 312 | Venezuela: Falcón (115) | 1149 | MN978642 | This study |
| paraguayana A YL 81 | Brazil: Minas Gerais (42) | 801 | JF281068 | Rocha et al. (2015) |
| paraguayana A MVZ 197594 | YL 92 | Brazil: Minas Gerais (42) | 801 | JF281069 | Rocha et al. (2015) |
| Haplogroup | Voucher | Field # | Locality | bp | GenBank | Source |
|-----------|---------|---------|----------|----|---------|--------|
| paraguayana A | [PUCMG?] | JEQ 01 | Brazil: Minas Gerais (43) | 803 | EF587303 | Dias et al. (2010) |
| paraguayana A | [PUCMG?] | CB 01 | Brazil: Minas Gerais (44) | 803 | EF587307 | Dias et al. (2010) |
| paraguayana A | YL 75 | Brazil: Minas Gerais (45) | 801 | GU112920 | Agrizzi et al. (2012) |
| paraguayana A | MVZ 197593 | YL 76 | Brazil: Minas Gerais (45) | 1149 | MN978643 | This study |
| paraguayana A | [UFMG?] | 266 | Brazil: Minas Gerais (46) | 801 | EF587288 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 1091 | Brazil: Minas Gerais (46) | 803 | EF587301 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 1427 | Brazil: Minas Gerais (46) | 803 | EF587302 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 890 | Brazil: Minas Gerais (46) | 803 | EF587308 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 1317 | Brazil: Minas Gerais (46) | 803 | EF587304 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 1421 | Brazil: Minas Gerais (46) | 803 | EF587306 | Dias et al. (2010) |
| paraguayana A | [UFMG?] | A 315 | Brazil: Minas Gerais (46) | 803 | EF587305 | Dias et al. (2010) |
| paraguayana A | LPC 792 | Brazil: São Paulo (56) | 801 | GU112922 | Agrizzi et al. (2012) |
| paraguayana A | TK 129697 | Paraguay: Canindeyú (91) | 801 | JN887140 | de la Sancha et al (2012) |
| paraguayana A | TK 129479 | Paraguay: Itapúa (92) | 801 | JN887139 | de la Sancha et al (2012) |
| paraguayana B | MN 46888 | CRB 1287 | Brazil: Rio de Janeiro (54) | 803 | EF587289 | Dias et al. (2010) |
| paraguayana B | MVZ 182064* | MAM 46 | Brazil: São Paulo (55) | 1146 | HM106372 | Gutierrez et al. (2010) |
| paraguayana B | MVZ 182065* | MAM 47 | Brazil: São Paulo (55) | 1146 | HM106373 | Gutierrez et al. (2010) |
| paraguayana B | MZUSP 29195 | Brazil: São Paulo (55) | 630 | JN887141 | de la Sancha et al (2012) |
| parda | FMNH 24139* | EH 6493 | Peru: Huánuco (100) | 475 | MN978644 | This study |
| perplexa | USNM 513425* | ALG 13224 | Ecuador: Loja (74) | 475 | MN978645 | This study |
| perplexa | UMMZ 176563* | LLW 1066 | Peru: Cajamarca (95) | 1149 | MN978646 | This study |
| phacea | INPA 2514 | VCSV 61 | Brazil: Amazonas (21) | 630 | MN992049 | Patton lab |
| phacea | INPA 2515 | VCSV 65 | Brazil: Amazonas (21) | 630 | MN992050 | Patton lab |
| phacea | CTUA 495 | JFD 109 | Colombia: Antioquia (60) | 1149 | MN978647 | This study |
| phacea | CTUA 497 | JFD 111 | Colombia: Antioquia (60) | 1149 | MN978648 | This study |
| Haplogroup | Vouchera | Field #c | Localityd | bp£ | GenBank | Source                  |
|------------|----------|----------|-----------|-----|---------|-------------------------|
| phaea      | FMNH 69863* | PH 3764  | Colombia: Antioquia (61) | 475 | MN978649 This study |
| phaea      | FMNH 69866* | PH 4747  | Colombia: Antioquia (62) | 726 | MN978650 This study |
| phaea      | FMNH 88543* | KS 23068 | Colombia: Cauca (64)     | 1149| MN978651 This study |
| phaea      | FMNH 70915* | PH 5281  | Colombia: Huila (67)     | 978 | MN978652 This study |
| phaea      | FMNH 70911* | PH 5320  | Colombia: Huila (67)     | 475 | MN978653 This study |
| phaea      | FMNH 70922* | PH 5389  | Colombia: Huila (68)     | 978 | MN978654 This study |
| phaea      | FMNH 70923* | PH 5381  | Colombia: Huila (69)     | 978 | MN978655 This study |
| phaea      | AMNH 277739* | EEG 136  | Venezuela: Aragua (113)  | 1149| MN978656 This study |
| phaea      | AMNH 277729* | RPA 341  | Venezuela: Aragua (113)  | 1149| MN978657 This study |
| rapposa A  | BMNH 98.11.6.13* |          | Peru: Cuzco (99)        | 498 | MN978658 This study |
| rapposa B  | [USNM]* | LHE 1307  | Bolivia: Chuquisaca (2)  | 1149| MN978659 This study |
| rapposa B  | [USNM]* | LHE 1299  | Bolivia: Chuquisaca (3)  | 1149| MN978660 This study |
| rapposa B  | MSB 63277* | NK 21697 | Bolivia: Chuquisaca (4)  | 1149| MN978661 This study |
| rapposa B  | AMNH 264924* | NK 30312 | Bolivia: Cochabamba (5)  | 1149| MN978662 This study |
| rapposa B  | CBF 7556* | EY 1917   | Bolivia: Cochabamba (6)  | 1149| MN978663 This study |
| rapposa B  | CBF 7551* | FGS 03-15 | Bolivia: Cochabamba (6)  | 1149| MN978664 This study |
| rapposa B  | TTT 34785* | WDW 967   | Bolivia: La Paz (7)      | 498 | MN978665 This study |
| rapposa B  | AMNH 275463* | NK 25648 | Bolivia: La Paz (8)      | 1149| MN978666 This study |
| rapposa B  | AMNH 275464* | NK 25729 | Bolivia: La Paz (8)      | 1149| MN978667 This study |
| rapposa B  | MSB 67019* | NK 22792  | Bolivia: Santa Cruz (10) | 1149| MN978668 This study |
| rapposa B  | MSB 59883* | NK 15501  | Bolivia: Santa Cruz (11) | 1146| HM106368 Gutierrez et al. (2010) |
| rapposa B  | AMNH 275466* | NK 23272 | Bolivia: Santa Cruz (12) | 1146| HM106369 Gutierrez et al. (2010) |
| rapposa B  | MSB 87093* | NK 23983  | Bolivia: Tarija (15)     | 1149| MN978669 This study |
| rapposa B  | USNM 390023* | MLK 12192 | Brazil: Mato Grosso do Sul (41) | 475 | MN978670 This study |
| rapposa B  | MSB 67000* | NK 22521  | Paraguay: Amambay (90)   | 1149| MN978671 This study |
| rapposa B  | UMMZ 174909* | GD 377   | Paraguay: San Pedro (93) | 1149| MN978672 This study |
| rapposa B  | UMMZ 174992* | GD 387   | Paraguay: San Pedro (93) | 384 | MN978673 This study |
| rapposa C  | USNM 582111* | LHE 1388 | Peru: Junín (101)            | 1149| MN978674 This study |
| rapposa C  | USNM 582112* | LHE 1396 | Peru: Junín (101)               | 1149| MN978675 This study |
| rutteri    | MVZ 190332* | MNFS 1232 | Brazil: Acre (16)                   | 1149| MN992051 This study |
| rutteri    | MVZ 190323* | JLP 15435 | Brazil: Amazonas (22)              | 1146| HM106370 Gutierrez et al. (2010) |
| rutteri    | MVZ 190324* | JLP 15436 | Brazil: Amazonas (22)              | 630 | JN887142 (2012) |
| rutteri    | FMNH 70966* | PH 5913   | Colombia: Caquetá (63)        | 475 | MN978676 This study |
| rutteri    | MVZ 154766* | JLP 7745  | Peru: Amazonas (94)           | 1149| U34675 Patton et al. (1996) |
| rutteri    | AMNH 273164* | DWF 659  | Peru: Loreto (105)             | 1149| MN978677 This study |
| rutteri    | KU 144095* | NW 505    | Peru: Madre de Dios (108)      | 1149| MN978678 This study |
TABLE 2 continued

| Haplogroupa | Voucherb | Field #c | Localityd | bp° | GenBank | Source |
|------------|---------|----------|-----------|-----|---------|--------|
| “Yasuni”   | ROM 118880* | F 41891 | Ecuador: Orellana (75) | 1149 | MN978679 | This study |
| “Yasuni”   | KU 157974* | RMT 4088 | Peru: Loreto (102) | 1149 | MN978680 | This study |
| “Yasuni”   | TTU 99000* | TK 73966 | Peru: Loreto (103) | 1149 | MN978681 | This study |

a Putative species as delimited by mPTP (see text).
b Asterisks indicate specimens examined by the authors. Square brackets enclose the assumed or conjectured repositories of uncataloged material or specimens for which we were unable to determine catalog numbers.
c Used to label terminals in figures 1–3. Some sequences obtained from morphological specimens lack entries in this column.
d Country and next-largest administrative unit (state, department, province, etc). Numbers in parentheses refer to gazetteer entries (appendix 1), which provide additional geographic information.
e Number of sequenced base pairs of cytochrome b.

Lian polymerase chain reaction (PCR) products were not present. We PCR-amplified the mitochondrial gene cytochrome b (CYTB), intron 14 of the X-linked gene encoding O-linked N-acetylgalactosamine transferase (OGT), and four autosomal loci (breast cancer activating gene 1 exon 11 [BRCA1], interphotoreceptor retinoid-binding protein exon 1 [IRBP], solute carrier family 38 intron 7 [SLC38], and an anonymous noncoding locus [Anon128]) using the primers and methods described in Voss and Jansa (2009), Giarla et al. (2010, 2014), Gutiérrez et al. (2010), and Pavan et al. (2014). Primers used to amplify cytochrome b from degraded DNA extracted from dried tissue are listed in appendix 2. The resulting PCR products were Sanger-sequenced on an ABI 3730xl automated sequencer.

Molecular data analysis: The cytochrome b sequences we analyzed are listed in table 2 and the nuclear gene sequences are listed in table 3. All sequences were edited and assembled in Geneious Pro version 7.0 (http://www.geneious.com, Kearse et al., 2012); length heterozygotes in the nuclear loci were resolved using Intelligent version 1.2 (Dmitriev and Rakitov, 2008). Individual genes were aligned using the default parameters of MUSCLE (Edgar, 2004), and alignments of all protein-coding loci were examined with reference to translated amino-acid sequences.

We estimated a maximum-likelihood (ML) cytochrome b phylogeny in IQ-TREE 1.6.11 (Nguyen et al., 2014) using IQ-TREE’s built-in substitution model testing (Kalyaanamoorthy et al., 2017) and partitioning capabilities (Chernomor et al., 2016) to simultaneously estimate the tree and the best-fitting model for each codon position. We evaluated nodal support using 1000 ultrafast bootstrap replicates (the UFBoot2 algorithm; Hoang et al., 2017). All other settings were left at their default values.

We obtained putative species delimitations from the CYTB tree using the multirate Poisson Tree Processes method (mPTP; Kapli et al., 2017). This approach accounts for differences in coalescent rates among lineages and has a Markov Chain Monte Carlo (MCMC) sampling method for assigning an average support value to each ML delimitation. Within mPTP, we estimated the minimum branch-length threshold and ignored branch lengths below it. This eliminates a bias that could arise due to the addition of arbitrarily small branches among identical sequences during phylogenetic inference. We conducted a ML delimitation analysis in mPTP, allowing a unique coalescent rate for each delimited species. We estimated support for the ML delimitation using 10 MCMC runs, each $1 \times 10^7$ generations long. Convergence between the different MCMC runs was assessed using the average standard deviation of delimitation support values across all runs.

We compiled a six-locus dataset (CYTB, BRCA1, IRBP, OGT, SLC38, and Anon128) in which a single exemplar specimen was chosen to
FIG. 1. Collection localities for sequenced specimens of *Marmosa (Micoureus)* corresponding to the putative species (haplogroups) alstoni, perplexa, germana A, germana B, and “Yasuni.” Numbers are keyed to localities listed in appendix 1. Symbols for sympatry include records from localities separated by <10 km without intervening riverine or other known barriers to dispersal.
represent each mPTP-delimited putative species. A maximum-likelihood tree was estimated from these concatenated data using IQ-TREE and the procedures described above for the CYTB analysis. This dataset was divided into 12 subsets: one for each codon position in the protein-coding genes (CYTB, BRCA1, IRBP) and one each for the noncoding loci (OGT, SLC38, Anon128). Nodal support was calculated using 1000 ultrafast bootstrap replicates.

We inferred a Bayesian tree with MrBayes 3.2.6 (Ronquist et al., 2012). Prior to Bayesian inference, we tested nucleotide substitution models and partitioning schemes on the subset of models available in MrBayes using PartitionFinder2 (Lanfear et al., 2016). We allowed for the same data subsets as described for the multilocus IQ-TREE analysis. In MrBayes, we applied the best-fitting substitution models and partitioning scheme. We ran the analysis for $10^7$ generations, initiating two independent MCMC runs, each with four chains. MCMC convergence was assessed in Tracer 1.7.1 (Rambaut et al., 2018). The posterior sample of trees was summarized in MrBayes after discarding 25% of the sample as burn-in.

FIG. 2. Collection localities for sequenced specimens of *Marmosa* (*Micoureus*) corresponding to the putative species *constantiae, demerarae, limae* A–D, *meridae, paraguayana* A, *paraguayana* B, and *phaea*. Numbers are keyed to localities listed in appendix 1.
Measurements: Except as noted otherwise, external measurements are those taken in the field by collectors using the standard American protocol (Hall, 1962). We transcribed total length (nose to fleshy tail tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen labels or field notes, but we sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by collectors, and we used our values whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm (the smallest decimal fraction of a millimeter that is consistently obtainable with repeated caliper measurements). The following dimensions were measured (fig. 4):

- Condylobasal length (CBL): Measured from the occipital condyles to the anteriormost point of the premaxillae
- Nasal breadth (NB): Measured across the triple-point sutures of the nasal, frontal, and maxillary bones on each side
- Least interorbital breadth (LIB): Measured at the narrowest point across the frontals between the orbits
Least postorbital breadth (LPB): Measured at the narrowest point across the frontals between the temporal fossae (behind the postorbital processes)

Zygomatic breadth (ZB): Measured at the widest point across both zygomatic arches

Palatal length (PL): Measured from the anterior-most point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present)

Palatal breadth (PB): Measured across the labial margins of the fourth molar (M4) crowns, at or near the stilar A position

Maxillary toothrow length (MTR): Measured from the anterior margin of the canine (C1) to the posterior margin of the fourth molar (M4)

Length of molars (LM): Measured from the anterior-most labial margin of M1 to the posterior-most point on M4

Length of M1–M3 (M1–M3): Measured from the anterior-most labial margin of M1 to the posterior-most point on M3

Width of M3 (WM3): Measured from the labial margin of the crown at or near the stilar A position to the lingual apex of the protocone

| TABLE 3 |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| **Ingroup and Outgroup Sequences Used for Multigene Phylogenetic Analyses** |
|               | CYTB\(^a\) | Anon128 | BRCA1 | IRBP | OGT | SLC38 |
| **INGROUP:**  |            |         |       |     |     |       |
| alstoni       | MN978600   | MN978682| MN978694| MN978706| MN978713| MN978725 |
| constantiae   | HM106375   | FJ159304| AF257693| KM071234| KM071140 |
| demerarae     | MN978623   | MN978683| MN978695| MN978707| MN978714 |
| germana A     | MN978627   | MN978684| MN978696| MN978708| MN978715 |
| germana B     | MN978632   | MN978685| MN978697| MN978716 |
| limae A       | MN978634   | MN978686| MN978698| MN978717 |
| limae B       | EF587292   |         |       |     |     |       |
| limae C       | JF281091   |         |       |     |     |       |
| limae D       | MN978639   | MN978687| MN978699| MN978718 |
| meridae       | MN978642   | MN978688| MN978700| MN978719 |
| paraguayaana A| MN978643   |         |       |     |     |       |
| paraguayaana B| HM106373   | KU171148| FJ159305| KJ129917| KJ129974 |
| parda         | MN978644   |         |       |     |     |       |
| perplexa      | MN978646   | MN978689| MN978701| MN978709| MN978720| MN978726 |
| phaea         | MN978648   | MN978690| MN978702| MN978721 |
| rapposa A     | MN978658   |         |       |     |     |       |
| rapposa B     | MN978669   | MN978691| MN978703| MN978710| MN978722| MN978727 |
| rapposa C     | MN978675   | MN978692| MN978704| MN978711| MN978723| MN978728 |
| rutteri       | MN992051   | KU171149| FJ159306| AT233780| KM819064| MN978729 |
| "Yasuni"      | MN978679   | MN978693| MN978705| MN978712| MN978724 |
| **OUTGROUP:** |            |         |       |     |     |       |
| Thylamys pusillus | HM583416 | KJ129877| FJ159319| AT957489| KJ129934| KJ129959 |

\(^a\) Column entries are GenBank accession numbers.
AGE DETERMINATION: Except as noted below, all analyzed morphological character data were obtained from adult specimens as determined by dental criteria. The third upper and lower premolars (P3/p3) are the last teeth to erupt in *Marmosa*, and we used the maxillary locus to define age classes: a specimen was judged to be *juvenile* if the deciduous third premolar (dP3) was still in place; *subadult* if dP3 had been shed, but P3 was still incompletely erupted; and *adult* if the permanent upper dentition was complete. In effect, specimens that we judged to be adult by these criteria correspond to age classes 6–9 of Rossi et al. (2010). Although we acknowledge that our adult material

FIG. 4. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Marmosa murina* (not a member of the subgenus *Micoureus*), showing the anatomical limits of craniodental measurements defined in the text.
FIG. 5. Phylogenetic tree based on maximum-likelihood analysis of 167 cytochrome \( b \) sequences. Numbers at nodes denote ML bootstrap support. For haplogroups with more than one sequence, tips of the phylogeny have been collapsed into black triangles, the breadth of which is proportional to the number of sequences within each clade and the depth of which is proportional to genetic diversity. The outgroup is not shown.
exhibits substantial ontogenetic variation in many cranial dimensions (as evidenced by the tendency for specimens with more heavily worn teeth to have larger measurement values for most dimensions than specimens with unworn teeth), we were unable to consistently distinguish toothwear-defined age classes in our material.

MOLECULAR ANALYSES

Results

The mPTP analysis identified 21 putative species (95% credible interval = 17–25 species), of which 20 could be resolved as reciprocally monophyletic haplogroups (fig. 5). Across the 10 independent MCMC runs, the average support value for the ML delimitation of 21 species was 87.9%, and the standard deviation of support values was 0.00034. At the base of the tree is a robustly supported dichotomy that separates taxa belonging to two main clades, of which the larger (Clade A) includes 15 haplogroups and the smaller (Clade B) only five. Fourteen haplogroups in Clade A can be provisionally associated with named taxa, but one highly divergent haplogroup (“Yasuni”) is unnamed. The putative species in Clade B can be confidently associated with named taxa based on revisionary research summarized in a subsequent section of this report.

Uncorrected average pairwise cytchrome b sequence comparisons among the putative species identified by mPTP range from 2% to 15%, but most values cluster in the range from 9% to 12% (table 4). Notably low values (2–4%) are mostly associated with comparisons among members of the monophyletic complex that includes demerarae, limae A, limae B, limae C, and limae D, but similarly low values were obtained for comparisons between germana A and germana B, between paraguayana A and paraguayana B, and between rapposa A and rapposa B. Average intraspecific distances (the bolded diagonal elements in table 4) are mostly small, but those for alstoni and perplexa are notably larger than the others.

All the putative species in figure 5, together with Clade B and several other internal nodes are robustly supported in this analysis of cytchrome b sequence data. Phylogenetic analyses based on the concatenated-gene dataset (fig. 6) provide strong support for most of the internal nodes that they have in common, including Clade A and Clade B. Additionally, there is robust support in the concatenated-gene data for the nested relationships (meridae (phaea (constantiae (demerarae + limae))), for paraguayana A + paraguayana B, for perplexa + “Yasuni,” for germana A + germana B, and for (rapposa C (rapposa A + rapposa B)). By contrast, one or both concatenated-gene analyses provide only weak support for the shared clades (alstoni (germana A + germana B)) and parda + rutteri. Topological differences between the maximum-likelihood and Bayesian results for these data concern relationships that are not strongly supported in either analysis.

Discussion

Single-locus species delimitation methods are useful for identifying operational taxonomic units that can subsequently be analyzed using other data. However, as repeatedly emphasized in the literature (e.g., Carstens et al., 2013; Sukumar and Knowles, 2017), these methods provide an inadequate basis for taxonomic inference on their own merits, so the putative species recovered by mPTP in this study should not be interpreted as valid taxa without additional supporting evidence. Nevertheless, the number of putative species recovered by mPTP and the substantial pairwise distances among some of them suggest that the subgenus Micoureus is more diverse than currently recognized. Later in this report we formally revise the species in Clade B based on morphological comparisons, but revisions of the species in Clade A are still in progress, and only preliminary remarks about geographic distributions and the application of names can be offered here.
### TABLE 4
Mean Uncorrected Pairwise Sequence Divergence at the Cytochrome b Locus within and among Putative Species of *Marmosa* (*Micoureus*)

|       | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|-------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|
| 1. *alstoni* | 0.05 |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |
| 2. *constantiae* | 0.10 | 0.03 |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |
| 3. *demerarae* | 0.09 | 0.05 | 0.02 |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |
| 4. *germana A* | 0.09 | 0.10 | 0.10 | 0.01 |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| 5. *germana B* | 0.09 | 0.09 | 0.09 | 0.04 | — |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| 6. *limae A* | 0.10 | 0.06 | 0.04 | 0.10 | 0.10 | 0.01 |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| 7. *limae B* | 0.10 | 0.05 | 0.04 | 0.10 | 0.10 | 0.04 | 0.01 |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| 8. *limae C* | 0.09 | 0.05 | 0.04 | 0.10 | 0.09 | 0.03 | 0.03 | — |   |    |    |    |    |    |    |    |    |    |    |    |    |
| 9. *limae D* | 0.09 | 0.05 | 0.04 | 0.10 | 0.09 | 0.03 | 0.04 | 0.02 | 0.00 |   |    |    |    |    |    |    |    |    |    |    |    |
| 10. *meridae* | 0.10 | 0.08 | 0.08 | 0.11 | 0.11 | 0.09 | 0.09 | 0.08 | 0.08 | 0.01 |   |    |    |    |    |    |    |    |    |    |    |
| 11. *paragua. A* | 0.10 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.01 |
| 12. *paragua. B* | 0.11 | 0.09 | 0.10 | 0.09 | 0.10 | 0.09 | 0.09 | 0.08 | 0.09 | 0.09 | 0.09 | 0.04 | 0.01 |   |    |    |    |    |    |    |
| 13. *parda* | 0.11 | 0.13 | 0.13 | 0.12 | 0.12 | 0.13 | 0.13 | 0.13 | 0.14 | 0.13 | 0.11 | 0.12 | — |   |    |    |    |    |    |    |
| 14. *perplexa* | 0.11 | 0.11 | 0.11 | 0.10 | 0.10 | 0.11 | 0.12 | 0.11 | 0.10 | 0.12 | 0.11 | 0.12 | 0.13 | 0.05 |   |    |    |    |    |    |
| 15. *phaea* | 0.10 | 0.06 | 0.05 | 0.10 | 0.10 | 0.05 | 0.05 | 0.05 | 0.05 | 0.08 | 0.09 | 0.10 | 0.14 | 0.11 | 0.03 |   |    |    |    |    |
| 16. *rapposa A* | 0.12 | 0.12 | 0.12 | 0.11 | 0.12 | 0.11 | 0.12 | 0.12 | 0.12 | 0.13 | 0.10 | 0.10 | 0.06 | 0.13 | 0.12 | — |   |    |    |    |
| 17. *rapposa B* | 0.13 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.11 | 0.12 | 0.06 | 0.15 | 0.14 | 0.03 | 0.01 |   |    |    |    |
| 18. *rapposa C* | 0.13 | 0.15 | 0.15 | 0.13 | 0.14 | 0.15 | 0.15 | 0.15 | 0.15 | 0.12 | 0.12 | 0.06 | 0.15 | 0.15 | 0.07 | 0.08 | 0.00 |   |    |    |
| 19. *rutteri* | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.12 | 0.12 | 0.05 | 0.14 | 0.13 | 0.07 | 0.08 | 0.09 | 0.02 |   |    |    |
| 20. “Y asuni” | 0.10 | 0.10 | 0.10 | 0.10 | 0.10 | 0.10 | 0.10 | 0.09 | 0.10 | 0.09 | 0.10 | 0.13 | 0.08 | 0.10 | 0.12 | 0.13 | 0.14 | 0.13 | 0.01 |
FIG. 6. Maximum-likelihood (left) and Bayesian (right) phylogenetic trees inferred from concatenated sequences of six genes (CYTB, BRCA1, IRBP, OGT, SLC38, and Anon128). Numbers at nodes denote ML bootstrap support or Bayesian posterior probabilities. Outgroups are not shown. Dotted lines connect the same taxon across the two trees to highlight differences.
Working our way downward from the top of the cartooned cytochrome \( b \) tree (fig. 5), the oldest name for \textit{demerarae}-like specimens from southeastern Amazonia is \textit{limae}, the application of which is supported by a 498 bp fragment of cytochrome \( b \) that we obtained from the holotype. The latter was recovered as a member of \textit{limae} B, which occurs east of the Tocantins in the Brazilian states of Ceará, Goiás, and southeastern Pará (fig. 2). Based solely on geography, it seems probable that \textit{pfrimeri} (with type locality in Goiás; table 1) is a synonym of \textit{limae}, but we have not seen the lectotype. No names are apparently available for the putative species we call \textit{limae} A (which occurs west of the Tocantins and east of the Xingu in the states of Mato Grosso, Pará, and Tocantins), \textit{limae} C (from Alagoas), and \textit{limae} D (from Bahia). However, pairwise distances among these four haplogroups are all small-to-modest (2%–4%), and we are not convinced that they are usefully recognized as distinct taxa. We have not made a close morphological study of this complex, which might not, in fact, be phenotypically distinguishable from \textit{demerarae}.

The haplogroup we call \textit{demerarae} includes all the sequences obtained from specimens collected north of the lower Amazon and east of the Rio Negro–Orinoco (the Guiana Region of zoogeographers; Tate, 1939). The type locality of \textit{demerarae} is in Guyana, from which we have several representative sequences, and this haplogroup also includes sequences from specimens collected reasonably near the type localities of \textit{arenticola}, and \textit{esmeraldae}, which we provisionally regard as synonyms following Gardner and Creighton (2008). However, not all the specimens with sequences assigned to this putative species share the phenotypic traits traditionally associated with \textit{demerarae}, an issue that will eventually need to be addressed in a revisionary context.

The application of the name \textit{constantiae} in our results is supported by a topotypical sequence (from OMNH 37209; table 2), as well as by the morphological similarity of sequenced specimens from Mato Grosso and easternmost Bolivia with Thomas’s (1904a) description and type material. Our distributional concept of \textit{constantiae} is similar to Silva et al.’s (2019), including sequences from specimens collected south of the Amazon from the lower slopes of the Andes to the right bank of the Tapajós. However, there is geographic variation in external morphology (Voss et al., 2019), as well as phylogeographic structure within \textit{constantiae}, both of which merit future revisionary attention. Based on our examination of type material, the nominal taxa \textit{mapi-riensis} (from the Andean foothills of Bolivia) and \textit{domina} (from the left bank of the Tapajós) are probably synonyms of \textit{constantiae}.

The sequences we assign to \textit{phaea} (next in vertical sequence after \textit{constatntiae} in fig. 5) are from a widely scattered array of localities that extend from the Colombian Andes to the coastal mountains of northern Venezuela and the Amazonian lowlands of northwestern Brazil. Although we have not made a close study of all the voucher material for sequences assigned to this clade, the specimens we sequenced from the Colombian departments of Cauca and Huila resemble the type series of \textit{phaea} (from Nariño), whereas other specimens (e.g., those from lowland Antioquia) exhibit obvious morphological differences. There is, additionally, strongly developed phylogeographic structure in this problematic haplogroup, which clearly warrants future study.

The highly divergent haplogroup that we tentatively identify as \textit{meridae} includes sequences from specimens collected at two localities, one in northern Colombia and the other in northwestern Venezuela. This material is phenotypically similar to the holotype and topotypical material of \textit{meridae}, but the type locality is not particularly close to where the vouchers were collected (Mérida is about 270 km SE of locality 65 and about 380 km SW of locality 115; fig. 2). Topotypical sequence data should help determine whether \textit{meridae} is the name that properly applies to this clade.

Sister to the complex of mostly Amazonian and northern-Andean haplogroups described above is a clade consisting of two putative species...
from the Atlantic Forest biome (the Mata Atlântica of Brazilian authors), both of which we associate with the name *paraguayana*. Whereas *paraguayana* A includes sequences from eastern Paraguay (the type locality of *paraguayana*) the other haplogroup, *paraguayana* B, includes a sequence from the Brazilian state of Rio de Janeiro—the type locality of *travassosi*. Without having seen the type of *travassosi* we hesitate to use the name even in this informal context, preferring to maintain the prevailing usage of *paraguayana* as the currently accepted senior synonym. However, the two haplogroups are about 4% divergent, on average, and they occur at adjacent localities in the state of São Paulo (appendix 1). The few specimens we examined (*N* = 15; from Paraguay, Minas Gerais, Rio de Janeiro, and São Paulo) exhibit no conspicuous character variation inter se, but the woolly mouse opossums of the Atlantic Forest would seem to merit taxonomic attention based on these results.

Two haplogroups that we associate with the name *germana* were obtained from specimens collected north of the Amazon in eastern Ecuador and northeastern Peru (fig. 1). Although *germana* is currently treated as a subspecies of *regina*,

\[2\] As explained elsewhere (Voss et al., 2019: 31), we follow Tate (1933: 83) in restricting the name *regina* to the holotype, which is strikingly unlike other nominal taxa of the subgenus *Micoureus*.

this is an unambiguously distinct lineage, the relationships of which are, apparently, either with *perplexa* + “Yasuni” (fig. 5) or with *alstoni* (fig. 6). However, our morphological material of *germana* does not closely resemble voucher specimens of any of the putative species with which it is associated phylogenetically. Whereas Gardner and Creighton (2008) treated *parda* and *rutteri* as junior synonyms of *germana*, we recognize *parda* and *rutteri* as valid species of the Rapposa Group (see below).

The sister-group relationship of *perplexa* and “Yasuni” is strongly supported in all our phylogenetic results. Although the former name has long been treated as a synonym of *phaea*, the cytochrome *b* sequences we refer to *perplexa* (from western Ecuador and northern Peru; see above) and *phaea* (from Colombia, northwestern Brazil, and northern Venezuela) are highly divergent (about 11%), and none of our analyses recovered them as sister lineages. Specimens of “Yasuni” (an Amazonian lineage from eastern Ecuador and northeastern Peru) are morphologically distinctive and do not closely resemble *perplexa* or any other nominal taxon. Our current working hypothesis is that they represent an undescribed species.

The haplogroup that we identify as *alstoni* includes sequences from specimens collected in Central America and in the trans-Andean lowlands of western Colombia and northwestern Ecuador. This haplogroup is strongly structured phylogeographically, and the associated voucher material is morphologically heterogeneous, including some of the largest and some of the smallest specimens in the subgenus. The next installment of our revisionary series will treat this haplogroup in substantive detail, but for now we follow the currently accepted taxonomy (Gardner, 2005), which treats *nicaraguae* as a junior synonym of *alstoni*.

**COMPARATIVE MORPHOLOGY**

The mitochondrial lineages of *Marmosa (Micoureus)* recognized as valid species in this report and those that follow can be phenotypically distinguished from one another by qualitative morphological characters and measurement data. Here we describe character variation among examined skins and skulls using anatomical terminology explained or referenced by Voss and Jansa (2003, 2009), with exceptions as noted below.

**SIZE AND EXTERNAL MORPHOLOGY**

Species of the subgenus *Micoureus* are externally rather similar, but they are consistently distinguishable from other congeners by their dull-colored (usually brownish-gray, never distinctly reddish) dorsal fur, large manual claws (typically extending just beyond the fleshy digital...
pad on each finger), possession of lateral and medial carpal tubercles in large adult males, and tails with rhomboidal scales in distinctly spiral series (Voss et al., 2014). However, some sympatric species of *Micoureus* are so alike externally that it can be difficult to tell them apart, with the result that field identifications are often challenging. Careful attention to age criteria, accurate external measurements, subtle differences in pelage length and pigmentation, and tail markings, however, can be taxonomically informative.

**Size:** Members of the subgenus *Micoureus* include the largest known species of *Marmosa*, but interspecific size differences within *Micoureus* are substantial. The smallest species is an unnamed Panamanian form with an average adult head-and-body length of 139 mm (observed range 121–150 mm; *N* = 7) and an average adult weight of just 58 g (observed range 40–68 g; *N* = 5). By contrast, *Marmosa rutteri*, one of the larger species, has an average adult head-and-body length of 179 mm (observed range 152–251 mm; *N* = 32) and an average adult weight of 122 g (observed range 63–180 g; *N* = 28). However, as can be seen from the observed ranges, there is substantial intraspecific variation in these dimensions, including sexual size dimorphism as well as ontogenetic variability among the specimens classed as “adults” (see Materials and Methods). The latter typically include smaller (presumably younger) individuals with almost-unworn dentitions and larger (presumably older) individuals with heavily worn teeth. Because sexual size dimorphism and ontogenetic variability are minimal for molar dimensions—which (unlike head-and-body length or weight) can be determined with high accuracy from museum specimens—we often use upper-molar toothrow length (LM) as a surrogate for size in species comparisons. For the unnamed Panamanian species mentioned above, LM averages 7.6 mm (observed range 7.3–8.0, *N* = 8); for *M. rutteri*, LM averages 9.0 mm (observed range 8.3–9.8 mm, *N* = 56).

**Dorsal pelage:** The dorsal fur of *Micoureus* is often described as “woolly” (e.g., by Gardner and Creighton, 2008) because the individual hairs of some species are strongly kinked. This trait is most pronounced in longer-furred taxa (e.g., *M. alstoni*, *M. paraguayana*), whose pelage has a distinctively fluffy texture, but it is less pronounced in shorter-furred species (e.g., *M. rutteri*). Fur length is positively correlated with altitude in species with wide elevational distributions (e.g., *M. rapposa*), although some lowland populations of *M. demerarae* are also long furred. Dorsal fur color in *Micoureus* is almost always some dull shade of brownish gray, but *M. paraguayana* has distinctly clear-grayish dorsal fur, at least in the few fresh skins we examined.

**Ventral pelage:** The ventral fur is taxonomically variable in the subgenus *Micoureus*, as it is in many other small opossums. Following Tate (1933), we use the prefix “self-” in combination with descriptors of ventral pelage color (e.g., self-yellow) to describe fur comprised of hairs that have the same coloration from base to tip; by contrast, fur comprised of hairs that are basally gray is described as “gray based” (gray-based yellow, for example). Whereas almost the entire ventral pelage can be self-colored in some species (e.g., *M. rapposa*), others (e.g., *M. demerarae*) have extensively gray-based ventral fur (fig. 7). Commonly, however, the ventral pelage includes both types of fur, sometimes with a self-colored midventral streak that extends from chin to groin and lateral zones of gray-based fur between the fore- and hind legs.

**Gular gland:** Adult male specimens of many opossums, including some species of *Marmosa*, have a naked patch of glandular skin on the midline of the throat or upper chest. Although the absence of such a gular gland was listed as a diagnostic trait of the subgenus *Micoureus* by Voss et al. (2014), a distinct gular gland is present on the holotype of *Marmosa regina* (BMNH 98.5.15.4), an old adult male (Thomas, 1898). Whether this is an individual peculiarity or a consistent trait of the species—currently known from a single specimen—is unknown.

**Tail:** The tail is always substantially longer than the combined length of the head and body in
the subgenus *Micoureus*, with computed sample means of the ratio LT/HBL × 100 ranging from about 130% to almost 150%. Unfortunately, artifactual variation in external dimensions measured in the field by different collectors is sufficiently high that relative tail length is generally unsuitable for diagnosis or identification. Instead, other caudal features are more consistently useful.

Soft body pelage (“fur” in the ordinary sense of the word) extends onto the base of the tail to a taxonomically variable extent, and this character is sometimes useful for distinguishing sympatric species (Patton et al., 2000). In many species (e.g., *M. parda*, *M. perplexa*, *M. rapposa*, *M. rutteri*) body fur extends for only a short distance (≤ 20 mm) along the base of the tail, and the caudal fur is short, resembling the condition seen in other subgenera of *Marmosa*. By contrast, in several other species (e.g., *M. alstoni*, *M. demerarae*, *M. meridae*, *M. paraguayana*), body fur extends for 25 mm or more (to 55 mm in some specimens) along the base of the tail, and in these same taxa the caudal fur also tends to be long (with hairs >10 mm), resulting in a conspicuously fluffy tail base (fig. 8).

The pigmentation of the unfurred (scaly) part of the tail is also taxonomically variable in *Micoureus*. In most species—including *Marmosa germana*, *M. parda*, *M. perplexa*, and *M. rutteri*—the scaly part of the tail is entirely dark (grayish or brownish) from base to tip, resembling the widespread, uniform caudal coloration seen in other subgenera. In others, however, the base of the tail is dark but the distal part is

FIG. 7. Taxonomic variation in ventral pelage color as exemplified by *Marmosa rapposa* (on the left, with self-yellow ventral fur) and *M. demerarae* (right, with gray-based yellow ventral fur). From left to right: AMNH 210398, 210399, 210400, 266427, 267370, 267818).
unpigmented (whitish or pinkish in life); this, the “particolored” phenotype (Voss and Jansa, 2009: 25), is the usual condition in *M. alstoni*, *M. meridae*, *M. nicaraguae*, *M. rapposa*, *M. para-
guayana*, and in some forms of the *M. demerarae* complex (fig. 8). A few species are polymorphic for pale caudal markings, but one condition or the other seems to predominate in most taxa.

**Craniodental Morphology**

Adult skulls of members of the subgenus *Micoureus*, like those of species in other subgenera of *Marmosa*, have short, wide rostrums; large orbits; well-developed postorbital processes; widely flaring zygomatic arches; and small bullae. Indeed, species of *Micoureus* seem to be exceptionally conservative in craniodental morphology, with the result that skulls of even quite distantly related taxa are hard to tell apart. Only a few non-metrical craniodental characters seem to be useful for the purposes of this revision, including details of palatal fenestration, the length of postprotocristae on the upper molars, and the occurrence of postcingulids on the lower molars.

**Maxillopalatine fenestrae**: Perforations in the didelphid hard palate include foramina and fenestrae (Voss and Jansa, 2009: 36–38). Spe-
cies of the subgenus *Micoureus* can have as many as four pairs of palatal perforations, including (from front to back) the incisive foramina, maxillopalatine fenestrae, palatine fenestrae, and posterolateral palatal foramina. All species have maxillopalatine fenestrae—nonvascular openings in the suture between the maxillary and palatine bones—but these can vary substantially in size. Maxillopalatine fenestrae are largest in species such as *Marmosa rapposa*, where they are wide and usually extend from a point opposite P3 to a point opposite M3 (fig. 9A), and they are smallest in species such as *M. germana*, where they are narrow and usually extend only from M1 to M2 (fig. 9B). However, many species have intermediate morphologies, and in all examined species there is appreciable variation in fenestral width and length.

**Palatine fenestrae:** Palatine fenestrae are openings contained entirely by the palatine bones, posterior to the maxillopalatine openings. In a few species, palatine fenestrae are normally present, but in others they are usually absent. As a result, although unilateral polymorphisms are not uncommon, this character is often useful for taxon diagnosis (e.g., Silva et al., 2019; Voss et al., 2019). For example, whereas palatine fenestrae are bilaterally present in 94% of examined specimens of *Marmosa rapposa* (fig. 9A), they are bilaterally absent in 100% of examined specimens of *M. germana* (fig. 9B).

**Postprotocristae:** Of the two enamel crests that diverge from the apex of the protocone on didelphid upper molars (Voss and Jansa, 2009: fig. 20), the preprotocrista passes anterolabially around the base of the paracone to join with the anterolabial cingulum, forming a continuous shelf along the anterior margin of the crown in all examined species of *Marmosa*. By contrast, the postprotocrista varies in length among species of the subgenus *Micoureus*. In species with a

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**FIG. 9.** Ventral views of palates of *Marmosa rapposa* (A, MSB 104347) and *M. germana* (B, TTU 101236). Both species have maxillopalatine fenestrae (**mpf**), but these openings are much larger in *M. rapposa* than in *M. germana*, and only the former species has palatine fenestrae (**pf**). Dental loci (**P3**, **M1**, **M2**, **M3**) are convenient landmarks for describing fenestral size.
“long” postprotocrista (e.g., *M. rapposa*; fig. 10A), this crest extends labially far beyond the base of the metacone, forming a narrow cingulum along the posterior surface of the tooth (the “posterior lingual cingulum” of Silva et al., 2019). By contrast, in species with a “short” postprotocrista (e.g., *M. constantiae*; fig. 10B), this crest terminates at or near the base of the metacone, and the posterior surface of the crown labial to the metacone is smooth and essentially featureless. Although generally reliable for diagnostic purposes, the extent of the postprotocristae can sometimes be hard to assess in specimens with heavily worn teeth.

**Posterior cingulids:** The posterior cingulid—a well-known feature of tribosphenic dentications that is also known as the postcingulid—is an enameled shelf that occurs along the posterobasal margin of the hypoconid on one or more lower molars in some species of the Rapposa Group.3 This feature is best developed on unworn m1–m3 of *Marmosa rapposa* (fig. 11A), but it often persists even on the worn dentitions of old adults of this species. Although posterior cingulids are less well developed in other members of the Rapposa Group, a small posterior cingulid is usually present on m2 and sometimes also on m1 and/or m3 of *M. parda* and *M. rutteri* (see below). Other congeneres (e.g., *M. constantiae*; fig. 11B) entirely lack this structure. Development of a posterior cingulid is correlated with the development of a

3 Until quite recently (Voss et al., 2018), this structure was not known to occur in any didelphid, so it was omitted from Voss and Jansa’s (2009: fig. 20) diagram of molar morphology. Outside the Rapposa Group of *Marmosa*, posterior cingulids are only known to occur in the recently described didelphine species *Philander pebas* (see Voss et al., 2018: fig. 20A).
labial cingulid (a shelf at the base of the hypoconulid; Silva et al., 2019: fig. 12), but in our experience the posterior cingulid provides a less subjective basis for scoring specimens.

TAXONOMIC ACCOUNTS

The following accounts summarize our conclusions about species limits in Clade B (hereinafter, the Rapposa Group) based on the molecular analyses described above and supporting morphological evidence. Our synonymies include only original descriptions, selected examples of usage represented in major works (e.g., Cabrera, 1958; Gardner, 2008), first instances of new name combinations, and incorrect subsequent spellings (if any). Except as noted otherwise, the species treated in this report conform to the morphological description of Marmosa provided by Voss and Jansa (2009: 101–104) and to the diagnosis of Micoureus in Voss et al. (2014). Therefore, only characters that vary within the subgenus are mentioned in the following accounts. Lists of specimens examined include only those personally

The Rapposa Group

We recognize three species in the Rapposa Group (“Clade B” in figs. 5, 6), members of which are distinguished from other species of Micoureus by the absence of a fluffy-furred tail base, by their long postprotocristae, by the presence of posterior cingulids (postcingulids), and by their highly divergent cytochrome b sequences. Insofar as known, all members of the Rapposa Group are Andean or cis-Andean; none is trans-Andean, nor is any known to occur in the Atlantic Forest. Collectively, they occur along the eastern slopes of the Andes (below about 2500 m) from central Peru to northern Argentina; in the Amazonian lowlands of Colombia, Ecuador, Peru, and western Brazil; and in the Cerrado (or Cerrado-like) landscapes of eastern Bolivia, central Brazil, and Paraguay.
Marmosa (Micoureus) rapposa
Thomas, 1899

*Marmosa rapposa* Thomas, 1899b: 42 (original description).

*Marmosa budini* Thomas, 1920a: 195 (original description).

*Marmosa constantiae constantiae*: Tate, 1933: 75 (part, based on misidentified material), not *constantiae* Thomas, 1904a.

*Marmosa constantiae budini*: Tate, 1933: 76 (new name combination).

*Micoureus constantiae*: Gardner, 1993 (part; *budini* treated as synonym), not *constantiae* Thomas, 1904.

*Micoureus regina*: Gardner, 1993: 20 (part; *rapposa* treated as synonym), not *regina* Thomas, 1898.

*Marmosa constantiae constantiae*: Anderson, 1997: 156 (part; based on misidentified material), not *constantiae* Thomas, 1904a.

*Micoureus constantiae budini*: Anderson, 1997: 156 (new name combination).

*Micoureus rapposa*: Gardner and Creighton, 2008: 81 (new name combination with inappropriate gender change).

*Marmosa (Micoureus) constantiae*: Voss and Jansa, 2009: 101 (part; *budini* treated as synonym), not *constantiae* Thomas, 1904a.

*Marmosa (Micoureus) regina*: Voss and Jansa, 2009: 101 (part; *rapposa* treated as synonym), not *regina* Thomas, 1898.

*Marmosa (Micoureus) constantiae*: de la Sancha et al., 2012 (misidentified material), not *constantiae* Thomas, 1904a.

*Marmosa (Micoureus) budini*: Silva et al., 2019: 254 (new name combination).

**Type material and type locality:** The holotype (by original designation, BMNH 98.11.6.13) consists of the skin and skull of a large adult female collected by Otto Garlepp in December 1897 on the “Vilcanota River just north of Cuzco” (Thomas, 1899b: 43) at 1500 m elevation in the Peruvian department of Cusco. As noted by Jenkins and Knutson (1983), the catalog number of this specimen was incorrectly reported by Thomas (as 98.11.1.13). Four juvenile paratypes (BMNH 98.11.6.14–98.11.6.17, also collected by Garlepp at the same locality in December 1897) are assumed to be offspring of the holotype (Thomas, 1899b; Tate, 1933).

According to Ceballos-Bendezú (1981), the type material of *Marmosa rapposa* was collected at Huaquinya in the district of Santa Teresa, province of La Convención (district and province are sequentially larger administrative units of Peruvian departments). Stephen and Traylor’s (1983) coordinates for Huaquinya (appendix 3: locality 52) place it ca. 85 km NW of Cuzco. According to Stephens and Traylor (1983) “Vilcanota” is a local synonym for the upper Urubamba.

**Distribution and sympatry:** Based on specimens that we examined and others examined by Silva et al. (2019), *Marmosa rapposa* occurs along the eastern slopes of the Andes (below about 2500 m) and in adjacent foothills from about 13° S in southeastern Peru (Junín and Cusco) to about 26° S in northwestern Argentina (Tucumán). Additionally, this species is widely distributed in the lowlands of eastern Bolivia, and we have also seen specimens from Brazil and Paraguay (fig. 12).

*Marmosa rapposa* occurs sympatrically with *M. constantiae* in eastern Bolivia (see below) and perhaps also in southeastern Peru, eastern Bolivia, and southwestern Brazil. Additionally, the geographic range of *M. rapposa* approaches that of *M. paraguayana* in eastern Paraguay (de la Sancha et al., 2012: fig. 2).

**Description:** The dorsal pelage of *Marmosa rapposa* is uniformly drab, ranging from a dull yellowish-gray—somewhat similar to Ridgway’s (1912) Grayish Olive—to a somewhat warmer

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4 “Raposa” is the vernacular term for opossum in Peruvian Spanish, so the epithet is to be understood as a noun standing in apposition to the generic name. Although incorrectly spelled according to Spanish orthography, *rapposa* is the correct original spelling in the sense of the Code (ICZN, 1999: article 32).

5 But note that *Marmosa rapposa* is identified as *M. constantiae* by de la Sancha et al. (2012).
brownish gray (near Ridgway’s Light Brownish Olive), often slightly paler in lowland specimens than in specimens from montane habitats, but otherwise remarkably constant in coloration throughout the wide geographic distribution of the species. Fur length at mid back ranges from 8 to 16 mm, but most specimens have middorsal fur that is 10–12 mm long; in general, lowland specimens are shorter furred than highland material. By contrast with the tonal uniformity observed in the dorsal pelage, the ventral fur varies considerably in color, from pale yellow (resembling Ridgway’s Cartridge Buff) to pinkish-orange (near Ochraceous Salmon), with yellowish hues predominating in lowland specimens and richer pigments primarily in highland material. A broad, continuous median streak of self-colored fur extends from the chin to the groin in most specimens (fig. 7), but at least some of the lateral fur is often gray based, and a few specimens (only 5% of those scored for this trait; table 5) have mostly gray-based ventral fur; the fur of the chin, throat, and groin, however, is always self-colored. The tail, usually about 130%–140% of head-and-body length, is covered with short fur for about 25 mm or less (usually <20 mm) at its base, and the naked part of the tail is almost always boldly marked or spotted with white distally (particolored). In a few specimens, as much as half of the unfurred distal part of the tail is white, but only the tip is white in many others, and a few specimens (mostly from the Andean foothills of eastern Bolivia) have all-dark tails. The manus and pes are covered dorsally with

FIG. 12. Collection localities for examined specimens of *Marmosa rapposa*. Numbers are keyed to entries in gazetteer (appendix 2). Lettered localities correspond to selected Argentinian specimens examined by Silva et al. (2019) from Salta (A–C) and Tucumán (D).
short, pale (usually yellowish) hairs in most specimens, but the metapodials are indistinctly darker in some individuals.

Mature adult skulls (fig. 13A, D) usually have short, wide rostrums; broadly flaring zygomatic arches; and distinct postorbital processes. The maxillopalatine fenestrae are usually widely open (seldom reduced to narrow slits), and often extend posteriorly from the level of P3 to the level of M3. Palatine fenestrae are almost always present and well developed. The auditory bullae are usually smoothly globular; none that we examined are acutely pointed ventrally (“conical” sensu Tate, 1933). The upper molar series (LM) is usually short (8.0–8.5 mm), the first three upper molars (M1–M3) have long postprotocristae, and posterior cingulids are usually present on m1–m3.

**VARIATION:** Qualitative variation in selected morphological traits is summarized in table 5. With the exceptions noted above (fur pigmentation in lowland versus highland material), no geographic variation in qualitative phenotypic traits was observed, and specimens exhibiting rare traits for one character are not unusual in other respects. For example, the single specimen we examined that lacks posterior cingulids (CM 4947) has well-developed palatine fenestrae, maxillopalatine foramina that extend from P3 to M3, and a particolored tail. Therefore, such variation has the aspect of intraspecific polymorphism rather than taxonomic heterogeneity.

Morphometric variation in our adult material (table 6) is typical of that observed in homogeneous mammalian samples (e.g., with coeffi-

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**TABLE 5**

Qualified Trait Frequencies for *Marmosa rapposa*

| Trait                              | Frequency |
|------------------------------------|-----------|
| Self-colored ventral fur (N = 42)  |           |
| continuous from chin to groin:      | 40 (95%)  |
| discontinuous (gray-based on abdomen): | 2 (5%)   |
| Tail coloration (N = 40)           |           |
| particolored (marked with white distally): | 33 (82.5%) |
| all-dark:                          | 7 (17.5%) |
| Maxillopalatine fenestrae (N = 40) |           |
| extend from P3 to M3:              | 28 (70%)  |
| extend from P3 to M2:              | 3 (7.5%)  |
| extend from M1 to M3:              | 9 (22.5%) |
| Palatine fenestrae (N = 48)        |           |
| bilaterally present:               | 45 (94%)  |
| unilaterally present:              | 2 (4%)    |
| absent:                            | 1 (2%)    |
| Posterior cingulids (N = 40)       |           |
| distinct on m1–m3:                 | 30 (75%)  |
| distinct on m1 & m2 only:          | 4 (10%)   |
| distinct on m2 only:               | 4 (10%)   |
| distinct on m2 & m3 only:          | 1 (2.5%)  |
| absent/indistinct:                 | 1 (2.5%)  |

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* These traits are less well developed in young adults, and a few adults (e.g., USNM 582111, from an isolated high-altitude site) have narrower skulls than usual.
FIG. 13. Dorsal and ventral cranial views (×1.75) of *Marmosa rapposa* (A, D; AMNH 210398), *M. parda* (B, E; FMNH 24139), and *M. rutteri* (C, F; MVZ 190331). All specimens are adult males.
Although the holotype of *budini* (BMNH 20.1.7.134, from Argentina) is a subadult, it is only slightly smaller than our smallest measured adult specimens (from Bolivia, Brazil, Peru, and Paraguay) in two nasal dimensions. By contrast, the old adult female holotype of *rapposa* (BMNH 98.11.6.13) is substantially larger than any other specimen (of either sex) in several craniodental dimensions, but other specimens from Cuzco (e.g., FMNH 65678, 66411) have unremarkable measurements, and a large (518 bp) fragment of cytochrome *b* that we were able to amplify and sequence from dried tissue scraped from the holotype skull supports the application of *rapposa* to specimens that share the external and craniodental traits described above. Therefore, we conclude that the type is simply an unusually large specimen. Other odd attributes of the holotype include a discontinuous facial mask (dark mystacial and circumocular markings are separated by a narrow line of yellowish fur; Thomas, 1899b) and short postprotocristae.

### TABLE 6

| Measurements (mm) and Weights (g) of *Marmosa rapposa* |
|---------------------------------|-----------------|-----------------|
| Males                          | BMNH 20.1.7.134 | Females         |
| HBL 153 ± 17 (131–186) 15       | "139"           | 150 ± 14 (118–170) 19 |
| LT 213 ± 16 (180–239) 15        | "186"           | 195 ± 19 (162–237) 19 |
| HF 25 ± 2 (22–29) 17            | 26              | 24 ± 2 (19–28) 23 |
| Ear 26 ± 2 (23–30) 17           | "22"            | 26 ± 2 (20–30) 18 |
| CBL 39.7 ± 2.1 (36.2–44.2) 20   | 36.7            | 37.8 ± 2.2 (34.4–41.5) 20 |
| NL 18.3 ± 1.1 (16.4–20.5) 19    | 16.3            | 17.2 ± 1.1 (15.3–18.7) 20 |
| NB 5.2 ± 0.4 (4.8–6.1) 20       | 4.6             | 5.1 ± 0.4 (4.3–6.1) 25 |
| LIB 7.1 ± 0.5 (6.3–8.6) 20      | 6.6             | 6.9 ± 0.6 (5.6–7.9) 25 |
| LPB 6.9 ± 0.5 (6.2–7.7) 17      | 6.9             | 7.1 ± 0.4 (5.9–8.0) 24 |
| ZB 22.6 ± 1.7 (20.2–26.1) 20    | 21.0            | 21.9 ± 1.6 (19.1–24.5) 24 |
| PL 22.1 ± 0.9 (20.6–23.7) 20   | 20.7            | 21.3 ± 1.1 (19.4–23.0) 23 |
| PB 13.0 ± 0.5 (12.0–13.8) 20   | 12.6            | 12.9 ± 0.6 (11.8–14.3) 25 |
| MTR 16.1 ± 0.5 (15.2–16.9) 20  | 15.6            | 15.6 ± 0.4 (14.8–16.5) 26 |
| LM 8.4 ± 0.2 (7.9–8.6) 20      | 8.6             | 8.3 ± 0.2 (8.0–9.0) 26 |
| M1-3 7.1 ± 0.2 (6.7–7.3) 20    | 7.2             | 7.0 ± 0.2 (6.7–7.7) 26 |
| WM3 2.8 ± 0.1 (2.6–2.9) 20     | 2.8             | 2.8 ± 0.1 (2.6–3.0) 26 |
| Weight 81 ± 23 (52–132) 20     | —               | 66 ± 19 (37–98) 18 |

\[\text{\textsuperscript{a}}\text{ The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 210398, 210399, 275464, 275466, 275468; CBF 14, 2332, 3569, 3570; MSB 6700, 70281, 70282, 140343, 140347, 140352; MVZ 172583; UMMZ 126676, 155910; USNM 390023, 390573.}\]

\[\text{\textsuperscript{b}}\text{ The subadult male holotype of *budini*. External measurements in scare quotes were not taken by the American method.}\]

\[\text{\textsuperscript{c}}\text{ The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 63860–63863, 72569, 210400, 264923, 264924, 275463, 275465, 275467; BMNH 76.631; CBF 2334, 7551, 7556; FMNH 65678, 66411; MSB 59883, 63277, 87093, 140348, 140349, 140351, 140415; UMMZ 126678, 126679.}\]

\[\text{\textsuperscript{d}}\text{ The female holotype of *rapposa*. External measurements in scare quotes were not taken by the American method.}\]

\[\text{\textsuperscript{e}}\text{ Measured by R.S.V. on the dried hind foot.}\]
topotypical paratype skins have continuous facial masks, and the molars of the only preserved topotypical paratype skull (BMNH 98.11.6.14) have long postprotocristae. The problem of atypical holotypes is well known (Daston, 2004) and requires no additional comment here.

**Comparisons:** *Marmosa rapposa* differs from other members of the Rapposa Group in several characters (table 7). Whereas the ventral pelage of *M. rapposa* usually includes a broad midventral zone of self-colored fur (sometimes entirely without lateral zones of gray-based hairs), the ventral pelage of *M. parda* is almost entirely gray based (occasionally with a narrow median streak of self-yellow hairs), and the self-colored ventral fur of *M. rutteri* is usually narrowed by lateral zones of gray-based hairs and is sometimes discontinuous. Most (>80%) examined specimens of *M. rapposa* have tails that are marked with white (“depigmented” sensu Silva et al., 2019) distally, but all examined specimens of *M. parda* and *M. rutteri* have completely dark tails. According to Silva et al. (2019), specimens of *M. rapposa* (which they called *M. budini*) usually have more than three hairs emerging from the posterior edge of each caudal scale, whereas specimens of *M. rutteri* (which they called *M. regina*) usually have only three hairs per scale, but we did not score this character for our study.

Craniodental traits provide other diagnostic criteria. In general, skulls of *Marmosa rapposa* are less robust than those of *M. parda* and *M. rutteri*, and they tend to have smaller (but usually distinct) postorbital processes. A less subjective basis for sorting specimens is the palatine fenestrae, which are bilaterally present in >90% of the specimens we examined of *M. rapposa* and in all examined specimens of *M. parda*, but which are usually absent (or, when present, are much smaller) in *M. rutteri*. Lastly, the upper molar toothrow is substantially shorter, on average, in *M. rapposa* than in *M. parda* and *M. regina*.

**Remarks:** We include several putative species identified by our mPTP analysis under this binomen (fig. 14). The haplogroup we call *rapposa A* consists of a single sequence from the Peruvian holotype, whereas *rapposa B* includes 17 sequences from widely scattered localities in Bolivia, Brazil, and Paraguay. A third haplogroup, *rapposa C*, includes two sequences from a single locality in the Cordillera Vilcabamba, an outlying spur of the Peruvian Andes. Sequence divergence between *rapposa A* and *rapposa B* is only about 3%, but *rapposa C* differs from the other haplogroups by about 7%–8% (table 4). Although the latter values are notably high for intraspecific sequence comparisons, we are unable to phenotypically distinguish specimens from the Cordillera Vilcabamba from other material of *M. rapposa*, so it seems best to treat all three haplogroups as conspecific in the absence of other evidence of lineage independence.

Specimens of *Marmosa rapposa* have long been misidentified as *M. constantiae* (e.g., by Tate, 1933; Anderson, 1997; Flores et al., 2007; Gardner and Creighton, 2008; Voss et al., 2009; de la Sancha et al., 2012). Indeed, the holotype (BMNH 3.7.7.157) and other specimens of *M.
FIG. 14. Relationships among 28 cytochrome b sequences of species in the Rapposa Group. This subtree shows the full details of the cartooned lineages belonging to Clade B in figure 5.
constantiae from eastern Bolivia (e.g., AMNH 209158–209162, 210397) and western Mato Grosso (AMNH 384, OMNH 37209) superficially resemble lowland material of M. rapposa by having a continuous median zone of self-yellow ventral fur and tails that are boldly marked with white. Externally, these species are difficult to tell apart where they occur together, although M. constantiae has a longer furry tail base (usually >25 mm). However, M. constantiae differs from M. rapposa in several craniodental traits, notably by lacking palatine fenestrae, by having short postprotocristae on M1–M3 (fig. 10), and by lacking any trace of posterior cingulids (fig. 11); additionally, M. constantiae has larger molars (LM = 8.7–9.2 mm) and bullae that tend to become distinctly conical in older adults.

For the last 25 years Marmosa rapposa has been treated as a synonym (Gardner, 1993) or subspecies (Gardner and Creighton, 2008) of M. regina, but there is no compelling evidence to support the hypothesis that these are closely related taxa. The type of M. regina (BMNH 98.5.15.4) consists of the skin and skull of an old adult male collected by G.D. Child in “W[est]. Cundinamarca (Bogotá region)” (Thomas, 1898: 275). As noted by Patton et al. (2000: 76), the type locality of regina is probably somewhere in the Río Magdalena valley of Colombia, which is separated from the rest of the enormous geographic range previously attributed to this species (Gardner and Creighton, 2008: map 35) by formidable elevations of the eastern Andean cordillera. Among other traits by which it differs from M. rapposa, the holotype of M. regina lacks palatine fenestrae and has distinctly redder dorsal fur (formerly near Prout’s Brown according to Tate [1933: 83], who saw the type when it was less than 40 years old), a well-developed gular gland, an all-dark tail, and short postprotocristae. Like Tate (1933), Voss et al. (2019) restricted the application of M. regina to the holotype, which does not closely resemble any other specimen of Micoureus that we have examined.

In a well-executed and meticulously documented study of mtDNA sequence data and craniodental morphology, Silva et al. (2019) identified the present species as Marmosa budini, a name that we treat as a junior synonym. The holotype of M. budini (BMNH 20.1.7.134) consists of the skin and skull of a subadult male collected by Emilio Budin on 23 July 1919 at 500 m on the Altura de Yuto near the Río San Francisco in the province of Jujuy, Argentina. Except for its slightly smaller nasal measurements (discussed above; see Variation), this specimen is morphologically indistinguishable from sequenced Bolivian material that clusters with the partial sequence we obtained from the type of M. rapposa.

One specimen of Marmosa rapposa—AMNH 72569, from Ñequejahuira at 8000 ft (2450 m) above sea level on the eastern slopes of the Cordillera Real of La Paz department, Bolivia—was part of Tate’s (1931) type series of M. mapiriensis, but it is not conspecific with the holotype (AMNH 72555), which was collected in the adjacent foothills at Ticunhuaya (1500 m). Among other noteworthy differences from M. rapposa, AMNH 72555 lacks palatine fenestrae and posterior cingulids; additionally, it has short postprotocristae, short and narrow maxillopalatine fenestrae, and strongly conical auditory bullae. As noted earlier, we provisionally regard mapiriensis as a junior synonym of M. constantiae.

HABITATS: Explicit descriptions of habitats in which specimens of Marmosa rapposa have been collected are uncommon. Ecological maps suggest that most Andean specimens were collected in montane (“cloud”) forest and that most lowland specimens were taken in dry forests, and these ecological associations are generally supported by brief notations on specimen tags and in field notes. According to Silva et al. (2019: 17), this species occurs in multiple ecoregions (sensu Olson et al., 2001) including “Cerrado, Chaco (savannic and humid), Pantanal, Parana/Paraiba interior forests, Bolivian Yungas, Andean Yun-
gas, south-western Amazonian moist forests, Chiquitania dry forests, and Bolivian montane dry forests,” but their list conveys little about the appearance of vegetation in which the species is actually found because many of these ecoregions (e.g., the Cerrado; Eiten, 1972) are mosaics of quite different habitat types. Detailed descriptions of the vegetation at distant localities where *M. rapposa* have been collected are in Ratter et al. (1973) and Holst (1997), but carefully conducted trapping programs at sites like these would be necessary to establish which local habitats are “sinks” and which are “sources” (Pulliam, 1988) for this species.

Despite their very broad geographic overlap, the only place where *Marmosa rapposa* and *M. constantiae* are known to occur sympatrically is the Serranía (or Cordillera) Mosetenes in Cochabamba department, Bolivia (appendix 3: locality 7). In September 2003, Fernando Guerra, Teresa Tarifa, and Eric Yenssen collected two specimens of *M. rapposa* (CBF 7551, 7556) and two specimens of *M. constantiae* (CBF 7515, 7540) in the Serranía Mosetenes at elevations ranging from 1200 to 1600 m. According to Tarifa et al. (2008), local habitats included bamboo thickets, regenerating montane forest, mature montane forest, and ridge forest; apparently, *M. constantiae* ("Micoureus demerarae") was captured only in montane forest, whereas *M. rapposa* ("Mic. regina") was captured in both montane forest and ridge forest. The ridge-forest habitat (figs. 15, 16) of *M. rapposa* was said to consist of stunted trees heavily laden with epiphytes, and to lack

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**FIG. 15.** Habitat of *Marmosa rapposa* in ridge-top forest at about 1600 m in the Serranía Mosetenes, Cochabamba department, Bolivia (photo by Teresa Tarifa).
FIG. 16. Interior of ridge-top forest in the Serranía Mosetenes, Cochabamba department, Bolivia (photo by Teresa Tarifa).
the “Amazonian elements” observed in mature montane forest.

**Specimens examined (N = 94):**

**Argentina—** Jujuy, Altura de Yuto (BMNH 20.1.7.134 [holotype of *budini*]).

**Brazil—** Mato Grosso, 264 km N Xavantina (BMNH 76.631); Mato Grosso do Sul, 10 km NE Urucum (USNM 390023).

**Bolivia—** Beni, 5 km N Estancia El Porvenir (CBF 14); Chuquisaca, 2 km E Chuyayacu (MSB 63276), El Limón (LHE 1307), Rinconada del Bufete (LHE 1299), Río Limón (MSB 63277).

**Chuquisaca—** 2 km E Chuyayacu (MSB 63276), El Limón (LHE 1307), Rinconada del Bufete (LHE 1299), Río Limón (MSB 63277).

**Cochabamba—** Serranía Mosetenes (CBF 7551, 7556), 4.4 km N Tablas Monte (AMNH 264924, CBF 3570, MSB 70281), 9.5 km NE Tablas Monte (AMNH 264923, CBF 3569, MSB 70282); La Paz, 4 km NW Alcoche (UMMZ 126679, 127170), Cajuata (CBF 6606, 6607), 20 km NNE Caranavi (UMMZ 126676–126678, 127171), La Reserva (AMNH 275463–275465, 275467; MSB 140341–140345, 140347–140351, 140415), 1 km S La Reserva (CBF 2332, 2334); Los Molinos de Titiamaya (CBF 4996), Ñequejahuira (AMNH 72569), 1 mi W Puerto Linares (TTU 34785); Santa Cruz, 53 km E Boyuibe (AMNH 275466), Buenavista (CM 5049; FMNH 25266, 51902–51905), Cerro Hosane (CM 4941, 4947, 4951), 2 km N Chapare River mouth (AMNH 210398, 210399), 54 km S Chapare River mouth (AMNH 210400), 1 km NE Estancia Cuevas (MSB 67019), Río Surutú (CM 5040), 27 km SE Santa Cruz (MSB 59883), Warnes (USNM 390573); Tarija, 3 km WNW Carapari (AMNH 275468), 5 km NNW Entre Ríos (MSB 87093).

**Paraguay—** Alto Paraguay, Puerto Casado (FMNH 5440); Amambay, Parque Nacional Cerro Cora (MSB 67000, UMMZ 134550); San Pedro, Ganadera La Carolina (UMMZ 174909, 174992), Cusco—Hacienda Cadena (FMNH 65678, 66411, 68330, 75102), Vilcanota River just north of Cuzco (BMNH 98.11.6.13 [holotype of *rapposa*], 98.11.6.14–98.11.6.17); Junín, “Camp Two” in Cordillera Vilcabamba (MUSM 13004, 13005; USNM 582111, 582112), 15 km by road SW San Ramón (UMMZ 155909–155911, 158013–158015), Utcuyacu (AMNH 63860–63863); Puno, 11 km NNE Ollachea (MVZ 172582), 14 km W Yanahuaya (MVZ 172583).

*Marmosa (Micoureus) parda* Tate, 1931

*Marmosa germana parda* Tate, 1931: 4 (original description).

*Marmosa (Marmosa) germana parda*: Cabrera, 1958: 15 (name combination).

*Micoureus regina*: Gardner, 1993: 20 (part; *parda* treated as synonym); not *regina* Thomas, 1898.

*Micoureus regina germanus*: Gardner and Creighton, 2008: 81 (part; *parda* treated as synonym); not *germania* Thomas, 1904.

*Marmosa (Micoureus) regina*: Voss and Jansa, 2009: 101 (part; *parda* treated as synonym); not *regina* Thomas, 1898.

**Type material and type locality:** The holotype (by original designation, FMNH 24140) consists of the skin and skull of an adult male collected by J.T. Zimmer on 28 September 1922 at Huachipa, Huánuco, Peru. Both elements of the type specimen are in excellent condition. In addition to the holotype, Tate (1931) mentioned that he had examined 15 other specimens of this taxon, all of which can be considered paratypes; Tate (1933: 82–83) listed this material, which included several BMNH specimens, but not all of these are conspecific with the holotype (see Remarks, below).

**Distribution and sympatry:** The material we refer to *Marmosa parda* is all from the upper Río Huallaga drainage between about 1000 and 2000 m in the departments of Huánuco and La Libertad, Peru (fig. 17). We are not aware that this species occurs sympatrically with any other member of the subgenus *Micoureus*.

**Description:** The dorsal pelage of *Marmosa parda* is dull brownish gray (near Ridgway’s Citrine Drab or Grayish Olive), with little tonal variation in the material we examined; at midback the fur ranges in length from 12 to 15 mm. The ventral fur is almost completely gray based, except
on the chin and groin, which have self-yellowish or buffy fur; additionally, a very narrow median streak of self-yellowish fur is present in some specimens. The tail seems to be slightly more than 130% of head-and-body length, judging from the few available specimens measured by the American method; it is covered with short fur for only about 25 mm or less at the base, and the exposed caudal skin is completely dark (brownish in dried specimens) without any bold whitish markings. The manus and pes are covered dorsally with pale hairs in most specimens, but a few have indistinctly darker metacarpal pelage.

Mature adult skulls of *Marmosa parda* are larger and more robust than those of *M. rapposa* in same-sex comparisons (fig. 13, table 8). However, these taxa are otherwise cranially similar, with short, wide rostrums; broadly flaring zygomatic arches; and well-developed postorbital processes. In ventral view, the maxillopalatine fenestrae are widely open and extend from M1 to M3 in most specimens. Palatine fenestrae are consistently present and usually well developed. The auditory bullae are smoothly globular in most specimens, but they are faintly conical in at least one (FMNH 24137), which has vascularized

FIG. 17. Collection localities for examined specimens of *Marmosa parda* and *M. rutteri*. Numbers are keyed to entries in gazetteer (appendix 3).
Sinuses on the ventral apex. The upper molar series is longer than those typically seen in *M. rapposa*, ranging from 8.5 to 9.1 mm in the specimens we measured. The first three upper molars have long postprotocristae. Most specimens have distinct postcingulids on m1–3, but these structures are indistinct (possibly worn away) in two specimens (FMNH 24138, 24139).

Comparisons: Comparisons of *Marmosa parda* with *M. rapposa* have already been provided, so it only remains to compare this species with its sister taxon, *M. rutteri*. These species are externally similar, but the dorsal fur is typically somewhat longer in *parda* (≥12 mm) than in *rutteri* (in which it is usually <12 mm). Additionally, the tail appears to be relatively shorter in *parda* than in *rutteri*, although this is hard to assess with measurements obtained in the field by collectors using different protocols. Lastly, the ventral fur is more extensively gray based in *parda* than in *rutteri*. Although Tate (1933: 83) claimed that *parda* and *rutteri* were not distinguishable cranially, the clearest distinction between these taxa is the consistent, bilateral presence of large palatine fenestrae in *parda* and the absence, unilateral presence, or reduced size of these openings in *rutteri*.

Remarks: Tate (1931) originally described *Marmosa parda* as a subspecies of *M. germana*, but *M. germana* is a distantly related taxon (fig. 6) that has short postprotocristae.

### TABLE 8

| Measurements (mm) and Weights (g) of *Marmosa parda* |
|-----------------------------------------------|
| FMNH   | FMNH | FMNH | FMNH | LSUMZ | BMNH | BMNH |
| 24139  | 24139 | 24137 | 24138 | 22324 | 27.11.1246 | 27.11.1248 |
| Sex    | male  | male  | female | male  | female | female |
| HBL    | 160\(^b\) | 171 | 147\(^b\) | 137\(^b\) | 177 | 159\(^b\) | 164\(^b\) |
| LT     | 242\(^b\) | 235 | 223\(^b\) | 210\(^b\) | 225 | 266\(^b\) | – |
| HF     | 28 | 28 | “24” | 26\(^c\) | 27\(^c\) | 27\(^c\) | 26\(^b\) |
| Ear    | – | – | – | – | 26 | 24.5\(^b\) | 24\(^b\) |
| CBL    | 43.6 | 43.6 | 41.6 | 40.0 | 41.1 | 40.6 | – |
| NL     | 19.6 | 20.0 | 19.3 | 18.6 | 18.5 | 19.0 | 19.2 |
| NB     | 6.2 | 7.0 | 6.5 | 5.8 | 6.0 | 6.5 | 6.2 |
| LIB    | 8.7 | 8.9 | 8.2 | 7.9 | 8.1 | 8.0 | 8.0 |
| LPB    | 8.0 | 8.7 | 8.1 | 7.9 | 8.3 | 7.8 | 7.5 |
| ZB     | 25.4 | 24.8 | 24.1 | 23.4 | 22.6 | 23.1 | 23.0 |
| PL     | 24.5 | 24.4 | 23.6 | 22.4 | 23.0 | 23.4 | 23.3 |
| PB     | 14.1 | 13.8 | 13.4 | 14.2 | 13.7 | 14.0 | 14.9 |
| MTR    | 16.7 | 17.7 | 16.4 | 16.5 | 16.8 | 17.0 | 17.0 |
| LM     | 8.5 | 9.1 | 8.7 | 9.0 | 8.8 | 9.0 | 8.8 |
| M1–3   | 7.2 | 7.5 | 7.4 | 7.6 | 7.2 | 7.4 | 7.3 |
| WM3    | 2.7 | 2.7 | 2.9 | 2.8 | 2.9 | 2.9 | 3.0 |
| Weight | – | – | – | 82 | – | – | – |

\(^a\) Holotype.
\(^b\) Measured by the British method.
\(^c\) Measured by R.S.V. from dried skin.
and lacks palatine fenestrae and postcingulids. Specimens that we refer to M. germana are only known from lowland localities north of the Amazon in northeastern Peru and eastern Ecuador.

Among the BMNH paratypes listed by Tate (1933: 82–83), only two that we examined (BMNH 27.11.1.246, 27.11.1.248), both from Huánuco, are conspecific with the holotype. The others, from Pasco (BMNH 12.1.15.8) and San Martín (BMNH 24.8.1.4, 27.1.1.174–27.1.1.176) are examples of M. constantiae, with longer, fluffier fur at the base of the tail and short postprotocristae; none has palatine fenestrae nor any trace of postcingulids on the lower molars.

Habitats: Nothing has been recorded about the habitats occupied by this species, but the typical vegetation of the eastern Andean slopes of central Peru between about 1000 and 2000 m is premontane or montane rainforest.

Specimens examined (N = 7): Peru—Huánuco, Chinchavita (BMNH 27.11.1.246, 27.11.1.248), Hacienda Porvenir (FMNH 24139), Hacienda San Antonio (FMNH 24137, 24138), Huachipa (FMNH 24140); La Libertad, on trail to Ongón (LSUMZ 22324).

Marmosa (Micourus) rutteri Thomas, 1924

Marmosa rutteri Thomas, 1924: 536 (original description).

Marmosa germana rutteri: Tate, 1933: 81 (name combination).

Marmosa (Marmosa) germana rutteri: Cabrera, 1958: 15 (name combination).

Micoureus regina: Gardner, 1993: 20 (part; rutteri treated as synonym); not regina Thomas, 1898.

Micoureus regina germanus: Gardner and Creighton, 2008: 81 (part; rutteri treated as synonym); not germana Thomas, 1904.

Marmosa (Micoureus) regina: Voss and Jansa, 2009: 101 (part, rutteri treated as synonym); not regina Thomas, 1898.

Type material: The holotype (by original designation, BMNH 24.2.22.67) consists of the skin and skull of an adult male collected by Latham Rutter on 10 September 1923 at “Tushemo, near Masisea” at an elevation of 1000 ft [305 m] in the Peruvian department of Ucayali.

Distribution and sympatry: Marmosa rutteri is a lowland Amazonian species that has been collected at or below about 800 m in southeastern Colombia, eastern Ecuador, eastern Peru, and western Brazil. It is known to occur sympatrically with several other members of the subgenus Micoureus, including M. constantiae (south of the Amazon in western Brazil and eastern Peru), M. germana (north of the Amazon in eastern Peru and eastern Ecuador), and an undescribed species (M. “Yasuni”; see above) that appears to have much the same geographic distribution as M. germana.

Description: The dorsal pelage of Marmosa rutteri ranges in color from a dull grayish hue (near Ridgway’s Deep Grayish Olive) to paler, more yellowish tones (close to Light Brownish Olive or even to Isabella Color); at midback the fur ranges in length from 8 to 16 mm, with longer fur typically in foothill material, but in most specimens we measured the middorsal fur is 9–11 mm long. The ventral pelage, at least along the midline from chin to groin, is usually self-yellowish (e.g., Antimony Yellow or Colonial Buff), although there are often broad lateral zones of gray-based fur on the lower thorax and abdomen (between the fore- and hind limbs), and a few skins have mostly gray-based ventral fur with self-yellowish fur only on the chin, throat, and groin. The tail is approximately 145% of head-and-body length, on average, and only a short part of the base (usually <20 mm) is covered with fur; the naked, scaly part of the tail is completely dark (grayish or grayish brown in life), and it is not marked with white in any specimen that we examined.

Adult skulls (fig. 13C, F) have short, wide rostrums and broadly flaring zygomatic arches. The postorbital processes, even of most young adults, are large and triangular. The maxillo-
palatine fenestrae extend from the level of M1 to the level of M3 in most specimens, but in many others they extend only from M1 to M2; however, these openings are seldom very wide, usually taking the form of narrow, bilaterally paired slits. Palatine fenestrae are bilaterally absent in most specimens, but small openings in the posterior palate are present unilaterally (e.g., in fig. 13F) and sometimes bilaterally in others. The first three upper molars (M1–M3) have long postprotocristae, and posterior cingulids are often distinct on m1–m3 (but always, at least, on unworn m2).

**Variation:** Summary statistics for external and craniodental measurements of *Marmosa rutteri* are provided in table 9, and qualitative trait variation is summarized in table 10. None of the morphometric or qualitative variation in this species seems particularly noteworthy, nor does this variability appear to be geographically structured. For example, we observed broad morphometric overlap between samples collected north and south of the upper Amazon. Although a few populations exhibit high frequencies of unusual phenotypes (e.g., 6 out of 10 specimens that we scored for ventral fur color from Amazonas

| Measure | BMNH 24.2.22.67 | BMNH 24.2.22.67 | BMNH 24.2.22.67 |
|---------|----------------|----------------|----------------|
| HBL     | 158±        | 184 ± 11 (164–203) 17 | 174 ± 16 (152–206) 15 |
| LT      | 213±        | 260 ± 17 (227–291) 17 | 240 ± 16 (210–269) 15 |
| HF      | 28±         | 29 ± 2 (25–33) 18 | 28 ± 2 (25–30) 18 |
| Ear     | 23±         | 26 ± 2 (23–29) 18 | 25 ± 1 (23–28) 17 |
| CBL     | 5.6±        | 45.0 ± 2.0 (41.6–49.7) 25 | 42.7 ± 2.0 (39.6–46.5) 24 |
| NL      | 18.1±       | 20.2 ± 1.5 (17.4–23.0) 29 | 19.2 ± 1.2 (17.2–21.6) 20 |
| NB      | 5.6±        | 6.4 ± 0.6 (5.5–7.7) 32 | 6.1 ± 0.5 (4.8–6.9) 26 |
| LIB     | 7.3±        | 8.4 ± 0.6 (7.2–9.6) 31 | 8.0 ± 0.5 (7.3–9.2) 26 |
| LPB     | 7.2±        | 7.4 ± 0.6 (5.9–8.6) 31 | 7.4 ± 0.6 (6.4–8.2) 26 |
| ZB      | 22.8±       | 25.0 ± 1.2 (22.5–27.6) 31 | 24.0 ± 1.0 (22.2–26.6) 25 |
| PL      | 13.3±       | 14.5 ± 0.7 (13.1–15.7) 29 | 14.4 ± 0.6 (13.4–16.2) 26 |
| PB      | 16.7±       | 17.9 ± 0.8 (16.7–19.4) 31 | 17.5 ± 0.6 (16.7–18.8) 26 |
| MTR     | 8.6±        | 9.0 ± 0.4 (8.3–9.8) 31 | 9.1 ± 0.3 (8.6–9.6) 26 |
| LM      | 7.3±        | 7.6 ± 0.3 (7.0–8.2) 32 | 7.7 ± 0.2 (7.2–8.1) 26 |
| WM3     | 2.9±        | 3.0 ± 0.2 (2.6–3.3) 32 | 3.0 ± 0.1 (2.7–3.2) 26 |
| Weight  | —           | 132 ± 30 (84–180) 17 | 105 ± 23 (63–151) 12 |

| a Holotype.  
| b The sample mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size based on measurements of the following series: AMNH 71958, 76302, 230021; BMNH 24.2.22.67, 28.5.2.231–28.5.2.235, 28.5.2.237, 28.5.2.240; FMNH 46110, 46111; KU 144110; MUSM 11055, 11063, 15316; MVZ 154749, 154755, 154762, 154764, 154766, 157629, 157630, 157631, 190319, 190320, 190323, 190329–190332.  
| c The sample mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size based on measurements of the following series: AMNH 71951, 72009, 72010, 74087, 98655, 98712, 273164; BMNH 28.5.2.241; FMNH 19635, 55467, 70966, 75100, 87118, 124613; KU 144093, 144095, 144100, 144102, 144107; LSMUZ 15674; MUSM 6086, 6087; MVZ 154758, 157628, 190321, 190326.  
| d Measured by the British method.
Comparisons: Comparisons of *Marmosa rutteri* with other members of the Rapposa Group are provided in the preceding accounts. *Marmosa rutteri* differs from other (non-Rapposa Group) species of the subgenus *Micoureus* with which it is sometimes sympatric (e.g., *M. constantiae* and *M. germana*) by its long postprotocristae on M1–M3, and by the presence of posterior cingulids on unworn m2 (and sometimes other lower molars); it is also substantially larger than the undescribed species of the Perplexa Group with which it co-occurs north of the Amazon (*M. “regina”* sensu Hice and Velazco, 2012). Additional comparisons between *M. rutteri* and *M. constantiae* were summarized by Voss et al. (2019: 27–29).

**Habitats:** The entire known geographic range of *Marmosa rutteri* is in western Amazonia, where the predominant natural climax vegetation is lowland rainforest. However, Amazonian vegetation is notoriously heterogeneous, including numerous distinct kinds of habitats, especially in riparian landscapes (Prance, 1979; Pires and Prance, 1985; Puhakka and Kalliola, 1995). Given that several species of the subgenus *Micoureus* have overlapping distributions in this region (see Distribution and sympatry, above), it would be reasonable to expect that some of them might be habitat specialists.

The most compelling evidence for habitat specialization by Amazonian species of *Marmosa* comes from an exemplary trapping study along the Rio Juruá in western Brazil (Patton et al., 2000). At numerous sites along this major white-
water river, *Marmosa rutteri* ("Micoureus regina") and *M. constantiae* ("Micoureus demerarae") were found to occur sympatrically, although usually not syntopically. Equal numbers of both species ($N = 55$ each) were collected. Of these, specimens of *M. rutteri* were trapped in both *várzea* (seasonally flooded forest; fig. 18) and *terra firme* (unflooded) habitats, whereas *M. constantiae* was taken almost exclusively in *terra firme* forest (table 11). Based on these results, it seems plausible that *M. rutteri* might be a *várzea* specialist or, at least, might utilize seasonally flooded habitats to a greater extent than sympatric congeners.8

The same two field studies also provide the best available data about microhabitat occupancy by *Marmosa rutteri*. In Patton et al.’s (2000) study, substantial numbers of traps were set on the ground and in trees at each sampled site along the Rio Juruá; all of the 55 specimens of *M. rutteri* they collected were taken in arboreal traps.

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8 In the commonly accepted terminology for Amazonian riparian vegetation (Prance, 1979), *várzea* refers to forests seasonally flooded by sediment-bearing (white-water) rivers, whereas *igapó* refers to forests seasonally flooded by sediment-free black- or clear-water rivers.
set 5–10 m above the ground, or were shot from arboreal perches >2 m above ground level. At Cuzco Amazónico, 20 out of 24 specimens of *M. rutteri* (ca. 83%) were trapped in trees (Woodman et al., 1995). These results are consistent with the commonly accepted notion that species of *Marmosa* are predominantly arboreal (Charles-Dominique et al., 1981; Miles et al., 1981; Vieira and Monteiro-Filho, 2003).

**Specimens Examined (N = 98):**
- **Brazil**—Acre, Igarapé Porongaba (MVZ 190332), Nova Vida (MVZ 190333); Amazonas, Boa Esperança (MVZ 190330, 190331), Igarapé Nova Empresa (MVZ 190321, 190323–190325), opposite Altamira (MVZ 190328, 190329), Penedo (MVZ 190319, 190320), Seringal Condor (MVZ 190326).
- **Colombia**—Amazonas, Leticia (USNM 536890); Caquetá, Tres Troncos (FMNH 70964–70966).
- **Ecuador**—Napo, “near the river Napo” (BMNH 34.9.10.234–34.9.10.237); Orellana, San José de Payamino (FMNH 124613); Sucumbios, Boca Río Lagartococha (AMNH 72008, 72009).
- **Peru**—Amazonas, La Poza (MVZ 157629), mouth of Río Cenepa (AMNH 98712), vicinity of Huampani (MVZ 153278, 154749, 154751, 154755, 154758, 154762, 154764, 154766, 157628, 157630, 157631), vicinity of Kayamas (MVZ 153281); Ayacucho, Santa Rosa on Río Santa Rosa (LSUMZ 15674); Cuzco, Quincemil (FMNH 75100); Loreto, Boca Río Curaray (AMNH 71951, 71956, 71958, 71964, 71966, 71968, 71975, 72010), Nuevo San Juan (AMNH 273164; MUSM 11055, 11063, 15315, 15316), Orosa (AMNH 74087), Otorongo (MUSM 33443), Pampa Chica (FMNH 87118), San Antonio (AMNH 98655), San Jerónimo (BMNH 28.5.2.231–28.5.2.241; FMNH 46110, 46111), Sarayacu (AMNH 76302, 76303), “Triunfo Chacras” (TTU 124799), Yurimaguas (FMNH 19635); Madre de Dios, Blanquillo (MUSM 8399), Reserva Cuzco Amazónico (KU 144091, 144093, 144095, 144100, 144102, 144107, 144110, 144111; MUSM 6083, 6086–6088, 6090–6092, 6100, 6101), 30 km above mouth of Río Tambopata (USNM 530907); Pasco, San Pablo (AMNH 230019, 230021); Ucayali, Tushemo (BMNH 24.2.22.67 [holotype]), Yarinacocha (FMNH 55467).

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**TABLE 11**

|                  | *M. constantiae* | *M. rutteri* | Totals |
|------------------|------------------|--------------|--------|
| Zone 1<sup>b</sup> | 5                | 6            | 11     |
| Zone 2<sup>c</sup> | 1                | 7            | 8      |
| **Totals**       | **6**            | **13**       | **19** |

<sup>a</sup> Both species identified as “*Micoureus regina*” by Woodman et al. (1991, 1995). Only specimens that we examined are included in these counts.

<sup>b</sup> Trapping area located in terra firme forest (Duellman and Koechlin, 1991).

<sup>c</sup> Trapping area located in seasonally flooded forest (Duellman and Koechlin, 1991).
Heath Garner (TTU); and Darrin Lunde and Nicole Edmison (USNM).

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APPENDIX 1

GAZETTEER OF SEQUENCED SPECIMENS OF
MARMOSA (MICOUREUS)

Below we list all the localities where sequenced specimens of the subgenus Micoureus were collected, including those sequenced by us and others corresponding to sequences we downloaded from GenBank (table 2). Italicized place names are those of the largest political units within each country (states, departments, provinces, etc.). Geographic coordinates (in decimal degrees) were obtained from primary sources (e.g., specimen labels; in parentheses) or secondary sources (institutional databases or publications, cited in square brackets). Numbers identify locality symbols plotted on maps in Materials and Methods (figs. 1–3).

BOLIVIA
1. Beni, Río Iténez frente Costa Marquez [12.48°S, 64.28°W; Anderson, 1997].
2. Chuquisaca, El Limón, 15.6 km N El Palmar [20.71°S, 64.31°W].
3. Chuquisaca, Rinconada del Bufete [= Cerro Bufete at 20.83°S, 64.38°W; Patton et al., 2015].
4. Chuquisaca, Río Limón (19.55°S, 64.13°W).
5. Cochabamba, 4.4 km by road N Tablas Monte [17.07°S, 65.98°W; Anderson, 1997].
6. Cochabamba, Chapare, Serranía Mosetenes [16.23°S, 66.42°W; Tarita et al., 2008].
7. La Paz, 1 mi W Puerto Linares [15.48°S, 67.52°W; Anderson, 1997].
8. La Paz, La Reserva [15.73°S, 67.52°W; Anderson, 1997].
9. Pando, La Cruz [11.45°S, 67.22°W].
10. Santa Cruz, 1 km NE Estancia Cuevas [18.18°S, 63.73°W].
11. Santa Cruz, 27 km SE Santa Cruz [17.97°S, 63.05°W].
12. Santa Cruz, 53 km E Boyuibe [20.45°S, 62.83°W; Anderson, 1997].
13. Santa Cruz, Parque Nacional Noel Kempff Mercado, El Refugio [14.77°S, 61.03°W].
14. Santa Cruz, Parque Nacional Noel Kempff Mercado, Flor de Oro [13.55°S, 61.01°W; USNM database].
15. Tarija, 5 km NNW Entre Ríos [21.48°S, 64.20°W].

BRAZIL
16. Acre, Igarapé Porongaba, right bank Río Juruá [8.67°S, 72.78°W].
17. Alagoas, São José de Lajes [8.96°S, 36.07°W; Rocha et al., 2015].
18. Amazonas, alto Río Urucu [4.85°S, 65.27°W; MVZ database].
19. Amazonas, Barcelos [0.06°S, 64.59°W; F.C. Almeida, personal commun.].
20. Amazonas, Barro Vermelho, left bank Río Juruá [6.47°S, 68.77°W; Patton et al., 2000].
21. Amazonas, Comunidade Colina, right bank Río Tiquié [0.12°N, 69.01°W; Patton et al., 2015].
22. Amazonas, Igarapé Nova Empresa, left bank Río Juruá [6.80°S, 70.73°W].
23. Amazonas, Penedo, right bank Río Juruá [6.83°S, 70.75°W; Patton et al., 2000].
24. Amazonas, Santa Isabel do Río Negro [0.76°S, 63.44°W; F.C. Almeida, personal commun.].
25. Amazonas, Seringal Condor, left bank Río Juruá [6.75°S, 70.85°W; Patton et al., 2000].
26. Amazonas, Villa Bella Imperatriz, Boca Rio Andira [2.75°S, 56.82°W; Paynter and Traylor, 1991].
27. Bahia, Fazenda Bolandeira, 10 km S Una [15.35°S, 39.00°W; MVZ database].
28. Bahia, Fazenda Santa Rita, 8 km E Andaraí [12.80°S, 41.27°W; Costa et al., 2003].
29. Bahia, Itacaré, Fazenda Rio Capitão [14.34°S, 39.09°W; F.C. Almeida, personal commun.].
30. Bahia, Itamar, Fazenda Alto São Roque [13.85°S, 39.67°W; F.C. Almeida, personal commun.].
31. Bahia, Nova Viçosa [17.81°S, 39.66°W; Rocha et al., 2015].
32. Bahia, Porto Seguro, Parque Nacional do Pau Brasil [16.52°S, 39.30°W; F.C. Almeida, personal commun.].
33. Bahia, Uruçuca, Fazenda Caititu [14.42°S, 39.07°W; F.C. Almeida, personal commun.].
34. Ceará, locality unknown [3.71°S, 38.50°W at Fortaleza, the state capital; Paynter and Traylor, 1991].
35. Goiás, Mimoso de Goiás [15.06°S, 48.19°W; F.C. Almeida, personal commun.].
36. Mato Grosso, Chapada dos Guimarães, Usina Hidrelétrica Manso [15.58°S, 56.10°W; Bonvicino et al., 2002].
37. Mato Grosso, Fazenda Lagoa Bonita, 36 km N Barra do Garças [15.58°S, 52.36°W; MVZ database].
38. Mato Grosso, Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira [12.64°S, 51.93°W; MVZ database].
39. Mato Grosso, 40 km N Alta Floresta (including sublocalities “left bank Rio Cristalino” and “Reserva Ecológica Cristalino”) [9.60°S, 55.93°W; MVZ database].
40. Mato Grosso, São José do Xingu [10.80°S, 52.74°W; F.C. Almeida, personal commun.].
41. Mato Grosso do Sul, Corumbá, São Marcus road, 10 km NE Urucum [19.10°S, 57.58°W; Gardner, 2008].
42. Minas Gerais, 13 km E Marliéria [19.72°S, 42.65°W; MVZ database].
43. Minas Gerais, Berilo, Usina Hidrelétrica de Irapé [16.74°S, 42.59°W; F.C. Almeida, personal commun.].
44. Minas Gerais, Casa Branca, Parque Estadual Rola Moça [20.12°S, 44.12°W; F.C. Almeida, personal commun.].
45. Minas Gerais, Estação Ecológica de Acauã, 17 km N Turmalina [17.17°S, 42.78°W; Carrara et al., 2013].
46. Minas Gerais, Marliéria, Parque Estadual do Rio Doce (including sublocalities “Campolina” and “Vinhático”) [19.76°S, 42.63°W; F.C. Almeida, personal commun.].
47. Pará, Kayapó Indigenous Area, Pinkaití Research Station [7.77°S, 51.97°W].
48. Pará, Novo Repartimento [4.11°S, 50.09°W; Rocha et al., 2015].
49. Pará, Santana do Araguaia [9.63°S, 50.14°W; Rocha et al., 2015].
50. Rio de Janeiro, Guapimirim [22.54°S, 42.98°W; F.C. Almeida, personal commun.].
51. São Paulo, Fazenda Intervales, Base do Carmo, 5.5 km S Capão Bonito, 700 m [24.33°S, 48.42°W].
52. São Paulo, Sorocaba, Floresta Nacional de Ipanema [23.44°S, 47.63°W; Patton et al., 2015].
53. São Paulo, S Pium [9.97°S, 50.03°W; Rocha et al., 2015].
54. Tocantins, Caseara [9.30°S, 49.96°W; Rocha et al., 2015].
55. Tocantins, N Pium [9.54°S, 50.09°W; Rocha et al., 2015].
56. Tocantins, S Pium [9.98°S, 50.03°W; Rocha et al., 2015].

COLOMBIA

60. Antioquia, Corregimiento El Cedro, Vereda Corcovado, Finca El Bosque, Bosque San Andrés (7.07°N, 75.42°W).
61. Antioquia, San Jerónimo, NW Medellín, 420 m [6.45°N, 75.75°W; Paynter, 1997].
62. Antioquia, Sonsón, 9 km E Río Negro, 2050 m [5.70°N, 75.30°W; Patton et al., 2015].
63. Caquetá, Río Caquetá, Tres Troncos [0.13°N, 74.68°W; Patton et al., 2015].
64. Cauca, Chisquio, 1700 m [2.48°N, 76.87°W; Paynter, 1997].
65. Cesar, Sierra Negra, Villanueva [10.60°N, 72.92°W; Patton et al., 2015].
66. Chocó, Río Baudó, Río Sandó [5.05°N, 76.95°W; Paynter, 1997].
67. Huila, Acevedo, San Adolfo, 1400 m [1.62°N, 75.98°W; Paynter, 1997].
68. Huila, San Augustín, [Río] San Antonio, 2300 m [1.95°N, 76.40°W; Apanaskevich et al., 2017].

COSTA RICA

70. Cartago, Agua Caliente [9.85°N, 83.93°W; VertNet database].
71. Puntarenas, Monteverde [10.25°N, 84.77°W; Clark et al., 2000].
72. San José, San José [9.93°N, 84.08°W; USBGN, 1956].

ECUADOR
73. Esmeraldas, Esmeraldas [0.98°N, 79.70°W; Paynter, 1993].
74. Loja, 12 km E (by road) Portovelo [3.72°S, 79.55°W; Paynter, 1993].
75. Orellana, 42 km S and 1 km E Pompeya Sur (0.68°S, 76.43°W).
76. Orellana, Parque Nacional Yasuní, 35 km S Pompeya Sur (0.63°S, 76.47°W).

FRENCH GUIANA (FRANCE)
77. Camp du Tigre [4.91°N, 52.31°W; Jiménez et al., 2011].
78. Les Nouragues [4.08°N, 52.67°W; Voss and Emmons, 1996].
79. Paracou [5.28°N, 52.92°W; Simmons and Voss, 1998].
80. Pic Matecho [3.75°N, 53.03°W; Byles et al., 2013].
81. Saül [3.62°N, 53.22°W; Byles et al., 2013].

GUYANA
82. Potaro-Siparuni, Iwokrama Reserve, 25 km SSW Kurupukari [4.28°N, 58.47°W; ROM database].
83. Potaro-Siparuni, Iwokrama Reserve, 5 km SW Kurupukari [4.63°N, 58.72°W].
84. Upper Demerara-Berbice, West Pibiri (5.03°N, 58.63°W).
85. Upper Takutu-Upper Essequibo, Chodikar River, 55 km SW Gunn’s Strip (1.37°N, 58.77°W).
86. Upper Takutu-Upper Essequibo, Quarter Mile Landing, Rupununi River, 5 km S Arrai [3.92°N, 59.10°W; ROM database].

NICARAGUA
87. Zelaya, Río Siquía [presumably the stream near Rama at 12.15°N, 84.22°W; USBGN, 1976].

PANAMA
88. Bocas del Toro, Isla San Cristobal, Bocatorito [9.23°N, 82.27°W; Siegel and Olson, 2008].
89. Colón, Parque Nacional Soberanía, Pipeline Road, 1 km N Río Mendoza [9.17°N, 79.75°W; Vencel et al., 2017].

PARAGUAY
90. Amambay, 33 km SE Pedro Juan Caballero, Parque Nacional Cerro Corá [22.67°S, 55.98°W; Paynter, 1989].
91. Canindeyú, Reserva Morombí [24.72°S, 55.43°W; de la Sancha et al., 2012].
92. Itapúa, Reserva San Rafael [26.57°S, 55.68°W; de la Sancha et al., 2012].
93. San Pedro, Ganadera La Carolina (24.09°S, 56.41°W).

PERU
94. Amazonas, Huampami, Río Cenepa (4.47°S, 78.17°W).
95. Cajamarca, San Ignacio, Tabaconas, Cerro La Viuda (5.28°S, 79.32°W).
96. Cuzco, 2 km SSW Tangoshiari, 530 m (11.77°S, 73.33°W).
97. Cuzco, Paucartambo, Consuelo, 15.9 km SW Pilcopata, 1000 m [13.02°S, 71.49°W; FMNH database].
98. Cuzco, Ridge Camp, 1000 m (11.78°S, 73.33°W).
99. Cuzco, Vilcanota River just north of Cuzco [13.12°S, 72.65°W; Ceballos-Bendezú, 1982].
100. Huánuco, Río Cayumba, Hacienda Porvenir [9.43°S, 76.00°W; Stephens and Traylor, 1983].
101. Junín, “Camp 2” in Cordillera Vilcabamba (11.55°S, 73.63°W).
102. Loreto, 1.5 km N Teniente López [2.60°S, 76.12°W; Duellman and Mendelson, 1995].
103. Loreto, 25 km S Iquitos, Estación Biológica Alpahuayo [3.97°S, 73.42°W; Hice and Velazco, 2012].
104. Loreto, Quebrada Orán, ca. 5 km N Río Amazonas [3.48°S, 72.52°W; Patton et al., 2015].
105. Loreto, Río Gálvez, Nuevo San Juan [5.25°S, 73.17°W; Voss and Fleck, 2011].
106. Loreto, San Jacinto [2.32°S, 74.87°W; Duellman and Mendelson, 1995].
107. Loreto, Teniente López [2.60°S, 76.12°W; Duellman and Mendelson, 1995].
108. *Madre de Dios*, 15 km E Puerto Maldonado, Reserva Cuzco Amazónico [12.58°S, 69.08°W; Duellman and Koechlin, 1991].

109. *San Martín*, Moyobamba, Wagonki, Área de Conservación Municipal Mishquiyacu-Rumi-yacu y Almendra, 1000 m [= Waqanki at 6.08°S, 76.98°W, 970 m; Velazco and Patterson, 2019].

VENEZUELA

110. *Amazonas*, Cerro Neblina Camp V [0.83°N, 65.98°W; USNM database].

111. *Amazonas*, Cerro Neblina Camp VII [0.84°N, 65.97°W; Patton et al., 2015].

112. *Amazonas*, Cerro Neblina Camp XI [0.87°N, 65.97°W; Patton et al., 2015].

113. *Aragua*, Estación Biológica de Rancho Grande [10.37°N, 67.68°W; Patton et al., 2015].

114. *Bolívar*, 126 km SW Río Cuyuní, 1400 m [5.68°N, 61.32°W; MVZ database].

115. *Falcón*, Serranía de San Luis, 9 km N Cabure [11.23°N, 69.61°W; Patton et al., 2015].
### APPENDIX 2

**Primers Used to Amplify CYTB from Degraded DNA**

| Primer name       | Primer sequence                  |
|-------------------|----------------------------------|
| CYTB-F1-Didelphidae | 5´ ATAACCTATGGCATGAAAAACCATTGTTG |
| CYTB-R1-Didelphidae | 5´ CCTTCATTGCTGGCTTTACAAGGC      |
| CYTB-420R-Didelphidae | 5´ GCTCCTCAGAAGGATATTGTCTCTCA   |
| CYTB-730R-Marmosa  | 5´ TCWCCTAATARRTCWGGTARATATTTGC  |
| CYTB-540F-Marmosa  | 5´ GAGGAGGMTTYTCHGTGTGATAAAGC    |
| CYTB-650F-Marmosa  | 5´ CTATTCCCTACGAAACAGGCTC        |
| CYTB-217R-Marmosa  | 5´ TCTGTAGCCCCAYATYTGCGWGAYG     |
| CYTB-70F-Marmosa   | 5´ CCMTCAATATTTCAGCCGTATG        |
| CYTB-365R-Micoureus | 5´ CAGTAAGTAGAAAGRATAACTCC       |
| CYTB-495R-Micoureus | 5´ CCTCARATTTCATCAACTAATG       |
| CYTB-220F-Micoureus | 5´ TTAACAGCATTYTCATCTGTAGC       |
APPENDIX 3
Gazetteer of Examined Specimens of the Rapposa Group

This gazetteer includes all localities from which we personally examined specimens of the Rapposa Group of the subgenus *Micoureus*. Italicized place names are those of currently recognized departments, provinces, or states; boldface identifies collection localities as they appear in the text of this report. Unless recorded by the collector, geographic coordinates and elevation above sea level are provided in square brackets with a cited secondary source for these data. The name(s) of species collected at each locality are separated from the locality name and geographic data by a colon, followed by the name(s) of the collector(s) and date(s) of collection in parentheses. Numbers identify locality symbols plotted on maps that accompany the species accounts in our text (figs. 12, 17).

ARGENTINA
1. **Jujuy**, Río San Francisco, *Altura de Yuto* [23.63°S, 64.47°W; Gardner, 2008], 500 m: *Marmosa rapposa* (E. Budin, 23 July 1919).

BOLIVIA
2. **Beni**, 5 km N Estancia El Porvenir, Isla de Bosque [14.51°S, 66.35°W], 201 m: *Marmosa rapposa* (J. Salazar, 10 August 1988).
3. **Chuquisaca**, 2 km E Chuyayacu [19.72°S, 63.85°W], 1200 m: *Marmosa rapposa* (E. Palma, 9 August 1990).
4. **Chuquisaca**, El Limón [20.72°S, 64.32°W], left bank Río Santa Marta, 15.6 km N El Palmar, 900 m: *Marmosa rapposa* (L.H. Emmons, 26 May 1995).
5. **Chuquisaca**, Rinconada del Bufete [20.83°S, 64.37°W; Schulenberg and Awbrey, 1997], 2050 m: *Marmosa rapposa* (L.H. Emmons, 19 May 1995).
6. **Chuquisaca**, Río Limón [19.55°S, 64.13°W], 1300 m: *Marmosa rapposa* (R.L. Cuéllar, 3 August 1990).

7. **Cochabamba**, Serranía Mosetenes [16.23°S, 66.42°W; Tarifa et al., 2008]: *Marmosa rapposa* (F. Guerra, 6–7 September 2003).
8. **Cochabamba**, 4.4 km by road N Tablas Monte, Río Jatun Mayu [17.07°S, 66.00°W], 1833 m: *Marmosa rapposa* (J.L. Dunnum, 13–16 July 1993; S.C. Peurach, 14 July 1993).
9. **Cochabamba**, 9.5 km NE Tablas Monte, Río Jatun Mayu [17.03°S, 65.98°W], 1500 m: *Marmosa rapposa* (J.L. Dunnum, 17 July 1993; C.T. Seaton, 16 July 1993; J. Peralta, 16 July 1993).
10. **La Paz**, 4 km NW Alcoche [15.67°S, 67.70°W], 425 m; Anderson, 1997]: *Marmosa rapposa* (G.K. Creighton, 10–11 May 1978).
11. **La Paz**, 20 km NNE Caranavi [15.70°S, 67.58°W, 2000 ft; Anderson, 1997]: *Marmosa rapposa* (G.K. Creighton, 6–7 May 1978).
12. **La Paz**, Cajuata [16.82°S, 67.25°W, ca. 1800 m; Paynter, 1992]: *Marmosa rapposa* (collector and dates unknown).
13. **La Paz**, La Reserva [15.73°S, 67.52°W], 840–950 m: *Marmosa rapposa* (AMNH/MSB expedition, 24–29 July 1992, 18–22 May 1996).
14. **La Paz**, 1 km S La Reserva [15.75°S, 67.52°W; Anderson, 1997], 1100 m: *Marmosa rapposa* (R.J. Vargas, 21 September 1992; E. Yenssen, 20 September 1992).
15. **La Paz**, Los Molinos de Titiamaya [ca. 16.92°S, 67.19°W; Mapcarta website], 2744 m: *Marmosa rapposa* (S.F. Moolenijzer, 1 August 1993).
16. **La Paz**, Ñequejahuira [ca. 16.33°S, 67.83°W; Paynter, 1992], 8000 ft: *Marmosa rapposa* (G.H.H. Tate, 23 May 1926).
17. **La Paz**, 1 mi W Puerto Linares [15.48°S, 67.52°W, ca. 500 m; Anderson, 1997]: *Marmosa rapposa* (W.D. Webster, 23 July 1979).
18. **Santa Cruz**, 53 km E Boyuibe [20.45°S, 62.83°W], 600 m: *Marmosa rappospa* (E. Palma, 6 July 1991).
19. **Santa Cruz**, Buenavista [17.45°S, 63.67°W; Anderson, 1997], 500 m: *Marmosa rapposa* (F. Steinbach, 1926–1929; J. Steinbach, 1920–1924).
20. Santa Cruz, Cerro Hosane [17.42°S, 64.00°W; Dirksen and De la Riva, 1999], 1300 m: *Marmosa rapposa* (J. Steinbach, 13–18 August 1917).

21. Santa Cruz, 2 km N Chapare River mouth [15.95°S, 64.68°W; Anderson, 1997]: *Marmosa rapposa* (D.E. Añez, 13–18 August 1917).

22. Santa Cruz, ca. 54 km S Chapare River mouth [16.48°S, 64.73°W; Anderson, 1997]: *Marmosa rapposa* (A. Ximénez, 22 July 1965).

23. Santa Cruz, 1 km NE Estancia Cuevas (18.18°S, 63.73°W), 1300 m: *Marmosa rapposa* (J.L. Dunnum, 25 May 1991).

24. Santa Cruz, 27 km SE Santa Cruz (17.97°S, 63.05°W), 365 m: *Marmosa rapposa* (B.J. Hayward, 29 May 1988).

25. Santa Cruz, Warnes [17.50°S, 63.17°W; Paynter, 1992]: *Marmosa rapposa* (R. Villalobos, 10 November 1991).

26. Tarija, 3 km NW Carapari (21.80°S, 63.78°W), 850 m: *Marmosa rapposa* (S. Anderson, 16 August 1991).

27. Tarija, 5 km NNW Entre Ríos (21.48°S, 64.20°W), 1600 m: *Marmosa rapposa* (E. Peñaranda, 27 January–1 February 1952).

**BRAZIL**

28. Acre, Igarapé Porongaba, right bank Rio Juruá [8.67°S, 72.78°W; Patton et al., 2000]: *Marmosa rutteri* (M.N.F. da Silva, 22 February 1992).

29. Acre, Nova Vida, right bank Rio Juruá [8.37°S, 72.82°W; Patton et al., 2000]: *Marmosa rutteri* (M.N.F. da Silva, 13 March 1992).

30. Amazonas, Boa Esperança, right bank Rio Juruá [6.53°S, 68.92°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 13 November 1991).

31. Amazonas, Igarapé Nova Empressa, left bank Rio Juruá [6.80°S, 70.73°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 31 August–3 September 1991).

32. Amazonas, opposite Altamira, left bank Rio Juruá [6.58°S, 68.93°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 13 November 1991).

33. Amazonas, Penedo, right bank Rio Juruá [6.83°S, 70.75°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 29 August–7 September 1991).

34. Mato Grosso, 264 km N Xavantina (12.85°S, 51.77°W, ca. 1750 ft): *Marmosa rapposa* (R.L. Jackson, 22 July 1968).

35. Mato Grosso do Sul, Corumbá, São Marcos Road, 10 km NE Urucum [19.10°S, 57.58°W; Gardner, 2008]: *Marmosa rapposa* (M.L. Kuns, 15 September 1965).

**COLOMBIA**

36. Amazonas, Leticia [4.15°S, 69.95°W, ca. 100 m; Paynter, 1997]: *Marmosa rutteri* (R.H. Rageot, March 1979).

37. Caquetá, Tres Troncos [0.13°N, 74.68°W; Paynter, 1992]: *Marmosa rapposa* (R. Villalobos, 27 January–1 February 1952).

**ECUADOR**

38. Napo, “near the river Napo” [0.98°S, 77.82°W; Voss, 1988], 2400–3000 feet: *Marmosa rutteri* (L. Söderström, June 1921–January 1923). Probably near Tena, which is close to where the old trail from Baeza to Puyo crossed the Napo.

39. Orellana, San José de Payamino [0.50°S, 77.28°W; Paynter, 1993], 300 m: *Marmosa rutteri* (R.M. Timm, 25 January 1984).

40. Sucumbios, Boca Lagarto Cocha [= Boca Rio Lagartococha at 0.65°S, 75.27°W; Paynter, 1993]: *Marmosa rutteri* (Olaña y Hijos, 15–16 January 1926). Misspelled “Voca Lagarto Cocha” on the original skin tags, this locality is on the Ecuadorian-Peruvian frontier, which is formed by the Río Lagartococha. As discussed by Wiley (2010: 37–38), it is not actually known whether specimens from this locality were collected on the Ecuadorian or the Peruvian side of the river.

**PARAGUAY**

41. Alto Paraguay, Puerto Casado [22.33°S, 57.92°W; Paynter, 1989], 150 m: *Marmosa rapposa* (P. Willim, 6 July 1960).
42. Amambay, Parque Nacional Cerro Corá [ca. 22.67°S, 55.98°W; Paynter, 1989]: Marmosa rapposa (E. Palma at “33 km SE Pedro Juan Caballero,” 26 May 1991; G.K. Creighton, 1979).

43. San Pedro, Ganadera La Carolina (24.09°S, 56.41°W): Marmosa rapposa (G. D’Elía, 29–31 March 2001).

44. Amazonas, La Poza [4.02°S, 77.77°W, 170 m; Patton et al., 1982] on Río Santiago: Marmosa rutteri (J.L. Patton, 17–24 August 1979).

45. Amazonas, mouth of Río Cenepa [4.58°S, 78.20°W; Stephens and Traylor, 1983]: Marmosa rutteri (J.M. Schunke, 24 October 1929). The original collector’s skin tag on AMNH 98712 gives this locality as “Mündung Cenipa Fluss.”

46. Amazonas, vicinity of Huampami, Río Cenepa, 700 ft [4.47°S, 78.17°W, 210 m; Patton et al., 1982]: Marmosa rutteri (J.L. Patton, 9 July 1977, 10 July–11 August 1978).

47. Amazonas, vicinity of Kayamas [4.45°S, 78.17°W; MVZ database], Río Cenepa: Marmosa rutteri (J.L. Patton, 2 August 1977).

48. Ayacucho, Santa Rosa on Río Santa Rosa (12.70°S, 73.72°W), ca. 800 m: Marmosa rutteri (J.P. O’Neill, 11 July 1970). The collector’s skin tag gives the longitude as 76°43’W, an obvious lapsus: the department of Ayacucho does not extend to 76°W, and Santa Rosa is known to be near Luisana (ca. 12.65°S, 73.73°W; Stephens and Traylor, 1983) on the Río Apurimac.

49. Cuzco, Hacienda Cadena [13.40°S, 70.72°W; Stephens and Traylor, 1983], 1000 m: Marmosa rapposa (C. Kalinowski, 22 December 1948, 25 November 1949).

50. Cuzco, La Convención, Kimbiri, Llaqtahuamaná [ca. 12.87°S, 73.52°W; Gardner, 2008], 1710 m: Marmosa rapposa (E. Vivar, 25 June 1998).

51. Cuzco, Quincemil [13.27°S, 70.63°W; Stephens and Traylor, 1983], 680 m: Marmosa rapposa (C. Kalinowski, 8 August 1953).

52. Cuzco, Vilcanota River just north of Cuzco [probably near Huadquiña at 13.12°S, 72.65°W; Stephens and Traylor, 1983], 1500 m: type locality of Marmosa rapposa (O. Garlepp, December 1897). This locality was recorded as “Vilcanota nord[l]ich, v[on].” Cuzco, Peru, 1500 m on original labels still attached to the paratypes.

53. Huánuco, Chinchavita [= Chinchavito, at 9.48°S, 75.92°W, ca. 1000 m; Stephens and Traylor, 1983]: Marmosa parda (R.W. Hendee, 26–29 December 1926).

54. Huánuco, Huachipa [ca. 9.50°S, 75.87°W, 855–1405 m; Stephens and Traylor, 1983]: Marmosa parda (I.T. Zimmer, 28 September 1922).

55. Huánuco, Río Cayumba, Hacienda Porvenir [ca. 6 km above Hacienda Éxito at 9.43°S, 76.00°W; Stephens and Traylor, 1983], 3000 ft: Marmosa parda (E. Heller, 18 August 1922).

56. Huánuco, Río Chinchao, Hacienda San Antonio [ca. 9.55°S, 75.87°W; Stephens and Traylor, 1983], 3000 ft: Marmosa parda (E. Heller, 3–19 September 1922).

57. Junín, “Camp Two” in Cordillera Vilcabamba (11.55°S, 73.63°W, 2050 m): Marmosa rapposa (L.H. Emmons, 28 June–1 July 1997; L. Luna W., 1 July 1997). “Camp Two” is the name assigned by Alonso et al. (2001) to the site with these coordinates visited by Conservation International’s Rapid Assessment Program (CI-RAP) expedition in 1997. Expedition personnel did not use this place name on specimen tags or in field notes, which only identified this camp by its coordinates and elevation.

58. Junín, Utcuyacu [ca. 11.20°S, 75.47°W, 1400–1465 m; Stephens and Traylor, 1983], including nearby sublocality 15 km by road SW San Ramón (1400 m): Marmosa rapposa (H. Watkins, 25 November–6 December 1919; G.K. Creighton, 19–20 May 1980).

59. La Libertad, Utcubamba, on trail to Ongón [ca. 8.27°S, 76.97°W; Stephens and Traylor, 1983], 1825 m: Marmosa parda (L.J. Barkey, 30 October 1979).
60. **Loreto, Boca Río Curaray** [2.37°S, 74.08°W; Wiley, 2010]: *Marmosa rutteri* (Olalla y Hijos, 29 October 1925–16 January 1926). See Wiley (2010: 34–37) for a discussion of this locality, which the Olallas consistently misspelled “Voca R. Curaray,” and which has often been misinterpreted as being in Ecuador.

61. **Loreto, Nuevo San Juan** [5.25°S, 73.17°W; Voss and Fleck, 2011], Río Gálvez: *Marmosa rutteri* (D.W. Fleck, 25 June 1995, 10 July 1996, 21–27 October 1999).

62. **Loreto, Orosa** [ca. 3.53°S, 72.18°W; Wiley, 2010], Río Amazonas: *Marmosa rutteri* (Olalla y Hijos, 26 October 1926).

63. **Loreto, Otorongo** [= Fuerte Militar Otorongo at 3.95°S, 73.37°W; Hice and Velasco, 2012], “km 21 carretera Iquitos-Nauta,” 120 m: *Marmosa rutteri* (W. Sánchez, 14 August 2003).

64. **Loreto, Iquitos, Pampa Chica** [ca. 3.75°S, 73.20°W, 106 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (C. Kalinowski, 29 August 1956). On modern maps “Pampachica” is shown as a suburb of Iquitos; in Kalinowski’s day it was probably a village just outside the city, whose coordinates and elevation are used as approximations for this locality.

65. **Loreto, Iquitos, “Triunfo Chacras”** [ca. 4.15°S, 73.47°W; Hurtado et al., 2014]: *Marmosa rutteri* (C.L. Hice, 4 February 2003). The locality name presumably refers to agricultural fields (chacras) near El Triunfo, a small community about 48 km SW of Iquitos on the road to Nauta.

66. **Loreto, Río Itaya, San Antonio** [4.17°S, 73.33°W, 150 m; Robinson and Wunderlin, 2005]: *Marmosa rutteri* (J.M. Schunke, 25 October 1927).

67. **Loreto, San Jerónimo**, 1000 ft [7.92°S, 74.91°W; Patton et al., 2015]: *Marmosa rutteri* (R.W. Hendee, 29 November–10 December 1927).

68. **Loreto, Sarayacu** [6.73°S, 75.10°W, 125 m; Stephens and Traylor, 1983], Río Ucayali: *Marmosa rutteri* (Olalla y Hijos, 2–27 April 1927).

69. **Loreto, Yurimaguas** [5.90°S, 76.08°W, 182 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (M.P. Anderson, 29 November–10 December 1927).

70. **Madre de Dios, Blanquillo** [12.43°S, 70.70°W, 273 m; S. Solari, personal commun.]: *Marmosa rutteri* (W. Sánchez, 14 August 2003).

71. **Madre de Dios, 15 km E Puerto Maldonado, Reserva Cuzco Amazónico** [12.55°S, 69.05°W, ca 200 m; Duellman and Koechlin, 1991]: *Marmosa rutteri* (C.A. Schmidt, R.M. Timm, and N. Woodman; 1989–1990).

72. **Puno, 11 km NNE Ollachea** [13.72°S, 70.44°W; MVZ collection database], 1880 m: *Marmosa rapposa* (J.L. Patton, 10–13 July 1986).

73. **Puno, 14 km W Yanahuaya** [14.27°S, 69.33°W; MVZ collection database], 2210 m: *Marmosa rapposa* (J.L. Patton, 28 July 1986).

74. **Ucayali, Tushemo** [8.60°S, 74.32°W, 225 m; Gardner, 2008], near Masisea: *Marmosa rutteri* (L. Rutter, 10 September 1923).

75. **Ucayali, Río Ucayali, Yarinacocha** [8.25°S, 74.72°W, ca. 100 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (J.M. Schunke, 5 June 1945).
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ON THE COVER: Holotype skull of Marmosa rapposa Thomas, 1899, an adult female specimen collected by Otto Garlepp in Cuzco de-
partment, Peru (BMNH 98.11.6.13).