Systematics of the American marsupial genus *Marmosops* (Didelphidae: Thylamyini) based on molecular and morphological data

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DEDICATION

This thesis is dedicated to my mom, Carito and Titi, three women from whom I have received the most important "lectures" of my life.

ABSTRACT

This research presents the results of a collaborative work with Sharon A. Jansa and Robert S. Voss on the taxonomy and systematics of the American marsupials of the genus *Marmosops* and some of its closely allied forms. Chapter 1 evaluates the species-level diversity of the genus *Marmosops* using mitochondrial sequences from >200 specimens, including exemplars of every currently recognized species together with a dense intraspecific sampling. These data are analyzed using the General Mixed Yule Coalescent (GMYC) model and the results suggest that the genus could be twice as speciose as currently recognized. Additionally, the phylogenetic relationships within *Marmosops* are evaluated using sequences of the Breast Cancer Type 1 susceptibility gene (BRCA1). These analyses reveal a basal dichotomy between two ancient, morphologically diagnosable clades. Based on the latter results, a taxonomic proposal is made with the description of a new subgenus, *Sciophanes*. Chapter 2 includes a revision of the species of subgenus *Sciophanes* in the context of the molecular analyses of Chapter 1. This revision recognizes 12 valid species in three monophyletic species groups: the Parvidens Group (including *M. pakaraimae*, *M. parvidens*, and *M. pinheiroi*), the Fuscatus Group (*M. carri*, *M. fuscatus*, *M. handleyi*, and *M. invictus*), and the Bishopi Group (*M. bishopi*, *M. juninensis*, *M. ojastii*, and two new species). For each species, information about type material, ecogeographic distribution, and diagnostic morphological characters is presented. Chapter 3 evaluates the phylogenetic relationships of the tribe Thylamyini (a clade that includes the genus *Marmosops*) by

using a multi-locus dataset. In particular, this chapter aims to resolve evolutionary relationships of the thylamyine genus *Chacodelphys*, a monotypic genus that has remained a phylogenetic enigma since its original description in 1930. A previous understanding of the species-level diversity within *Marmosops* is crucial for constructing a phylogeny of Thyamyini because this genus accounts for almost 45% of the diversity within the tribe. Phylogenetic analyses of these data convincingly resolves *Chacodelphys* as the sister taxon of *Cryptonanus*, a genus with which it had not previously been thought to be closely related, and supports most of the previous phylogenetic arrangements obtained within *Marmosops.*

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INTRODUCTION

American marsupials of the genus *Marmosops* Matschie, 1916, are small (<200 g) opossums distributed from Panama to southern Bolivia and southeastern Brazil. Although the genus is mostly restricted to wet forests, species of *Marmosops* occur in a variety of lowland and highland regions, including the Andes, Pantepui, Amazonia, and the Atlantic Forest (Emmons, 1997; Gardner and Creighton, 2008; Voss et al., 2013). Most of these areas are now recognized as important biodiversity hotspots due to their high levels of species richness and endemism (Myers, 1988; Myers et al., 2000; Loyola et al., 2009). Given this widespread distribution, *Marmosops* is an attractive group to undertake studies on Neotropical diversification processes, but such research is hindered by the fact that we do not yet understand species limits or phylogenetic relationships within the genus.

Current usage of *Marmosops* as a valid genus dates from Gardner and Creighton (1989), and the morphological diagnosis and phylogenetic position of the genus within the family Didelphidae was recently assessed by Voss and Jansa (2009). Although 39 nominal taxa have been referred to *Marmosops*, many of these names are thought to be synonyms of just 17 currently recognized species (Voss and Jansa, 2009; Voss et al.,

2013; García et al., 2014) (table 1). The last comprehensive taxonomic treatment of most of the species now referred to *Marmosops* was Tate's (1933) monographic revision of "mouse opossums" (*Marmosa* sensu lato), with subsequent publications on the systematics and taxonomy of this group limited to lists of species (Cabrera, 1958; Gardner and Creighton, 1989; Gardner, 2005), descriptions of new taxa (Handley and Gordon, 1979; Pine, 1981; Gardner, 1990; Voss et al., 2013; García et al., 2014), re-descriptions based on newly collected material (Díaz-N. et al., 2011), revisions of locally co-occurring species (Patton et al., 2000; Voss et al., 2001; Voss et al., 2004), phylogeographic studies (Mustrangi and Patton, 1997; Steiner and Catzeflis, 2004), and phylogenetic analyses based on a few exemplar species (Patton et al., 1996; Jansa and Voss, 2000; Voss and Jansa, 2003, 2009; Steiner et al., 2005; Flores, 2009; Nascimento et al., 2015). To date, no study has attempted to assess the validity of all of the currently recognized species of *Marmosops*, nor has any phylogenetic analysis included more than 50% of them. That the genus is still taxonomically problematic is suggested by improbably wide geographic distributions of some species, high levels of intraspecific molecular variation in others, and numerous specimens that cannot be assigned to any currently recognized taxon.

Table 1. Valid species and synonyms currently referred to the genus *Marmosops* (after Voss and Jansa, [2009] but including subsequently described forms).

Taxa
M. bishopi Pine, 1981
M. cracens Handley and Gordon, 1979
M. creightoni Voss *et al.*, 2004
M. fuscatus Thomas, 1896
carri J.A. Allen and Chapman, 1897
perfuscus Thomas, 1924
M. handleyi Pine, 1981
M. impavidus Tschudi, 1845
caucae Thomas, 1900
celicae Anthony, 1922
madescens Osgood, 1913
oroensis Anthony, 1922
sobrinus Thomas, 1913
ucayalensis Tate, 1931
M. incanus Lund, 1840
bahiensis Tate, 1931
scapulatus Burmeister, 1856
M. invictus Goldman, 1912
M. juninesis Tate, 1931
M. neblina Gardner, 1990
M. noctivagus Tschudi, 1845
albiventris Tate, 1931
collega Thomas, 1920
dorothea Thomas, 1911
keaysi J.A. Allen, 1900
leucastrus Thomas, 1927
lugendus Thomas, 1927
neglectus Osgood, 1915
politus Cabrera, 1913
purui Miller, 1913
stollei Miranda-Ribeiro, 1936
yungasensis Tate, 1931
M. ocellatus Tate, 1931
M. ojastii García *et al.,* 2014
M. pakaraimae Voss *et al.*, 2013
M. parvidens Tate, 1931
M. paulensis Tate, 1931
M. pinheiroi Pine, 1981
woodalli Pine, 1981

In this study, I assess species diversity in *Marmosops* based on analyses of the mitochondrial cytochrome-*b* gene (CYTB). Given its high mutation rate and relatively

rapid coalescent time (Brown et al., 1979; Moore, 1995), mitochondrial DNA (mtDNA) is the most widely used marker for assessing species limits of didelphid marsupials (Mustrangi and Patton, 1997; Patton et al., 2000; Solari, 2010; Giarla et al., 2010; Gutiérrez et al., 2010; de la Sancha et al., 2012). I sequenced CYTB from holotypes, paratypes, or topotypical material of most of the 39 nominal taxa in the genus, and sequenced numerous specimens from as many localities as possible of geographically widespread taxa. Because preliminary analyses of mtDNA sequences suggested a basal dichotomy in the genus, and because I was unable to obtain CYTB sequence data from one species, I additionally sequenced a large fragment of the nuclear Breast Cancer Activating 1 gene (BRCA1 exon 11) from one representative of each putative species identified by analyses of cytochrome-*b*. Together, these molecular data provide important new perspectives on both recent diversity and ancient-lineage membership. As a basis for future revisionary work, I name a new subgenus and discuss the probable application of names to the CYTB clades recovered in these analyses.

METHODS

Taxon Sampling and specimen identification

I sequenced 151 samples, consisting either of preserved tissue or dried fragments of museum skins, from at least one representative specimen of every currently recognized species of *Marmosops* (table 2). For most species, I sequenced multiple specimens, and made a particular effort to obtain sequence data from material collected throughout the range of widespread forms. In the absence of any recent comprehensive revision, I made a special attempt to sequence representative material of nominal taxa currently treated as

subjective junior synonyms (ICZN, 1999) that might provide appropriate names for previously unrecognized lineages. In total, I obtained partial or complete CYTB sequences for 31 nominal forms of *Marmosops*: 5 sequences from holotypes, 1 from a paratype, and 25 from topotypical material (see below). To further increase my ingroup geographic sampling, I downloaded an additional 62 CYTB sequences from Genbank and other sources for a total mtDNA dataset of 213 sequences. I subsequently obtained BRCA1 sequence data from 35 specimens—one each from most of the haplotype groups (putative species) identified from phylogenetic analyses of the CYTB data—and also obtained a BRCA1 sequence from *M. juninensis*, a species from which I was unable to amplify CYTB. For all of my phylogenetic analyses, I obtained CYTB and/or BRCA1 sequences from other members of the tribe Thylamyini and more distantly related didelphids used as outgroups (Table 2).

Laboratory methods and sequence alignment

In order to associate haplogroups (putative species; see below) with named taxa, I examined type specimens (Voss et al., 2004: table 1) and matched them with relevant voucher material based on measurements and qualitative morphological characters described by Voss et al. (2004, 2013), Voss and Jansa (2009), and Díaz-N. et al. (2011). Haplogroups that could not be confidently associated with Latin epithets were provisionally labeled with geographic or alphabetic designations.

Table 2. Sequences of *Marmosops* and outgroups included in this report. Samples in bold font identify sequences used in GMYC analyses. Sequences amplified from skins lack information in the Tissue column. In the Locality column, numbers in parentheses correspond to localities mapped in figures 1–3 and are listed in the gazetteer (Appendix 1). All voucher specimens and associated tissues sampled for this study are preserved in the following collections: 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 (Pittsburg); CTUA, Colección Teriológica Universidad de Antioquia (Medellín); EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay); FMNH, Field Museum of Natural History (Chicago); ICN, Instituto de Ciencias Naturales (Bogotá); KU, Biodiversity Institute, University of Kansas (Lawrence); LSU, Louisiana State University, Museum of Natural Science (Baton Rouge); MHNUC, Museo de Historia Natural, Universidad de Caldas (Manizales); MNK, Museo de Historia Natural Noel Kempff Mercado (Santa Cruz); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); MZUSP, Museu de Zoologia Universidade de São Paulo (São Paulo); QCAZ, Museo de Zoología, Pontificia Universidad Católica del Ecuador (Quito); ROM, Royal Ontario Museum (Toronto); TTU, Museum of Texas Tech University (Lubbock); UMMZ, University of Michigan, Museum of Zoology (Ann Arbor); USNM, United States National Museum of Natural History (Washington).

Putative species	Voucher	Tissue	Locality	CYTB	BRCA1	Source
bishopi A	**MVZ 190283**	**JLP15826**	Brazil: Amazonas (20)	1149	-	This report
bishopi A	**MPEG 28041**	**JUR476**	Brazil: Amazonas (22)	1149	-	Patton et al. (2000)
bishopi A	**MVZ 191188**	**MNFS1757**	Brazil: Amazonas (22)	1149	-	This report
bishopi A	**FMNH 169800**	**SS1796**	Peru: Madre de Dios (110)	1149	-	This report
bishopi A	FMNH 169801	SS1856	Peru: Madre de Dios (110)	635	-	This report
bishopi A	FMNH 203328	PMV2365	Peru: San Martín (116)	1149	876	This report
bishopi A	**FMNH 203509**	**PMV2361**	Peru: San Martín (116)	1149	-	This report
bishopi B	**AMNH 268938**	**NK25679**	Bolivia: La Paz (6)	1149	-	This report
bishopi C	**ICN 18338**	**-**	Colombia: Amazonas (50)	629	-	This report
bishopi D	**CBF 7531**	**EY1909**	Bolivia: Cochambaba (2)	1149	-	This report
bishopi D	**MSB 55843**	**NK12946**	Bolivia: Santa Cruz (18)	1149	-	This report
bishopi E	**MNK**	**LHE1498**	Bolivia: Santa Cruz (14)	423	-	This report
bishopi E	USNM 584464	LHE1541	Bolivia: Santa Cruz (14)	1149	612	This report
bishopi F	**TTU 101239**	**TK75131**	Peru: Loreto (104)	1149	882	This report
bishopi F	**KU 157969**	**RMT4042**	Peru: Loreto (107)	391	-	This report

bishopi F	KU 157971	RMT4091	Peru: Loreto (108)	1149	-	This report
carri	**AMNH 188353**	**-**	Trinidad and Tobago: Trinidad (122)	379	-	This report
carri	**EBRG 27001**	**EGC137**	Venezuela: Aragua (124)	1149	885	This report
carri	**USNM 406931**	**-**	Venezuela: Monagas (129)	379	-	This report
carri	**USNM 372933**	**-**	Venezuela: Trujillo (131)	379	-	This report
carri	USNM 372934	-	Venezuela: Trujillo (131)	379	-	This report
caucae A	**FMNH 70939**	**-**	Colombia: Antioquia (53)	1149	-	This report
caucae A	**CTUA 427**	**JFD125**	Colombia: Antioquia (55)	1149	882	This report
caucae A	**ICN uncatalogued**	**BVG257**	Colombia: Caldas (58)	1149	-	This report
caucae A	ICN uncatalogued	BVG258	Colombia: Caldas (58)	1149	-	This report
caucae A	ICN uncatalogued	BVG272	Colombia: Caldas (58)	1149	-	This report
caucae A	**USNM 280889**	**-**	Colombia: Cesar (63)	1000	-	This report
caucae A	**FMNH 70930**	**-**	Colombia: Huila (64)	1000	-	This report
caucae A	**FMNH 70933**	**-**	Colombia: Huila (64)	1000	-	This report
caucae A	**FMNH 70938**	**-**	Colombia: Huila (65)	1000	-	This report
caucae A	FMNH 70944	-	Colombia: Huila (66)	1000	-	This report
caucae A	**AMNH 136157**	**-**	Colombia: Meta (67)	538	-	This report
caucae A	**AMNH 139226**	**-**	Colombia: Meta (67)	194	-	This report
caucae A	**QCAZ 8665**	**KMH2254**	Ecuador: Cotopaxi (70)	1149	-	This report
caucae A	**QCAZ 8666**	**MP59**	Ecuador: Cotopaxi (70)	1149	-	This report
caucae A	QCAZ 8667	MP73	Ecuador: Cotopaxi (70)	1149	-	This report
caucae A	QCAZ 8668	TK149092	Ecuador: Cotopaxi (70)	1149	-	This report
caucae A	**AMNH 47180**	**-**	Ecuador: El Oro (71)	878	-	This report
caucae A	**AMNH 47182**	**-**	Ecuador: Loja (72)	194	-	This report
caucae A	**QCAZ 8836**	**DFA413**	Ecuador: Morona-Santiago (73)	1149	-	This report
caucae A	**USNM 574501**	**JFJ668**	Ecuador: Pastaza (76)	1149	-	This report
caucae A	TTU 84898	TK104126	Ecuador: Pastaza (77)	1149	-	This report
caucae A	TTU 84923	TK104151	Ecuador: Pastaza (77)	1149	-	This report

caucae A	**USNM 513424**	**-**	Ecuador: Zamora-Chinchipe (78)	538	-	This report
caucae A	**ROM 116281**	**F-48823**	Panama: Darién (88)	1149	-	This report
caucae A	**AMNH 268099**	**DPL233**	Peru: Cajamarca (91)	1149	-	This report
caucae A	**UMMZ 176705**	**LLW1214**	Peru: Cajamarca (92)	1149	-	This report
caucae A	UMMZ 176576	LLW1079	Peru: Cajamarca (93)	1149	-	This report
caucae A	**UMMZ**	**LHL111**	Peru: Cajamarca (94)	1149	-	This report
caucae A	UMMZ	RCO1031	Peru: Cajamarca (94)	1149	-	This report
caucae A	UMMZ 176774	LLW991	Peru: Cajamarca (95)	1149	-	This report
caucae A	**FMNH 81444**	**-**	Peru: Piura (112)	1000	-	This report
caucae A	**USNM 560732**	**ALG14410**	Venezuela: Amazonas (123)	1149	-	This report
caucae A	USNM 560735	ALG14436	Venezuela: Amazonas (123)	1149	-	This report
caucae A	**USNM 418507**	**-**	Venezuela: Táchira (130)	383	-	This report
caucae A	USNM 418509	-	Venezuela: Táchira (130)	362	-	This report
caucae B	**MVZ 190270**	**MNFS1067**	Brazil: Acre (19)	1149	-	This report
caucae B	**MVZ 190272**	**JLP15450**	Brazil: Amazonas (21)	1149	882	This report
caucae B	**FMNH 203324**	**PMV2408**	Peru: San Martín (115)	1149	-	This report
caucae B	**FMNH 203325**	**RCO1009**	Peru: San Martín (115)	1149	-	This report
caucae B	FMNH 203326	SVS419	Peru: San Martín (115)	1149	-	This report
"Condor A"	**USNM 581930**	**LHE1094**	Peru: Amazonas (90)	1149	882	This report
"Condor B"	**QCAZ 8844**	**DFA421**	Ecuador: Morona-Santiago (73)	1149	-	This report
"Condor B"	QCAZ 8850	DFA427	Ecuador: Morona-Santiago (73)	1149	882	This report
creightoni	**CBF 7641**	**GVA314**	Bolivia: La Paz (7)	1149	882	This report
creightoni	**CBF 6552**	**EY1705**	Bolivia: La Paz (9)	1149	-	This report
"East Magdalena"	**FMNH 70926**	**-**	Colombia: Boyacá (57)	391	-	This report
"East Magdalena"	**ICN 18788**	**-**	Colombia: Santander (68)	191	-	This report
"East Magdalena"	ICN 19924	-	Colombia: Santander (69)	379	882	This report
fuscatus	**USNM 418503**	**-**	Venezuela: Falcón (126)	619	-	This report
fuscatus	USNM 442719	-	Venezuela: Falcón (126)	579	-	This report

fuscatus	**AMNH 276509**	**JOG4531**	Venezuela: Falcón (127)	1149	885	This report
fuscatus	**BMNH 1903.1.5.2**	**-**	Venezuela: Mérida (128)	1008	-	This report
"Gálvez"	AMNH 272760	RSV2202	Peru: Loreto (106)	1149	-	This report
"Gálvez"	**MUSM 13284**	**RSV2114**	Peru: Loreto (106)	1148	882	This report
handleyi	FMNH 69823	-	Colombia: Antioquia (54)	208	-	This report
handleyi	**CTUA 413**	**JFD122**	Colombia: Antioquia (55)	1149	-	This report
handleyi	CTUA 415	JFD162	Colombia: Antioquia (56)	1149	879	This report
incanus A	**MZUSP 29173**	**MAM186**	Brazil: Rio de Janeiro (42)	1149	882	Voss *et al.* (2013)
incanus A	MZUSP 29174	MAM188	Brazil: Rio de Janeiro (42)	400	-	Mustrangi & Patton (1997)
incanus B	MZUSP 29186	MAM5	Brazil: São Paulo (45)	777	-	Mustrangi & Patton (1997)
incanus B	MZUSP 29170	MAM137	Brazil: São Paulo (46)	397	-	Mustrangi & Patton (1997)
incanus B	MVZ 182061	MAM71	Brazil: São Paulo (47)	718	-	Mustrangi & Patton (1997)
incanus B	**Not catalogued**	**CRS279**	Brazil: São Paulo (48)	1149	705	This report
incanus B	MVZ 192502	JLP16299	Brazil: São Paulo (49)	400	-	Mustrangi & Patton (1997)
incanus C	-	MF26	Brazil: Espírito Santo (27)	398	-	Mustrangi & Patton (1997)
incanus C	MZUSP 29175	MAM192	Brazil: Espírito Santo (27)	400	-	Mustrangi & Patton (1997)
incanus C	**-**	**LPC1080**	Brazil: Espírito Santo (28)	801	-	Agrizzi et al. (2012)
incanus C	-	MF34	Brazil: Espírito Santo (29)	801	-	Mustrangi & Patton (1997)
incanus C	**-**	**MF35**	Brazil: Espírito Santo (29)	400	-	Mustrangi & Patton (1997)
incanus C	**MZUSP 29176**	**MAM194**	Brazil: Espírito Santo (29)	1149	879	This report
incanus C	**-**	**YL444**	Brazil: Espírito Santo (30)	798	-	Agrizzi et al. (2012)
incanus C	-	MAM203	Brazil: Minas Gerais (32)	384	-	Mustrangi & Patton (1997)
incanus C	-	MAM204	Brazil: Minas Gerais (32)	801	-	Mustrangi & Patton (1997)
incanus C	**-**	**MAM206**	Brazil: Minas Gerais (32)	270	-	Mustrangi & Patton (1997)
incanus C	-	MAM207	Brazil: Minas Gerais (32)	335	-	Mustrangi & Patton (1997)
incanus C	**MVZ 182768**	**MAM201**	Brazil: Minas Gerais (32)	1149	-	This report
incanus C	MVZ 182769	MAM202	Brazil: Minas Gerais (32)	1149	-	This report
incanus C	**-**	**GM3**	Brazil: Minas Gerais (33)	335	-	Mustrangi & Patton (1997)

incanus C	**-**	**LC22**	Brazil: Minas Gerais (33)	398	-	Agrizzi et al. (2012)
incanus C	**-**	**LC49**	Brazil: Minas Gerais (36)	797	-	Agrizzi et al. (2012)
incanus C	**-**	**AL3035**	Brazil: Minas Gerais (37)	386	-	Mustrangi & Patton (1997)
incanus C	**-**	**JCN893**	Brazil: Minas Gerais (37)	400	-	Mustrangi & Patton (1997)
incanus C	**-**	**LC81**	Brazil: Minas Gerais (38)	801	-	Agrizzi et al. (2012)
incanus D	**MVZ 197435**	**LPC231**	Brazil: Bahia (26)	1149	879	This report
incanus D	**MVZ 197761**	**LPC201**	Brazil: Bahia (26)	781	-	Agrizzi et al. (2012)
invictus	**USNM 337962**	**-**	Panama: Darién (89)	483	388	This report
juninensis	AMNH 230016	-	Peru: Junín (102)	-	882	This report
"Juruá"	**MSB 57002**	**NK14140**	Bolivia: Pando (10)	1149	-	This report
"Juruá"	**MVZ 190269**	**MNFS1319**	Brazil: Acre (19)	1149	-	This report
"Juruá"	**MVZ 190268**	**MNFS760**	Brazil: Amazonas (20)	1149	-	This report
"Juruá"	**MVZ 190267**	**JLP15633**	Brazil: Amazonas (25)	1149	-	This report
"Juruá"	**UMMZ 176449**	**LLW869**	Peru: San Martín (113)	1149	-	This report
"Juruá"	UMMZ 176464	LLW884	Peru: San Martín (113)	1149	882	This report
noctivagus A	**FMNH 70946**	**-**	Colombia: Caquetá (62)	362	-	This report
noctivagus A	**QCAZ 8833**	**DFA410**	Ecuador: Morona-Santiago (74)	1149	888	This report
noctivagus A	**ROM 105316**	**F37644**	Ecuador: Napo (75)	1149	-	This report
noctivagus A	TTU 98590	TK73933	Peru: Loreto (103)	1149	-	This report
noctivagus A	**TTU 100924**	**TK73278**	Peru: Loreto (104)	1149	-	This report
noctivagus A	**LSU 28016**	**LJB2318**	Peru: Loreto (105)	1149	-	This report
noctivagus A	**KU 157961**	**RMT4047**	Peru: Loreto (107)	1149	-	This report
noctivagus A	KU 157967	RMT4068	Peru: Loreto (108)	1149	-	This report
noctivagus B	**UMMZ 176459**	**LLW879**	Peru: San Martín (113)	1149	-	This report
noctivagus B	UMMZ 176497	LLW917	Peru: San Martín (114)	1149	-	This report
noctivagus B	**FMNH 203327**	**PMV2353**	Peru: San Martín (116)	1149	882	This report
noctivagus C	AMNH 262402	NK14139	Bolivia: Pando (10)	1149	-	This report
noctivagus C	**AMNH 262404**	**NK13990**	Bolivia: Pando (11)	202	-	This report

noctivagus C	**MVZ 191194**	**JRM251**	Brazil: Amazonas (23)	1149	-	This report
noctivagus C	INPA 2931	MNFS381	Brazil: Amazonas (24)	1149	-	Mustrangi & Patton (1997)
noctivagus C	**MVZ 190275**	**JLP15353**	Brazil: Amazonas (24)	1149	-	Mustrangi & Patton (1997)
noctivagus C	**MVZ 190277**	**JLP15566**	Brazil: Amazonas (25)	1149	-	This report
noctivagus C	**USNM 545537**	**-**	Brazil: Mato Grosso (31)	1149	-	This report
noctivagus C	USNM 545538	-	Brazil: Mato Grosso (31)	1149	-	This report
noctivagus C	**USNM 545540**	**-**	Brazil: Pará (41)	416	-	This report
noctivagus C	USNM 588014	LHE1482	Peru: Cuzco (100)	1149	-	This report
noctivagus C	**FMNH 169786**	**BDP3775**	Peru: Cuzco (101)	424	-	This report
noctivagus C	**MVZ 173930**	**JLP13887**	Peru: Cuzco (96)	1149	-	This report
noctivagus C	**MVZ 173931**	**JLP13888**	Peru: Cuzco (96)	783	-	Mustrangi & Patton (1997)
noctivagus C	**MVZ 171408**	**JLP11895**	Peru: Cuzco (97)	1149	-	This report
noctivagus C	UMMZ 160470	PM4804	Peru: Cuzco (97)	791	-	This report
noctivagus C	MVZ 173932	JLP13905	Peru: Cuzco (98)	1149	-	Mustrangi & Patton (1997)
noctivagus C	MVZ 173933	JLP13906	Peru: Cuzco (98)	1149	-	Mustrangi & Patton (1997)
noctivagus C	MVZ 173934	JLP13947	Peru: Cuzco (98)	1149	-	Mustrangi & Patton (1997)
noctivagus C	MVZ 173935	JLP13948	Peru: Cuzco (98)	1149	-	Mustrangi & Patton (1997)
noctivagus C	**USNM 588013**	**LHE1473**	Peru: Cuzco (99)	1149	-	This report
noctivagus C	AMNH 272775	RSV2225	Peru: Loreto (106)	1149	-	This report
noctivagus C	AMNH 272782	RSV2242	Peru: Loreto (106)	1149	-	This report
noctivagus C	AMNH 272809	RSV2294	Peru: Loreto (106)	1149	-	This report
noctivagus C	MUSM 13289	RSV2224	Peru: Loreto (106)	1149	-	This report
noctivagus C	**MUSM 13292**	**RSV2131**	Peru: Loreto (106)	1149	882	This report
noctivagus C	**KU 144070**	**NW518**	Peru: Madre de Dios (109)	1149	-	This report
noctivagus C	KU 144085	NW737	Peru: Madre de Dios (109)	1149	-	This report
noctivagus D	**AMNH 275451**	**NK30258**	Bolivia: Cochabamba (3)	1149	882	This report
noctivagus D	AMNH 275458	NK30333	Bolivia: Cochabamba (4)	414	-	This report
noctivagus D	**CBF 7527**	**CBF7527**	Bolivia: Cochabamba (2)	538	-	This report

noctivagus D	CBF 7560	TTS715	Bolivia: Cochabamba (2)	401	-	This report
noctivagus D	CBF 7573	CBF7573	Bolivia: Cochabamba (2)	1149	-	This report
noctivagus D	CBF 7577	TTS718	Bolivia: Cochabamba (2)	420	-	This report
noctivagus D	AMNH 268936	NK25272	Bolivia: La Paz (5)	551	-	Mustrangi & Patton (1997)
noctivagus D	AMNH 268937	NK25274	Bolivia: La Paz (5)	1149	-	This report
noctivagus D	**AMNH 275459**	**NK25203**	Bolivia: La Paz (5)	551	-	This report
noctivagus D	**AMNH 72561**	**-**	Bolivia: La Paz (8)	394	-	This report
ocellatus	**MSB 63275**	**NK21845**	Bolivia: Chuquisaca (1)	1149	-	This report
ocellatus	**MSB 58511**	**NK15126**	Bolivia: Santa Cruz (12)	764	-	Mustrangi & Patton (1997)
ocellatus	AMNH 261265	NK13053	Bolivia: Santa Cruz (13)	1149	-	This report
ocellatus	USNM 584467	LHE1573	Bolivia: Santa Cruz (14)	1149	-	This report
ocellatus	AMNH 275462	NK23270	Bolivia: Santa Cruz (15)	1149	-	This report
ocellatus	**USNM 581979**	**ECH7**	Bolivia: Santa Cruz (16)	1149	882	This report
ocellatus	**MSB 67021**	**NK22947**	Bolivia: Santa Cruz (17)	1149	-	This report
ojastii	**USNM 371299**	**-**	Venezuela: Falcón (125)	635	882	This report
pakaraimae	ROM 115129	F-46739	Guyana: Cuyuni-Mazaruni (82)	1149	-	Voss et al. (2013)
pakaraimae	**ROM 114698**	**F-46454**	Guyana: Potaro-Siparuni (85)	1149	-	Voss et al. (2013)
pakaraimae	ROM 115841	F-47080	Guyana: Potaro-Siparuni (86)	1149	882	Voss et al. (2013)
parvidens	ISEM V-1633	ISEM T-3832	French Guiana: Les Nouragues (79)	800	-	This report
parvidens	AMNH 267817	LHE1161	French Guiana: Paracou (80)	800	-	This report
parvidens	**ISEM V-1399**	**-**	French Guiana: Paracou (80)	799	-	Steiner & Catzefis (2004)
parvidens	ISEM V-1581	-	French Guiana: Paracou (80)	1149	-	Steiner & Catzefis (2004)
parvidens	MNHN1998-1830	-	French Guiana: Saint-Eugène (81)	645	-	Steiner & Catzefis (2004)
parvidens	**ROM 97938**	**FN-33439**	Guyana: Upper Takutu-Upper Essequibo (87)	645	882	This report
parvidens	**ROM 114144**	**F-41219**	Surinam: Brokopondo (118)	1149	-	Voss et al. (2013)
parvidens	ROM 114299	F-41329	Surinam: Brokopondo (118)	755	-	Steiner & Catzefis (2004)
parvidens	ROM 114322	F-41352	Surinam: Brokopondo (118)	773	-	Steiner & Catzefis (2004)
parvidens	**ROM 117348**	**F-54669**	Surinam: Sipaliwini (121)	1149	-	This report

paulensis A	**-**	**MP405**	Brazil: Minas Gerais (34)	1149	882	This report
paulensis A	**-**	**YL19**	Brazil: Minas Gerais (35)	782	-	Mustrangi & Patton (1997)
paulensis B	**MZUSP 29184**	**MAM475**	Brazil: Rio de Janeiro (43)	371	-	Mustrangi & Patton (1997)
paulensis B	**MZUSP 29185**	**MAM481**	Brazil: Rio de Janeiro (43)	1139	-	Mustrangi & Patton (1997)
paulensis B	**uncatalogued**	**EEB1021**	Brazil: São Paulo (44)	247	705	This report
paulensis C	MVZ 182059	MAM25	Brazil: São Paulo (45)	1149	-	This report
paulensis C	**MVZ 183243**	**JLP16216**	Brazil: São Paulo (45)	1149	-	Voss *et al.* (2013)
paulensis C	**MVZ 183244**	**JLP16217**	Brazil: São Paulo (45)	1149	882	This report
paulensis C	**MZUSP 29166**	**MAM20**	Brazil: São Paulo (45)	376	-	Mustrangi & Patton (1997)
paulensis C	MZUSP 29167	MAM31	Brazil: São Paulo (45)	787	-	Mustrangi & Patton (1997)
paulensis C	MZUSP 29168	MAM32	Brazil: São Paulo (45)	399	-	Mustrangi & Patton (1997)
paulensis C	MZUSP 29169	MAM33	Brazil: São Paulo (45)	385	-	Mustrangi & Patton (1997)
pinheiroi	**-**	**ISEM V-955**	French Guiana: Les Nouragues (79)	800	-	Steiner & Catzefis (2004)
pinheiroi	**ROM 108920**	**F-43900**	Guyana: Potaro-Siparuni (83)	1149	-	Voss et al. (2013)
pinheiroi	**ROM 111558**	**F-44687**	Guyana: Potaro-Siparuni (84)	799	-	Steiner & Catzefis (2004)
pinheiroi	**ROM 114318**	**F-41348**	Surinam: Brokopondo (118)	800	-	Steiner & Catzefis (2004)
pinheiroi	**CM 63506**	**TK10169**	Surinam: Nickerie (119)	1149	882	Voss et al. (2013)
pinheiroi	ROM 116974	F-54337	Surinam: Sipaliwini (120)	1149	-	Voss et al. (2013)
ucayaliensis	**KU 144088**	**NW509**	Peru: Madre de Dios (109)	1149	882	This report
ucayaliensis	KU 144090	RMT3920	Peru: Madre de Dios (109)	1149	-	This report
ucayaliensis	**AMNH 230025**	**-**	Peru: Pasco (111)	362	-	This report
ucayaliensis	AMNH 230027	-	Peru: Pasco (111)	362	-	This report
ucayaliensis	AMNH 76532	-	Peru: Ucayali (117)	194	-	This report
"West Magdalena"	**CTUA 434**	**CACE004**	Colombia: Antioquia (51)	1149	882	This report
"West Magdalena"	FMNH 69837	-	Colombia: Antioquia (52)	391	-	This report
"West Magdalena"	FMNH 69822	-	Colombia: Antioquia (54)	391	-	This report
"West Magdalena"	FMNH 70925	-	Colombia: Caldas (59)	379	-	This report
"West Magdalena"	MHNUC 986	-	Colombia: Caldas (60)	396	-	This report

"West Magdalena"	MHNUC 750	-	Colombia: Caldas (61)	391	-		This report
woodalli	**USNM 549294**	**MDC589**	Brazil: Pará (39)	1149		882	Voss et al. (2013)
woodalli	**USNM 545543**	**-**	Brazil: Pará (40)	421	-		Voss et al. (2013)
Outgroups							
Cryptonanus unduaviensis	AMNH 262401	NK14234	Bolivia: Pando, Independencia	1149		888	This report
Didelphis marsupialis	USNM 578138	FMG2573	Panama: Bocas Del Toro, Peninsula Valiente, Punta Alegre	1149		879	This report
Gracilinanus microtarsus	MVZ 182055	MAM38	Brazil: São Paulo, Fazenda Intervales, Capao Bonito	1149		888	This report
Lestodelphis halli	CNP 889	CNP889		1149		887	Giarla et al. (2010)
Marmosa murina	USNM 549291	LHE503	Brazil: Pará, Altamira, 52 Km SSW, E Bank Rio Xingu	1146		885	This report
Metachirus nudicaudatus	MUSM 13293	RSV2329	Peru: Loreto, Rio Gálvez	1149		882	Giarla & Jansa (2014)
Monodelphis arlindoi	CM 68359	TK17069	Surinam: Nickerie, Kayserberg Airstrip	1146		882	This report
Thylamys pallidior	OMNH 23482	ARG43	Argentina: Mendoza	1149		884	This report

Methods for DNA extraction from preserved tissue and dried museum specimens follow Voss and Jansa (2009) and Giarla et al. (2010), respectively. For DNA of high molecular weight (extracted from preserved tissue), I PCR-amplified CYTB either in a single 1149 bp piece or in two overlapping 600-700 bp fragments. For fragmented DNA (extracted from dried tissue), I developed internal primers to sequence CYTB as six overlapping fragments (ca. 200–300 bp each). Similarly, a fragment of the BRCA1 gene of approximately 882 bp was PCR-amplified in a single reaction or in two overlapping fragments (ca. 500 bp each). Primers for all loci are listed in appendix 2. For CYTB I used touchdown-PCR conditions as described in Gutiérrez et al. (2010) and modified PCR annealing temperatures as required for particular samples. Amplification protocols for BRCA1 closely resembled those described in Voss et al. (2014). DNA was sequenced using amplification primers and dye-terminator chemistry on an ABI-3730xl automated sequencer. Sequences were assembled using Sequencher ver. 4.8 (Gene Codes Inc.) and aligned using the default settings of MUSCLE (Edgar, 2004) in Geneious Pro ver. 5.6.3 (Biomatters, Inc.; available from http://www.geneious.com). The resulting alignments were inspected with reference to translated amino acid sequences. All sequences have been deposited in GenBank: CYTB (KT437693– KT437880), BRCA1 (KT453993–KT454030).

Putative species delimitation based on CYTB sequences

I performed phylogenetic analyses of aligned CYTB sequences using maximum likelihood (ML) searches and Bayesian Inference (BI). Missing bases were coded as unknown characters in all analyses. The best-fitting nucleotide substitution model was

determined under the Bayesian Information Criterion (BIC) in jModelTest (Posada, 2008). I conducted four independent ML searches in GARLI 2.0 (Zwickl, 2006) and evaluated nodal support based on bootstrap analyses of 1,000 pseudoreplicated datasets with the same parameters as the initial searches. Bootstrap support (BS) values were summarized on the ML tree using Sumtrees version 3.3.1 (Sukumaran and Holder, 2010). Bayesian Inference was implemented in MrBayes v3.2 (Ronquist et al., 2012) by running two independent Markov Chain Monte Carlo (MCMC) analyses for 50 million generations each, sampling every 5,000 generations and including one cold chain and three heated chains. To ensure convergence, the results of the MCMC runs were inspected in Tracer v1.5 (Rambaut and Drummond, 2007) and AWTY (Nylander et al., 2008). I discarded the first 50% of trees of each run as burnin and combined the remaining trees into a final set of 10,000 trees. Tree topology, mean lnL value, nodal support (Posterior Probability, PP), and remaining parameters were summarized in a maximum-clade-credibility tree with TreeAnnotator v1.7.2 (Drummond et al., 2012).

To identify putative species, I used the likelihood version of the General Mixed Yule Coalescent model (GMYC) as implemented by the software package SPLITS (Pons *et al.*, 2006), as well as the Bayesian version implemented by bGMYC (Reid and Carstens, 2012). To avoid confusion, I refer to the general model developed by Pons et al. (2006) as GMYC, I use "LGMYC" for its likelihood implementation in SPLITS, and "BGMYC" for the Bayesian version. GMYC methods delimit putative species by estimating the point of transition between intra- and inter-specific evolutionary processes on an ultrametric tree and, unlike other methods, they do not require prior assignment of

sequences to taxa or populations (Pons et al., 2006). However, LGMYC operates under a maximum-likelihood framework whereas BGMYC uses a Markov Chain Monte Carlo simulation (MCMC) to account for error in phylogenetic estimation and uncertainty of model parameters (e.g., tree topology and branch lengths) (Pons et al., 2006; Reid and Carstens, 2012). For the purposes of this report, I recognize putative species as strongly supported mtDNA clades (PP $\geq$ 0.95) that fall within the 95% confidence interval flanking the species-delimitation threshold for LGMYC and/or BGMYC. I associate species names with these putative species based on routine taxonomic criteria (genetic or morphological similarity with type material) whenever possible.

Because it has been shown that the accuracy of GMYC methods is compromised by the presence of duplicate haplotypes (Monaghan et al., 2009; Fujisawa and Barraclough, 2013) I only used unique haplotypes across the aligned region (129 terminals; table 2). All LGMYC analyses permitted a single shift from a Yule process (by which branch lengths result from lineage birth) to a coalescent process (by which branch lengths result from intra-lineage haplotype dynamics) (Pons et al., 2006). I did not implement the LGMYC analyses allowing multiple shifts across the phylogeny because—based on empirical and simulated datasets—it has been demonstrated that such analyses have a strong tendency to overestimate the diversity of a clade (Fujisawa and Barraclough, 2013). For BGMYC I first evaluated the MCMC parameters and appropriate burnin value by checking the likelihood plots of the "single.phy" option (Reid and Carstens, 2012) using the maximum clade credibility tree from BEAST (see below). Subsequently I obtained 100 random trees from the posterior distribution of the

BEAST analyses using the R package APE (Paradis et al., 2004) and ran the program for 50,000 generations, sampling every 100 generations and discarding the first 40,000 trees as burnin for a total of 10,000 trees retained.

To implement the LGMYC and BGMYC analyses I constructed an ultrametric tree in BEAST v1.7.2 (Drummond et al., 2012) using a lognormal relaxed-clock model, a coalescent constant-size tree prior, and relative time set with a prior on the ingroup age of one (normal distribution: mean=1, SD=0.01). I ran two independent Markov Chain Monte Carlo (MCMC) analyses for 50 million generations each, sampling every 5,000 generations. Analyses of convergence, burnin, and summarization process followed those described for the MrBayes analysis. All phylogenetic analyses (including those described in the next paragraph) were implemented in the CIPRES Science Gateway (Miller et al., 2010). I estimated uncorrected (*p*-) and model-corrected genetic distances within and among putative species using MEGA5 (Tamura et al., 2011).

Phylogenetic analyses of BRCA1 and BRCA1 + CYTB

I analyzed two additional matrices to reconstruct phylogenetic relationships among putative species of *Marmosops*, one that included only BRCA1 sequences and another that added CYTB sequences from the same taxa. The BRCA1 matrix was analyzed using ML and BI methods as previously described for the CYTB dataset (see above), with the exception that each of the two independent MCMC analyses were run for 1 million generations, sampling every 100 generations. I performed partitioned analyses on the combined-gene (BRCA1 + CYTB) matrix using ML and BI methods as implemented in GARLI 2.0 (Zwickl, 2006) and MrBayes v3.2 (Ronquist et al., 2012),

respectively. I estimated the best data-partitioning scheme and substitution model(s) using the BIC as implemented in PartitionFinder v1.0 (Lanfear et al., 2012) with unlinked branch lengths and the greedy algorithm search strategy (Table 3). For MrBayes I ran two independent MCMC analyses for 20 million generations each, sampling every 2,000 generations, including one cold chain and three heated chains. All subsequent steps of BI analyses (i.e., convergence, burnin, and summarization) followed those previously described for the putative species delimitation analyses.

Table 3. Optimal partitioning scheme and substitution models for the two-gene concatenated dataset (BRCA1+CYTB). Parameters=119, aligned sites=2,046, BIC= 34290.67.

Partition	Best Model	Characters
1	HKY+Γ	BRCA1 position 1, BRCA1 position 2
2	HKY	BRCA1 position 3
3	SYM+I+Γ	CYTB position 1
4	HKY+I+Γ	CYTB position 2
5	GTR+I+ Γ	CYTB position 3

RESULTS

Phylogenetic analyses and species delimitation based on CYTB sequence data

The final CYTB matrix contained 213 *Marmosops* sequences from 131 localities plus eight outgroup sequences; analyzed CYTB sequences ranged in length from 194 to 1149 bp, representing 77.2% nucleotide coverage overall (figures 1–3, table 2). I was unable to obtain any CYTB sequence from *M. juninensis* because I consistently co-amplified a nuclear pseudogene from my only available sample (a scrap of dried skin).

The best-fit nucleotide substitution model for all of the mitochondrial analyses was GTR+Γ+I.

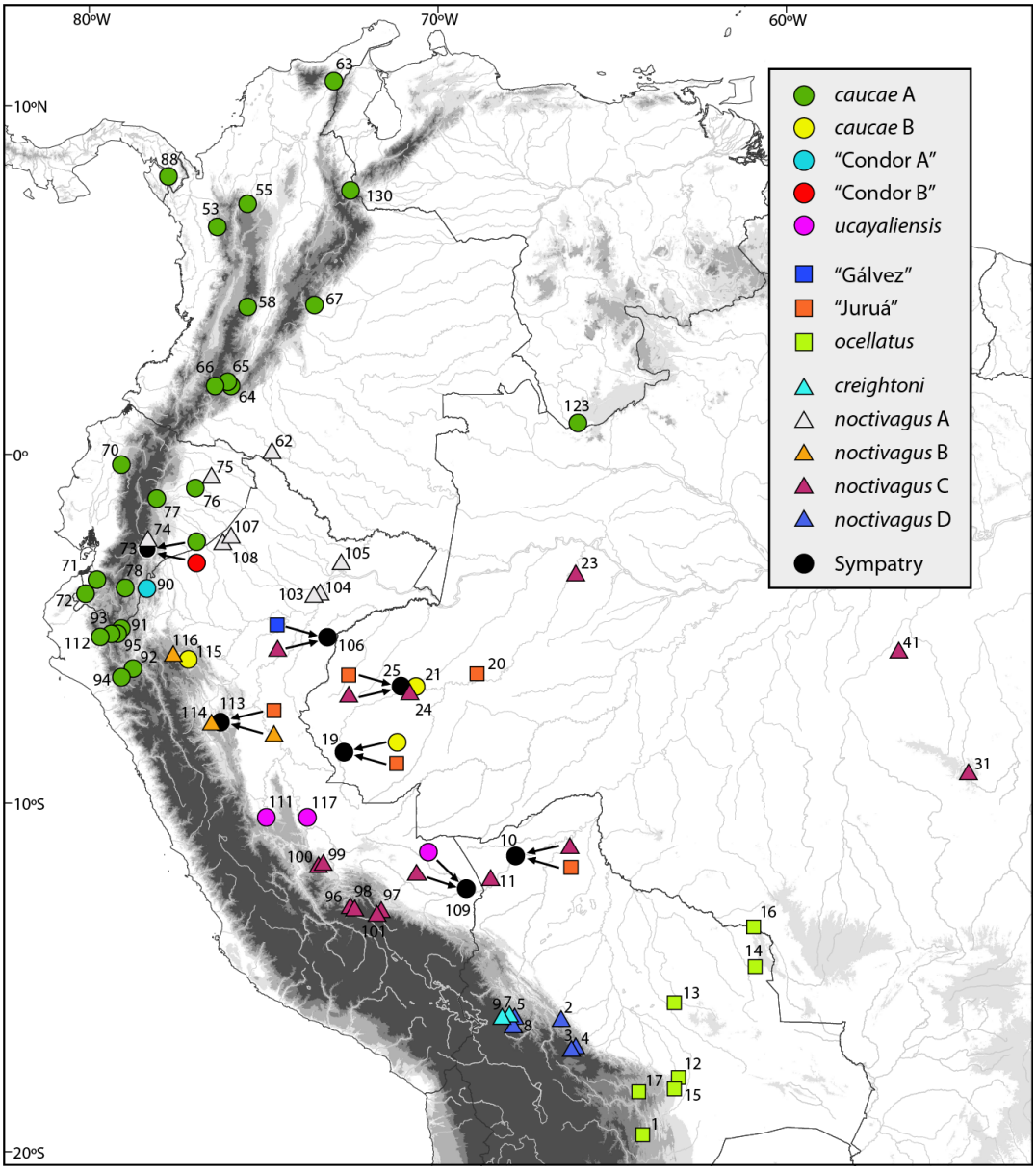

Figure 1. Collection localities for sequenced specimens of clades D, E and F in subgenus II of *Marmosops*. Progressively darker shading indicates the following elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, and darkest gray ≥3000 m.

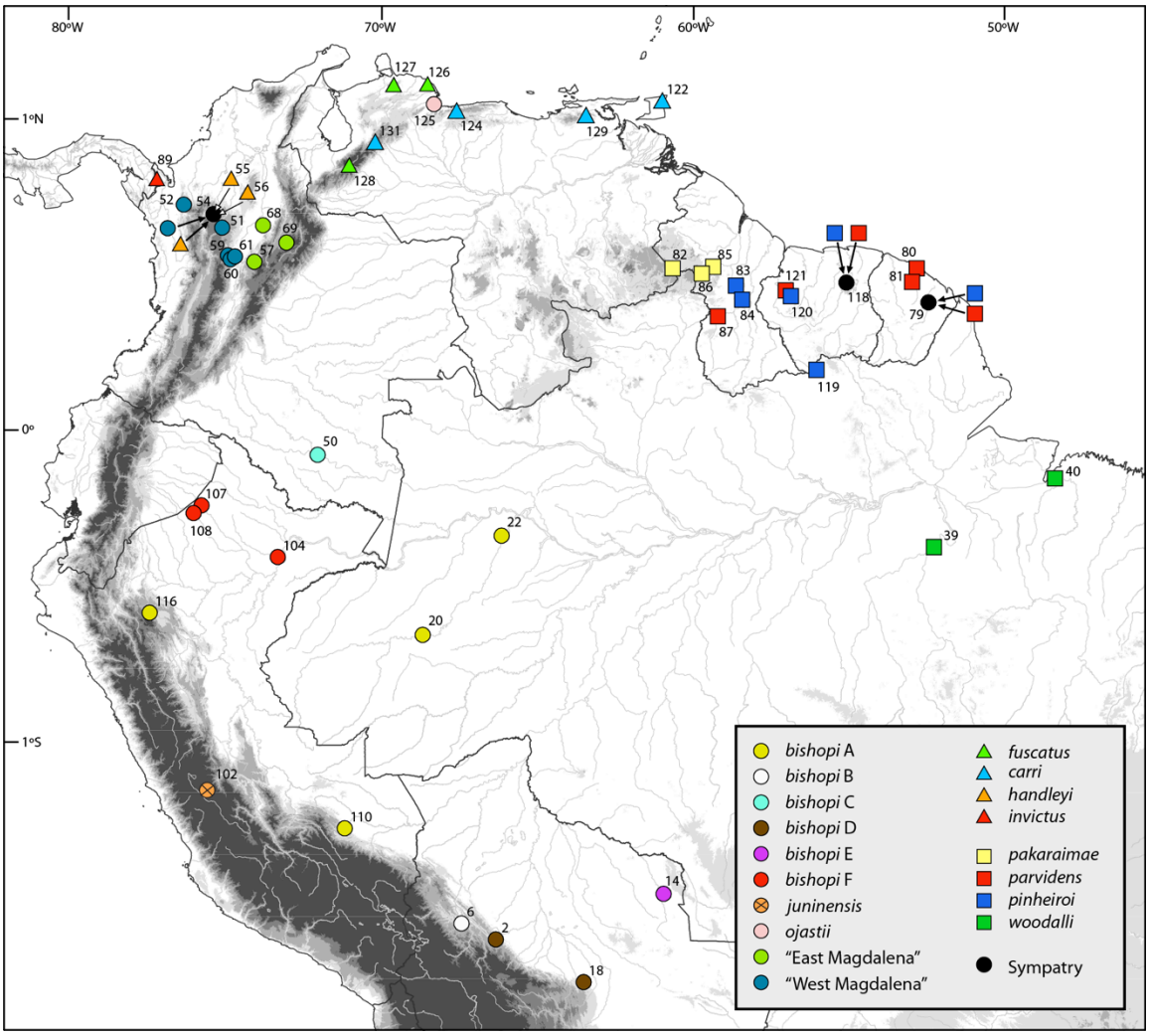

Figure 2. Collection localities for sequenced specimens of subgenus I of *Marmosops*. Progressively darker shading indicates the following elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, and darkest gray ≥3000 m.

Salient features of the CYTB analyses (figure 4, appendices 3 and 4) are (1) strong support for the monophyly of *Marmosops*, and (2) a basal dichotomy within the genus between two robustly supported clades that I propose to recognize as subgenera (see below). The latter clades are both apparently speciose, containing numerous strongly supported, geographically coherent, and divergent mitochondrial haplogroups. A total of 18 lineages cross the LGMYC species threshold (dashed line in Figure 4);

another 19 strongly-supported haplogroups fall within the 95% confidence interval of the LGMYC threshold and, by this criterion, a total of 37 haplogroups merit recognition as putative species. By the same logic, BGMYC recovered 36 putative species, the same as those recovered by LGMYC with but one exception: LGMYC recognizes three putative species among the sequences referable to *Marmosops paulensis* of current usage, whereas only two such clades were recovered by BGMYC.

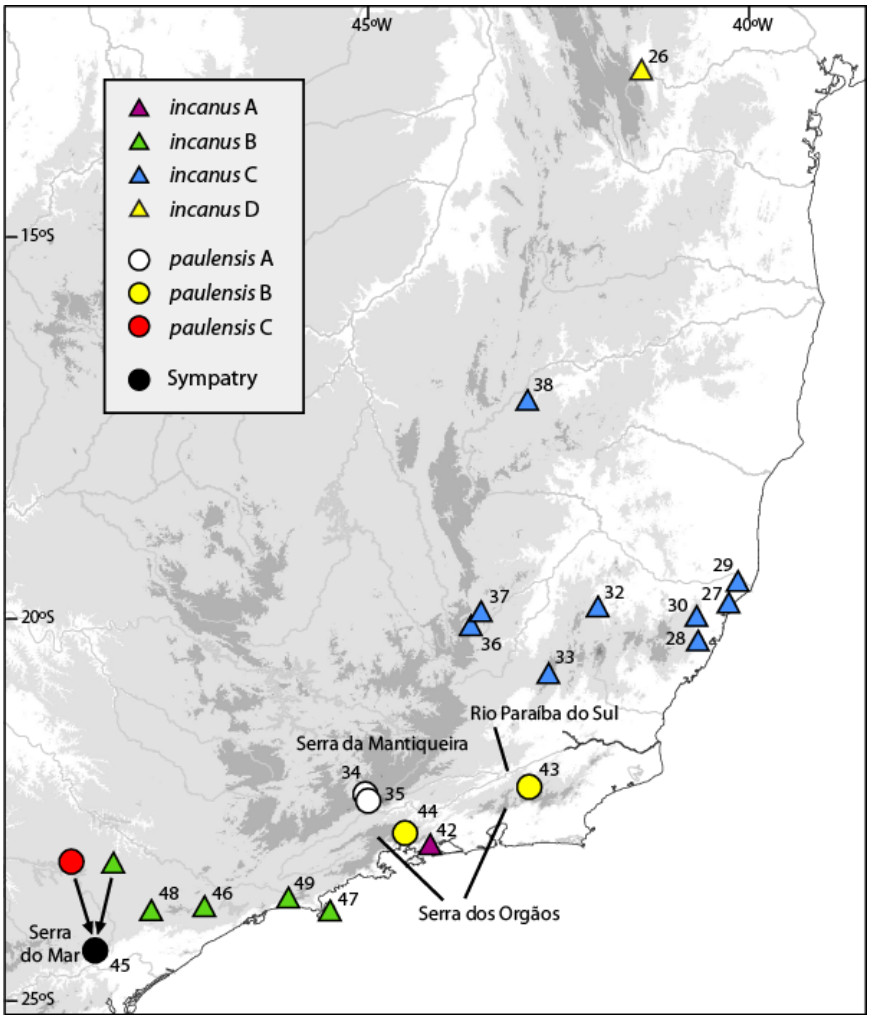

Figure 3. Collection localities for sequenced specimens of Atlantic Forest species included in subgenus II of *Marmosops*. Colors of the circles and triangles represent putative species (see text). Progressively darker shading indicates the following elevations: pale gray ≥500 m, medium gray ≥1000 m, and dark gray ≥2000 m.

Although many of the taxa recognized by recent authors (e.g., Gardner and Creighton, 2008; Voss and Jansa, 2009; Voss et al., 2013) were recovered as well-supported (PP ≥ 0.95; BS ≥ 75%), reciprocally monophyletic groups that correspond to putative species according to the LGMYC and BGMYC analyses, there are important exceptions. *Marmosops* "*impavidus*" (sensu Gardner and Creighton, 2008; Voss and Jansa, 2009), for example, includes five putative species (*caucae* A, *caucae* B, *ucayaliensis*, "Gálvez," and "Juruá") that do not form a monophyletic group. Other currently recognized species (e.g., *M. bishopi* and *M. incanus*) contain highly divergent mtDNA lineages that either intersect the LGMYC and BGMYC thresholds or fall within their 95% confidence intervals. Lastly, some putative species (labeled by geographic descriptors in figure 4) lack available names.

Phylogenetic relationships

Both ML and BI analyses of CYTB sequences recovered a monophyletic *Marmosops*, and most nodes representing phylogenetic relationships among putative species in the genus were also recovered with consistently strong support. In particular, the basal dichotomy described earlier (subtending subgenera I and II) is robustly supported by both analyses of these data, as are several multi-species clades. The latter include some groups previously recognized by authors (e.g., the group comprising *pakaraimae* + *parvidens* + *pinheiroi*; Voss *et al.*, 2013) and others that were previously unrecognized (e.g., *creightoni* + *noctivagus*). By contrast, nine internal nodes are weakly supported by both analyses of CYTB, including some nodes of key importance for future

biogeographic analyses. To corroborate and extend these results, additional sequence data from other loci are clearly needed.

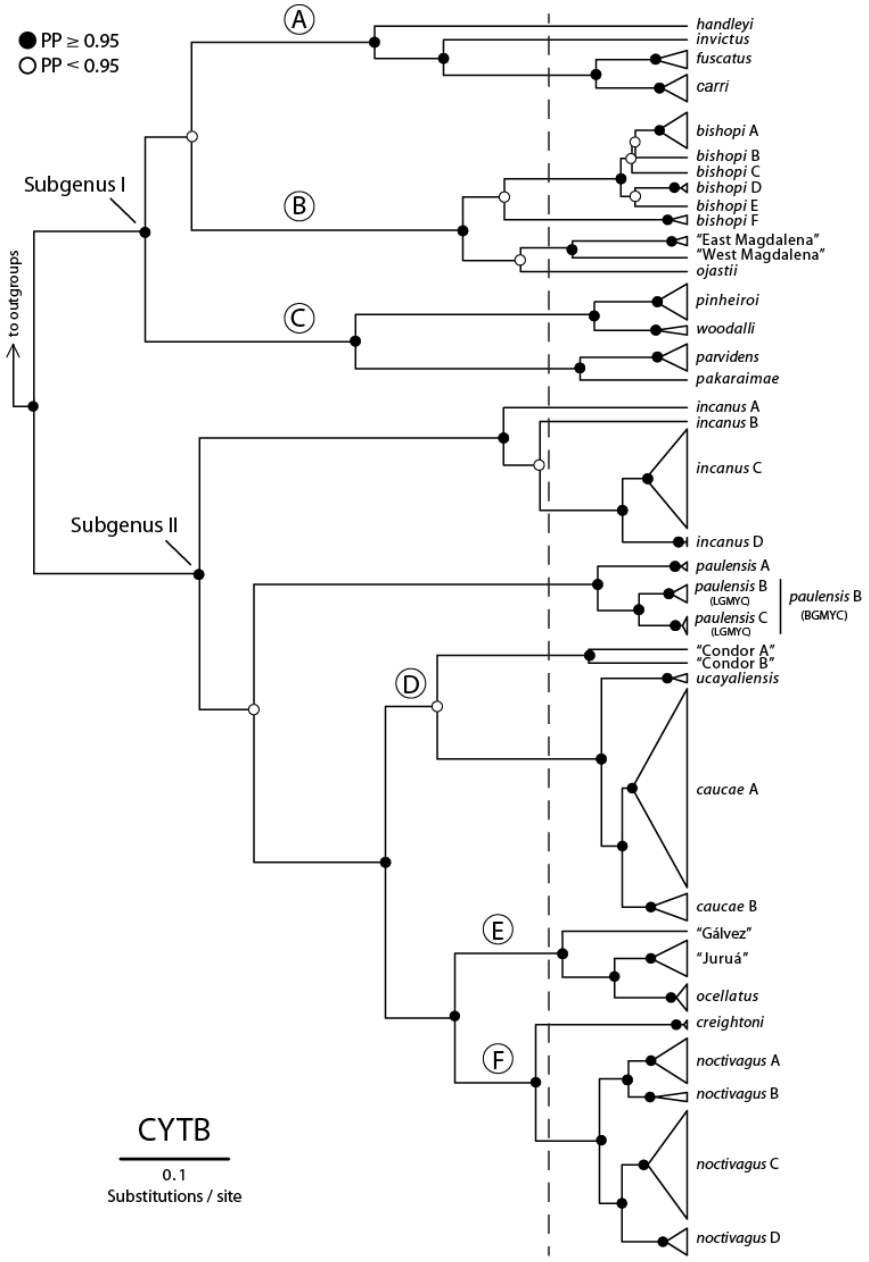

Figure 4. BEAST ultrametric tree based on CYTB sequences with putative species (as cartooned terminals). Dashed vertical line shows the threshold between Yule and coalescent branching processes as estimated by the likelihood implementation of the General Mixed Yule Coalescent model (LGMYC). Areas of triangles at branch tips are proportional to the number of sequences in each clade. Filled circles at internal nodes represent high support (PP ≥ 0.95).

Phylogenetic analyses of BRCA1 alone (not shown) and of the concatenated-gene matrix (BRCA1 + CYTB) both recovered a monophyletic *Marmosops* as well as the basal dichotomy between subgenera I and II that were obtained from the analyses of CYTB (figure 5). The concatenated analyses additionally recovered three well-supported groups within Subgenus I: one comprising *carri, fuscatus, handleyi,* and *invictus* (clade A); another including *juninensis, ojastii*, "East Magdalena", "West Magdalena," and a *bishopi* complex (clade B); and a third including *pakaraimae, parvidens, pinheiroi* and *woodalli* (clade C). I was unable to obtain CYTB sequence for *juninensis*, but the nuclear sequence obtained for this taxon indicates that it is clearly distinct from other members of Clade B. Although each of these three groups (clades A, B, and C) is strongly supported, the relationships among them are not. Additionally, the relationships of *ojastii* and relationships within the *bishopi* complex cannot be convincingly resolved with these data, and the position of *invictus* within Clade A is only strongly supported by the ML analysis.

The concatenated-gene analyses also produced a topology with several strongly supported groups within Subgenus II. The first (Clade D) includes "Condor A", "Condor B", *caucae* A, *caucae* B, and *ucayaliensis*; a second (Clade E) groups *ocellatus*, "Gálvez," and "Juruá"; and a third (Clade F) includes *creightoni*, and a *noctivagus* complex. These three clades form a nested set of monophyletic groups in the sequence (D (E + F)), with monophyletic *paulensis* and *incanus* complexes as successively more distant sister groups. Relationships within the *noctivagus* complex and within clade E, however, remain to be convincingly resolved.

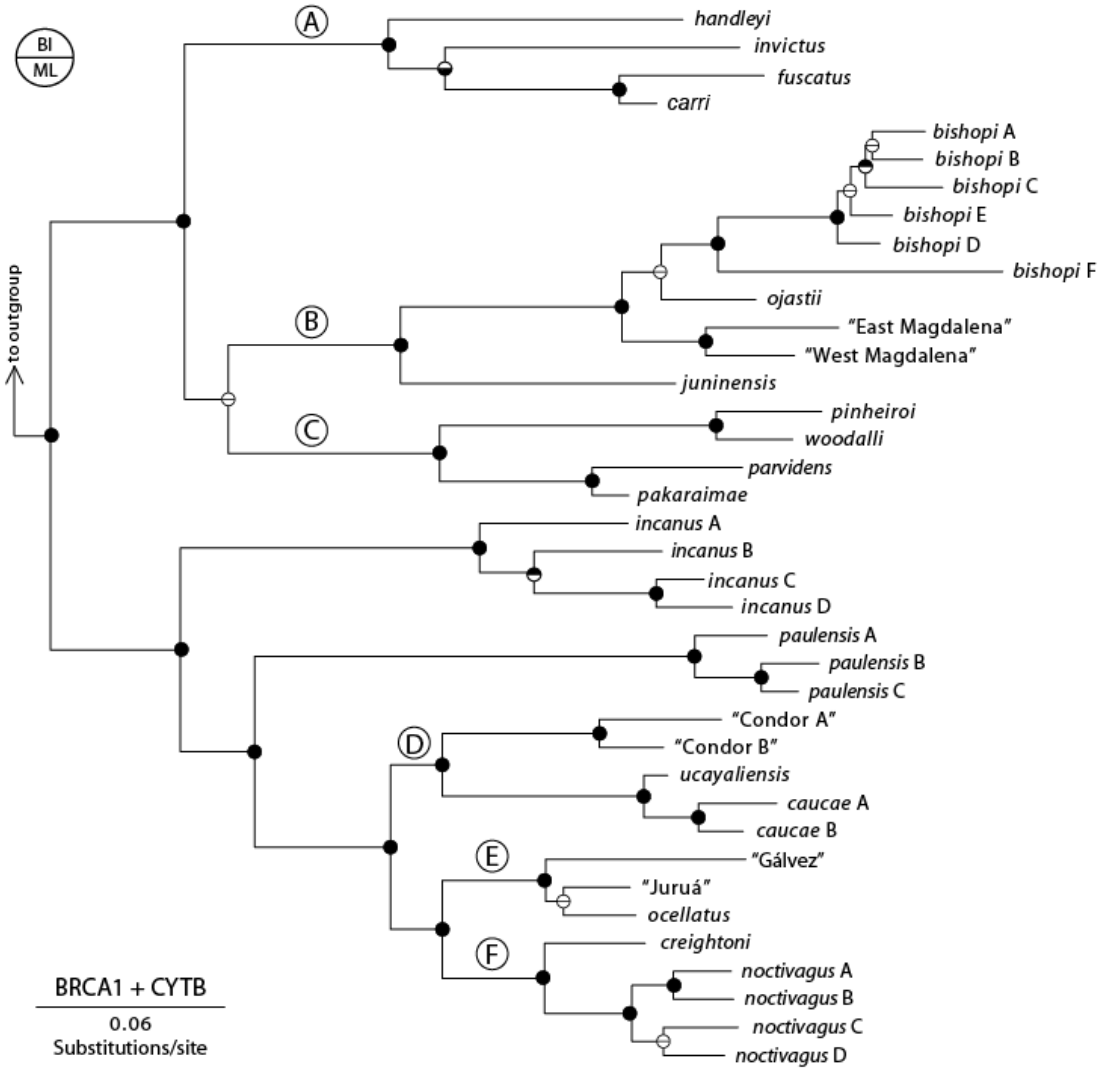

Figure 5. Phylogeny of *Marmosops* obtained by Bayesian analysis of a concatenated-gene (CYTB + BRCA1) dataset. Terminals are putative species recovered by GMYC analyses of CYTB plus *M. juninensis* (uniquely represented by a BRCA1 sequence). Filled semicircles at internal nodes indicate high support (PP ≥ 0.95, Bootstrap ≥ 75).

DISCUSSION

Assessment of species-level diversity and phylogenetics in *Marmosops*

A recent overview of opossum systematics (Voss and Jansa, 2009) recognized a monophyletic *Marmosops* containing 15 species, and subsequent descriptions of new taxa (Voss et al., 2013; García et al., 2014) raised the total to 17 species currently recognized as valid. However, Voss and Jansa (2009:138) noted that "few of the currently recognized species have received critical revisionary attention, and it seems likely that several widespread taxa (e.g., *M. fuscatus, M. impavidus,* and *M. noctivagus*) will prove to be composite". This study is the first to assess intra- and inter- specific variation for *Marmosops* by sequencing representatives of all currently recognized species, including multiple individuals from many widespread taxa. My findings suggest that the diversity of *Marmosops* is underestimated by the currently accepted taxonomy, and that the genus might contain as many as 37 species. However, GMYC analyses are based on a number of assumptions about evolutionary processes that need to be considered.

The GMYC model operates in a coalescent-based framework that identifies the point(s) at which the phylogeny shifts from interspecific (Yule) to intraspecific (coalescent) processes, so differences in branching rate within and between species are crucial for methodological success. In particular, when the coalescent branching rate is much higher than the Yule branching rate, GMYC is likely to be reasonably accurate (Reid and Carstens, 2012). However, in clades with large population sizes and high speciation rates, the coalescent and Yule processes tend to have similar rates and, in such situations, GMYC has proven to be less accurate (Esselstyn et al., 2012; Fujisawa and

Barraclough, 2013). When implementing the likelihood version of GMYC with these data, the shift from interspecific to intraspecific branching processes was only marginally significant ($p = 0.0512$), suggesting that the rates in question are not very different, perhaps because speciation rates are high and population sizes are large in *Marmosops*. Unfortunately, there are currently no independent data with which to evaluate these possibilities.

The likelihood version of the GMYC model has, additionally, several other potential sources of error. Notably, the model does not take into account uncertainty in the evaluated parameters (e.g., coalescent and Yule processes) nor does it account for phylogenetic error (Reid and Carstens, 2012). By contrast, the Bayesian implementation of GMYC takes uncertainty of the parameters and phylogenetic error into account. Also, in this application, BGMYC suggests that the coalescent branching rate is substantially larger than the Yule rate: the mean values I obtained across 10,000 generations suggest that the rate of branching for the coalescent process is an order of magnitude larger than that for the Yule process (by about 44.1 to 4.4). Therefore, BGMYC could be providing a better estimate of species-level diversity within *Marmosops* than the corresponding likelihood implementation. However, because the single discrepancy between the two models is nested (Figure 4), their results are not incongruent; in fact, they provide a scenario that can be further tested with additional evidence (see below).

It is important to highlight that the GMYC model was originally devised to delimit species from single-locus gene trees in the absence of additional information (Fujisawa and Barraclough, 2013). Whenever other information—such as sequences

from multiple loci, morphological data, or geography—is available, however, that information should be used to inform the results from GMYC (Fujisawa and Barraclough, 2013). Although this current dataset does not include relevant genetic data from other loci, I consider morphology and geographic distributions in the following accounts, which discuss the possibility that some putative species delimited by GMYC methods might actually be evolutionarily independent lineages (valid species). In effect, my results provide, for the first time, a set of testable hypotheses based on methodologically explicit data analyses that can serve as the basis for future revisionary work.

My second principal result, the discovery of a strongly supported basal dichotomy in the genus, implies an ancient speciation event that gave rise to two speciose lineages with broadly overlapping geographic distributions. Based just on the samples analyzed for this report (figures 1–3), members of subgenus I and subgenus II are found together throughout much of western Amazonia, in the northern Andes, and in eastern Panama. Apparently, only members of subgenus I occur in northern Venezuela, in the Guianas, and in eastern Amazonia, whereas only subgenus II occurs in southeastern Brazil. These distributions, together with an estimated divergence age of about 9 million years—based on the time tree in Jansa et al. (2014)—and a consistent difference in mean size between members of the two subgenera where they occur sympatrically (e.g., Patton et al., 2000; Díaz-N et al., 2011; Hice and Velazco, 2012) suggests a long independent history of geographic dispersion and ecological adaptation.

Taxonomic accounts

The following accounts formalize recognition of the basal dichotomy in *Marmosops* as Linnaean subgenera. Formal recognition seems warranted because these two clades are old, strongly supported by molecular sequence data, morphologically diagnosable, and ecogeographically distinctive. Although taxonomic rank is biologically arbitrary, treating these taxa as subgenera rather than as full genera has the advantage that current binomial usage is conserved. Subgenus II is nominotypical because it contains *incanus* Lund, 1840, type species of *Marmosops*. By contrast, no genus-group name is based on any nominal species in Subgenus I, for which I provide a new name below.

Additionally, these accounts justify my assignment of nominal taxa to each subgenus based on morphological, geographic, and/or molecular criteria. Although I comment briefly on relevant issues of synonymy and usage, a formal taxonomic revision of the species-level nomenclature (including descriptions of new taxa) is postponed to subsequent reports that will treat the subgenera separately in much greater detail.

Sciophanes, new subgenus

TYPE SPECIES: *Marmosops parvidens* (Tate, 1931).

CONTENTS: I refer 12 nominal taxa to *Sciophanes*, including *bishopi* Pine, 1981; *carri* Allen and Chapman, 1897; *cracens* Handley and Gordon, 1979; *fuscatus* Thomas, 1896; *handleyi* Pine, 1981; *invictus* Goldman, 1912; *juninensis* Tate, 1931; *ojastii* García et al., 2014; *pakaraimae* Voss et al., 2013; *parvidens* Tate, 1931; *pinheiroi* Pine, 1981; and *woodalli* Pine, 1981.

The nominal taxon *perfuscus* Thomas, 1924, was previously regarded as a synonym or subspecies of *Marmosops fuscatus* (e.g., by Tate, 1933; Cabrera, 1958; Gardner and Creighton, 2008), but my examination of the holotype suggest that this name is a junior synonym of *M. caucae* (a member of the nominotypical subgenus, see below).

DIAGNOSIS: Specimens that I refer to the subgenus *Sciophanes* can be distinguished morphologically from those that I refer to the nominotypical subgenus by their shared possession of an anteroposteriorly elongated subsquamosal fenestra, accessory upper canine cusps, and two antebrachial vibrissae.

Of these distinguishing traits, the most consistently useful is the morphology of the subsquamosal foramen, a lateral opening in the squamosal bone that exposes the underlying petrosal just dorsal to the ear region (figure 6). In *Sciophanes*, the subquamosal fenestra is anteroposteriorly elongated, revealing not only the sulcus for the prootic sinus, but also a substantial strip of the relatively featureless lateral surface of the *pars canalicularis* behind that groove.[1] By contrast, the subsquamosal fenestra in the nominotypical subgenus is shorter and does not extend posteriorly much behind the sulcus for the prootic sinus. These contrasting morphologies, first described by Díaz-N. *et al.* (2011) to distinguish Colombian exemplars of these clades, appear to provide complete discrimination among the tissue vouchers and examined type material that I refer to *Sciophanes* on the one hand and to the subgenus *Marmosops* on the other.

All species of *Sciophanes* also have accessory upper canine cusps, but there is taxonomic variation in the expression of this trait. In members of clade A—e.g., *Marmosops (S.) handleyi* (see Díaz-N. *et al.*, 2011)—the accessory cusps of C1 are

[1] See Wible (2003) for a detailed description and illustrations of didelphid petrosal morphology.

sexually dimorphic, usually occurring only in females. By contrast, both sexes seem to have upper-canine accessory cusps in species that belong to clade C, in which C1 is a short and strikingly premolariform tooth (Voss *et al.,* 2001: figure 23). Although sample sizes are too small for several taxa in clade B to be assessed for sexual dimorphism, both sexes of some species—e.g., *M. (S.) bishopi*—and at least some females in others have either one or two C1 accessory cusps.[2] Based on the material I examined, the upper canine lacks distinct accessory cusps in all species of the nominotypical subgenus (in which this tooth is consistently unicuspid).

In addition to these craniodental traits, all species of *Sciophanes* have two antebrachial vibrissae, long tactile hairs on the dorsolateral surface of the forearm, by contrast with the single antebrachial vibrissa normally found in most species of the subgenus *Marmosops* (Díaz-N. *et al.*, 2011: figure 5). The only exceptional species of the latter clade known to me is *M. (M.) ocellatus*, of which most examined specimens appear to have two antebrachial vibrissae.

REMARKS: Most of the nominal taxa that comprise clade A are unrevised. The unique exception is *handleyi*, recently redescribed by Díaz-N. *et al.* (2011), who also documented its apparently restricted distribution in the Cordillera Central of northern Colombia; among other material unambiguously referable to this species, the validity of which is clearly supported by my analyses, I sequenced a paratype (FMNH 69823). The unique sequence of *invictus*, one of only two species of *Marmosops* known to occur in

[2] Voss *et al.* (2001: 48) described *Marmosa (Sciophanes) juninensis* as lacking distinct C1 accessory cusps, but their material consisted of mature adults with worn teeth. Subsequently examined specimens, among them LSU 25902 (a juvenile male) and two young adult females described by (Peralta & Pacheco, 2014), all have distinct posterior accessory cusps on C1.

Panama, was obtained from a specimen that I compared directly with Goldman's (1912) type material, which it closely resembles in all relevant external and craniodental details; the very large CYTB distances among this taxon and all other members of clade A (10.6–17.5%, uncorrected) are obviously consistent with its currently accepted status as a valid species. Although I sequenced both the holotype (USNM 418503) and a paratype (USNM 442719) of *cracens* from the Caribbean coast of northern Venezuela, I provisionally treat this name as a junior synonym of *fuscatus* based on close morphological and sequence similarity with topotypical material of the latter taxon (e.g., BMNH 1903.1.5.2, from the Mérida Andes of western Venezuela). I use *carri* (previously considered to be a synonym of *fuscatus*; e.g., by Gardner & Creighton, 2008) for sequences obtained from Trinidad (the type locality of *carri*) and from the adjacent Venezuelan mainland. The CYTB sequences I refer to *fuscatus* (including *cracens*) and *carri* are substantially divergent (4.9%, uncorrected), and relevant voucher material is unambiguously distinguishable by dental measurements, so I provisionally regard these taxa as valid species.

Clade B is also unrevised and contains both currently recognized species and putative species that lack available names. My unique BRCA1 sequence of *juninensis* was obtained from a specimen collected near the Peruvian type locality (in Junín department), and which I compared directly with the holotype (AMNH 63864). I have not personally examined type material of *ojastii*, but the sequence I associate with this name was obtained from a specimen collected near the type locality (in north-central Venezuela), and which conforms to the morphological diagnosis provided by García *et*

al. (2014). Large CYTB differences (7.7–10.2%, uncorrected) between *ojastii* and other nominal taxa in Clade B seem consistent with its proposed status as a valid species. Sister to *ojastii* is a complex of putative species that are morphologically indistinguishable from *Marmosops bishopi*. These taxonomically problematic lineages differ from one another by 3.5 to 11.3% in mean uncorrected CYTB sequence comparisons (table 4) and, in default of available names, I distinguish them by alphabetic labels. The name *bishopi* is based on a type from south of the Amazon, so the epithet would apply to the clade labeled "A" if it were to be used in a formally restricted sense. The remaining terminals belonging to Clade B are two unnamed haplogroups from northern Colombia, one from either side of the Río Magdalena—an important zoogeographic barrier (Chapman, 1917; Gutiérrez-Pinto *et al.*, 2012)—that differ by about 5.9% at the cytochrome-*b* locus; because they are also morphologically diagnosable (see chapter 2), I regard them as valid species.

Clade C has received some revisionary attention, most recently from Voss *et al.* (2013), who analyzed morphological data and CYTB sequences to establish *pakaraimae*, *parvidens*, and *pinheiroi* as valid species. My samples from this clade are identical to theirs, and include several sequences from the type series of *pakaraimae*. Identifications of sequences that I assign to *parvidens* and *pinheiroi* are supported by direct comparisons of voucher specimens with type material based on external and craniodental characters described by Voss *et al.* (2001). Indeed, the only noteworthy issue here concerns the status of *woodalli*, currently treated as a subspecies (Pine, 1981) or junior synonym (Gardner & Creighton, 2008) of *pinheiroi*. The CYTB clade that I associate with

woodalli, consisting of sequences from two specimens (including a paratype, USNM 545543) collected south of the Amazon, is only 3.9% divergent from typical *pinheiroi* (from north of the Amazon), and I am not aware of any consistent phenotypic character by which these nominal taxa can be distinguished. I am, therefore, inclined to regard *pinheiroi* and *woodalli* as conspecific.

ETYMOLOGY: From the ancient Greek (σκιοφανής) for shadowy or phantomlike, in reference to the elusive habits of these small forest creatures.

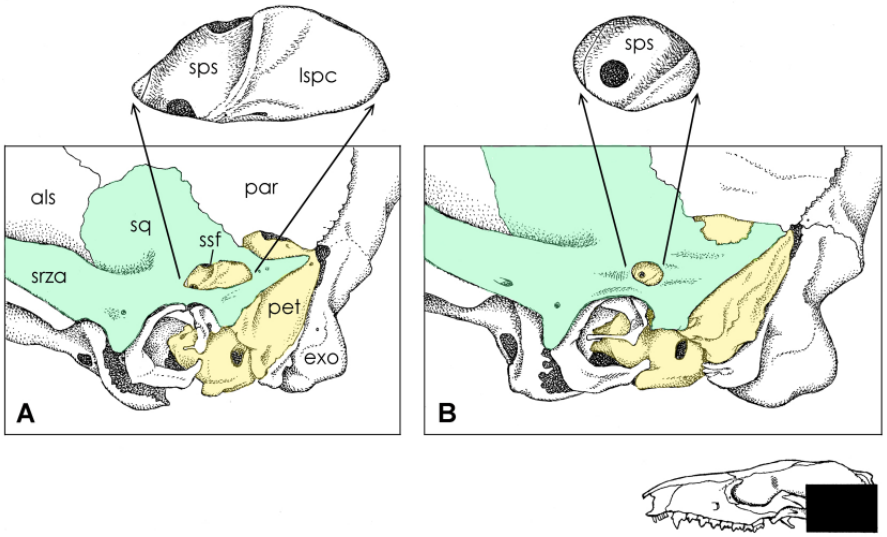

Figure 6. Lateral view of posterior braincase of *Marmosops (Sciophanes) pinheiroi* (A, AMNH 267345) and *M. (M.) noctivagus* (B, MUSM 13288) illustrating diagnostic subgeneric morphologies of the squamosal (green) and petrosal (yellow). Abbreviations: als, alisphenoid; exo, exoccipital; lspc, lateral surface of *pars canalicularis* (of petrosal); par, parietal; pet, petrosal; sps, sulcus for the prootic sinus (of petrosal); sq, squamosal; srza, squamosal root of zygomatic arch; ssf, subsquamosal foramen.

Subgenus *Marmosops* Matschie, 1916

TYPE SPECIES: *Marmosops incanus* (Lund, 1840).

CONTENTS: I refer 25 nominal taxa to the subgenus *Marmosops*, including *albiventris* Tate, 1931; *bahiensis* Tate, 1931; *caucae* Thomas, 1900; *celicae* Anthony, 1922; *collega* Thomas, 1920; *creightoni*, Voss et al., 2004; *dorothea* Thomas, 1911; *keaysi* Allen, 1900; *leucastrus* Thomas, 1927; *lugendus* Thomas, 1927; *madescens* Osgood, 1913; *neblina* Gardner, 1990; *neglectus* Osgood, 1915; *noctivagus* Tschudi, 1845; *ocellatus* Tate, 1931; *oroensis* Anthony, 1922; *paulensis* Tate, 1931; *perfuscus* Thomas, 1924; *politus* Cabrera, 1913; *purui* Miller, 1913; *scapulatus* Burmeister, 1856; *sobrinus* Thomas, 1913; *stollei* Miranda-Ribeiro, 1936; *ucayaliensis* Tate, 1931; and *yungasensis* Tate, 1931.

The nominal species *impavidus* Tschudi, 1845, is not certainly identifiable as a member of the genus *Marmosops* despite current usage of this name for at least two distinct species in the nominotypical subgenus. Briefly (a fuller account will be provided elsewhere), no type specimen is known to exist, the name cannot be applied with confidence based on characters described by Tschudi, its application as a senior synonym for *caucae* is inconsistent with Tschudi's description, and its application to specimens with *ocellatus*-like CYTB sequences from western Brazil and northeastern Peru is inconsistent with Tschudi's type locality. In my opinion, *impavidus* is best regarded as a *nomen dubium* and should be retired from taxonomic service.

Table 4. Percent pairwise CYTB sequence divergence among putative species of *Marmosops* subgenus I. Uncorrected net average *p*-distance (below diagonal) and net average Maximum Likelihood corrected distance (above diagonal) between groups, and mean uncorrected within-group distances (diagonal, shaded cells).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1. *bishopi* A	2.0	4.2	6.2	4.8	5.0	16.7	27.6	16.2	30.5	28.4	32.1	14.8	29.6	29.3	31.3	27.6	15.1
2. *bishopi* B	3.5	-	6.0	5.6	5.5	17.2	25.7	14.5	36.1	30.4	34.5	12.5	31.8	29.6	34.8	31.8	16.3
3. *bishopi* C	5.0	4.9	-	6.1	6.4	18.5	28.2	16.4	34.0	32.7	22.5	13.2	31.3	34.7	34.0	27.2	16.2
4. *bishopi* D	3.9	4.6	4.9	0.6	4.3	17.1	28.2	13.4	33.2	31.9	38.2	12.3	31.8	30.6	33.2	28.7	13.6
5. *bishopi* E	4.1	4.6	5.3	3.7	0.5	17.9	27.1	12.6	34.1	30.5	36.2	12.3	32.0	29.9	32.6	27.8	13.5
6. *bishopi* F	10.4	10.8	11.4	10.7	11.3	1.5	31.3	12.8	37.2	31.5	38.4	14.7	32.4	30.0	28.7	25.6	13.7
7. *carri*	13.9	14.0	14.8	14.5	14.0	16.0	1.4	21.8	5.2	16.9	17.8	27.2	25.3	20.7	26.4	23.7	23.5
8. "East Magdalena"	10.5	9.8	11.2	9.2	8.7	8.8	12.5	0.8	22.8	24.0	16.4	10.3	26.5	32.8	24.8	20.4	7.4
9. *fuscatus*	14.9	17.2	16.9	16.0	16.3	17.4	4.1	12.9	1.6	19.3	19.8	26.4	29.0	26.3	28.6	25.9	24.1
10. *handleyi*	13.9	15.3	16.2	15.3	14.8	15.4	10.4	12.9	11.5	0.6	24.6	28.3	27.3	27.2	34.0	31.7	25.1
11. *invictus*	15.5	16.8	13.7	17.4	16.8	17.5	12.0	10.6	12.7	14.0	-	24.1	34.3	29.7	29.7	29.9	22.3
12. *ojastii*	10.3	9.2	9.7	9.0	9.1	10.2	14.9	7.7	14.6	14.9	14.1	-	25.0	28.3	28.5	25.6	11.0
13. *pakaraimae*	14.9	16.1	16.3	15.8	16.0	15.8	14.1	14.4	15.0	14.3	17.2	14.0	0.1	9.2	21.1	19.4	27.0
14. *parvidens*	14.4	15.1	16.7	15.2	15.0	14.6	12.2	16.0	13.8	13.9	15.8	14.5	6.9	1.6	24.3	23.0	33.2
15. *pinheiroi*	14.8	16.4	16.3	15.7	15.5	14.0	13.7	13.7	13.9	15.5	14.4	14.5	12.3	13.2	1.3	5.1	25.7
16. *woodalli*	13.0	15.0	13.7	13.8	13.6	12.5	12.2	11.3	12.5	14.2	13.8	13.1	11.3	12.1	3.9	2.4	22.0
17. "West Magdalena"	10.3	11.1	11.5	9.7	9.7	9.4	13.0	5.9	13.4	13.4	13.1	8.4	14.8	16.3	13.7	12.0	0.3

Table 5. Percent pairwise CYTB sequence divergence among putative species of *Marmosops* subgenus II. Uncorrected net average *p*-distance (below diagonal) and net average Maximum Likelihood corrected distance (above diagonal) between groups, and mean uncorrected within-group distances (diagonal, shaded cells).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1. *caucae* A	3.9	2.4	21.0	18.2	21.1	24.0	28.9	32.9	27.2	32.6	16.0	21.0	21.9	19.9	21.5	20.2	34.2	31.3	32.4	5.7
2. *caucae* B	2.0	1.8	20.1	17.6	20.8	23.1	28.9	29.7	27.6	31.4	16.7	19.7	21.1	18.4	19.8	20.6	33.3	29.7	30.6	4.8
3. *condor* A	11.6	11.9	-	9.9	22.7	19.7	28.6	27.4	25.8	27.2	18.8	21.9	21.4	20.3	22.4	20.6	32.3	31.4	30.0	20.3
4. *condor* B	10.2	10.6	7.5	0.1	21.8	23.6	30.4	25.7	22.8	25.7	17.8	22.9	23.0	21.3	23.0	19.1	30.9	24.2	27.1	19.1
5. *creightoni*	11.5	12.1	13.1	12.7	0.3	20.5	29.8	26.4	24.3	27.0	14.1	11.4	13.2	11.1	13.2	18.0	32.5	26.9	30.2	17.1
6. "Gálvez"	12.2	12.5	11.7	13.1	11.9	0.4	27.9	26.6	23.9	28.8	11.0	22.2	23.2	21.1	21.2	13.0	31.5	28.9	30.3	22.0
7. *incanus* A	13.7	14.6	15.5	15.8	15.4	14.8	0.0	15.3	13.8	15.3	25.0	26.1	27.2	26.0	29.0	31.3	38.3	34.6	34.0	28.0
8. *incanus* B	14.9	14.6	15.1	14.3	14.5	14.5	10.7	0.2	10.3	13.6	25.9	25.9	27.9	29.2	27.9	28.4	34.6	31.3	31.1	29.5
9. *incanus* C	12.4	13.4	14.1	12.6	13.2	12.9	9.6	7.4	2.5	5.3	23.6	21.9	23.9	23.7	25.4	27.2	30.0	26.9	29.1	26.1
10. *incanus* D	14.3	14.9	14.6	13.9	14.1	14.7	10.8	9.5	4.2	0.0	28.1	28.3	27.8	25.0	28.9	33.5	36.6	30.9	33.2	32.1
11. "Juruá"	8.9	9.9	11.3	10.6	9.2	7.4	13.1	13.7	12.3	14.1	2.3	14.8	14.9	13.6	15.7	5.4	27.2	27.3	27.3	16.9
12. *noctivagus* A	11.0	11.1	12.4	12.8	8.0	12.0	13.4	13.6	11.4	13.9	9.0	2.0	3.5	5.1	6.4	18.1	28.9	25.6	28.3	18.9
13. *noctivagus* B	11.4	11.8	12.2	12.7	9.0	12.4	13.7	14.3	12.2	13.7	9.1	2.9	2.1	5.1	6.6	18.9	34.3	29.3	30.7	18.2
14. *noctivagus* C	10.3	10.3	11.6	12.0	7.7	11.4	13.2	14.7	12.1	12.7	8.3	3.9	3.9	2.6	3.7	16.1	30.1	27.6	27.5	17.2
15. *noctivagus* D	11.2	11.2	12.6	12.8	9.0	11.6	14.4	14.5	13.0	14.2	9.4	4.8	4.9	2.8	1.4	16.7	31.6	28.2	28.2	18.7
16. *ocellatus*	10.9	11.7	12.3	11.5	11.3	8.7	15.8	14.8	13.9	16.3	4.2	10.9	11.2	9.7	10.2	0.7	28.6	28.0	28.7	20.0
17. *paulensis* A	14.4	15.1	15.6	14.8	15.3	14.8	17.2	16.1	14.0	16.9	13.2	13.3	15.0	13.7	14.3	13.9	0.6	8.3	8.5	35.0
18. *paulensis* B	13.8	14.1	15.6	12.8	13.6	14.3	15.9	15.2	12.9	14.8	13.3	12.4	13.7	13.2	13.5	14.1	6.1	0.9	3.4	33.0
19. *paulensis* C	14.3	14.5	15.0	13.8	15.0	14.7	16.1	15.3	14.0	16.0	13.4	13.5	14.2	13.2	13.5	14.3	6.5	2.9	0.2	32.6
20. *ucayaliensis*	4.2	3.8	12.1	11.5	10.7	12.4	14.9	15.3	13.4	15.5	10.2	10.9	10.5	10.0	11.0	11.9	15.8	15.4	15.5	1.0

REMARKS: The sequences I identify as *incanus* are from southeastern Brazilian material that exhibits the diagnostic morphological traits of *Marmosops incanus* as described and illustrated by Mustrangi & Patton (1997). As in their study, I found substantial geographically structured cytochrome-*b* sequence divergence among *incanus*-like specimens, which GMYC analysis suggests represent four putative species (differing by 4.2–10.8%, on average, in uncorrected pairwise comparisons). Although I use alphabetic designations for these haplogroups, the type locality of *incanus* (Lagoa Santa, in Minas Gerais) falls within the geographic range of "*incanus* C" (north of the Rio Paraíba do Sul), to which this epithet would presumably belong if it were to be applied in a stricter sense than it is at present. Additionally, at least on the basis of geography, the name *scapulatus* (also based on a specimen from Minas Gerais) seems to apply to *incanus* C, and the name *bahiensis* (based on a type from Bahia) is geographically closest to *incanus* D. Apparently, there are no available names for "*incanus* A" (from the southern coastal plain of Rio de Janeiro) or "*incanus* B" (from São Paulo). However, pending morphological analysis of this complex, and in the absence of any other evidence for nuclear-gene divergence, it seems premature to suggest that *M. incanus* includes more than a single valid species.

Similarly, I apply the name *paulensis* to specimens from southeastern Brazil that share the diagnostic morphological traits of *Marmosops paulensis* as described by Mustrangi & Patton (1997). The three putative species identified by LGMYC in this complex occur allopatrically, each on a different mountain range ("*paulensis* A" in the Serra da Mantiqueira, "*paulensis* B" in the Serra dos Orgaõs, "*paulensis* C" in the Serra

do Mar) and differ by 3.0–6.5%, on average, in uncorrected pairwise CYTB sequence comparisons. The holotype (FMNH 26576) is from the Serra dos Orgaõs, so the epithet would properly apply to "*paulensis* B" if it were to be applied in a stricter sense. No names are currently available for "*paulensis* A" or "*paulensis* C," but in the absence of diagnostic morphological characters (which I have yet to discover) or other evidence for nuclear-gene divergence, formal taxonomic recognition is inappropriate.

Clade D includes two putative species represented by three sequences from morphologically distinctive specimens recently collected in the Cordillera del Condor of northeastern Peru and from the immediately adjacent Cordillera Oriental of southern Ecuador. No name is available for either putative species, which I distinguish alphabetically. Sequenced specimens of "Condor A" and "Condor B" were collected over 1700 m above sea level on opposite sides of the Río Zamora, and their cytochrome-b sequences differ by about 7.5% (uncorrected)—an impressive difference for material obtained only 98 airline kilometers apart—but I lack sequence data from the headwaters of the Zamora, where intermediates might be expected to occur.

The *caucae* complex (also part of Clade D) includes one of the most geographically widespread series of specimens recovered by my analyses. My sequenced material spans an enormous range, from about 11°N (in northern Colombia) to 7°S (in northern Peru), and from about 66°W (in southern Venezuela) to 80°W (in western Ecuador); most sequenced specimens were collected in montane habitats, but several are from lowland Amazonian sites. As might be expected, there is substantial sequence variation within this complex (4.1%, uncorrected), but only two haplogroups ("*caucae* A"

and "*caucae* B") were recovered as weakly divergent (2%, uncorrected; table 5) putative species. The name *caucae* is based on a Colombian specimen that morphologically resembles all of the referred material I examined from that country; other names that can be associated with this complex based on morphology and geography include *celicae*, *madescens*, *neblina*, *oroensis*, *perfuscus*, and *sobrinus*. Sequence data that I obtained from type material (holotypes and/or paratypes) of *celicae* (AMNH 47182), *neblina* (USNM 560732, 560735), and *oroensis* (AMNH 47180) are likewise consistent with the hypothesis that these names are junior synonyms of *caucae*. The type locality of *madescens* is geographically closest in airline distance to my material of "*caucae* B" (e.g., locality 115, appendix 5) but the type was collected at a much higher elevation.[3] Consequently, I am unable to confidently associate a name with "*caucae* B" pending a proper revision of this complex.

Sister to the *caucae* complex is a putative species consisting of five sequences from three localities in southeastern Peru; one of these sequences is from a paratype of *ucayaliensis* (AMNH 76532), which appears to be the only available name that is definitely assignable to this haplogroup, although *purui* (from western Brazil; appendix 5) might be a senior synonym. The average pairwise uncorrected difference between CYTB sequences of *caucae* (including haplogroups A andB) and *ucayaliensis* is just 3.9%, and I am not aware of any consistent morphological differences among relevant voucher specimens. In effect, there is, as yet, no compelling evidence that these are distinct species.

[3] The type locality of *madescens* is in the highlands at approximately 2700 m above sea level, whereas geographically adjacent material of "*caucae* B" was collected in the lowlands (below 815 m).

Clade E consists of two putative species that lack available names ("Gálvez" and "Juruá") and a third that corresponds to *Marmosops ocellatus* as diagnosed by Voss et al. (2004); all are lowland haplogroups that occur in eastern Bolivia, eastern Peru, and/or western Brazil. Voss et al. (2004) described morphological differences between Bolivian material of *ocellatus* and "Juruá" (the latter represented by a sequenced specimen they called *M. impavidus*), which might be valid species despite modest sequence divergence (4.2%, uncorrected). "Juruá" and "Gálvez" differ by an average pairwise cytochrome-*b* distance of about 7.4% and also appear to be phenotypically distinct.

Clade F includes *creightoni*, a morphologically distinctive species (Voss et al., 2004), of which I sequenced the holotype (CBF 6552) and another specimen, both from the eastern Andean versant of northern Bolivia. Sister to *creightoni*, and differing from it by average uncorrected distances of 7.7–9.0%, is a strongly supported group of three putative species that collectively correspond to *Marmosops noctivagus* of current usage (sensu Gardner and Creighton, 2008). I use alphabetic designations to distinguish these haplogroups, which differ *inter se* by only 2.8–4.9%, because the application of available names is uncertain.

Tschudi's (1844) original description of *noctivagus* was based on specimens collected in east-central Peru (Junín department), which, unfortunately, is in-between the known geographic ranges of "*noctivagus* B" and "*noctivagus* C." Because I do not have sequence data from any surviving syntypes, and because morphological differences between voucher specimens of these haplogroups are not apparent, Tschudi's epithet could apply to either of them. The application of *keaysi*, the next-oldest name based on

noctivagus-like material, is also uncertain because Allen's (1900) type locality in southern Peru (Puno department) is in-between the known geographic ranges of "*noctivagus* C" and "*noctivagus* D." Geography can be used to associate *albiventris* (based on a type from Cusco department, Peru) and two names based on material from Amazonian Brazil (*collega* and *stollei*) with "*noctivagus* C," and the same logic suggests that *politus* (from eastern Ecuador) applies to "*noctivagus* A." Three names currently treated as synonyms of *noctivagus* that are based on types from northern Peru (*leucastrus*, *lugendus*, and *neglectus*) might apply to "*noctivagus* B," but until this complex is revised taxonomically, these are mere conjectures. My sequences of "*noctivagus* D" include one from a paratype of *yungasensis*, but the name *dorothea* (based on a type from La Paz department, Bolivia) is a senior synonym (Voss et al., 2004).

CHAPTER 2.
A REVISION OF THE DIDELPHID MARSUPIAL GENUS *MARMOSOPS* PART 1. SPECIES OF THE SUBGENUS *SCIOPHANES*

INTRODUCTION

Members of the genus *Marmosops* are small (<200 g) didelphid marsupials that collectively range from eastern Panama to southern Bolivia and southeastern Brazil. Black-masked, long-tailed, and pouchless, they were classified for many years in the genus *Marmosa* along with other superficially similar taxa (e.g., by Tate, 1933; Cabrera, 1958). However, subsequent morphological and molecular research (reviewed by Voss et al., 2004; Voss and Jansa, 2003) has shown that the species referred to *Marmosops* by Matschie (1916), together with those later refered to the genus by Gardner and Creighton (1989), form a strongly supported monophyletic group that is not closely related to *Marmosa* (sensu stricto). Instead, *Marmosops* is now placed in the didelphine tribe Thylamyini, a clade that also includes *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, and *Thylamys* (Voss and Jansa, 2009).

Unlike most other thylamyines, which occur in dry forests, savannas, grasslands, and high-latitude deserts, species of *Marmosops* typically inhabit humid-forest habitats. In particular, the genus is widespread—perhaps ubiquitous—in cis-Andean lowland rain forests (Mustrangi and Patton, 1997; Patton et al., 2000; Voss et al., 2001), and it also occurs in premontane and montane rain forests of the Andes, the Venezuelan coastal cordilleras, and Pantepui (Díaz-N. et al., 2011; Voss et al., 2013; García et al., 2014).

Insofar as known, these are scansorial opossums that are primarily active on the ground and within a few meters of the ground in understory vegetation (Malcolm, 1991; Patton et al., 2000; Voss et al., 2001; Cunha and Vieira, 2002; Vieira and Monteirho-Filho, 2003; Loretto and Vieira, 2008), where they apparently forage for arthropods (mostly insects) and fruit (Passamani, 1995; Leiner and Silva, 2007; Lessa and Costa, 2008). At least in the Atlantic Forest of southeastern Brazil, species of *Marmosops* appear to be semelparous breeders that experience almost complete post-reproductive mortality, such that successive adult generations are nonoverlapping (Lorini et al., 1994; Leiner et al., 2008).

The genus as a whole has never been revised, although taxonomic analyses of specimens collected in the course of regional faunal surveys have contributed numerous insights (Mustrangi and Patton, 1997; Voss et al., 2001, 2004, 2013; Díaz et al., 2011; García et al., 2014). The current classification formally recognizes 17 valid species of *Marmosops*, a total that includes the 15 species recognized by Gardner and Creighton (2008) and two others subsequently described as new (Voss et al., 2013; García et al., 2014). Among other didelphid genera, only *Monodelphis* (with 22 currently recognized species; Pavan et al., 2014; Pavan, 2015) and *Marmosa* (with 19 species; Voss et al., 2014) are comparably diverse.

Although molecular sequence data have been analyzed in a few taxonomic studies of *Marmosops* (e.g., by Mustrangi and Patton, 1997; Patton et al., 2000; Voss et al., 2004, 2013), much of the current nomenclature is based exclusively on phenotypic comparisons. Unfortunately, the morphology-based primary taxonomic literature is

inadequate to confidently identify several species, secondary sources (e.g., field guides and keys) that are routinely consulted for identification purposes are sometimes unreliable, and some currently accepted synonymies are not based on first-hand examination of type material. Not surprisingly, museum specimens of *Marmosops* are often misidentified.

This report, the first installment of a comprehensive generic revison, is based on a multi-year study of morphological specimens (including all relevant type material), the results of which I interpret in the context of the results obtained from the molecular sequence data in Chapter 1. Among the more robustly-supported outcomes of that analysis was the discovery of a basal dichotomy in the genus, resulting in two clades that I formally recognized as subgenera. This report concerns the subgenus *Sciophanes*, which contains *Marmosops parvidens* (the type species), and 11 additional species, including two previously undescribed.

MATERIALS AND METHODS

SPECIMENS: The morphological specimens I examined and others mentioned below are preserved in the following collections (listed in order of their standard institutional abbreviations): AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, London), CM (Carnegie Museum, Pittsburgh), CTUA (Colección Teriológica de la Universidad de Antioquia, Medellín), EPN (Escuela Politécnica Nacional, Instituto de Ciencias Biológicas, Quito), FMNH (Field Museum, Chicago), ICN (Coleccion de Mamíferos Alberto Cadena García, Instituto de Ciencias

Naturales, Bogotá), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), ISEM (Institut des Sciences de l'Evolution de Montpellier, Montpellier), KU (University of Kansas Biodiversity Institute, Lawrence), LACM (Los Angeles County Museum, Los Angeles), LSUMZ (Louisiana State University Museum of Zoology, Baton Rouge), MHNUC (Museo de Historia Natural, Universidad de Caldas, Manizales), MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque), MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito), ROM (Royal Ontario Museum, Toronto), UF (Florida Museum of Natural History, University of Florida, Gainesville), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), and USNM (National Museum of Natural History, Washington).

MEASUREMENTS: I transcribed total length (nose to fleshy tail-tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels, and computed head-and-body length (HBL) by subtracting LT from TL. I 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 sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by the collector, and used my values whenever large discrepancies were found. (In a few instances I omitted problematic collectors' measurements when computing sample means, and observed ranges.) 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 as skulls were viewed under low (6–12×) magnification. Measurement values were recorded to the nearest 0.01 mm, but those reported herein are rounded to the nearest 0.1 mm. The following dimensions were measured (figure 7):

Condylo-Basal Length (CBL): measured from the occipital condyles to the anteriormost point of the premaxillae.

Nasal Length (NL): the greatest anteroposterior dimension of either bone.

Nasal Breadth (NB): measured between 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, even when the postorbital constriction (between the temporal fossae) is narrower.

Zygomatic Breadth (ZB): measured at the widest point across both zygomatic arches.

Palatal Length (PL): measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present).

Palatal Breadth (PB): measured across the labial margins of the M4 crowns, at or near the stylar A position.

Maxillary Toothrow Length (MTR): measured from the anterior margin of C1 to the posterior margin of M4.

Length of Molars (LM): measured from the anteriormost labial margin of M1 to the posteriormost point on M4.

Length of M1–M3 (M1–M3): measured from the anteriormost labial margin of M1 to the posteriormost point on M3.

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

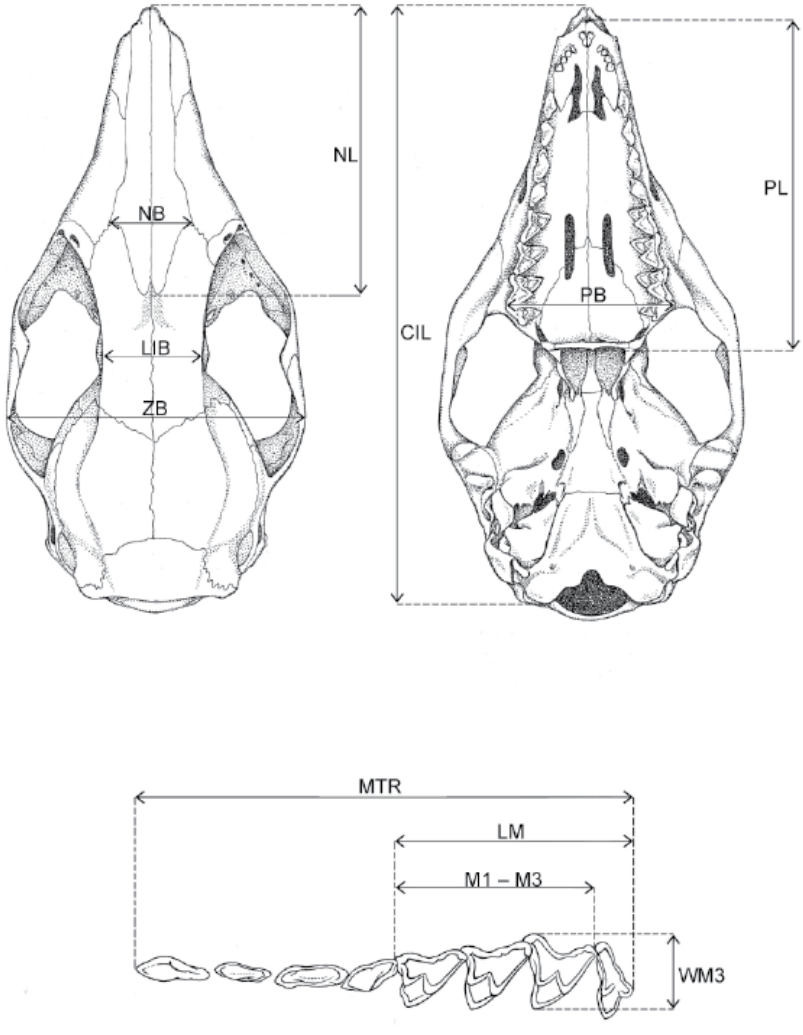

Figure 7. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Marmosops pinheiroi*, showing the anatomical limits of 11 craniodental measurements defined in the text.

AGE CRITERIA: Unless otherwise noted below, I recorded measurements and scored qualitative morphological data from adult specimens only. Following Voss et al. (2001), a specimen was judged to be juvenile if dP3 is still in place; subadult if dP3 has been shed but P3 is still incompletely erupted; and adult if the permanent upper dentition (I1–I5, C1, P1–P3, M1–M4) is complete. Because dP3 is molariform, juvenile specimens have only two premolariform teeth (P1 and P2) between the upper canine and the first molariform tooth (dP3), whereas adults have three fully erupted premolariform teeth (P1, P2, and P3) between the upper canine and the first molariform tooth (M1).

COMPARATIVE MORPHOLOGY

Species of *Marmosops* can be distinguished from one another by qualitative differences in numerous characters of the integument, skull, and dentition. I describe and illustrate these characters in the accounts that follow, using anatomical terminology defined or referenced by Voss and Jansa (2003, 2009) and Díaz-N. et al. (2011). For the most part, my usage is consistent with morphological descriptors defined by Brown (1971), Brown and Yalden (1973), Bown and Kraus (1979), and Wible (2003), which should also be consulted for relevant explanations and illustrations.

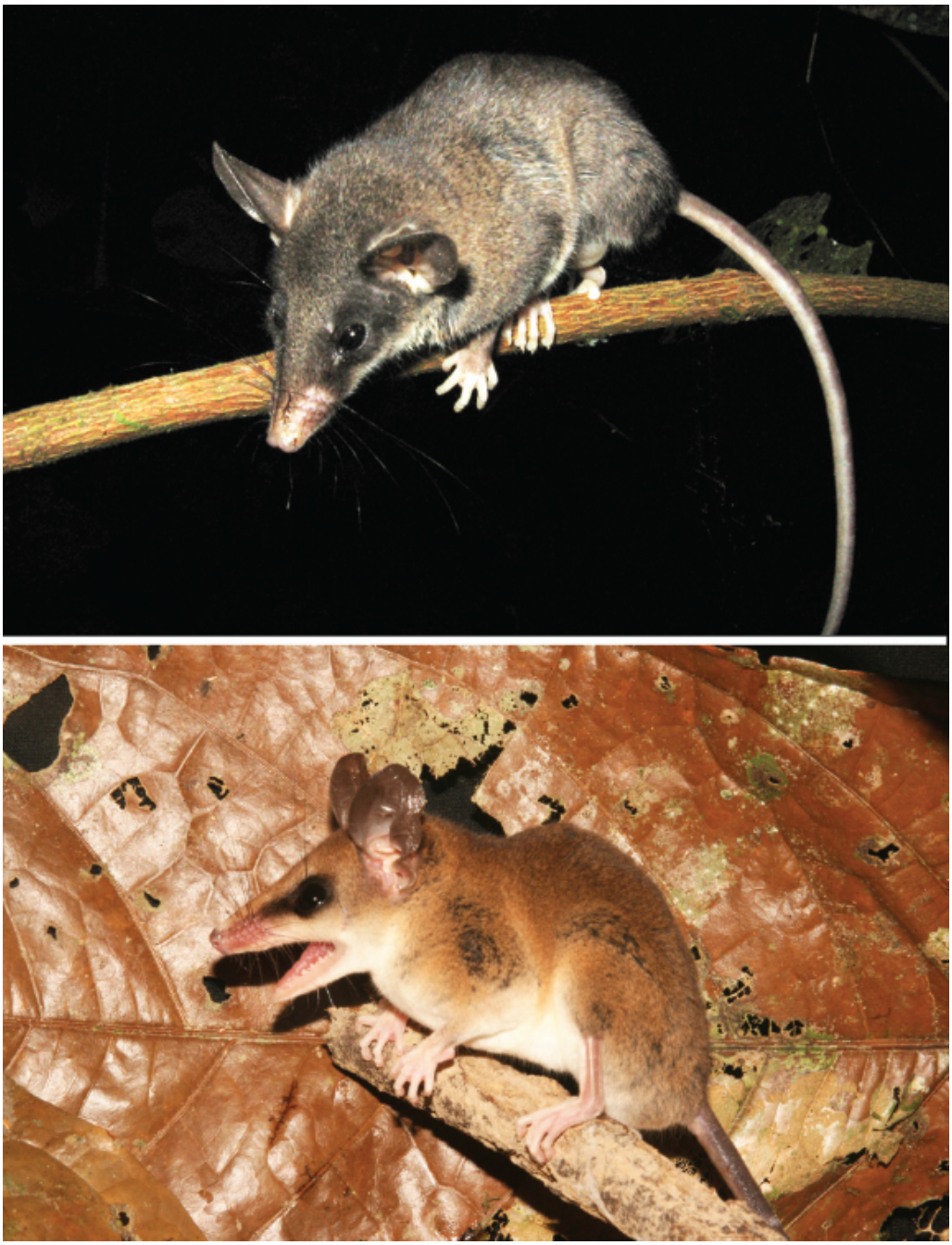

Figure 8. *Marmosops handleyi* (above; photographed by J. Díaz-Nieto at Finca Costa Rica, Antioquia, Colombia) and *M. parvidens* (below; photographed by T. Semedo near Urucará, Amazonas, Brazil). In addition to obvious differences in body pelage color, these species differ in forefoot markings: whereas *M. handleyi* has dark metacarpal fur that contrasts with the pale fur of the manual digits, *M. parvidens* has all-pale forefeet.

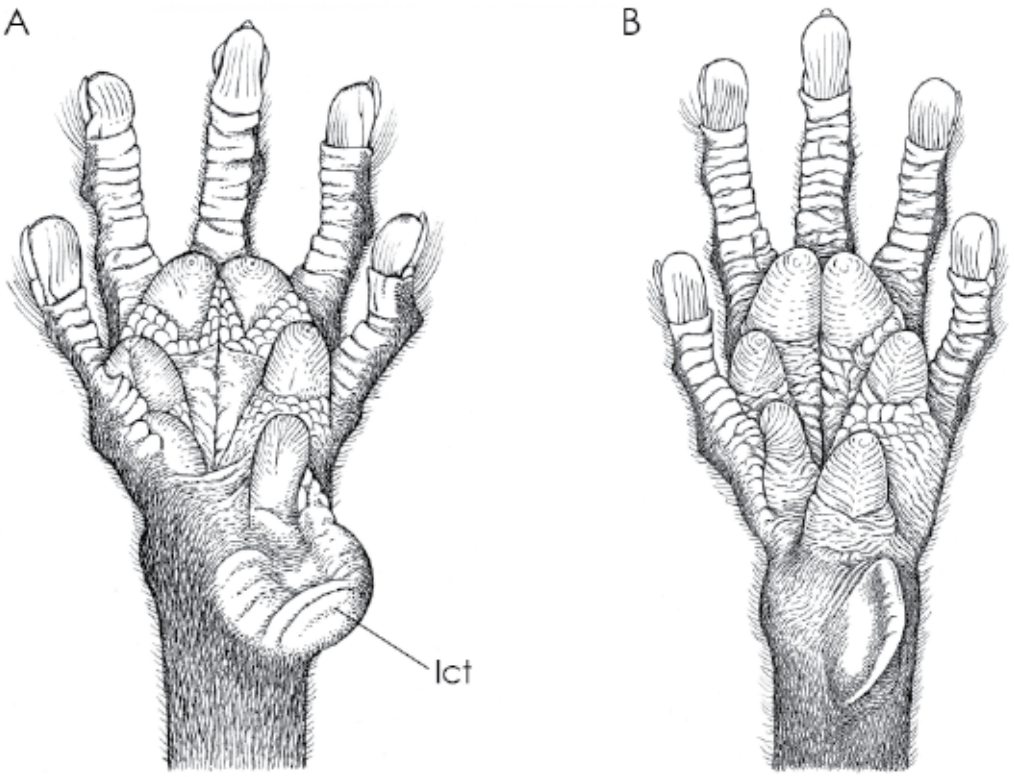

Figure 9. Plantar views of left forefoot (manus) and wrist of *Marmosops pinheiroi* (A, AMNH 267346) and *M. bishopi* (B, MUSM 23801) illustrating different morphologies of the lateral carpal tubercle (lct), which is spoon-shaped in adult males of *M. pinheiroi* and blade-like (laterally compressed) in adult males of *M. bishopi*.

INTEGUMENT

DORSAL PELAGE COLOR: As in many other groups of small nocturnal mammals, dorsal pelage color exhibits a limited range of variation among species of *Marmosops*. In general, the species treated in this report are soberly colored in various dull, substrate-matching shades of brown, but coat-color contrasts are sometimes striking (figure 8). Ordinary color descriptors (e.g., "pale grayish-brown") are sufficient for most comparative purposes, but I also cite Ridgway's (1912) terminology, which is always capitalized (e.g., Dark Umber).

VENTRAL PELAGE COLOR AND PATTERN: Ventral pelage hairs can be the same color from base to tip, or they can be grayish basally with paler tips. Ventral fur composed of hairs that are the same color from base to tip is said to be self-colored (e.g., self-white, self-buffy, etc.; Tate, 1933), whereas ventral fur composed of hairs with gray bases is said to be gray-based. In general, the fur of the chin (including the oral margins), and groin (including the scrotum) is self-whitish in *Marmosops*, but the coloration of the throat, chest, abdomen, and the inside surfaces of the fore- and hindlimbs is taxonomically variable. In several species of the subgenus *Sciophanes*, the entire ventrum (except the chin and groin) is covered with gray-based fur, but in other species there is a continuous midventral zone of self-colored fur that extends from the chin to the groin. In some species the self-whitish midventral fur is much narrowed by lateral zones of gray-based fur, and in others the self-colored fur is reduced to a discontinuous midventral streak. The short fur surrounding the mammae of lactating adult females is sometimes reddish or brownish; within the subgenus *Sciophanes* I observed this trait in specimens of *M. bishopi* (e.g., TTU 101238), *M. chucha* (FMNH 69837), *M. magdalenae* (ICN 19924), and *M. pinheiroi* (USNM 393529).

GULAR GLAND: Many species in the nominotypical subgenus of *Marmosops* have a conspicuous midventral patch of naked skin on the throat that is presumably homologous with the gular gland of other didelphids (Barnes, 1977), but species of the subgenus *Sciophanes* lack any external trace of glandular activity in the throat region, which is uniformly furred and unstained by cutaneous secretions.

DORSAL PELAGE OF MANUS AND PES: The dorsal surface of the manus is covered with short hairs that are uniformly pale in some species, whose forefeet lack any pigmental contrast between the metacarpal and digital pelage. In other species, however, the metacarpals are covered with dark (brownish or grayish) hairs that contrast abruptly in color with the paler digital fur. (See figure 8 for contrasting examples of manual pelage markings.) Hindfeet exhibit similar variation in the nominotypical subgenus of *Marmosops*, some species of which have dark metatarsals that contrast with abruptly paler digits, but all species of the subgenus *Sciophanes* have uniformly pale-furred hindfeet.

CARPAL TUBERCLES: Prominent carpal tubercles that are supported internally by the pisiform bone (Lunde and Schutt, 1999; Voss et al., 2001: figure 20) are present on the lateral surface of the wrist of adult males of most species of *Marmosops*, but these are sexually dimorphic structures that do not occur in females, and they are often inapparent on the wrists of immature males. In the subgenus *Sciophanes*, carpal tubercles are taxonomically variable in shape. In some species they are spoon-shaped (broadly concave anteriorly; figure 9A), whereas in others they are blade-like (laterally flattened and aligned with the long axis of the wrist; figure 9B).

ANTEBRACHIAL VIBRISSAE: Most didelphids, including most species of the nominotypical subgenus of *Marmosops*, have a single long vibrissa on the dorsolateral surface of the forearm, but species of the subgenus *Sciophanes* consistently have two antebrachial vibrissae (Díaz-N. et al., 2011: figure 5). The only exceptional species

known to me is *M. (M.) ocellatus*, of which most examined specimens appear to have two antebrachial vibrissae.

MAMMAE: Didelphid mammae are typically restricted to the inguinal or abdominal region, where they form a roughly circular array that often includes an unpaired median teat (Voss and Jansa, 2009: figure 5b). I summarize mammary morphology as teat counts using the formula R–M–L = T (Right–Median–Left = Total). Thus, a species with three teats on the right side, one unpaired median teat, and three teats on the left side would have a mammary formula of 3–1–3 = 7. In species with nine or fewer teats, all of the mammae are circularly arranged and abdominal-inguinal, but in species with 11 or more mammae—for example, *Marmosops (Marmosops) ocellatus*, with mammary fomula 6–1–6 = 13 (Voss et al., 2004)—one or more pairs are said to be "pectoral" (Tate, 1933) because they are positioned anterior to the circular abdominal-inguinal array, although none that I have seen actually occur on the chest. Insofar as known, species in the subgenus *Sciophanes* have no more than 9 mammae, all of which are abdominal-inguinal.

CAUDAL COLORATION: The tail in *Marmosops* is furred only at the base and appears to be completely naked because the three bristle-like hairs emerging from each scale are visible only under magnification. Some species have unicolored tails that are dark from base to tip on both the dorsal and ventral surfaces, but in other species the caudal integument is more heavily pigmented dorsally and/or basally than it is ventrally and/or distally. Tails that are distinctly darker dorsally than ventrally are said to be

bicolored, whereas tails that are darker basally and paler near the tip are said to be *particolored*. No species of the subgenus *Sciophanes* has a distinctly particolored tail.

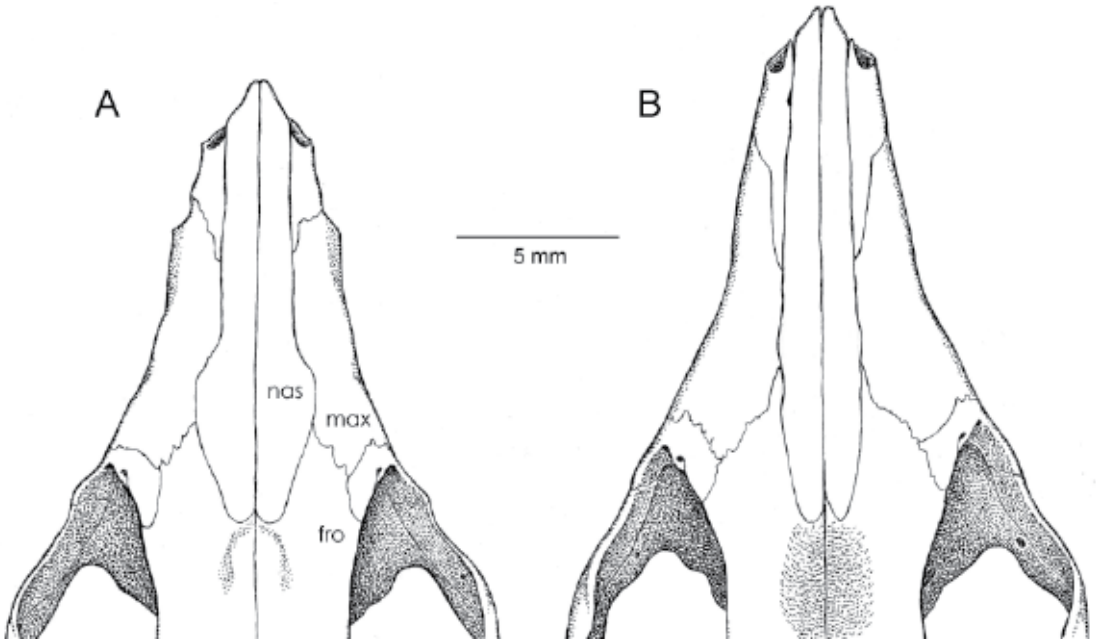

Figure 10. Dorsal views of the rostrum of *Marmosops invictus* (A, USNM 306386) and *M. fuscatus* (B, FMNH 22174), illustrating taxonomic differences in nasal width. Abbreviations: fro, frontal; max, maxillary; nas, nasal.

SKULL

NASAL SHAPE: The paired nasal bones are narrow and parallel-sided anteriorly, but in most species of *Marmosops* they are much wider posteriorly than anteriorly because they are laterally expanded at or near the frontal-maxillary suture (figure 10A). However, in some species of the nominotypical subgenus (e.g., *M. incanus*) and in two species of *Sciophanes* (namely *M. carri* and *M. fuscatus*), the nasals are almost as narrow

posteriorly as they are anteriorly, with only slight lateral expansion near the frontal-maxillary suture (figure 10B).

LACRIMAL FORAMINA: The lacrimal foramina transmit the lacrimal canaliculi and a small accompanying vein through the lacrimal bone, which forms the anterodorsal margin of the didelphid orbital fossa (Wible, 2003). Most species of *Marmosops* have two lacrimal foramina on each side, but the position of these openings is taxonomically variable. In some species of *Sciophanes* the foramina (or foramen, when only one is present) are more-or-less concealed from lateral view inside the anterior orbital margin (figure 19A), but in others they are laterally exposed anterior to the orbit (figure 19B). Yet other species, however, exhibit an intermediate morphology in which one foramen (usually the dorsalmost) is completely or partially concealed inside the orbit and the other (usually the ventralmost) is exposed on the orbital margin, and this character is sometimes quite variable even in local populations.

SQUAMOSAL-JUGAL OVERLAP: The zygomatic process of the squamosal is more-or-less acutely pointed and broadly overlapped dorsally by the jugal in most species of *Marmosops* (fig. 28A). But in *M. (Sciophanes) juninensis* the squamosal zygomatic process is rounded and not dorsally overlapped by the jugal, or is only shallowly overlapped by that bone (fig. 28B).

SUBSQUAMOSAL FORAMEN: The subsquamosal foramen[4] is a lateral opening in the squamosal bone that exposes the underlying petrosal just dorsal to the ear region of many

[4] The use of the term "subsquamosal foramen" is consistent with its original definition (Cope, 1880) and with well-established anatomical usage in the marsupial literature (e.g.,

marsupials. In the subgenus *Sciophanes* the subquamosal fenestra is anteroposteriorly elongated, revealing not only the sulcus for the prootic sinus, but also a substantial strip of the relatively featureless lateral surface of the pars canalicularis behind that groove (figure 6A). By contrast, the subsquamosal fenestra in the nominotypical subgenus is shorter and does not extend posteriorly much behind the sulcus for the prootic sinus (figure 6B).

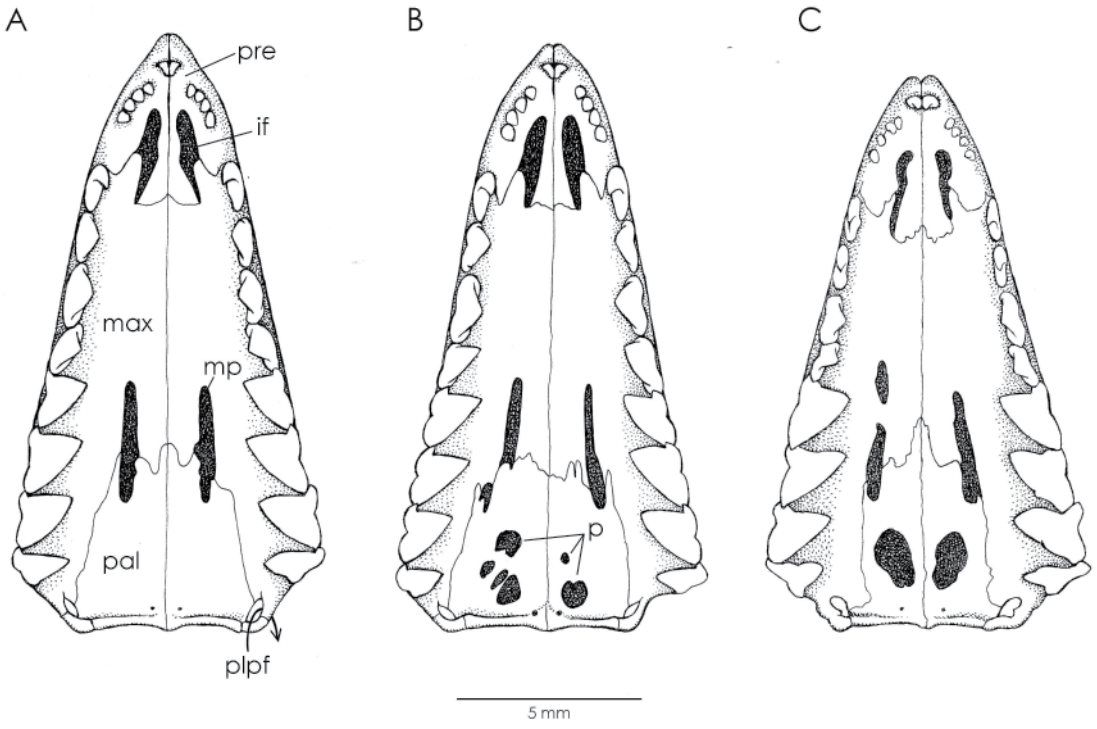

Figure 11. Ventral views of the palates of *Marmosops parvidens* (A, AMNH 267359), *M. juninensis* (B, AMNH 230016), and *M. magdalenae* (C, ICN 19926) illustrating species differences in the presence, absence, and morphology of palatal fenestrae and foramina. Abbreviations: if, incisive foramen; max, maxillary bone; mp, maxillopalatine fenestra; p, palatine fenestrae; pal, palatine bone; plpf, posterolateral palatine foramen.

Gregory, 1910; Archer, 1976), but Wible (2003: 183) referred to this opening as the "suprameatal foramen," a neologism.

PALATINE FENESTRAE: The didelphid bony palate is perforated by several pairs of foramina (transmitting ducts, nerves, and/or blood vessels) and fenestrae (which do not transmit anything), some of which exhibit important taxonomic variation (figure 11). All didelphids have incisive foramina, which occupy the the premaxillary-maxillary suture and transmit the nasopalatine ducts between the oral and nasal cavities; in most species of *Marmosops* the incisive foramina only extend posteriorly between the upper canines, but in at least one species of the nominotypical subgenus they are much longer, extending posteriorly between the first upper premolars (Mustrangi and Patton, 1997: figure 15). Most didelphids also have maxillopalatine fenestrae and posterolateral palatal foramina, both of which are in the maxillary-palatine suture, but these openings are not known to exhibit noteworthy variation among species of *Marmosops*. Instead, the presence or absence of palatine fenestrae—which penetrate the palatine bone just behind the maxillopalatine fenestrae—is a diagnostically useful character for species recognition in both subgenera.

Some species of the subgenus *Sciophanes* have completely ossified palatines that lack any trace of fenestration (figure 11A), whereas others have large palatine fenestrae. In some species the palatine fenestrae may consist of multiple irregular openings on each side (figure 11B), whereas other species may have a single large palatine fenestra on each side (figure 11C). Although palatine fenestrae sometimes vary in number, shape, and size among conspecific individuals, they tend to be consistently present or consistently absent in most species. Unfortunately the thin bone of the posterior palate is often damaged by

careless specimen preparation, so it is sometimes impossible to determine whether palatine fenestrae were present or absent.

ETHMOID FORAMEN: The didelphid ethmoid foramen is a small perforation in the medial wall of the orbit that transmits the ophthalmic artery and the ethmoidal nerve through the suture between the frontal and orbitosphenoid bones (Wible, 2003). In some species of the subgenus *Sciophanes* the dorsolateral margin of the foramen is consistently formed by the orbitosphenoid, whereas in others it seems to be consistently formed by the frontal. I have not surveyed variation in this character among species of the nominotypical subgenus.

DENTITION

C1 ACCESSORY CUSPS: The upper canine (C1) is a simple, recurved, unicuspid tooth in most marsupials, including all species in the nominotypical subgenus of *Marmosops*. By contrast, the subgenus *Sciophanes* is richly endowed with unusual upper-canine phenotypes, including sexual dimorphism. In both sexes of three species of *Sciophanes*, C1 is short and provided with both anterior and posterior accessory cusps (figure 12A), resulting in a strikingly premolariform tooth. In other species of *Sciophanes*, however, females have both anterior and posterior C1 accessory cusps, whereas males have only a posterior accessory cusp (figure 12B). In some species, both males and females usually have only posterior accessory C1 cusps; and in two species, females usually have only posterior C1 accessory cusps, whereas males have unicuspid teeth (figure 12C).

As noted previously (Voss and Jansa, 2009: 48), some care is needed in determining C1 crown morphology because accessory cusps are sometimes obliterated by wear, and because false posterior accessory cusps are sometimes created when the trailing edge of C1 is notched by occlusion with p1. Therefore, C1 morphology is best determined from subadult or young adult specimens.

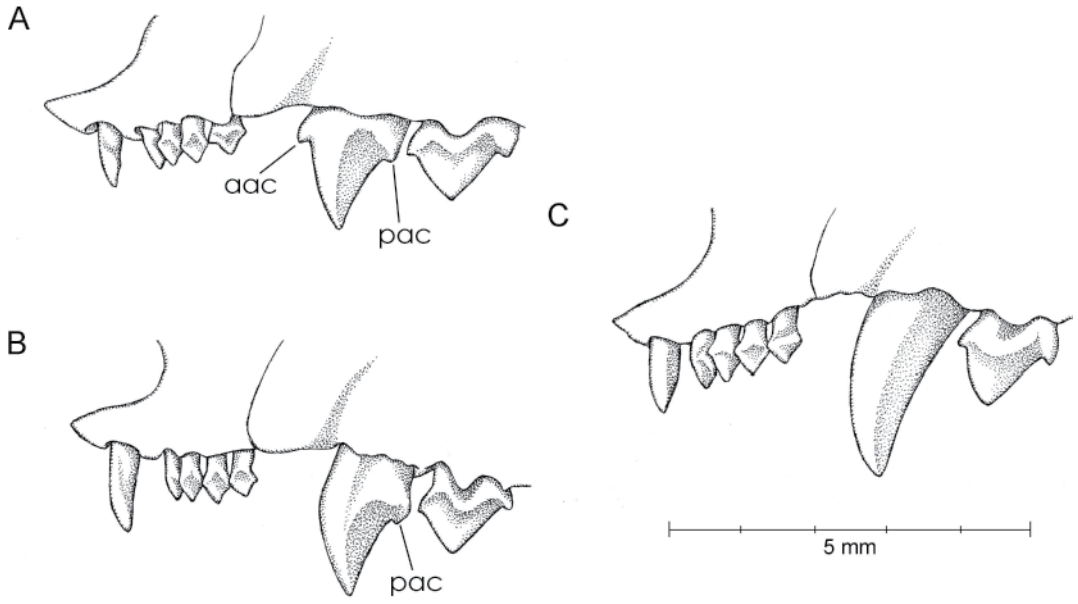

Figure 12. Lateral view of anterior left upper dentition (I1–P1) of *Marmosops pinheiroi* (A, AMNH 267349), *M. chucha* (B, ICN 18788), and *M. carri* (C, KU 120254) illustrating species differences in the presence or absence of accessory upper canine (C1) cusps. All illustrated specimens are males. Abbreviations: aac, anterior accessory cusp; pac, posterior accessory cusp.

M3 ANTERIOR CINGULUM: A continuous shelf along the anterior (mesial) border of the upper molars in some didelphid species is formed by the union of the anterolabial cingulum with the preprotocrista; in other didelphids, the anterior cingulum is incomplete because the preprotocrista terminates at the base of the paracone (Voss and Jansa, 2003:

figure 13; Voss and Jansa, 2009: 52–54). Both conditions are seen in *Marmosops*, but a complete anterior cingulum, when present, is never very wide in this subgenus, and careful examination of unworn teeth under relatively high magnification and good lighting is sometimes necessary to determine this character. Because this character sometimes varies along the toothrow, I scored it from the third upper molar (M3).

LOWER CANINE MORPHOLOGY: Like C1, the lower canine (c1) is a simple, recurved, more-or-less erect, unicuspid tooth in most didelphids, including some species in the nominotypical subgenus of *Marmosops*. By contrast, in most species of the subgenus *Sciophanes* c1 is a strikingly premolariform tooth, procumbent, subequal in height to the first lower premolar (p1), and with a distinct posterior accessory cusp (figure 13A). In two species of *Sciophanes*, however, c1 is distinctly taller than p1 and lacks a distinct posterior accessory cusp (figure 13B).

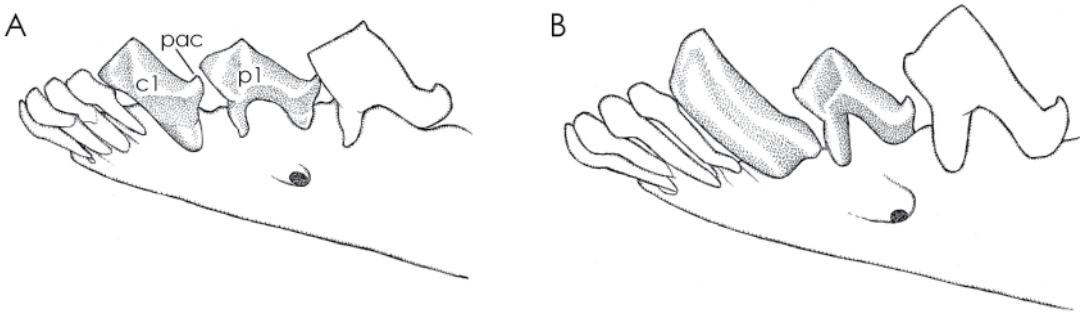

Figure 13. Lateral view of anterior left lower dentition of *Marmosops parvidens* (A, AMNH 266425) and *M. carri* (B, KU 120254) illustrating species differences in lower canine (c1) morphology. In *M. parvidens*, c1 is subequal in height with the first lower premolar (p1), and it has a distinct posterior accessory cusp (pac). By contrast, c1 in *M. carri* is distinctly taller than p1 and lacks a posterior accessory cusp. Both illustrated specimens are males.

In addition to the posterior accessory cusp described above, a distinct lingual accessory cusp is present on c1 in *Marmosops (Sciophanes) handleyi* (see Díaz-N. et al.,

2011: figure 9B). However, this unusual structure occurs polymorphically in other species of *Sciophanes*, and it is sometimes difficult to decide whether it is present or absent in older specimens with worn canines.

RELATIVE HEIGHTS OF M1 ENTOCONID AND M2 PARACONID: The lower first molar (m1) entoconid is conspicuously shorter than the immediately adjacent m2 paraconid in some species of the subgenus *Sciophanes* (figure 14A), but in other species these cusps are subequal in height (figure 14B). I have not surveyed this trait among members of the nominotypical subgenus of *Marmosops*, or among other didelphid taxa.

TALONID ON M4: In most didelphids the lower molar talonid is consistently provided with three cusps (hypoconid, entoconid, and hypoconulid), but the lower fourth molar (m4) talonid is bicuspid, apparently because the entoconid and hypoconulid are not distinguishable as separate cusps.

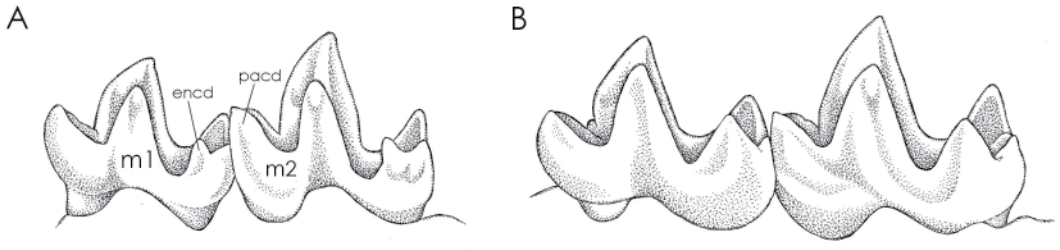

Figure 14. Lingual view of the first two lower right molars (m1 and m2) of *Marmosops bishopi* (A, AMNH 276697) and *M. carri* (B, AMNH 234953) illustrating taxonomic differences in the cusp height. In *M. bishopi* the entoconid (encd) of m1 is shorter than the adjacent paraconid (pacd) of m2, whereas these cusps are subequal in height in *M. carri*.

TAXONOMY

Marmosops Matschie, 1916

TYPE SPECIES: *Marmosops incanus* (Lund, 1840) by original designation.

CONTENTS: At least 19 species (as recognized by Voss and Jansa, 2009; Voss et al., 2013; Díaz-Nieto et al., 2016a; and this report) in two subgenera.

DESCRIPTION:[5] Combined length of adult head and body ca. 90–195 mm; adult weight ca. 20–140 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland consistently present in adult males of some species (e.g., *M. incanus*, *M. noctivagus*) but apparently absent in others (e.g., *M. caucae*, *M. parvidens*). Dorsal pelage unpatterned, usually some shade of dull grayish-brown, but distinctly redder or grayer in some species; dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-colored (whitish, buffy, or brown) or entirely or partially gray-based. Manus mesaxonic (dIII > dIV); manual claws small, shorter than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; lateral carpal tubercles externally conspicuous on wrists of large adult males of most species; medial carpal tubercles absent in both sexes. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel macroscopically naked (a microscopic pelage of very short hairs, not coarse fur, is usually present). Pouch absent; mammae varying among examined species

[5] After Voss and Jansa (2009: 134–137), but including minor corrections and supplementary observations of character variation discovered in the course of this study.

from 3–1–3 = 7 to 7–1–7 = 15 (anteriormost pairs "pectoral" when mammae ≥ 11; e.g., in *M. ocellatus*); cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate), and macroscopically naked (without a conspicuously furred base); naked caudal integument uniformly dark (usually grayish), bicolored (dark above, pale below), or particolored (dark proximally, paler distally); caudal scales in spiral series, each scale with three bristle-like hairs emerging from caudal margin; median hair of each caudal-scale triplet usually much thicker and darker than lateral hairs; ventral caudal surface modified for prehension distally (with naked median groove and apical pad bearing dermatoglyphs).

Premaxillary rostral process long and well-developed in some species (e.g., *M. parvidens*, *M. pinheiroi*) but short in others (e.g., *M. noctivagus*) and apparently absent in some (*M. incanus*). Nasals long, extending anteriorly beyond I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture except in *M. carri*, *M. fuscatus*, and *M. incanus* (which have narrow, more-or-less parallel-sided nasals). Maxillary turbinals (viewed through nasal orifice) elaborately branched. Lacrimal foramina usually two on each side, concealed from lateral view inside orbit (e.g., in *M. parvidens*) or exposed on orbital margin (e.g., in *M. pinheiroi*). Interorbital region without abrupt constrictions; supraorbital margins rounded in some species (e.g., *M. parvidens*), beaded in others (e.g., *M. noctivagus*); postorbital processes usually absent. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal consistently exposed laterally through fenestra in

parietal-squamosal suture in most species (but fenestra polymorphically absent in *M. incanus* and *M. noctivagus*). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae present in some species (e.g., *M. creightoni*), but absent in others (e.g., *M. pinheiroi*); maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly lingual to M4 protocones; posterior palate with prominent lateral corners (the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process small, often bluntly conical or laterally compressed (never smoothly globular), always with a well-developed anteromedial process enclosing the extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, increasing in length (mesio-distal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture;

C1 without accessory cusps in some species (e.g., *M. creightoni*), or with only posterior accessory cusp (e.g., *M. invictus*), or with both anterior and posterior accessory cusps (e.g., *M. parvidens*). First upper premolar (P1) smaller than posterior premolars but well-formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars strongly carnassialized (postmetacristae much longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow or indistinct on M1, shallow but usually distinct on M2, and consistently deep on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3 in some species (e.g., *M. noctivagus*) but anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete) in others (e.g., *M. parvidens*); postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) a distinctively tall, recurved, unicuspid tooth in some species (e.g., *M. noctivagus*), but smaller and premolariform in others (e.g., *M. pinheiroi*). Second lower premolar (p2) subequal in height to p3 in some species (e.g., *M. incanus*) but distinctly taller than p3 in most others; lower milk premolar (dp3) trigonid complete. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid usually taller than hypoconulid on m1–m3.

REMARKS: As discussed by Voss and Jansa (2009:137–138), the monophyly of the genus *Marmosops* is strongly supported by phylogenetic analyses of nuclear exon

sequences and by combined analyses of nuclear genes and morphological characters. In the latter analyses, several morphological traits optimized as generic synapomorphies, including (1) spirally arranged caudal scales, (2) the petiolate morphology of the central hair in each caudal-scale triplet, and (3) the presence of a distinct rostral process of the premaxillae. Generic monophyly is also supported by unique deletions at the DMP1 and BRCA1 loci (Voss and Jansa, 2009: figures 29, 31). The monophyly of *Marmosops* has been additionally corroborated in my recent phylogenetic analyses with much denser taxon sampling (figures 5, 38) and using additional genes not included in Voss and Jansa's (2009) study. As previously discussed elsewhere (Voss and Jansa, 2003: 56–57), DNA-DNA hybridization results reported by Kirsch and Palma (1995) and Kirsch et al. (1997) that recovered *Gracilinanus* nested inside the genus *Marmosops* are unambiguously attributable to misidentified voucher material. Diagnostic morphological comparisons among *Marmosops* and other didelphid genera with which it was formerly confused (*Gracilinanus*, *Marmosa*, and *Thylamys*) were described, illustrated, and tabulated by Voss et al. (2004).

Subgenus *Sciophanes* Díaz-Nieto et al., 2016

TYPE SPECIES: *Marmosops parvidens* (Tate, 1931).

CONTENTS: Twelve species as described below.

DESCRIPTION: Combined length of head and body usually < 120 mm and adult weight usually < 30 g (except in *Marmosops carri* and *M. fuscatus*, both of which are substantially larger). Gular gland absent in all examined material. Lateral carpal tubercles

consistently present in mature adult males; forearm with two widely separated antebrachial vibrissae. Mammae 3–1–3 = 7 or 4–1–4 = 9, all abdominal-inguinal (but note that mammary morphology is unknown for *M. fuscatus, M. juninensis, M. ojastii*, *M. pakaraimae*, and *M. magdalenae*). Scrotal integument consistently unpigmented and covered with self-whitish fur.

Nasals laterally expanded at or near maxillary-frontal suture (except in *M. carri* and *M. fuscatus*, which have very narrow, almost parallel-sided nasals). Interorbital region with rounded or squared supraorbital margins, without distinct beading and without distinct postorbital processes. Fenestra in parietal-squamosal suture consistently present; subsquamosal foramen anteroposteriorly elongate, exposing lateral surface of petrosal pars canalicularis behind sulcus for prootic sinus. Incisive foramina short, extending posteriorly between but not behind C1.

Upper canine (C1) with accessory cusps in one or both sexes (males of *Marmosops carri* and *M. fuscatus* lack C1 accessory cusps). Upper third molar (M3) with or without complete anterior cingulum (anterolabial cingulum and preprotocrista discontinuous in some species). Lower canine (c1) premolariform (procumbent, subequal in height to p1, and provided with a posterior accessory cusp) in most species (but not in males of *M. carri* and *M. fuscatus*, which have taller c1s that lack accessory cusps). Lower first molar (m1) entoconid and adjacent lower second molar (m2) paraconid subequal in height in some species, but m1 entoconid shorter than m2 paraconid in others.

COMPARISONS WITH THE NOMINOTYPICAL SUBGENUS: As explained in chapter 1 (see also Díaz-Nieto et al., 2016a), species of *Sciophanes* can be unambiguously distinguished from species in the subgenus *Marmosops* by the morphology of the subsquamosal foramen (anteroposteriorly elongate in *Sciophanes*, anteroposteriorly constricted in *Marmosops*; figure 6), C1 accessory cusps (present in one or both sexes in *Sciophanes*, consistently absent in *Marmosops*), and number of antebrachial vibrissae (two in *Sciophanes*, one in most *Marmosops*). However, the two subgenera also differ in their modal expression of other characters. In particular, most species of *Sciophanes* are small (HBL usually < 120 mm, weight usually < 30 g), whereas most members of the nominotypical subgenera are substantially larger. There is some size overlap, however, because two species of *Sciophanes* (*M. carri* and *M. fuscatus*; see below) are large, and because some species in the nominotypical subgenus (e.g., *M. ocellatus*; see Voss et al., 2004) are smaller than the subgeneric average. Nevertheless, wherever the two subgenera occur together (along the Rio Juruá, for example; Patton et al., 2000), species of *Sciophanes* are always smaller than sympatric members of the nominotypical subgenus.

Another potentially useful character for subgeneric identification is the morphology of the lower canine (c1), which is small (subequal in height to p1) and premolariform (with a well-developed posterior accessory cusp) in both sexes of most species of *Sciophanes*. By contrast, c1 is a larger tooth (always distinctly taller than p1) and often lacks a distinct posterior accessory cusp in members of the nominotypical subgenus. The noteworthy exceptions in this context are male specimens of the largest

species of *Sciophanes* (*M. carri* and *M. fuscatus*), in which c1 is taller than p1 and lacks a distinct posterior accessory cusp.

Among external traits that are sometimes observed in the nominotypical subgenus, no species of *Sciophanes* has a gular gland, and none has dark-furred hind feet, "pectoral" mammae, or pigmented scrotal epithelium. Additionally, no species of *Sciophanes* has distinctly beaded supraorbital margins, develops postorbital processes, has long incisive foramina (extending behind the upper canines), or lacks a fenestra in the squamosal-parietal suture.

REMARKS: The monophyly of *Sciophanes* is strongly supported by taxon-dense phylogenetic analyses of both nuclear and mitochondrial genes (chapter 1; see also Díaz-Nieto et al., 2016a, 2016b).

The same molecular analyses that provided strong support for the monophyly of *Sciophanes* also recovered three well-supported species groups within this subgenus. In chapter 1 I referred to these groups using alphabetical labels (figure 4; see also Díaz-Nieto et al. 2016a), but I herein substitue such labels for other names: the Fuscatus Group (for "clade A," including *Marmosops carri*, *M. fuscatus*, *M. handleyi*, and *M. invictus*), the Bishopi Group (for "clade B," including *M. bishopi*, *M. juninensis*, *M. ojastii*, and two new species), and the Parvidens Group ("clade C," including *M. pakaraimae*, *M. parvidens*, and *M. pinheiro*i). All three groups are morphologically diagnosable (table 6).

Table 6. Diagnostic Comparisons Among Species Groups of *Marmosops* (*Sciophanes*).

	Parvidens Group	**Fuscatus Group**	**Bishopi Group**
Geographic distribution:	cis-Andean	Andean & trans-Andean	widespread
Ventral pelage:	variable[a]	entirely gray-based	variable[a]
Relative tail length:[b]	ca. 150%	< 130%	< 140%
Lateral carpal tubercles:	spoon-shaped	blade-like	blade-like
Mammae:	3–1–3 or 4–1–4[c]	3–1–3[d]	4–1–4[e]
Palatine fenestrae:	absent	variable[a]	variable[a]
C1 accessory cusps:	present in both sexes[c]	variable[a]	variable[a]
M3 anterior cingulum:	variable[a]	variable[a]	narrowly present
m1 entoconid & m2 paraconid:	entoconid shorter	usually subequal	entoconid shorter

[a] Varies among member species.

[b] Length of tail divided by length of head-and-body, expressed as a percentage.

[c] Females of *Marmosops pakaraimae* are unknown.

[d] This character could not be scored for *Marmosops fuscatus*.

[e] This character could not be scored for *Marmosops juninensis*, *M. magdalenae*, or *M. ojastii*.

Species of the Parvidens Group

Species of the Parvidens Group are distinguished from other members of the subgenus *Sciophanes* by their very long tails (averaging about 150% of head-and-body length), spoon-shaped lateral carpal tubercles in adult males, consistent lack of palatine fenestrae, C1 with anterior and posterior accessory cusps in both sexes, and c1 subequal in height to p1 (table 6). The three recognized species are all cis-Andean: restricted to the Guianas, eastern Venezuela, and eastern Amazonian Brazil (figure 10). The following accounts are only slightly modified from those in Voss et al. (2013) and are based on substantially the same material that was examined in that earlier study. Diagnostic quantitative and qualitative comparisons are summarized in tables 7–9.

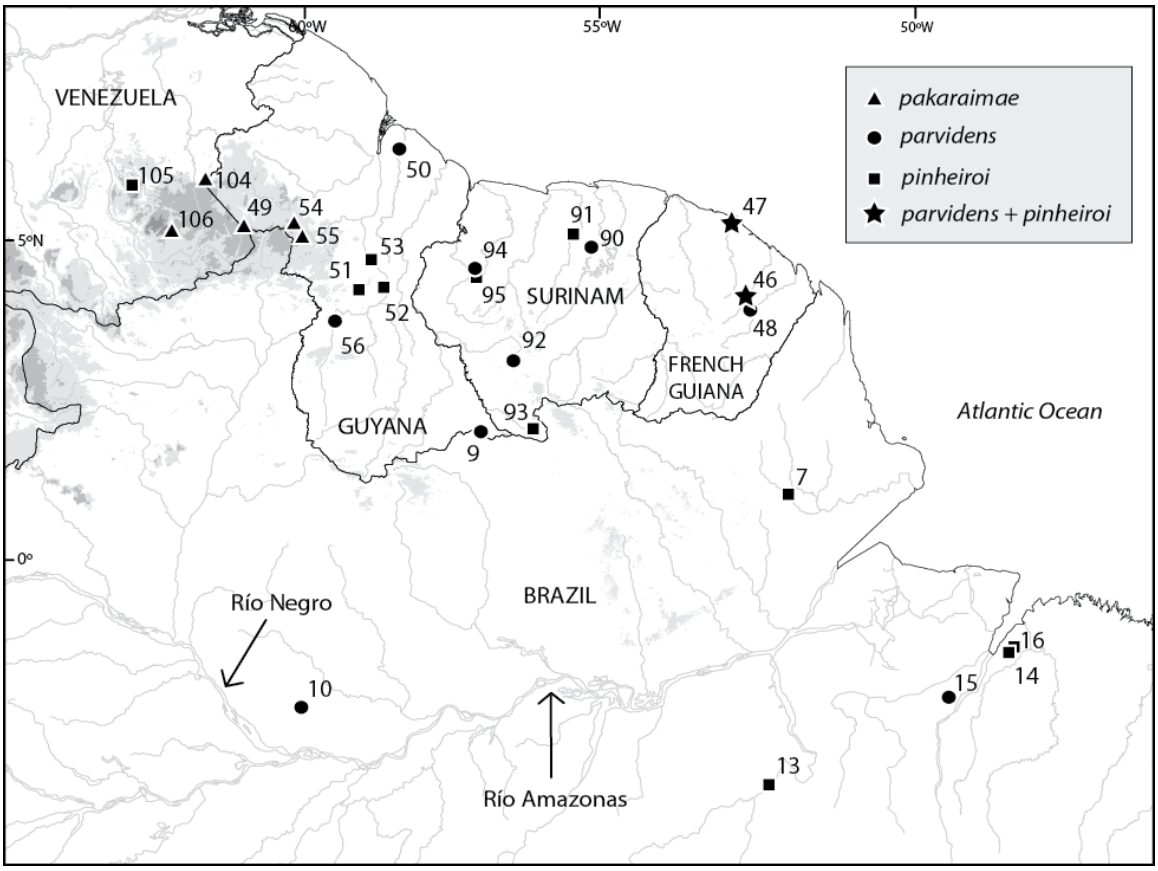

Figure 15. Collecting localities of examined specimens of the Parvidens Group of *Sciophanes*. Numbers are keyed to entries in the gazetteer (appendix 6). Progressively darker shading indicates higher elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, dark gray ≥ 2000 m, darkest gray ≥ 3000 m.

Marmosops pakaraimae (Voss et al., 2013)

Figures 16–18

Marmosops pakaraimae Voss et al., 2013: 6 (original description).

TYPE MATERIAL: The holotype (by original designation) consists of the skin, skull, postcranial skeleton, and preserved tissues of an adult male (ROM 115129; original number F46739) collected by Burton K. Lim and Deirdre M. Jafferally on 26 February

2003 at “Second Camp” on Mount Roraima (figure 10: locality 49), Cuyuni-Mazaruni Region, Guyana. The other seven specimens listed below are all paratypes.

DISTRIBUTION, HABITATS, AND SYMPATRY: *Marmosops pakaraimae* is currently known from just five localities, of which three are in the Pakaraima Highlands of western Guyana and two are in the adjacent highlands of eastern Venezuela. Recorded elevations at these localities range from 800 m to about 1500 m above sea level, and recorded habitats are premontane or lower montane rain forest (Voss et al., 2013). This species is not definitely known to occur sympatrically with any congeneric species, although it might be expected to come into contact with *M. parvidens* and/or *M. pinheiroi* at lower elevations in western Guyana or eastern Venezuela.

DESCRIPTION: Body pelage dark brown (near Dark Umber) middorsally, but indistinctly paler laterally, and about 8–9 mm long at mid-back; ventral pelage superficially whitish (the ventral coloration contrasting abruptly with the brownish flanks), but hairs of throat, chest, abdomen, and inner surfaces of fore- and hindlimbs uniformly gray-based (only the apex of the chin, the oral margins, and the scrotum have self-white fur). Manus covered dorsally with uniformly pale hairs in some specimens (e.g., ROM 114698), but metacarpals distinctly darker than digits in others (ROM 115129); lateral carpal tubercles spoon-shaped in all examined adult males. Mammary formula unknown (no female specimens examined). Tail much longer than combined length of head and body (mean LT/HBL × 100 = 148%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Table 7. Measurements (mm) and weights (g) of adult male specimens of the Parvidens Group of *Marmosops* (*Sciophanes*).

	M. pakaraimae[a]	***M. parvidens***[b]	***M. pinheiroi***[c]
HBL	109 (104–116) 7	100 (93–107) 10	101 (85–121) 12
LT	161 (151–169) 7	150 (142–160) 10	150 (142–160) 12
HF	18 (17–19) 7	16 (15–17) 10	17 (16–18) 12
Ear	22 (22–23) 7	22 (21–24) 9	22 (20–25) 12
CBL	30.8 (29.8–31.9) 7	28.3 (27.3–29.1) 9	29.1 (28.4–29.8) 12
NL	14.6 (14.2–15.2) 4	13.7 (12.7–14.4) 9	14.1 (13.2–14.7) 11
NB	3.8 (3.5–4.0) 7	3.4 (2.9–3.6) 12	3.7 (3.1–4.2) 12
LIB	6.0 (5.8–6.2) 7	5.3 (4.9–5.5) 11	5.4 (5.2–5.7) 12
LPB	6.2 (6.0–6.6) 7	5.5 (5.2–5.7) 11	5.6 (5.2–5.9) 11
ZB	15.2 (14.8–15.7) 7	14.5 (13.9–15.0) 10	15.1 (14.6–16.0) 12
PL	17.3 (16.5–17.9) 7	16.0 (15.0–16.8) 10	16.3 (16.0–16.7) 11
PB	8.9 (8.2–9.4) 7	8.3 (8.0–8.7) 12	8.6 (8.2–8.9) 12
MTR	12.2 (11.9–12.6) 7	11.2 (11.0–11.6) 11	11.6 (11.3–12.0) 12
LM	6.1 (6.0–6.3) 7	5.5 (5.3–5.7) 12	5.7 (5.6–5.9) 12
M1–3	5.2 (5.2–5.4) 7	4.8 (4.6–5.2) 12	5.0 (4.8–5.2) 12
WM3	2.0 (2.0–2.1) 7	1.9 (1.8–2.0) 12	1.9 (1.8–2.0) 12
Weight	30 (25–33) 6	25 (21–31) 9	27 (22–33) 12

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the type series (ROM 114698, 115129, 115148, 115254, 115841, 115845; USNM 385046).

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 93970, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-930, 1995-933; ROM 114144, 117348; USNM 579989.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 266423, 267341, 267342, 267345, 267346, 267349, 267352, 267357; CM 63506; FMNH 95320; MNHN 1995-931, 1995-932; ROM 108920, 111558, 111663; USNM 461459, 461460, 461462–461465.

Table 8. Measurements (mm) and weights (g) of adult female specimens of the Parvidens Group of *Marmosops* (*Sciophanes*)[a].

	***M. parvidens*[b]**	***M. pinheiroi*[c]**
HBL	96 (94–97) 2	100 (95–108) 15
LT	136 (133–138) 2	141 (125–154) 15
HF	16 (15–17) 2	16 (14–17) 15
Ear	21 (20–21) 2	20 (18–23) 15
CBL	27.3 (26.7–28.0) 4	28.5 (27.9–29.8) 14
NL	12.9 (12.7–13.4) 4	13.9 (13.4–14.6) 9
NB	3.1 (2.8–3.5) 5	3.3 (2.9–3.8) 14
LIB	5.2 (4.9–5.4) 4	5.4 (5.2–5.5) 15
ZB	14.5 (13.9–14.8) 5	15.1 (14.6–15.9) 12
PL	15.3 (14.9–15.8) 4	16.0 (15.5–16.8) 9
PB	8.3 (8.1–8.7) 5	8.8 (8.4–9.3) 14
MTR	11.1 (11.1–11.2) 5	11.6 (11.2–12.1) 15
LM	5.5 (5.3–5.6) 5	5.8 (5.5–6.2) 15
M1–3	4.8 (4.7–4.9) 5	5.0 (4.8–5.4) 15
WM3	1.9 (1.9–2.0) 5	2.0 (1.8–2.1) 15
Weight	22	22 (19–25) 11

[a] Female specimens of *Marmosops pakaraimae* are unknown.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 97333, 267344; FMNH 18545; USNM 548439, 579990.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 130570, 267342 267352; CM 63506; FMNH 95320; USNM 393529–393532, 461459, 461460, 461462, 461464, 461465, 545543.

Nasal bones long (consistently extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canine (C1) short, with anterior and posterior accessory cusps in males (female specimens are unknown). Upper third molar (M3) anterolabial cingulum

narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 apparently subequal to adjacent m2 paraconid;[6] unworn m4 talonid with three distinct cusps.

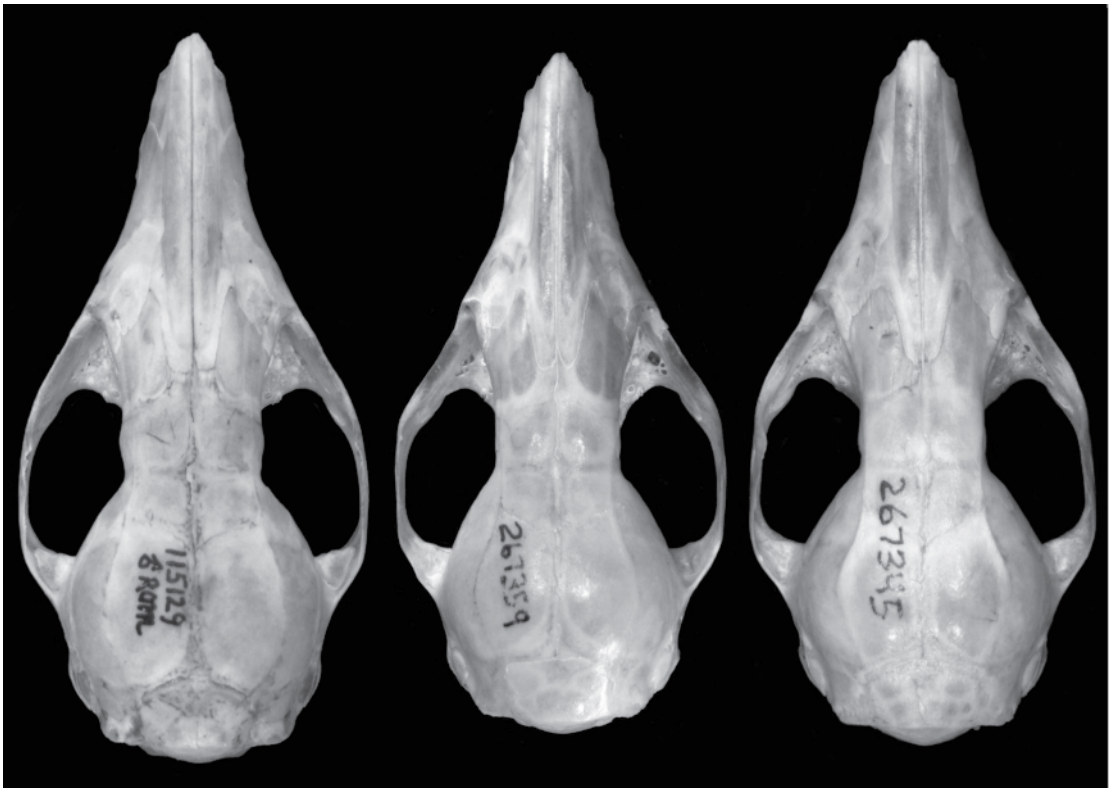

Figure 16. Dorsal views of skulls of the Parvidens Group of *Sciophanes*. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

COMPARISONS: *Marmosops pakaraimae* averages larger than *M. parvidens* in most measured external dimensions (table 7), and the two species differ strikingly in dorsal pelage coloration (dark brown in *pakaraimae* versus paler and distinctly reddish-

[6] This character is difficult to evaluate because specimens with unworn molars (juveniles and subadults) are unavailable.

brown in *M. parvidens*; Voss et al., 2013: figure 2). The difference in ventral pelage coloration (op. cit.: figure 3) is even more striking: whereas *M. pakaraimae* has almost completely gray-based ventral fur, all examined specimens of *M. parvidens* have a continuous streak of self-whitish fur that extends from chin to groin. *Marmosops pakaraimae* is consistently larger than *parvidens* in all measured craniodental dimensions, especially in five variables (CBL, LIB, LPB, MTR, LM) that exhibit nonoverlapping variation between the male samples (no female specimens of *M. pakaraimae* are known). Side-by-side comparisons of representative skulls (figures 16–18) reveal that *M. pakaraimae* has a visibly broader interorbital region but relatively smaller orbits than *M. parvidens*. In qualitative aspects of craniodental morphology, however, these species are notably similar, both having lacrimal foramina that are mostly concealed from lateral view inside the anterior orbital margin, upper third molars with narrowly complete anterior cingula, and consistently tricuspid m4 talonids.

Marmosops pakaraimae also averages larger than *M. pinheiroi* in most external dimensions, and the two species differ in dorsal pelage color (dark brown in *M. pakaraimae* versus paler brownish gray in *M. pinheiroi*). The ventral fur of *M. pakaraimae* is also more extensively gray-based than the ventral fur of *M. pinheiroi*, which usually includes a narrow, discontinuous midventral streak of self-white hairs. *Marmosops pakaraimae* is also larger on average than *M. pinheiroi* in craniodental measurements, especially in three dimensions (LIB, LPB, and LM) that exhibit nonoverlapping variation in my samples. Visual comparisons of representative skulls (figures 16–18) reveal similar proportional differences between *M. pakaraimae* and *M.*

pinheiroi to those previously noted between *M. pakaraimae* and *M. parvidens*, namely that *M. pakaraimae* has a relatively broader interorbit but smaller orbits. Additionally, the lacrimal foramina are more prominently exposed laterally, M3 never has a complete anterior cingulum, and m4 often has a bicuspid talonid in *M. pinheiroi*.

SPECIMENS EXAMINED ($N = 8$): **Guyana**—*Cuyuni-Mazaruni,* Mt. Roraima (ROM 115129, 115148, 115254); *Potaro-Siparuni,* Mt. Ayanganna (ROM 114698), Mt. Wokomung (ROM 115841, 115845). **Venezuela**—*Bolívar,* 85 km SSE El Dorado (USNM 385046), Churi-tepui (AMNH 176353).

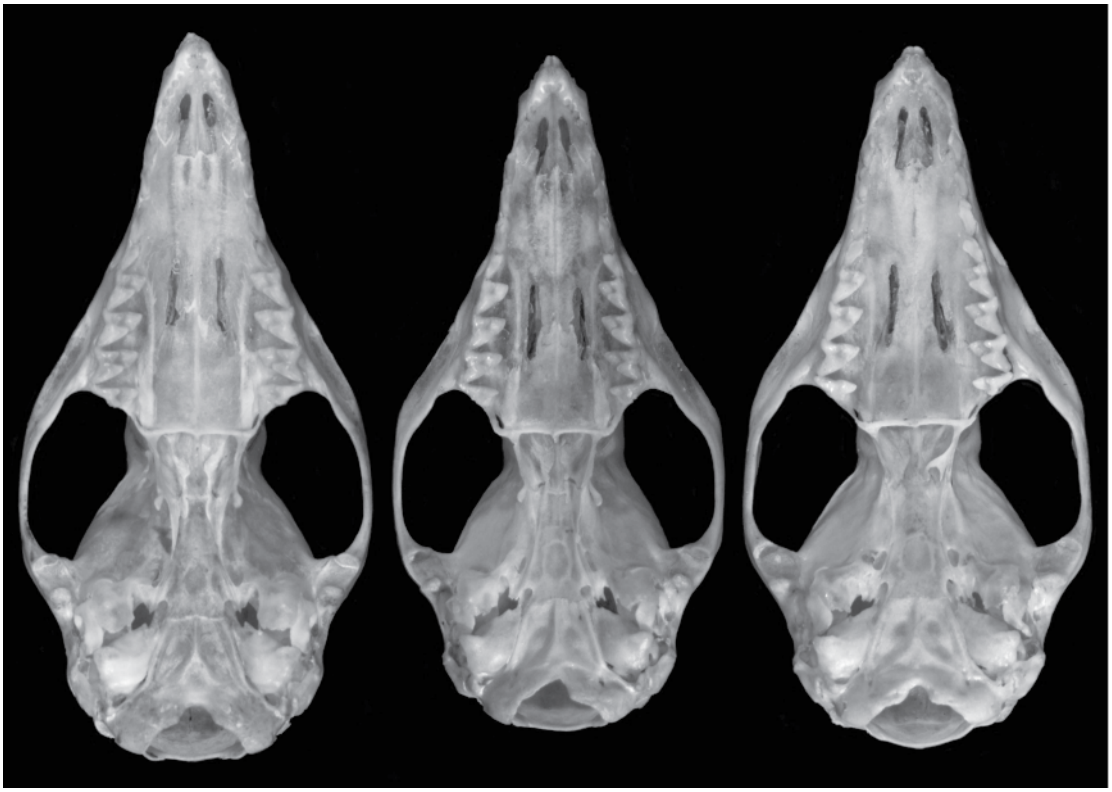

Figure 17. Ventral views of skulls of the Parvidens Group of *Sciophanes*. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

Marmosops parvidens (Tate, 1931)
Figures 8, 11, 13, 16–19

Marmosa parvidens Tate, 1931: 13 (original description).

Marmosa parvidens parvidens: Pine, 1981: 60 (name combination).

Marmosops parvidens: Gardner and Creighton, 1989: 4 (name combination).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult female (FMNH 18545; original number 8) collected by S.B. Warren on 8 September 1906 at Hyde Park (figure 15: locality 50), a locality near sea level on the Demerara River in East Demerara-West Coast Berbice about 35 km south of Georgetown. No other specimens were mentioned in the original description of this species.

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens suggest that *Marmosops parvidens* occurs throughout most of the Guiana Region (north of the Amazon and east of the Rio Negro), but the species appears to be unknown from Venezuela (García et al., 2014), and I have not examined any material from northern Pará. Although I have not personally examined material from Amapá, *M. parvidens* has recently been reported to occur there (Silva et al., 2013). A single specimen is also known from SE Amazonia (on the lower Rio Tocantins, figure 15: locality 13). All specimens associated with definite elevational data were collected between sea level and about 500 m. The predominant vegetation throughout the range of this species, which broadly

overlaps that of *M. pinheiroi*, is lowland rain forest (e.g., in French Guiana, where both species occur sympatrically; Voss et al., 2001; Catzeflis et al., 2014).

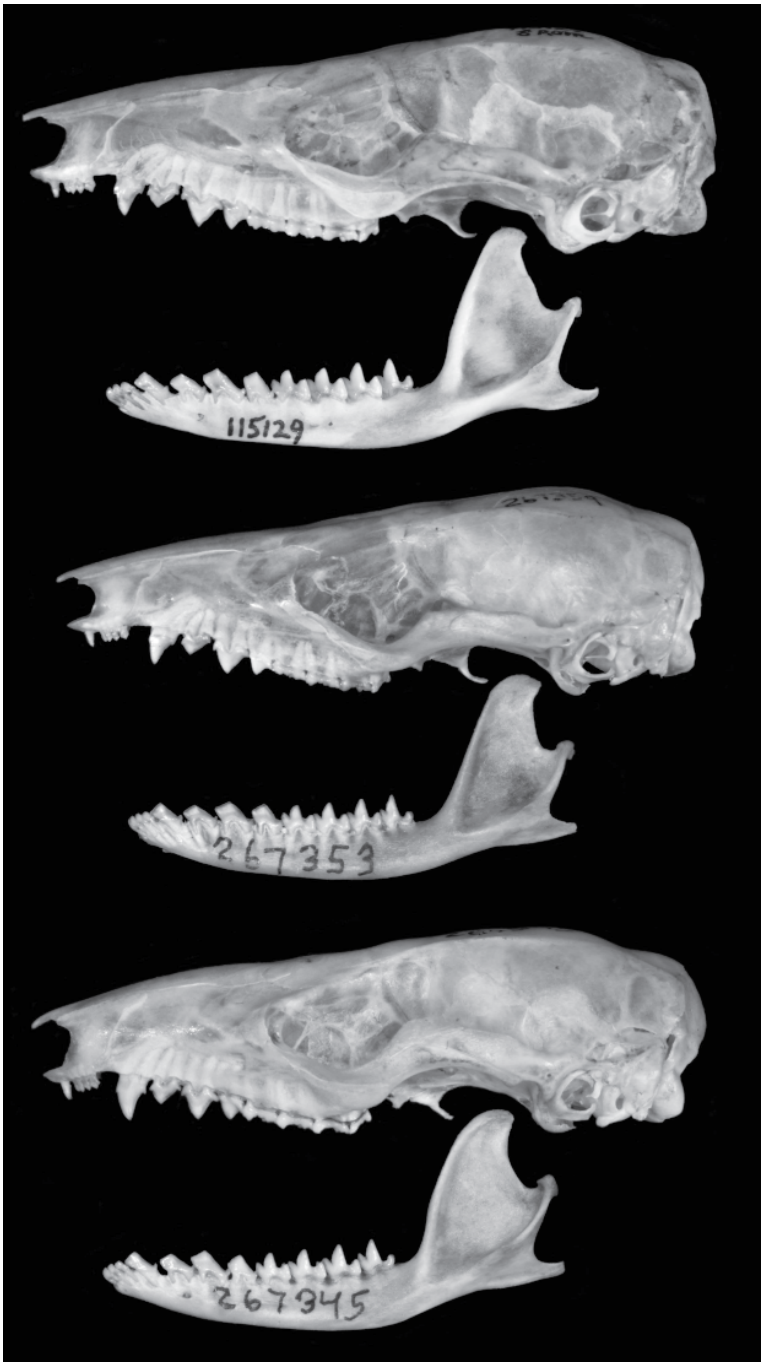

Figure 18. Lateral views of skulls and mandibles of the Parvidens Group of *Sciophanes*. Top to bottom: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359 [skull], 267353 [mandible]), and *M. pinheiroi* (AMNH 267345). All views about ×3.

DESCRIPTION: Body pelage dusty reddish-brown (near Bister or Snuff Brown) middorsally, but indistinctly paler laterally, and about 6–8 mm long at mid-back; ventral pelage extensively self-white from chin to anus (including the inner surfaces of the fore- and hindlimbs), usually with only narrow lateral-abdominal borders of gray-based fur. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles spoon-shaped in all examined adult males. Mammae 3–1–3 = 7 or 4–1–4 = 9. Tail much longer than combined length of head and body (mean LT/HBL × 100 = 150%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen usually formed by the orbitosphenoid.

Upper canine (C1) short, with anterior and posterior accessory cusps in both sexes. Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: *Marmosops parvidens* is approximately the same size as *M. pinheiroi* (tables 7, 8) in external dimensions, and differences in dorsal pelage coloration

(usually some shade of dusty reddish-brown in *M. parvidens* versus dull brownish-gray in *M. pinheiroi*) are sometimes less than obvious. By contrast, ventral pelage coloration provides a consistently useful external criterion for separating these broadly sympatric species: whereas *M. parvidens* has a broad, continuous band of self-whitish fur that extends from from chin to groin and along the inner surfaces of the fore- and hind-limbs, *M. pinheiroi* has a much narrower, discontinuous midventral streak of self-white hairs that apparently never extends onto the throat nor along the inner surfaces of the fore- and hindlimbs. *Marmosops parvidens* averages smaller than *pinheiroi* in most craniodental dimensions (WM3 in males is the unique exception; tables 7, 8), but all measurements show overlapping variation between the two species, so none is diagnostic (despite unambiguous multivariate separation; Voss et al., 2001: figure 24). Instead, qualitative aspects of craniodental morphology provide better characters for species identification: (1) whereas *M. parvidens* has lacrimal foramina that are usually concealed within the orbit, the lacrimal foramina of *M. pinheiroi* are more prominently exposed laterally; (2) the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid in *M. parvidens*, whereas the corresponding bony margin in *M. pinheiroi* is often formed by the frontal; (3) the unworn M3 of *M. parvidens* has a narrowly complete anterior cingulum, whereas the anterolabial cingulum and preprotocrista of this tooth are discontinuous in *M. pinheiroi*; (4) the talonid of m4 is consistently tricuspid in *M. parvidens* but often appears to be bicuspid in *M. pinheiroi*.

Comparisons between *Marmosops parvidens* and *M. pakaraimae* were provided in the account of the latter species (above).

Table 9. Diagnostic morphological comparisons among members of the Parvidens Group of *Marmosops* (*Sciophanes*).

Character	*M. pakaraimae*	*M. parvidens*	*M. pinheiroi*
Dorsal pelage:	dark brown	paler, usually reddish brown	paler, usually grayish brown
Ventral pelage:	gray-based	mostly self-whitish	mostly gray-based, but variable
Lacrimal foramina:	concealed inside orbit	concealed inside orbit	laterally exposed anterior to orbit
M3 anterior cingulum:	narrowly complete	narrowly complete	incomplete
m4 talonid:	tricuspid	tricuspid	often bicuspid

REMARKS: The binomina "*Marmosa parvidens*" and "*Marmosops parvidens*" were previously applied to specimens of several distinct species, including *M. bishopi*, *M. juninensis*, *M. ojastii*, *M. pakaraimae*, and others (e.g., by Handley, 1976; Pine, 1981; Linares, 1998; Patton et al., 2000). The restricted sense in which this species is now understood was first defined by Voss et al. (2001). Current phylogeographic sampling of *M. parvidens* consists of 10 cytochrome-*b* sequences from six localities in French Guiana, Guyana, and Surinam; these differ from one another by an average uncorrected distance of just 1.6%, well below the threshold value for species recognition in coalescent analyses performed in chapter 1 (see also Díaz-Nieto et al. 2016a). Additionally, I have not observed any geographic variation in morphology that corresponds to geographic variation in cytochrome-*b* sequence data from this species.

I carefully reexamined AMNH 97333, which remains the only specimen of *Marmosops parvidens* collected south of the Amazon. Although this specimen differs from material collected north of the Amazon in having the dorsolateral margin of the ethmoid foramen bordered by the frontal, and by lacking a continuous anterior cingulum on M3, it closely resembles typical *M. parvidens* in other respects, notably in its

extensively self-white ventral pelage. Although molecular confirmation that *M. parvidens* occurs south of the Amazon would be very welcome, I feel reasonably confident in the current identification of this unique specimen.

SPECIMENS EXAMINED (*N* = 42): **Brazil**—*Amazonas,* Boca Rio Paratucu (AMNH 93970), 80 km N Manaus (INPA 1758, 1762–1769, 1772–1779; USNM 579985–579989); *Pará,* Ilha do Taiuna (AMNH 97333). **French Guiana**—Les Nouragues (ISEM V-1633), Paracou (AMNH 267344, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-933, 1995-939), River Arataye (USNM 548439). **Guyana**— *Demerara-Mahaica,* Hyde Park (FMNH 18545), *Upper Takutu-Upper Essequibo,* Karanambo (ROM 97938). **Surinam**—*Brokopondo,* Brownsberg Nature Park (ROM 113997, 114009, 114144); *Nickerie,* Kayser Gebergte Airstrip (FMNH 93169); *Sipaliwini,* Bakhuis Transect 13 (ROM 117348).

Marmosops pinheiroi **(Pine, 1981)**
Figures 6, 7, 9, 12, 16–19

Marmosa parvidens pinheiroi Pine, 1981: 61 (original description).

Marmosa parvidens woodalli Pine, 1981: 62 (subjective junior synonym). Type locality "Nova Area Experimental, Utinga (the wooded area surrounding the Belém waterworks), Belém (1°27′ S, 48°29′ W), Pará, Brazil."

Marmosops parvidens: Gardner, 1993: 20, part (name combination; *pinheiroi* and *woodalli* listed as synonyms).

Marmosops pinheiroi: Voss et al., 2001: 49 (first use of current binomial).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult male (USNM 461459, original numbers T-391 and L5049), said to have been collected by personnel of the Instituto Evandro Chagas on 8 May 1969 at Rio Amapari, Serra do Navio (figure 15: locality 7), Amapá, Brazil. In addition, Pine (1981) examined 15 other specimens (paratypes), but one of these (USNM 385045) is also a paratype of *M. pakaraimae*, and two others (AMNH 130521, USNM 385046) might also be referrable to the latter species (Voss et al., 2013).

DISTRIBUTION, HABITATS, AND SYMPATRY: Based on the material I examined, *Marmosops pinheiroi* occurs in eastern Venezuela, Guyana, Surinam, French Guiana, and Brazil (Amapá and southeastern Pará). I have not examined the specimens that Nascimento et al. (2015) recently identified as *M. pinheiroi* from the Brazilian state of Maranhão, which would be a significant ecogeographic range extension if their material were correctly identified (see Remarks, below). Throughout its known range, this species probably co-occurs with *M. parvidens*, but the two have only been collected sympatrically in French Guiana (Voss et al., 2001; Catzeflis et al., 2014). Specimens of *M. pinheiroi* associated with definite elevational data were collected from near sea level to about 500 m. The predominant vegetation throughout the geographic range of this species—as documented by examined specimens—is lowland rain forest (e.g., at Paracou, French Guiana; Voss et al., 2001).

DESCRIPTION: Body pelage brownish-gray (near Olive Brown or Fuscous) middorsally, but indistinctly paler laterally, and about 6–8 mm long at mid-back; ventral pelage superficially whitish but extensively gray-based in most specimens (only the chin, groin, and a narrow midventral streak of abdominal fur are usually self-white); inner surfaces of fore- and hindlimbs covered with gray-based fur, apparently never self-white. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles spoon-shaped in all examined adult males. Mammae 3–1–3 = 7 or 4–1–4 = 9. Tail much longer than combined length of head and body (mean LT/HBL × 100 = 150%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually exposed in lateral view; zygomatic process of squamosal bone broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid in some specimens (e.g., ROM 108920, AMNH 267340, 267346), by the frontal in others (e.g., AMNH 267341, 267342), occasionally with bilateral variation (e.g., AMNH 267345).

Upper canine (C1) short, apparently always with anterior and posterior accessory cusps in both sexes. Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter than adjacent m2 paraconid

in some specimens (e.g., AMNH 266423, 267342, 267345), but these cusps subequal in others (e.g., AMNH 267349, 267357); unworn m4 talonid often with only two distinct cusps.

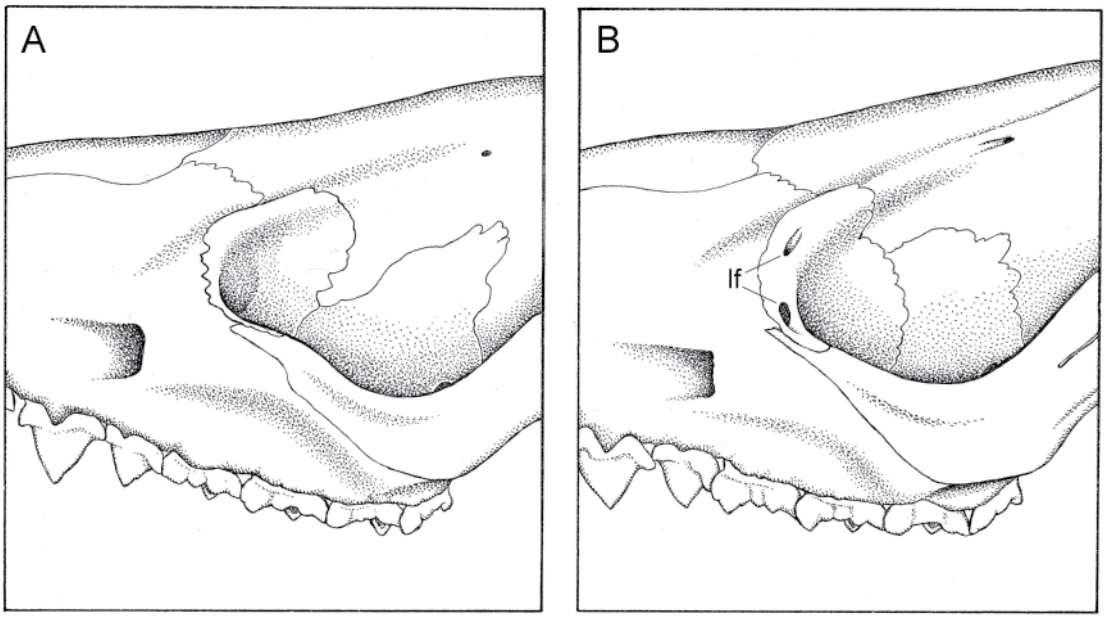

Figure 19. Lateral views of the anterior orbital region of *Marmosops parvidens* (A, AMNH 267359) and *M. pinheiroi* (B, AMNH 267345) illustrating species differences in the lacrimal foramina (lf), which are usually concealed inside the orbit in *M. parvidens*, but which are laterally exposed on the orbital margin of *M. pinheiroi*.

COMPARISONS: Diagnostic comparisons of *Marmosops pinheiroi* with *M. pakaraimae* and *M. parvidens* are provided in earlier species accounts (see above).

REMARKS: In my previous analyses of molecular sequence data (chapter 1; see also Voss et al., 2013; Díaz-Nieto et al., 2016a), I recovered two cytochrome-*b* haplogroups among the material here referred to *Marmosops pinheiroi*, the first consisting of six sequences from the Guianas and the second including two sequences from southeastern Pará (south of the Amazon and east of the Rio Xingu). On the assumption that these haplogroups are physically separated by the lower Amazon, then

the epithet *pinheiroi* could be associated with the former group and *woodalli* with the latter. Although this phylogeographic structure is robustly supported, these haplogroups differ on average by only 3.9% in uncorrected pairwise sequence comparisons, and I am unable to morphologically distinguish their corresponding voucher material. Therefore, I continue to treat *woodalli* as a junior (subjective) synonym.

The specimens that Nascimento et al. (2015) identified as *Marmosops pinheiroi* extend the potential range of this species by almost 700 km, into the Brazilian state of Maranhão. These specimens are also remarkable for having been collected in savanna, whereas all others known to me have been taken in lowland rain forest. Unfortunately, the identification of this interesting material is apparently based only on sequence analysis and external measurements. Supporting evidence from craniodental morphology would be very welcome.

SPECIMENS EXAMINED ($N = 33$): **Brazil**—*Amapá,* Serra do Navio (USNM 461459, 461460, 461462–461465); *Pará,* 52 km SSW Altamira (USNM 549294), Belém (USNM 545543), Utinga (USNM 393529–393532, 393534). **French Guiana**—Paracou (AMNH 266423, 267340, 267341, 267342, 267345, 267346, 267349, 267352, 267357; MNHN 1995-931, 1995-932). **Guyana**—*Potaro-Siparuni,* Forest Canopy Walkway (ROM 119852), 10 km NW Kurupukari (ROM 108920), Kabukalli Landing (ROM 111558, 111663). **Surinam**—*Bokopondo,* Finisanti (FMNH 95320); *Nickerie,* Sipaliwini Airstrip (CM 63506); *Sipaliwini,* Bakhuis Transect (ROM 116974). **Venezuela—***Bolívar,* Auyántepui (AMNH 130568, 130570).

Species of the Fuscatus Group

Species of the *Marmosops fuscatus* group are distinguished from other members of the subgenus *Sciophanes* by their entirely gray-based ventral fur, blade-like lateral carpal tubercles (in adult males), females with 3–1–3 = 7 mammae, and m1 entoconid usually subequal to the adjacent m2 paraconid. The four recognized species are found in eastern Panama, the northern part of the Cordillera Central of Colombia, the Cordillera de Mérida in western Venezuela, the coastal sierras and adjacent rain-forested lowlands of northern Venezuela, and the continental-shelf islands of Trinidad and Tobago. Diagnostic quantitative and qualitative comparisons are summarized in tables 10–12.

Marmosops carri (Allen and Chapman, 1897)
Figures 12–14, 20, 21

Thylamys carri Allen and Chapman, 1897: 27 (original description).

Didelphys (Marmosa) carri: Trouessart, 1905: 856 (name combination).

Marmosa (Thylamys) carri: Cabrera, 1919: 40 (name combination).

Marmosops fuscatus: Gardner, 1993: 19; part (*carri* treated as a subjective junior synonym of *fuscatus* Thomas, 1896)

Marmosops fuscatus carri: Gardner and Creighton, 2008: 66 (name combination).

Marmosops fuscatus fuscatus: Gardner and Creighton, 2008: 66 (name combination); part (Venezuelan material of *carri* misidentified as *M. f. fuscatus*).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult male (AMNH 7314/5922, original number 731) collected by Frank M. Chapman at Caparo (fig. 17: locality 97), Trinidad, on 20 March 1894. Two other specimens (paratypes) were also part of Allen and Chapman's type series: one is AMNH 7313/5921 (a young adult female), and the other was AMNH 7315/5923 (said to be an adult male; not examined and presumed lost).

DISTRIBUTION, HABITATS, AND SYMPATRY: *Marmosops carri* is known from Trinidad, Tobago, and Venezuela (figure 22)[7]. On the Venezuelan mainland, examined specimens have been collected in premontane and montane rain forest along the northern coastal cordilleras (e.g., at Hotel Humboldt; Handley, 1976: 79) and the Cordillera de Trujillo (e.g., at Hacienda Misisí; Handley, 1976: 71) between about 1000 m and 2300 m (but see Remarks). On Trinidad, however, it is definitely known to occur near sea level (e.g., at Rio Grande Forest; Appendix 1), presumably in lowland rain forest. Although the known range of *M. carri* overlaps with that of *M. ojastii* (a member of the Bishopi Group; see below) and might be expected to contact that of *M. fuscatus*, these species have apparently not been collected sympatrically.

DESCRIPTION: Body pelage grayish-brown (near Fuscous or Hair Brown) middorsally, sometimes indistinctly paler laterally, and about 7–9 mm long at mid-back; ventral pelage superficially whitish, but hairs of throat, chest, and abdomen uniformly gray-based in most specimens (a few have patches or narrow streaks of self-white fur on

[7] The material of *Marmosops carri* from Tobago, the first to be reported from that island, was originally identified as such by Darrin P. Lunde.

the throat, chest, groin, or along the insides of the thighs; e.g, AMNH 144832; USNM 370037, 418515, 517259). Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles blade-like in all examined adult males. Mammae 3–1–3 = 7 in all examined females with visible teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 120%); dorsal caudal surface dark, but indistinctly paler distally in some specimens; ventral caudal surface distinctly paler than dorsal surface.

Nasal bones long (extending well behind the lacrimals) and uniformly narrow, without conspicuous lateral expansion at the maxillary-frontal suture. Interorbital region broad, with rounded supraorbital margins in females and young adult males, but relatively narrower and tending to develop squared supraorbital margins in large adult males; postorbital processes absent or indistinct. Lacrimal foramina usually visible in lateral view; zygomatic process of the squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present or absent (when present, palatine fenestrae usually consist of several small irregular perforations, but in a few specimens they are large). Dorsolateral margin of ethmoid foramen usually formed by the orbitosphenoid.

Upper canine (C1) sexually dimorphic: longer and consistently unicuspid in males, shorter and consistently with one or two accessory cusps in females.[8] Second and third upper premolars (P2, P3) subequal in height; P3 not oblique (in line with C1–P2)

[8] All examined females have posterior accessory C1 cusps, and insular populations (from Trinidad and Tobago) usually also have small anterior accessory cusps (e.g., AMNH 5921, 234951, 234954, 234956, 259979). By contrast, females from mainland populations usually lack anterior accessory cusps on C1 (e.g., AMNH 144832; USNM 370030, 517256).

when fully erupted in most specimens. Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) sexually dimorphic: conventionally caniniform (erect, without accessory cusps) and taller than p1 in males versus premolariform (procumbent, with posterior accessory cusp) and subequal in height to p1 in females; c1 anterolingual accessory cusp usually absent in both sexes. Entoconid of m1 apparently subequal to m2 paraconid (but few specimens with unworn molars examined for this trait); unworn m4 talonid with three distinct cusps.

COMPARISONS: *Marmosops carri* is externally similar to *M. fuscatus* (with which it was formerly synonymized; see Remarks) but has somewhat paler dorsal fur, averages larger in all external measurements (tables 10, 11), and has a relatively longer tail (e.g., LT/HBL ×100 = 122% in male *carri* versus 110% in male *fuscatus*). *Marmosops carri* averages larger than *M. fuscatus* in all measured craniodental dimensions (except nasal breath, NB) but especially in three dental dimensions (MTR, LM, M1–3) that exhibit nonoverlapping variation. In other (qualitative) aspects of craniodental morphology the two species cannot be consistently distinguished, although there are modal differences in some characters. For example, the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid in *M. carri*, whereas this foramen is bordered dorsolaterally by the frontal in *M. fuscatus*. Handley and Gordon (1979) implied that *carri* and *fuscatus* (which they regarded as no more than subspecifically distinct) differ in nasal morphology—the nasals were said to be more expanded posteriorly in *fuscatus* than in *carri*—but I did not observe a consistent taxonomic difference in the comparisons of representative specimens of these taxa.

Table 10. Measurements (mm) and weights (g) of adult male specimens of the Fuscatus Group of *Marmosops* (*Sciophanes*).

	M. carri[a]	***M. fuscatus***[b]	***M. handleyi***[c]	***M. invictus***[d]
HBL	139 (126–155) 17	136 (132–140) 2	116 (110–122) 2	111 (106–115) 5
LT	169 (152–183) 17	149 (147–150) 2	149 (149–149) 2	136 (124–147) 5
HF	21 (20–23) 17	20 (19–20) 2	19 (19–20) 2	18 (17–19) 5
Ear	26 (23–29) 17	25	21 (20–21) 2	21 (21–22) 3
CBL	36.7 (33.8–41.2) 20	33.3 (31.8–35.4) 5	29.1 (27.7–30.5) 2	30.0 (29.8–30.3) 4
NL	18.1 (15.6–20.4) 17	15.9 (15.2–16.7) 5	14.2 (12.7–15.6) 2	14.5 (14.1–14.9) 5
NB	3.1 (2.7–3.5) 22	3.1 (2.7–3.3) 5	3.6 (3.5–3.7) 2	3.5 (3.2–3.8) 5
LIB	6.5 (6.2–7.0) 20	6.3 (6.0–6.6) 5	5.8 (5.5–6.0) 2	5.9 (5.7–6.0) 5
ZB	19.5 (17.1–21.8) 20	17.7 (16.5–19.5) 4	15.0 (14.5–15.5) 2	15.8 (15.2–16.1) 4
PL	20.8 (19.1–23.0) 21	18.9 (18.4–19.6) 5	16.1 (15.3–17.0) 2	16.6 (16.2–17.0) 5
PB	10.9 (10.1–11.8) 22	10.0 (9.7–10.7) 5	8.5	9.0 (8.6–9.5) 5
MTR	15.2 (14.3–17.2) 22	13.6 (13.3–13.9) 5	12.0 (11.6–12.5) 2	12.3 (12.1–12.5) 5
LM	7.2 (7.0–7.7) 22	6.6 (6.5–6.7) 5	6.1 (6.0–6.3) 2	6.3 (6.3–6.5) 5
M1–3	6.2 (5.9–6.5) 22	5.7 (5.7–5.7) 5	5.3 (5.2–5.5) 2	5.4 (5.3–5.7) 5
WM3	2.3 (2.1–2.5) 22	2.2 (2.1–2.2) 5	1.7	2.1 (2.0–2.2) 5
Weight	60 (41–85) 10	69	30	—

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 150007, 186437, 186438, 214439, 259978; KU 372934; USNM 370023, 370024, 370031, 370034, 370035, 370039, 372934, 406926, 406928, 406931, 418515, 443787, 443789, 517258–517260.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 276509, 276580; BMNH 3.1.5.2, 3.1.5.3; FMNH 22174.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 433; FMNH 69823.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: USNM 178708, 309265, 309267, 337960, 337962.

Marmosops carri is substantially larger than *M. handleyi* in all external measurements, especially in three dimensions (HBL, LT, and Ear) that exhibit nonoverlapping variation in same-sex sample comparisons. In qualitative external comparisons, these species principally differ in coloration: whereas *M. carri* has grayish-

brown dorsal body pelage and entirely white forefeet, *M. handleyi* has dark-brown dorsal pelage and dark metacarpals that contrast in color with its whitish manual digits. Skulls and dentitions of *M. carri* are considerably larger than those of *M. handleyi*, exhibiting nonoverlapping variation in same-sex comparisons of eight dimensions (CBL, ZB, PL, PB, MTR, LM, M1–3, and WM3). Overall, the skull of *M. carri* is more heavily built (especially in males) by comparison with the more delicate cranial construction of *M. handleyi*. In qualitative aspects of craniodental morphology, *M. carri* principally differs from *M. handleyi* by its uniformly narrow nasals (the nasals are posteriorly expanded in *M. handleyi*); unicuspid male C1 (this tooth has a posterior accessory cusp in male *M. handleyi*), and absence of a lingual accessory cusp on c1 in most specimens of both sexes (a lingual accessory cusp on c1 is present in both sexes of *M. handleyi*).

Marmosops carri is much larger than *M. invictus*, with no overlapping variation in same-sex comparisons of most measured dimensions. These species also differ strikingly in dorsal pelage coloration (much paler in *M. carri* than in *M. invictus*), coloration of the forefeet (entirely whitish in *M. carri*, whereas the metacarpals are dark in *M. invictus*), and tail markings (the tail is much more distinctly bicolored in *M. carri*). Qualitative craniodental comparisons reveal several additional contrasting differences. Among others, *M. carri* has uniformly narrow nasals, whereas the nasals are laterally expanded near the maxillary-frontal suture in *M. invictus*; at least the ventral lacrimal foramina is consistently visible in lateral view in *M. carri*, whereas this foramen is concealed inside the orbit in *M. invictus*; palatine fenestrae are often present in *M. carri*, whereas palatine perforations are consistently absent in *M. invictus*); c1 is a tall unicuspid tooth in male *M.*

carri, whereas this tooth is short and premolariform in male *M. invictus*; and the m1 entoconid is subequal in height to the adjacent m2 paraconid in *M. carri*, whereas the m1 entoconid is shorter than the m2 paraconid in *M. invictus*.

REMARKS: *Marmosops carri* exhibits noteworthy sexual size dimorphism, with adult males averaging larger than adult females in most measured dimensions, especially those prone to strong positive allometry (e.g., zygomatic breadth; tables 10, 11). The sexes additionally differ in interorbital and canine morphology as described above. Maturational changes in the interorbital morphology of adult males appear to result from enlargement of the temporalis musculature, which is accommodated by an increasingly well-defined postorbital constriction and by supraorbital remodelling.

This species was long regarded (e.g., by Tate, 1933) as endemic to Trinidad, but Handley and Gordon (1979) correctly observed that specimens from the coastal cordilleras on the adjacent Venezuelan mainland are morphologically indistinguishable from Trinidadian material. Handley and Gordon recognized that specimens referable to *Marmosops carri* are distinctively larger than topotypical material of *Marmosops fuscatus* (from the Mérida Andes), but they judged these taxa to be conspecific and used the older name (*fuscatus*) for both.

Although *Marmosops carri* and *M. fuscatus* are morphologically similar (in particular, these are the only species of *Sciophanes* that exhibit large size and uniformly narrow nasals), they form distinct cytochrome-*b* haplogroups (figure 4), and measured specimens have nonoverlapping molar dimensions: LM = 7.0–7.7 mm in *M. carri* (N = 28) versus 6.0–6.7 mm in *M. fuscatus* (N = 8). The specimen from Trujillo (USNM

372934) that Handley and Gordon (1979) believed to be intermediate to *M. carri* and *M. fuscatus* has large molars (LM = 7.0 mm) and belongs to the same haplogroup that occurs on Trinidad (Appendix 3); therefore, I refer this specimen (and others collected in the Cordillera de Trujillo) to *M. carri*.

Table 11. Measurements (mm) and weights (g) of adult female specimens of the Fuscatus Group of *Marmosops* (*Sciophanes*).

	***M. carri*[a]**	***M. fuscatus*[b]**	***M. handleyi*[c]**	***M. invictus*[d]**
HBL	130 (125–134) 5	—	109 (104–113) 5	109 (104–112) 5
LT	156 (145–171) 5	—	135 (129–141) 5	133 (124–140) 5
HF	20 (19–21) 5	—	18 (17–19) 5	17 (17–18) 5
Ear	25 (24–26) 5	—	20 (19–21) 5	22 (21–22) 4
CBL	33.7 (32.3–34.9) 6	—	29.9 (29.4–30.7) 5	29.3 (28.2–29.9) 5
NL	16.1 (15.1–16.5) 6	—	15.1 (14.5–15.5) 5	14.1 (13.6–14.9) 5
NB	2.9 (2.5–3.2) 6	3.6	3.5 (3.3–3.7) 5	3.6 (3.3–4.1) 5
LIB	6.2 (6.0–6.4) 6	6.1	6.0 (5.9–6.2) 5	5.9 (5.7–6.1) 5
ZB	17.1 (16.1–17.7) 4	—	15.1 (14.5–15.5) 4	15.7 (14.9–16.2) 5
PL	19.3 (19.1–19.6) 5	18	16.7 (16.3–17.0) 5	16.5 (16.0–17.0) 5
PB	10.7 (10.3–11.3) 5	9.4	9.0 (8.8–9.4) 5	9.2 (9.1–9.5) 5
MTR	14.4 (13.9–15.0) 6	13	12.5 (12.0–12.9) 5	11.9 (11.8–12.1) 5
LM	7.2 (7.0–7.6) 6	6.3	6.3 (5.9–6.6) 5	6.2 (6.0–6.4) 5
M1–3	6.2 (5.9–6.5) 6	5.5	5.4 (5.2–5.6) 5	5.3 (5.2–5.5) 5
WM3	2.3 (2.2–2.6) 6	2.2	1.6	2.1 (2.0–2.1) 5
Weight	42 (41–42) 2	—	27 (21–31) 4	—

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 5921; USNM 370030, 370037, 406929, 443786, 517256.

[b] Measurement of the following specimen: BMNH 96.11.1.6.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 411, 413, 414, 416; FMNH 69838.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: USNM 178709, 306386, 309266, 337959, 337961

I have not examined any voucher material from two ecological studies of mouse opossums identified as *Marmosops fuscatus*, one by O'Connell (1979) and the other by

Cordero (2001). O'Connell's study was carried out at Parque Nacional Guatopo in the interior coastal range of northern Venezuela (ca. 10°05′N, 66°30′W; on the border between the states of Miranda and Guárico), where "*M. fuscatus*" was said to occur only at higher elevations, presumably in premontane rain forest. Cordero's study was carried out at a field station of the Universidad Simón Rodríguez, close to the Caribbean coast in northern Venezuela (10°20′N, 66°15′W; in Miranda), where "*M. fuscatus*" was trapped in lowland rain forest near sea level. Based on their geographic locations (figure 22), I expect that the species observed in both of these studies was *M. carri*. Also unexamined by me are a substantial number of Venezuelan specimens identified as *M. fuscatus* (see Pérez-Hernández, 1989), many of which seem likely to represent *M. carri*. A careful review of this and subsequently collected in-country material should contribute to a more accurate assessment of the geographic ranges of these taxa, and I encourage additional sequencing efforts to test the correlation between haplotype membership and morphometric divergence upon which my hypothesis of full species status is largely based.

SPECIMENS EXAMINED ($N = 70$): **Trinidad and Tobago—***Tobago,* near Charlotteville (AMNH 259970, 259978, 259979); *Trinidad,* Caparo (AMNH 7313/5921, 7314/5922), Cedros (AMNH 234951), Cumaca (AMNH 169759, 169760), Rio Grande Forest (AMNH 186437, 186438, 188353), St. Augustine (AMNH 150007), Turure Forest (AMNH 214439, 214441, 234952–234956, 234959, 234974). **Venezuela**—*Aragua,* Rancho Grande (AMNH 144832; USNM 517256–517260); *Carabobo,* 4 km NW Montalbán (USNM 418515, 443731, 443783–443789, 496520, 496521), Cumbre de

Valencia (AMNH 31531); *Distrito Federal,* Los Venados (USNM 370022–370024); *Miranda/Vargas,* Hotel Humboldt (USNM 370027–370031, 370033–370039, 370041, 370042, 371300, 496517); *Monagas,* San Agustín (USNM 406925–406932, 4069324); *Trujillo*, 13–14 km E Trujillo (KU 120254, USNM 372933, 372934).

Table 12. Diagnostic morphological comparisons among members of the Fuscatus Group of *Marmosops* (*Sciophanes*).

Character	*M. carri*	*M. fuscatus*	*M. handleyi*	*M. invictus*
Dorsal pelage of manus:	all-white	all-white	metacarpals dark	metacarpals dark
Nasal shape:	uniformly narrow	uniformly narrow	wider posteriorly	wider posteriorly
Palatine fenestrae:	variable	variable	present	absent
C1 accessory cusps:	♂: absent; ♀: variable	♂: absent; ♀: post. only	♂: posterior only; ♀: ant. & post.	♂: posterior only; ♀: posterior only
Heights c1, p1 (males):	c1 > p1	c1 > p1	c1 ≈ p1	c1 ≈ p1
c1 lingual accessory cusp:	absent	absent	present	usually present
m1 entoconid, m2 paraconid:	subequal	subequal	subequal	m2 paraconid taller
Length of molars (LM):	7.0–7.7 mm	6.0–6.7 mm[a]	5.9–6.6 mm	6.0–6.5 mm

[a] Observed range includes measurements from two subadults (USNM 418503, 442719) with completely erupted molar dentitions (not included in tables 5 and 6).

Marmosops fuscatus (Thomas, 1896)
Figures 10, 20, 21

Marmosa fuscata Thomas, 1896: 313 (original description).

Didelphys (Marmosa) fuscata: Trouessart, 1898: 1240 (name combination).

Marmosa (Marmosa) fuscata: Cabrera, 1919: 36 (name combination).

Marmosa cracens Handley and Gordon, 1979: 66 (subjective junior synonym). Type locality "near La Pastora, 14 km ENE Mirimire, Falcón, Venezuela."

Marmosa crascens: Reig et al., 1985: 342 (incorrect subsequent spelling of *M. cracens* Handley and Gordon, 1979).

Marmosops cracens: Gardner and Creighton, 1989: 4 (name combination).

Marmosops fuscatus: Gardner and Creighton, 1989: 4 (first use of current binomial).

Marmosa (Marmosops) cracens: Pérez-Hernández et al., 1994: 35 (name combination).

Marmosa (Marmosops) fuscatus: Pérez-Hernández et al., 1994: 35 (name combination); part (not including misidentified specimens of *M. carri*).

Marmosops fuscatus fuscatus: Gardner and Creighton, 2008: 66 (name combination); part (not including misidentified specimens of *M. carri*).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an old adult female (BMNH 1896.11.1.6) collected by "S. Briceno" (= Salomón Briceño-Gabaldón, a commercial collector) at 1630 m elevation along the Río Albarregas (misspelled "Abbaregas" by Thomas, 1896) near the city of Mérida (figure 22: locality 114) in the Venezuelan state of Mérida on 6 April 1896.

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens of *Marmosops fuscatus* are from four Venezuelan localities, two in the Mérida Andes (Cordillera de Mérida), one in the Serranía de San Luis of western Falcón, and one in the Caribbean coastal lowlands of eastern Falcón (figure 22). Although recorded elevations range from 125 to 2350 m above sea level, capture habitats seem to be either premontane or montane

rain forest.[9] Previous reports of this species from Colombia (e.g., Gardner and Creighton, 2008: map 28) were based on misidentified material (see Remarks, below). *Marmosops fuscatus* is not known to occur sympatrically with any congeneric species, although it could be expected to do so with *M. carri* and *M. ojastii*, which have adjacent or overlapping geographic ranges.

DESCRIPTION: Body pelage dark grayish-brown (near Sepia) middorsally, indistinctly paler laterally, and about 7–9 mm long at mid-back (shorter in specimens from lower elevations than in those from the Mérida Andes); ventral pelage superficially whitish but uniformly gray-based except for the apex of the chin, oral margins, and scrotum (which are covered with self-whitish hairs). (One examined specimen, AMNH 276509, has small patches of self-white hairs along the insides of the thighs.) Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting in color with the digits); lateral carpal tubercles blade-like in all examined adult males. Mammary formula unknown. Tail longer than combined length of head and body (mean LT/HBL × 100 = 110%); dorsal caudal surface dark, but indistinctly paler distally in some specimens; ventral surface distinctly paler.

[9] Handley and Gordon (1979) reported that the type series of *Marmosa cracens* was collected between 125 and 170 m above sea level on "the steep, moist, north slope of an isolated, low mountain" near the Caribbean coast. Vegetation of distinctly montane character can extend downslope to within 100 m above sea level on such isolated peaks, which intercept moisture-laden sea breezes and are often shrouded in low-lying clouds. The cloud forest (montane rain forest) vegetation at capture localities in the Serranía de San Luis was briefly described by Anderson et al. (2012).

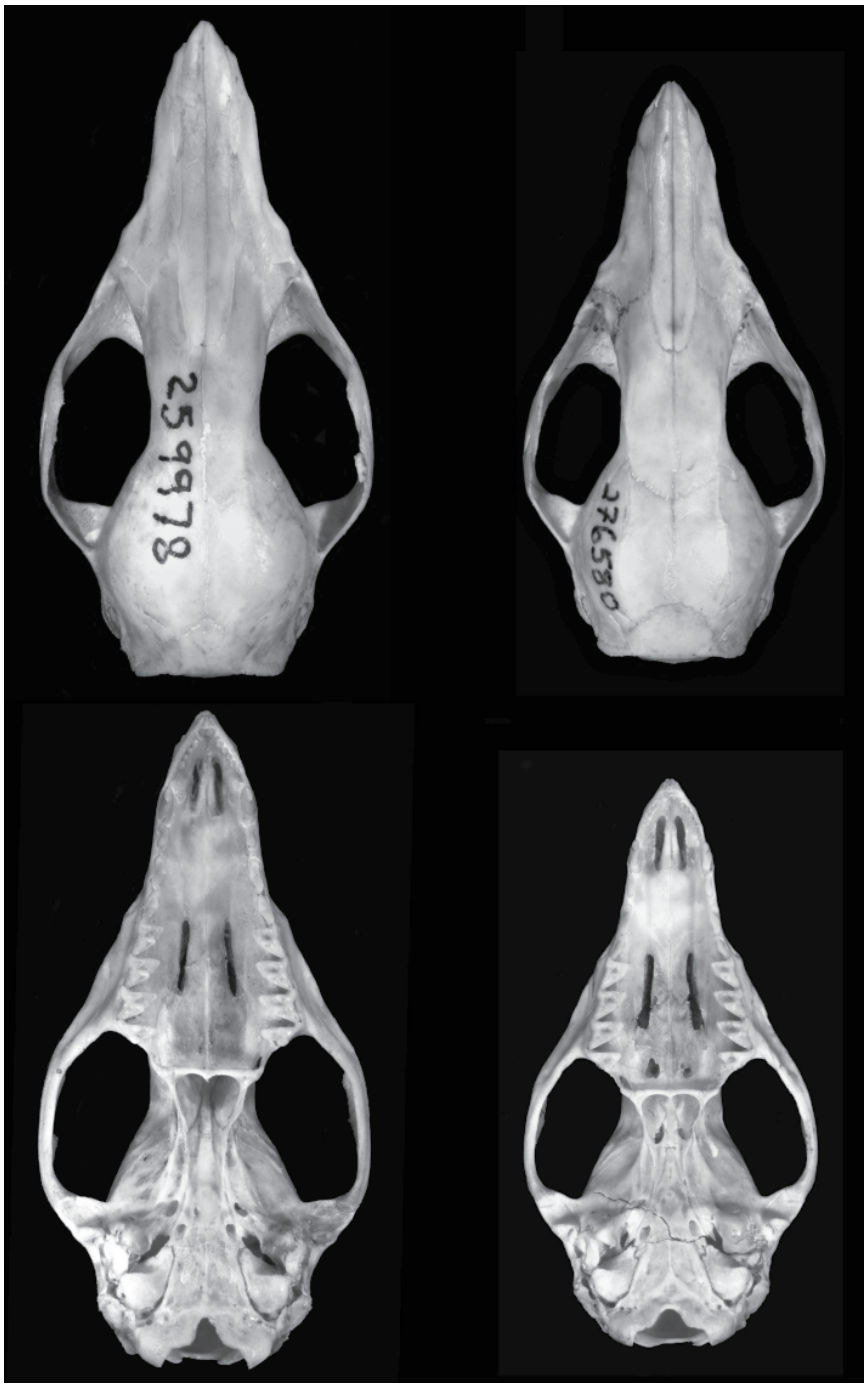

Figure 20. Dorsal and ventral views of skulls of *Marmosops carri* (left, AMNH 259978) and *M. fuscatus* (right, AMNH 276580). All views about ×2.5.

Nasal bones long (extending well behind the lacrimals) and uniformly narrow (without distinct lateral expansion at the maxillary-frontal suture). Interorbital region broad, with rounded supraorbital margins in females and young adult males, but relatively narrower and tending to develop squared supraorbital margins in large adult males; postorbital processes absent or indistinct. Lacrimal foramina variable (the upper foramen is usually not visible in lateral view, but the lower foramen can be either laterally visible or concealed inside the anterior orbital margin)[10]; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present or absent (when present these can appear as a single small perforation on each side or as several small irregular perforations on both sides). Dorsolateral margin of ethmoid foramen usually formed by the frontal.

Upper canine (C1) sexually dimorphic: longer and unicuspid in males, shorter and with posterior accessory cusp in young female specimens with unworn teeth (e.g., USNM 442719). Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) sexually dimorphic: conventionally caniniform (erect, without a posterior accessory cusp) and taller than p1 in males versus premolariform (procumbent, with a posterior accessory cusp) and subequal in height to p1 in females; c1 anterolingual accessory cusp usually absent in both sexes.

[10] The lower lacrimal foramen is laterally visible in some specimens (e.g., BMNH 3.1.5.2, 3.1.5.3, FMNH 22174, USNM 442719) but not in others (e.g., AMNH 276580, 276509). The specimens in which this foramen is visible are the largest in overall size and have the most heavily ossified skulls, but I lack sufficient material to determine whether or not this trait is age-correlated.

Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: Comparisons between *Marmosops fuscatus* and *M. carri* have already been described (see above).

Marmosops fuscatus is substantially larger than *M. handleyi* in head-and-body length and has a proportionately shorter tail (tables 10, 11). Externally the two species differ in the same characters described between *M. carri* and *M. handleyi*, namely dorsal pelage coloration (dark grayish-brown in *fuscatus*, dark brown in *handleyi*) and forefoot coloration (the manus is entirely whitish in *fuscatus*, whereas the pale digits contrast with the dark metacarpals in *handleyi*). *Marmosops fuscatus* also averages larger than *M. handleyi* in most craniodental dimensions, including four measurements (CBL, ZB, PL, MTR, and WM3) that exhibit nonoverlapping variation in same-sex comparisons. These species also differ in some of the same qualitative craniodental characters that distinguish *M. carri* and *M. handleyi*; in particular, *M. fuscatus* has much narrower nasals than *M. handleyi* (in which these bones are conspicuously expanded laterally at the maxillary-frontal suture), and males of *M. fuscatus* have unicuspid C1 and c1, whereas these teeth consistently have a small posterior accessory cusp in males of *M. handleyi*. Additionally, the dorsolateral margin of the ethmoid foramen is usually formed by the frontal in *M. fuscatus*, whereas the dorsolateral margin of this foramen is formed by the orbitosphenoid in *M. handleyi*. Lastly, the distinct lingual accessory cusp of c1 that appears to be consistently present in *M. handleyi* is absent in *M. fuscatus*.

Marmosops fuscatus is substantially larger than *M. invictus* in all external dimensions. In qualitative external characters, *M. fuscatus* is most readily distinguished from *M. invictus* by its paler dorsal coloration (the dorsal pelage of *invictus* is consistently much darker), by its entirely pale forefeet (the metacarpals are dark in *M. invictus*), and by its more distinctly bicolored tail (the tail is only indistinctly paler ventrally than dorsally in *M. invictus*). *Marmosops fuscatus* averages larger than *M. invictus* in most craniodental dimensions, including five measurements (CBL, NL, ZB, PL, MTR) that exhibit nonoverlapping variation in same-sex comparisons. Craniodental qualitative differences between these quite dissimilar species include the shape of the nasals (uniformly narrow in *M. fuscatus*, laterally expanded in *M. invictus*), dorsolateral margin of the ethmoid foramen (usually formed by the frontal in *M. fuscatus*, by the orbitosphenoid in *M. invictus*), C1 posterior accessory cusp (absent in males of *M. fuscatus*, present in both sexes of *M. invictus*), M3 anterior cingulum (incomplete in *M. fuscatus*, narrowly complete in *M. invictus*), c1 morphology (erect and unicuspid in male *M. fuscatus*, procumbent and premolariform in *M. invictus*), c1 lingual accessory cusp (absent in *M. fuscatus*, usually present in *M. invictus*), and m1 entoconid (subequal to adjacent m2 paraconid in *fuscatus*, shorter than m2 paraconid in *M. invictus*).

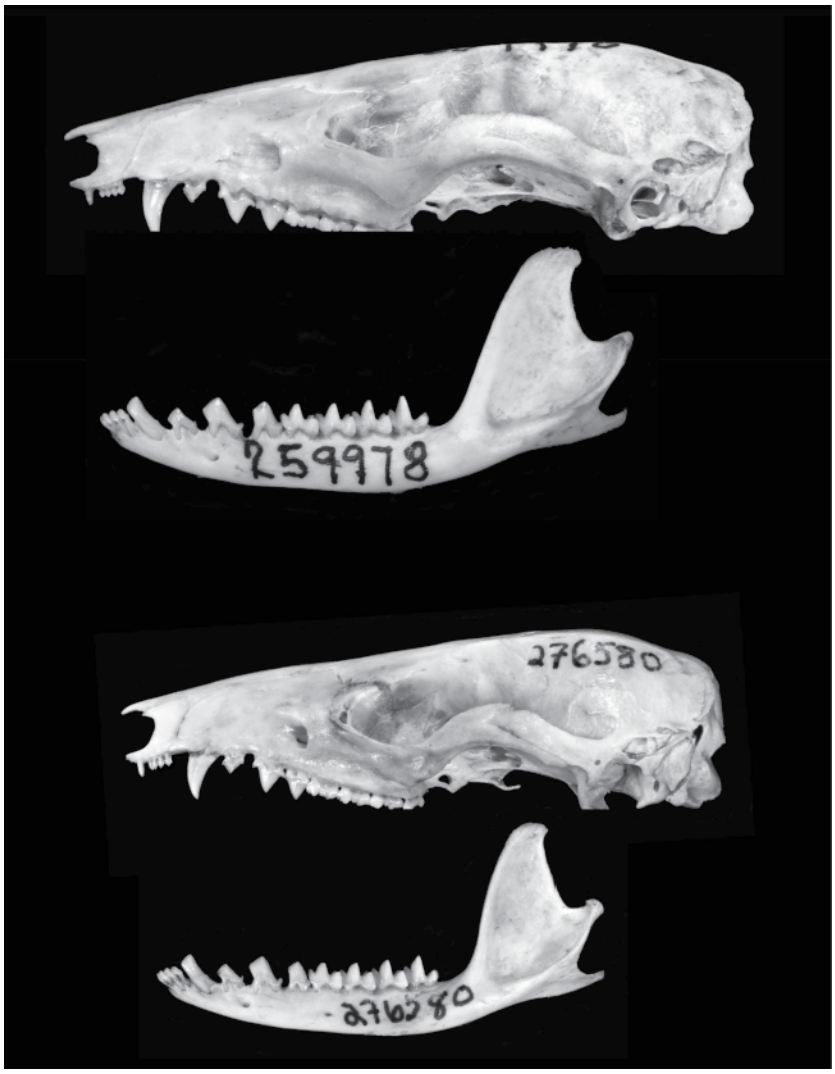

Figure 21. Lateral views of skulls and mandibles of *Marmosops carri* (above, AMNH 259978) and *M. fuscatus* (below, AMNH 276580). All views about ×2.5.

REMARKS: *Marmosa perfusca*, a nominal species that Thomas (1924) described from the Cordillera Oriental of Colombia, was synonymized with *M. fuscatus* by Tate (1933: 173), and some authors (e.g., Gardner and Creighton, 2008: 66) have treated it as a valid subspecies ("*Marmosops fuscatus perfuscus*"). However, the type of *perfusca* (BMNH 1923.11.13.18, consisting of the skin and skull of an old adult female) has

posteriorly widened nasals, a short subsquamosal foramen (not exposing the petrosal behind the sulcus of the prootic sinus), and only one antebrachial vibrissa. In these and other characters it closely resembles *Marmosops caucae* (Thomas, 1900), a member of the nominotypical subgenus of *Marmosops*. A second Colombian specimen that Tate (1933) referred to *Marmosa fuscata* is AMNH 34641, also from the Cordillera Oriental;[11] like BMNH 1923.11.13.18, this specimen appears to represent *M. caucae*. To the best of my knowledge, there are no valid records of *Marmosops fuscatus* from Colombia.

Handley and Gordon (1979: 67) described *Marmosa cracens* as "in almost every respect of pelage and skull character ... a miniature replica of *M. fuscata*, distinguishable from it only by its small size and the short, broad shape of its palate." Indeed, the male holotype of *cracens* (USNM 418503) is substantially smaller than any adult male specimen of *Marmosops fuscatus* that I measured. For example, the condylobasal length of the skull of USNM 418503 is 28.4 mm, whereas the range of condylobasal lengths of five adult male *M. fuscatus* is 31.8–35.4 mm. However, this size difference is plausibly explained by ontogeny: the type series of *cracens* consists of subadults (with incompletely erupted P3s), not young adults (contra Handley and Gordon, 1979). The subadult holotype and paratype of *cracens* do have relatively wider palates (PB/PL = 0.57–0.59) than topotypical adult *fuscatus* (0.51–0.53), but relative width of the palate is

[11] This specimen was collected by G. O'Connell on 4 April 1913 at "El Roble," a locality that Tate (1933: 173) erroneously placed in Departamento Cauca and that Gardner and Creighton (2008: 66) located in Departamento Quindío (on the western slope of the Cordillera Central; Paynter, 1997). However, Geoffroy O'Connell was a member of the 1913 AMNH expedition that worked at a different place called El Roble, "... a posada on the trail from Bogotá to Fusugasugá" on the western slope of the Cordillera Oriental (Chapman, 1917: 645); according to Paynter (1997), this locality is near 4°23′N, 74°19′W.

another ontogenetically variable trait because didelphid palates become proportionately longer and narrower with advancing age (Abdala et al., 2001). Lastly, I (appendix 3; see also Díaz-Nieto et al., 2016a) amplified partial (579–619 bp) cytochrome-*b* sequences from the holotype and a paratype of *cracens*, which differ by only 2.2% (uncorrected) from a partial (1008 bp) cytochrome-*b* sequence that I amplified from a topotype of *M. fuscatus* (BMNH 1903.1.5.2). Because this genetic distance is well within the range of values commonly obtained from comparisons of conspecific sequences of other mammals, and because the phenotypic differences that Handley and Gordon (1979) alleged between *cracens* and *fuscatus* seem to be attributable to the immaturity of their type series, I treat the former as a subjective junior synonym.

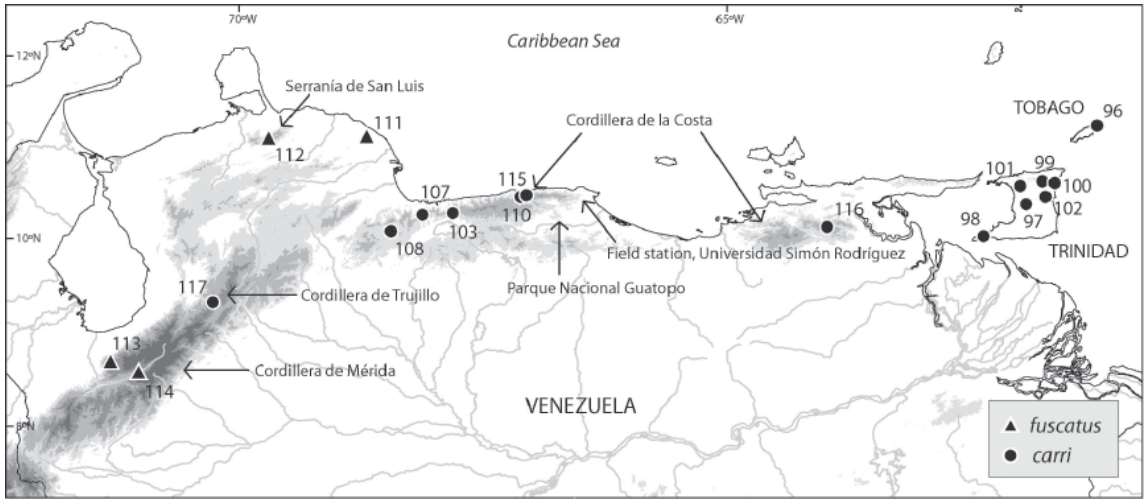

Figure 22. Collecting localities of examined specimens of *Marmosops carri* and *M. fuscatus*. Numbers are keyed to entries in the gazetteer (appendix 6). Progressively darker shading indicates higher elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, dark gray ≥ 2000 m, darkest gray ≥ 3000 m.

SPECIMENS EXAMINED (*N* = 8): **Venezuela**— *Falcón,* Near La Pastora (USNM 418503 [holotype of *cracens*], 442719), Serranía de San Luís (AMNH 276509, 276580); *Mérida,* La Azulita (FMNH 22174), Mérida (BMNH 1896.11.1.6 [holotype], 1903.1.5.2, 1903.1.5.3).

Marmosops handleyi (Pine, 1981)
Figures 8, 23, 24

Marmosa handleyi Pine, 1981: 67 (original description).

Marmosops handleyi: Gardner and Creighton, 1989: 4 (first use of current binomial).

TYPE MATERIAL: The holotype (by original designation) consists of the skin, skull, and postcranial skeleton of an adult female (FMNH 69838; original number PH 4371) collected by Philip Hershkovitz at a site 9 km south of Valdivia (figure 25: locality 24) in the Colombian department of Antioquia at an elevation of 1400 m on 16 June 1950. In addition, Pine's (1981) original material included an adult male paratype (FMNH 70926).

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens of *Marmosops handleyi* are all from the northern terminus of the Cordillera Central (central Andes) of Colombia, where they have been collected in humid premontane and montane rain forest at elevations ranging from 1400 to 1950 m above sea level (figure 25). This species has been collected sympatrically with *M. chucha* (a new species of the Bishopi Group; see below) and with *M. caucae* (a member of the nominotypical subgenus; Díaz-N. et al., 2011).

DESCRIPTION: Body pelage dark brown to chestnut brown middorsally, indistinctly paler laterally, about 9–10 mm long at midback, and somewhat woolly in texture; ventral pelage superficially whitish, but hairs of throat, chest, and abdomen uniformly gray-based (only the apex of the chin, the oral margins, the scrotum, and mammary region consistently have self-white fur).[12] Metacarpals covered dorsally with dark hairs (contrasting in color with the pale manual digits); lateral carpal tubercles blade-like. Mammary formula 3–1–3 = 7 in all examined females with conspicuous teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 125%), dorsal caudal surface dark gray but somewhat paler distally; ventral caudal surface distinctly paler.

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Upper lacrimal foramen not visible in lateral view, but lower foramen laterally exposed; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present (usually as a pair of large rounded perforations). Dorsolateral margin of ethmoid foramen with equal contribution of frontal and orbitosphenoid.

Upper canine (C1) short in both sexes but sexually dimorphic in shape: male C1 with posterior accessory cusp only, female C1 with both anterior and posterior accessory cusps. Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) premolariform (procumbent, with

[12] Pine (1981: 68) described the dorsal pelage as "fuscous," a grayer shade than I observed in fresh skins. Unfortunately, none were compared by me with color swatches in Ridgway (1912). One specimen (CTUA 415, a subadult male) has a 5 ×15 mm midventral streak of self-white abdominal hairs.

posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp present. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: Comparisons of *Marmosops handleyi* with *M. carri* and *M. fuscatus* have already been described (see above).

Although *Marmosops handleyi* averages slightly larger than *M. invictus* in most same-sex comparisons of external dimensions (tables 10, 11), sample sizes for both species are small and it seems unlikely that any external measurement will prove to be diagnostic as more material becomes available. A more consistent external difference between these species is pelage color (distinctly brownish in *handleyi* versus dark grayish-brown to blackish-gray in *invictus*) and fur length (9–10 mm middorsally in *handleyi* versus 6–7 mm in *invictus*). The two species broadly overlap in craniodental measurements, none of which is therefore useful for identification. Instead, *M. handleyi* is more readily distinguished from *M. invictus* by the consistent presence of palatine fenestrae (consistently absent in *M. invictus*), by the presence of both anterior and posterior accessory C1 cusps in females (females usually have only a posterior accessory C1 cusp in *M. invictus*), by lacking a comple M3 anterior cingulum (M3 has a narrowly complete anterior cingulum in *M. invictus*), and by having an m1 entoconid that is subequal in height to the adjacent m2 paraconid (the m1 entoconid is shorter than the m2 paraconid in *invictus*).

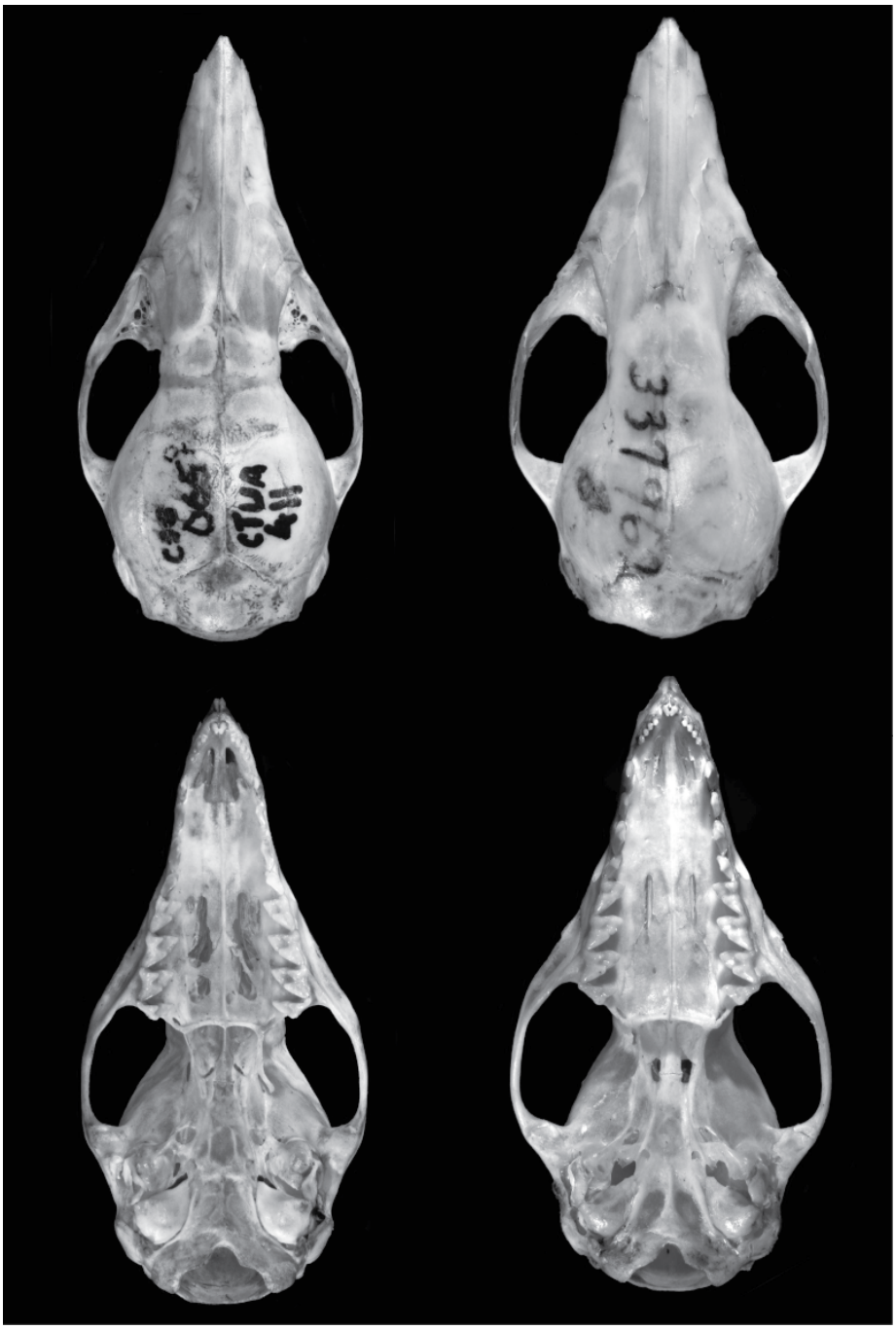

Figure 23. Dorsal and ventral views of skulls of *Marmosops handleyi* (left, CTUA 411) and *M. invictus* (right, USNM 337962). All views about ×3.

REMARKS: *Marmosops handleyi* had not been collected for sixty years before it was rediscovered and redescribed by Díaz-N. et al. (2011), whose report should be

consulted for additional morphological, geographical, and ecological information. Using the dichotomous key in Gardner and Creighton (2008), this species would be misdidentified as *M. juninensis*.

SPECIMENS EXAMINED ($N = 10$): **Colombia—***Antioquia,* Finca Costa Rica (CTUA 410–412, 433); Finca El Bosque (CTUA 413, 414), Finca Villa Nueva (CTUA 415, 416), 9 km S Valdivia (FMNH 69823, 69838).

***Marmosops invictus* (Goldman, 1912)**
Figures 10, 23, 24

Marmosa invicta Goldman, 1912: 3 (original description).

Didelphis (Marmosops) invicta: Matschie, 1916: 270 (name combination).

Marmosops invictus: Gardner and Creighton 1989: 4 (first use of current binomial).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult male (USNM 178708; original number 21517) collected by E.A. Goldman at Cana (figure 25: locality 57), in Darién province, Panama, on 14 March 1912. In addition to the holotype, Goldman's original material included an adult female paratype (USNM 178709).

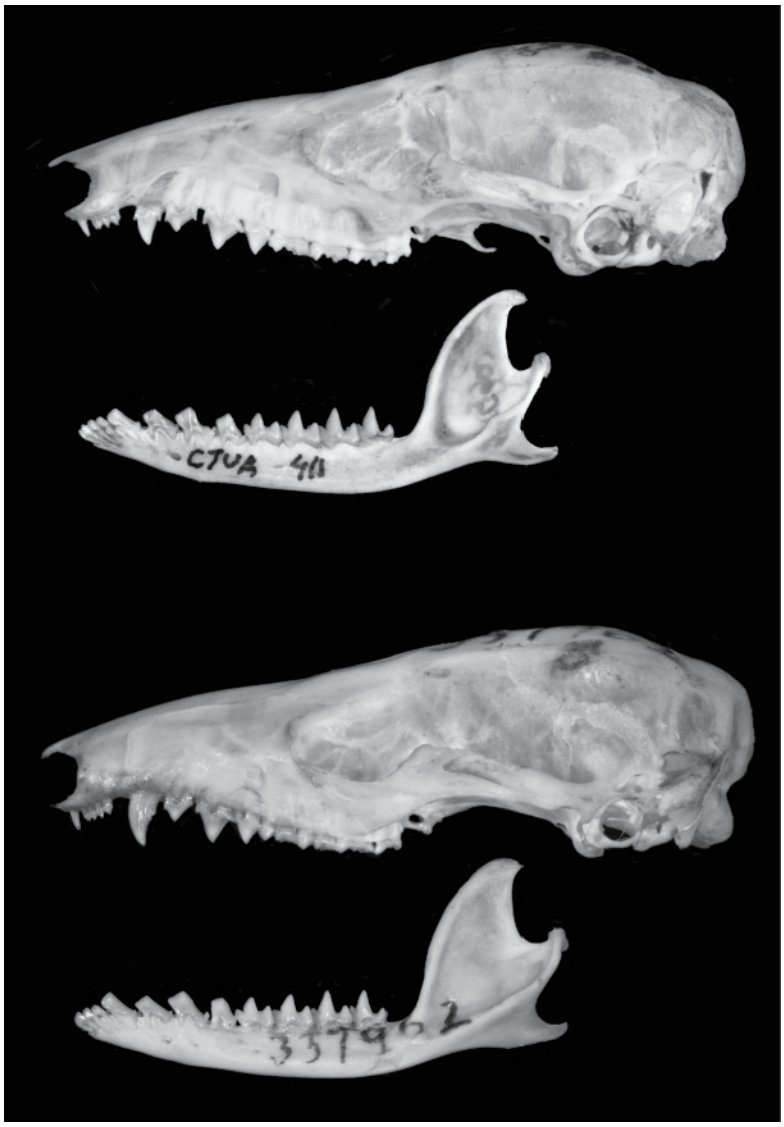

Figure 24. Lateral views of skulls and mandibles of *Marmosops handleyi* (above, CTUA 411) and *M. invictus* (below, USNM 337962). All views about ×3.

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens of *Marmosops invictus* are all from eastern Panama with recorded elevations between 600 and 1500 m above sea level (figure 25). Handley (1966), who may have examined more material than I have seen, gave the elevational range as ca. 450–1200 m and remarked that the species might occur throughout Panama in suitable habitat. Although the lower elevations at

which this species occurs would support lowland rain forest in Amazonia, humid forests of distinctly montane character (e.g., those at the type locality; Goldman, 1920: figures 1, 2) can be found well below 1000 m on the low mountains and foothills of Central America (Myers, 1969). Premontane rain forest seems likely to be the usual habitat of this species, which is not known to occur sympatrically with any other species of the subgenus *Sciophanes*. However, *M. caucae*, a member of the nominotypical subgenus, occurs at elevations >1400 m in the Darién highlands of eastern Panama (Loma Cana and Cerro Pirre) and probably coexists with *M. invictus* in some places.

DESCRIPTION: Dorsal body pelage uniformly dark grayish-brown to blackish-gray (near Bone Brown to Blackish Brown)—not appreciably paler laterally—and only about 6–7 mm long at mid-back; ventral fur silvery-gray (the hairs with dark-gray bases and whitish tips) over throat, chest, and abdomen (only the chin, oral margins, and groin have self-white fur). Manus with dark fur over all or part of metacarpals (contrasting in color with whitish digits); lateral carpal tubercles blade-like. Mammae 3–1–3 = 7 in all examined females with visible teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 122%); dorsal caudal surface dark gray from base to tip; ventral caudal surface indistinctly paler in some specimens (e.g., USNM 306386), almost as dark as dorsal surface in others (e.g., USNM 309265).

Nasal bones long (extending well behind the lacrimals in most specimens) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine

fenestrae absent (but some specimens have minute palatine perforations on one or both sides). Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canine (C1) short, usually with posterior accessory cusps in male and female specimens (two females—USNM 178709, 306386—have indistinct anterior accessory C1 cusps, and the holotype completely lacks accessory cusps). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp usually present. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: Comparisons of *Marmosops invictus* with other members of the Fuscatus Group have already been described (see above).

REMARKS: All of the material I examined for this revision was collected >50 years ago, and I am not aware of any recently collected specimens. However, Mangan and Adler (2000) reported trapping *Marmosops invictus* in the course of an ecological study in western Panama, well outside the specimen-documented range of this species. In the absence of voucher material, the identity of the animals they trapped and released remains to be determined.

In a recent discussion of cytochrome oxidase subunit I (COI) barcoding results, Lim (2012) reported the occurence of *Marmosops invictus* in Panama and Ecuador, but

the specimens he sequenced (ROM 116281, 118844, and F41897)[13] appear to have been misidentified. I examined the Panamanian specimen (ROM 116281), which consists of a skin and skull with all the diagnostic attributes of the nominotypical subgenus, not *Sciophanes*. In addition, its teeth are larger than those of any measured specimen of *M. invictus* (e.g., LM = 6.8 mm versus 6.0–6.5 mm), its ventral pelage includes a median streak of self-white fur, and it has well-developed palatine fenestrae. In these and other traits ROM 116281 resembles numerous specimens of a widespread species (or species complex) for which *M. caucae* is the oldest available name, and the cytochrome-*b* sequence that I (table 2, appendix 4) obtained from ROM 116281 also unequivocally associates this specimen with the *M. caucae* complex. The two Ecuadorean specimens (ROM 118844, F41897) cannot be found at present (Jacqueline Miller, personal commun.), but as their COI barcodes clustered with the barcode obtained from ROM 116281, it seems likely that they are also members of the *M. caucae* complex, which is abundantly represented among other sequenced Ecuadorean material (figure 2).

SPECIMENS EXAMINED (*N* = 10): **Panama—***Darién,* Cana (USNM 178708 [holotype], 178709), Cerro Tacarcuna (USNM 337959–337962), Tacarcuna Casita Camp (USNM 309265), Tacarcuna Laguna Camp (USNM 309266, 309267); *Panamá,* Cerro Azul (USNM 306386).

[13] Corresponding to records ABSMS616-06, ABECB166-08, and ABRMM151-07 in the Barcode of Life Data system (www.boldsystems.org; accessed in January 2016).

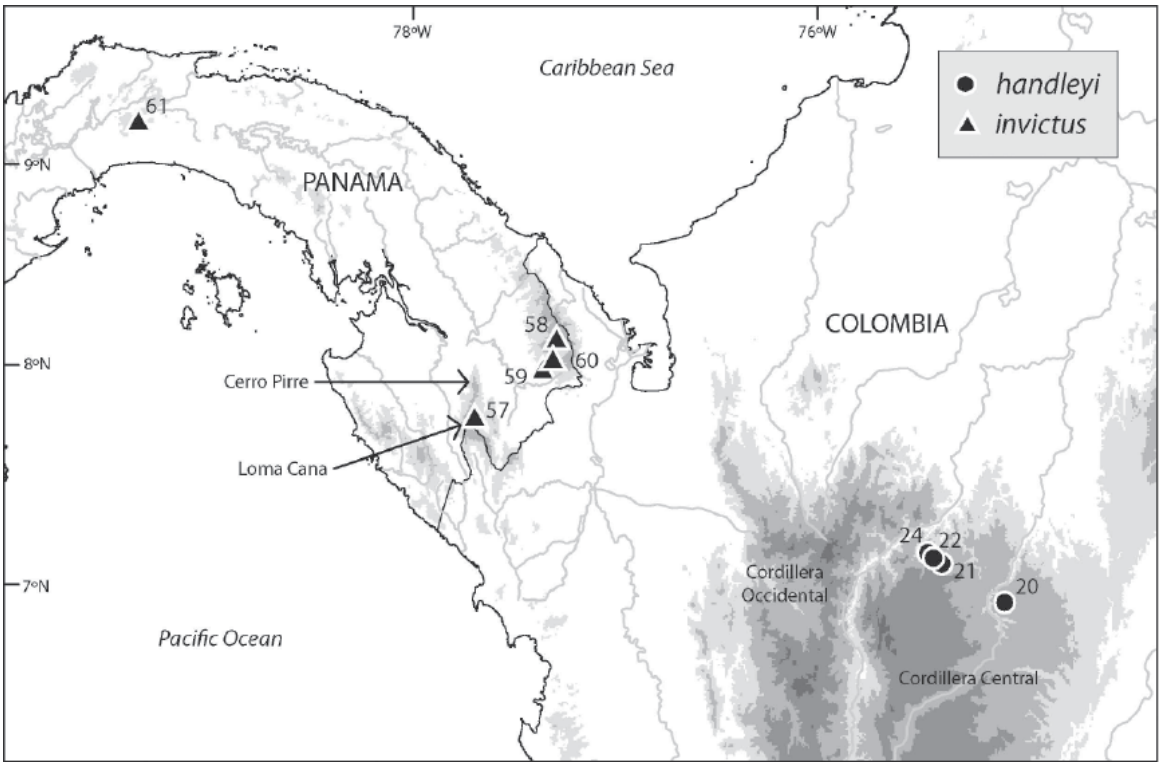

Figure 25. Collecting localities of examined specimens of *Marmosops handleyi* and *M. invictus*. Numbers are keyed to entries in the gazetteer (appendix 6). Progressively darker shading indicates higher elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, dark gray ≥ 2000 m, darkest gray ≥ 3000 m.

Species of the Bishopi Group

Species of the *Marmosops bishopi* group are distinguished from other members of the subgenus *Sciophanes* by their extensively self-white ventral fur (except *M. juninensis*), blade-like lateral carpal tubercles, 4–1–4 = 9 mammae, narrowly complete M3 anterior cingulum, and an m1 entoconid that is shorter than the adjacent m2 paraconid. This clade is widely distributed in western Amazonia, along the eastern slopes

of the Peruvian Andes, in northern Colombia, and in northwestern Venezuela. Diagnostic quantitative and qualitative comparisons are summarized in tables 13–15.

Tabla 13. Measurements (mm) and weights (g) of adult male specimens of the Bishopi Group of *Marmosops* (*Sciophanes*).

	M. bishopi[a]	***M. juninensis***[b]	***M. ojastii***[c]	***M. chucha***[d]	***M. magdalenae***[e]
HBL	103 (93–111) 20	98	94 (90–97) 2	105 (99–109) 5	103 (99–106) 2
LT	141 (126–153) 21	135	134 (130–138) 2	137 (134–141) 5	129 (125–132) 2
HF	17 (15–19) 19	17 (16–18) 2	18 (17–18) 2	18 (17–19) 5	18 (17–18) 2
Ear	21 (18–23) 20	21 (20–21) 2	20 (19–22) 2	21 (20–21) 4	19 (18–19) 2
CBL	28.3 (26.4–29.8) 20	27.7	25.8 (25.3–26.3) 2	28.9	28.3 (27.3–28.9) 3
NL	13.1 (12.2–13.9) 17	—	—	13.4 (13.3–13.6) 2	13.1 (12.5–13.9) 3
NB	3.6 (3.2–4.1) 24	3.7 (3.6–3.7) 2	3.0 (2.9–3.2) 2	3.9 (3.8–3.9) 2	3.8 (3.7–3.8) 3
LIB	5.6 (5.1–6.0) 24	5.6 (5.6–5.7) 2	5.3 (5.3–5.3) 2	5.6 (5.5–5.9) 4	5.5 (5.5–5.6) 3
ZB	14.7 (13.7–15.6) 24	13.9 (13.8–14.1) 2	13.6 (13.3–13.8) 2	15.2	15.1 (14.8–15.5) 3
PL	15.8 (14.6–16.8) 22	15.8	14.2 (13.8–14.7) 2	15.8 (15.7–15.9) 2	15.6 (14.9–16.0) 3
PB	8.6 (8.0–9.0) 24	8.3 (8.3–8.3) 2	8.2 (8.2–8.3) 2	8.9 (8.8–9.0) 2	8.7 (8.5–8.8) 3
MTR	11.5 (10.6–12.0) 24	11.3 (11.2–11.4) 2	10.6 (10.5–10.8) 2	11.4 (10.9–11.7) 3	11.3 (10.8–11.6) 3
LM	5.9 (5.4–6.3) 24	5.8 (5.7–5.8) 2	5.6 (5.6–5.6) 2	5.9 (5.7–6.1) 4	6.0 (5.9–6.1) 3
M1–3	5.1 (4.8–5.4) 24	5.0 (4.9–5.1) 2	5.0 (4.9-5.0) 2	5.2 (5.1–5.3) 4	5.2 (5.1–5.2) 3
WM3	1.9 (1.8–2.1) 24	1.8 (1.8–1.8) 2	1.8 (1.8–1.9) 2	1.9 (1.7–2.0) 4	1.9 (1.9–2.0) 3
Weight	25 (18–34) 16	—	—	26 (25–26) 2	24

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 276700, 276705; CBF 7531; EPN 127, 10706; FMNH 84251, 169802, 203328, 203509; ICN 18338; KU157969; MSB 55843; MUSM 16237, 16240, 16803, 17691, 17723, 17930; MVZ 168966; QCAZ 10308; TTU 99031, 99032, 101239; USNM 584464.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 230014, 230016.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: EBRG 27474, 29540 (data from García et al., 2024); USNM 371299.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: FMNH 69825, 70925, 70927; MHNUC 986, MHNUC uncataloged (DCV069).

[e] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: FMNH 70926; ICN 18788, ICN uncataloged (YMS1820).

Marmosops bishopi (Pine, 1981)
Figures 14, 26–28

Marmosa parvidens bishopi Pine, 1981: 63 (original description).

Marmosops parvidens bishopi: Gardner, 1993: 20 (name combination).

Marmosops bishopi: Voss et al., 2001: 48 (first use of current binomial).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult female (USNM 393535; original number RHP 5157) collected by Ronald H. Pine near the base camp of the Royal Geographical Society's Xavantina-Cachimbo expedition, 264 km N (by road) Xavantina in the Serra do Roncador, Mato Grosso, Brazil (figure 29: locality 12). Although Pine (1981) did not examine any other referred material, he mentioned two topotypical BMNH specimens that I have been unable to locate.

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens that I refer to *Marmosops bishopi* are from the western Amazonian lowlands of southeastern Colombia, eastern Ecuador, eastern Peru, northeastern Bolivia, and western Brazil; the eastern Andean foothills of Peru and Bolivia; and the Cerrado of central Brazil and eastern Bolivia (figure 29). The species has been collected from gallery forest in savanna-dominated landscapes (e.g., at the Serra do Roncador; Ratter et al., 1973; Eiten, 1975), in lowland rainforest (Patton et al., 2000; Hice and Velazco, 2012), and in premontane rain forest. Recorded elevations range from 100 to 1300 m above sea level. Not surprisingly, the broad geographic range of *M. bishopi* overlaps those of several congeneric species.

Among other reports of sympatry, this species has been collected together with *M. juninensis* (in eastern Peru; Peralta and Pacheco, 2014); *M. noctivagus*, *M. caucae*, and an undescribed species (in western Brazil; Patton et al., 2000); and *M. ocellatus* (in eastern Bolivia; Emmons, 2006).

Table 14. Measurements (mm) and weights (g) of adult female specimens of the Bishopi Group of *Marmosops* (*Sciophanes*)[a].

	***M. bishopi*[b]**	***M. juninensis*[c]**	***M. chucha*[d]**	***M. magdalenae*[e]**
HBL	101 (90–114) 7	104 (96–110) 3	100 (90–112) 4	99 (99) 2
LT	129 (116–141) 7	131 (122–137) 3	126 (119–133) 4	130 (129–130) 2
HF	16 (15–18) 8	16 (14–18) 3	16 (13–17) 4	17 (17) 2
Ear	20 (18–22) 8	19 (17–20) 2	19 (18–20) 4	20 (20) 2
CBL	27.5 (26.6–29.6) 9	28.3	27.2 (26.9–27.6) 3	27.1 (26.9–27.3) 2
NL	12.2 (11.7–13.1) 3	13.1 (13.0–13.3) 2	12.4 (11.7–12.7) 4	12.7 (12.5–12.8) 2
NB	3.5 (3.2–3.8) 11	3.4 (3.3–3.4) 2	3.5 (3.4–3.6) 4	3.7
LIB	5.4 (5.1–5.6) 11	5.7 (5.6–5.9) 3	5.4 (5.4–5.5) 4	5.5 (5.4–5.5) 2
ZB	14.6 (13.4–15.5) 11	14.2 (13.9–14.5) 2	14.4 (14.2–14.5) 2	14.8
PL	15.3 (14.7–16.3) 9	15.8 (15,7–16.0) 2	15.2 (14.9–15.4) 3	14.9 (14.9) 2
PB	8.8 (8.4–9.3) 10	8.6 (8.3–8.9) 3	8.4 (8.3–8.5) 3	8.8 (8.7–8.8) 2
MTR	11.4 (11.0–11.8) 11	11.4 (11.1–11.7) 3	11.2 (10.9–11.6) 4	10.9 (10.8–11.1) 2
LM	5.9 (5.6–6.1) 11	5.9 (5.6–6.0) 3	5.8 (5.5–6.0) 4	5.8 (5.8–5.9) 2
M1–3	5.1 (4.8–5.3) 11	5.1 (4.9–5.2) 3	5.0 (4.8–5.2) 4	5.1 (5.1–5.2) 2
WM3	2.0 (1.8–2.1) 11	1.9 (1.8–2.1) 3	1.9 (1.8–2.0) 4	2.0 (1.9–2.0) 2
Weight	21 (17–29) 5	27	18	—

[a] I have not examined any female specimen of *Marmosops ojastii*; according to García et al. (2014), adult female specimens of *M. ojastii* are unknown.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 268938; MUSM 17661, 23802, 24432, 33487; QCAZ 8168, 8169; TTU 98964, 101238, 101257; USNM 393535.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 63864; 230015; MUSM 40617.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 434; FMNH 69822, 69837, 70928.

[e] Measurement of the following specimen: ICN 19924.

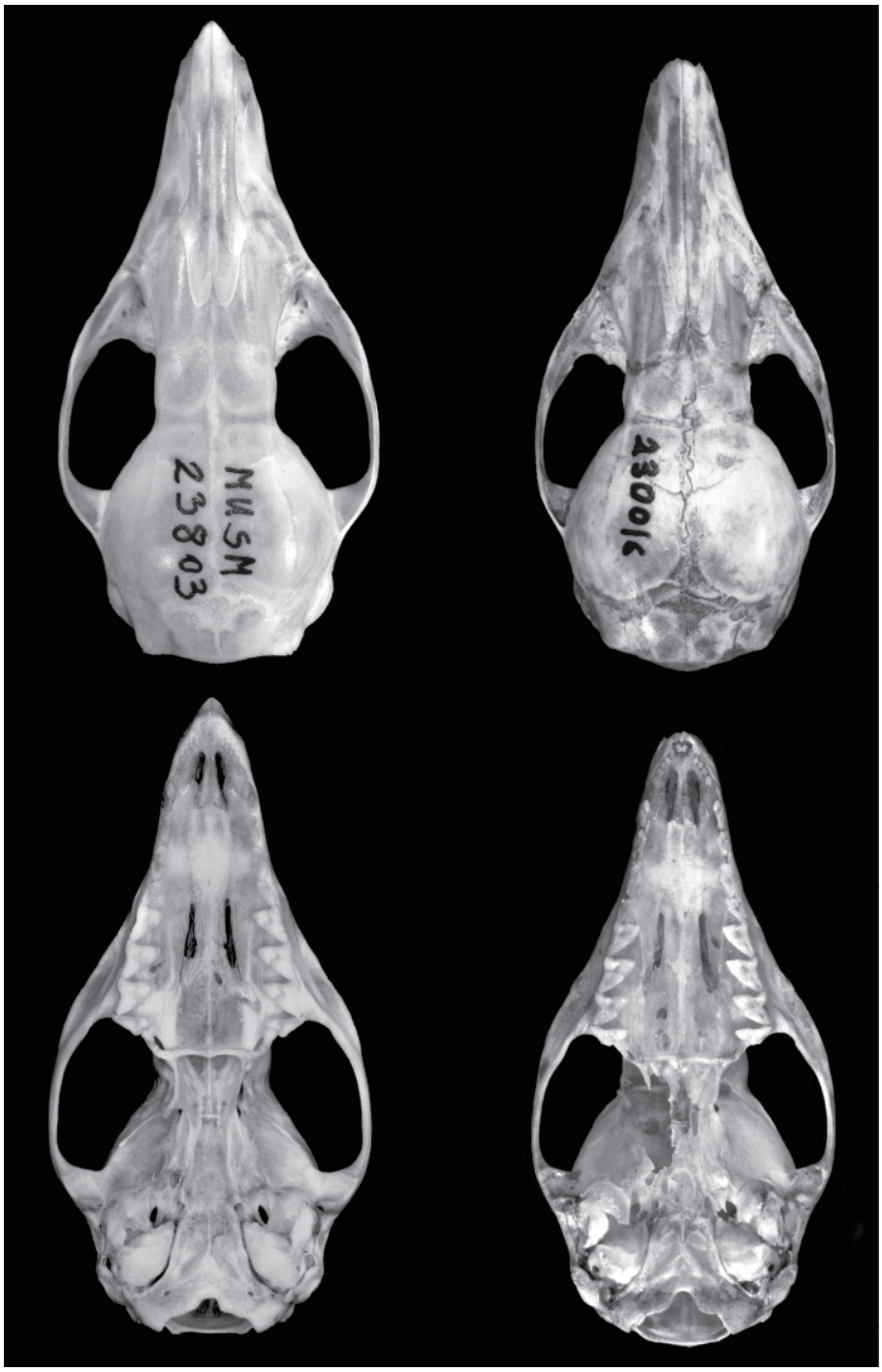

Figure 26. Dorsal and ventral views of skulls of *Marmosops bishopi* (left, MUSM 23803) and *M. juninensis* (right, AMNH 230016). All views about ×3.

DESCRIPTION: Dorsal body pelage geographically variable, but usually some shade of grayish-brown (near Bister) middorsally,[14] often indistinctly paler laterally, and about 7–9 mm at mid-back; ventral pelage predominantly self-white from chin to groin (including the inside surfaces of the fore- and hindlimbs), with or without narrow lateral borders of gray-based abdominal fur. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles blade-like. Mammae 4–1–4 = 9 in all examined females with visible teats. Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 130%); often indistinctly bicolored (dark above, somewhat paler below), but unicolored-dark in some specimens (e.g., AMNH 276723) and distinctly bicolored in others (e.g., USNM 584464).

Nasals proportionately shorter than in species of Parvidens and Fuscatus groups (often not extending behind lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually concealed from lateral view inside anterior orbital margin (but in some specimens—e.g., AMNH 67243, KU 157970, MUSM 23803—the lower foramen is partially exposed in lateral view); zygomatic process of the squamosal broadly overlapped dorsally by jugal. Distinct palatine fenestrae absent (but a few specimens have minute palatine perforations on one or both sides). Dorsolateral margin of ethmoid foramen formed by the frontal.

[14] Cerrado specimens (e.g., USNM 393535, 584464) are paler (near Snuff Brown) than those from lowland rain forest, and a few specimens (e.g., FMNH 84251) are distinctly reddish (near Cinnamon Brown).

Upper canine short and sexually dimorphic: males with posterior accessory C1 cusp, females with both posterior and anterior accessory cusps. Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter (sometimes much shorter) than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Table 15. Diagnostic comparisons among members of the Bishopi Group of *Marmosops* (*Sciophanes*).

Character	*M. bishopi*	*M. juninensis*	*M. ojastii*	*M. chucha*	*M. magdalenae*
Distribution:	cis-Andean	Andean	trans-Andean	trans-Andean	trans-Andean
Self-white ventral fur:	broad	absent	broad	broad	broad
Squamosal-jugal overlap:	broad	shallow/absent	broad	broad	broad
Palatine fenestrae:	usually absent	large/multiple	absent	absent	large
C1 accessory cusps:	♂: post. only; ♀: variable[a]	♂: post. only; ♀: post. only	♂: post. only; ♀: post. only[b]	♂: post. only; ♀: ant. & post.	♂: post. only; ♀: post. only

[a] All females have a posterior accessory cusp, but some also have an anterior accessory cusp.
[b] I did not examine females of this species, but García et al. (2014) described juvenile females with posterior accessory cusps.

COMPARISONS: *Marmosops bishopi* overlaps broadly in all measured external and craniodental dimensions with *M. juninensis*, from which it cannot be distinguished morphometrically (tables 13, 14). Similarly, the coloration of the dorsal pelage offers no useful criterion for identifying these species due to the wide variation in this trait observed in *M. bishopi*. By contrast, the ventral pelage is taxonomically diagnostic:

whereas a broad zone of self-white fur extends continuously from chin to anus, including the inside surfaces of the fore- and hindlimbs in *M. bishopi*, the ventral fur of *M. juninensis* is almost entirely gray-based (including the insides of the fore- and hindlimbs), with only a narrow, discontinuous midventral streak of self-white fur in some specimens. Additionally, *M. bishopi* can be distinguished from *M. juninenis* by having the zygomatic process of the squamosal broadly overlapped dorsally by the jugal (the zygomatic process of the squamosal is not or only slightly overlapped by the jugal in *M. juninensis*; figure 28), by having unfenestrated palatines (palatine fenestrae are consistently present in *M. juninensis*), and by lacking a c1 anterolingual accessory cusp (c1 usually has a small anterolingual accessory cusp in *M. juninensis*).

Marmosops bishopi is substantially larger, on average, than *M. ojastii* in head-and-body length and in many craniodental measurements, but these morphometric comparisons need to be interpreted cautiously because only two adult males of *M. ojastii* have been measured, and one of these (USNM 371299) is quite young. The dorsal pelage of the single skin of *M. ojastii* that I examined (USNM 371299) is somewhat paler than is usual in *M. bishopi*, but this contrast does not seem to be consistent with pelage color descriptors used by García et al. (2014: table 2). Instead, those authors distinguished *M. bishopi* from *M. ojastii* based on several other characters, including the size and shape of the lateral carpal tubercle (said to be larger and more flattened in *M. bishopi* versus smaller and triangular in *M. ojastii*), size and position of the hypothenar pad of the manus (said to be larger than the interdigital pads in *M. bishopi* versus smaller than the interdigitals in *M. ojastii*), position of the lacrimal foramina (said to be exposed outside

the orbit in *M. bishopi* versus concealed from lateral view inside the orbit in *M. ojastii*), development of lambdoid crests on the occiput (said to be larger in *M. bishopi* than in *M. ojastii*), position of the posterolateral palatal foramina (said to be larger and to extend anteriorly to the protocone of M4 in *M. bishopi* versus smaller and not extending anteriorly to the protocone of M4 in *M. ojastii*), and width of the masseteric fossa of the mandible (said to differ in some undefined way between these species). Although my observations (based on USNM 371299) are not entirely consistent with García et al's (2014), I have not examined their type material. The only other potentially diagnostic character I noted is the dorsolateral margin of the ethmoid foramen, which is usually formed by the frontal in *M. bishopi*, whereas the dorsolateral margin of this foramen is formed by the orbitosphenoid in USNM 371299.

Marmosops bishopi is morphometrically similar to *M. chucha*, with which it exhibits overlapping variation in all same-sex comparisons of homologous measurement values. Apparently, the only diagnostically useful external character for these species is the coloration of the ventral pelage, which is almost entirely self-white in most specimens of *M. bishopi*, whereas the self-white midventral fur of *M. chucha* is often narrowed by lateral zones of gray-based fur. Craniodentally, these species can be distinguished by the dorsolateral margin of the ethmoid foramen (which is usually formed by the frontal bone in *M. bishopi*, but by the orbitosphenoid in *M. chucha*) and by the morphology of c1 (which has only a posterior accessory cusp in both sexes of *M. bishopi*, whereas female specimens of *M. chucha* have both anterior and posterior accessory cusps.

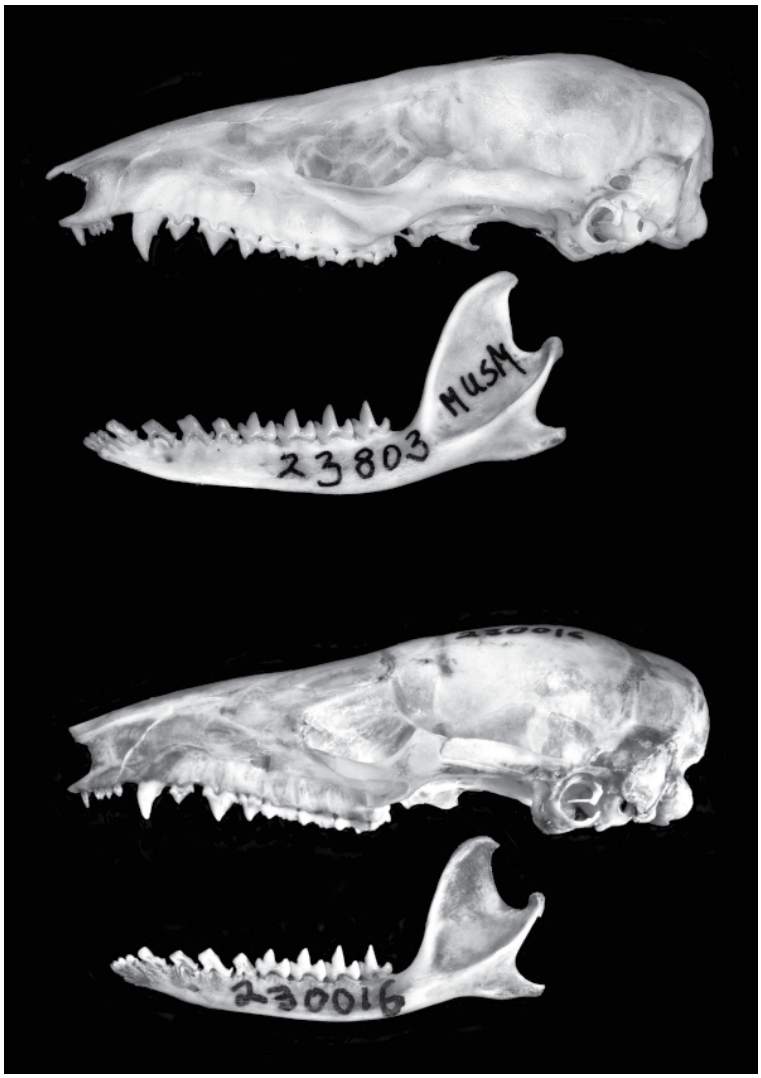

Figure 27. Lateral views of skulls and mandibles of *Marmosops bishopi* (above, MUSM 23803) and *M. juninensis* (below, AMNH 230016). All views about ×3.

Marmosops bishopi is also morphometrically similar to *M. magdalenae*, with which it overlaps broadly in all external and craniodental measurements. However, these species differ—to about the same extent already described between *M. bishopi* and *M. chucha*—in ventral pelage color pattern: whereas most specimens of *M. bishopi* have entirely self-white ventral fur, all examined specimens of *M. magdalenae* have a narrower midventral zone of self-white fur flanked by broad lateral bands of gray-based

hairs that sometimes extend onto the fore- and hindlimbs. In addition, palatine fenestrae are consistently absent (or present as small, usually unilateral or asymmetrical perforations) in *M. bishopi*, whereas palatine foramina are large and well-developed in *M. magdalenae*. Lastly, the talonid of m4 seems to be consistently tricuspid in *M. bishopi*, whereas the m4 talonid is usually bicuspid in *M. magdalenae*.

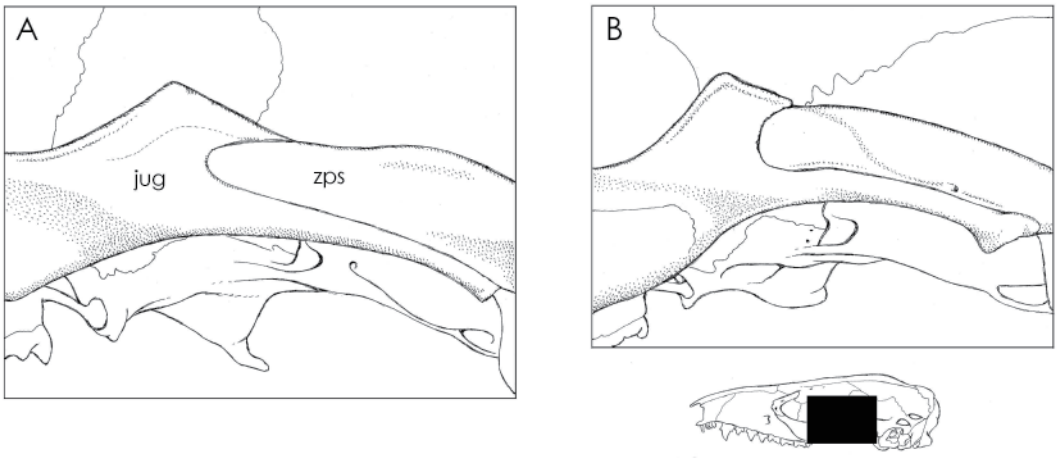

Figure 28. Lateral view of zygomatic arch of *Marmosops bishopi* (A, MUSM 23803) and *M. juninensis* (B, AMNH 230016) illustrating species differences in the extent of dorsal overlap between the zygomatic process of the squamosal (zps) and the jugal (jug).

REMARKS: *Marmosops bishopi* is a very widespread species that includes at least six cytochrome-*b* haplogroups, which I distinguished by alphabetic labels (table 16). Genetic divergence among these haplogroups is impressively high, but I am unable to distinguish them morphologically. The most divergent haplogroup is "F," which differs from all of the others by >10% in uncorrected pairwise cytochrome-*b* sequence comparisons, whereas pairwise cytochrome-*b* distances among haplogroups A–E range from 3.5 to 5.3% (Table 4). I did not obtain any sequence data from the holotype, but the

type locality is closest (geographically and ecologically) to the Cerrado site in eastern Bolivia (figure 29: locality 5) where specimens with haplotype "E" were collected.

Table 16. Cytochrome-b Haplogroups of *Marmosops bishopi*[a].

Haplogroup	N[b]	Distribution[c]	Biome(s)	Habitat(s)
A	7	eastern Peru & western Brazil	Amazonia & Andean foothills	lowland & premontane rain forest
B	1	northeastern Bolivia	Andean foothills	premontane rain forest
C	1	southeastern Colombia	Amazonia	lowland rain forest
D	2	northeastern Bolivia	Andean foothills	lowland & premontane rain forest
E	2	eastern Bolivia	Cerrado	semideciduous gallery forest
F	3	northeastern Peru	Amazonia	lowland rain forest

[a] Following results of chapter 1 (figure 4).

[b] Number of sequences.

[c] See figure 2 for mapped localities.

SPECIMENS EXAMINED ($N = 91$): **Bolivia—***Beni,* 1 km E La Emboscada (UMMZ 156014); *Cochabamba,* Serranía Mosetenes (CBF 7531); *La Paz,* Alto Río Madidi (USNM 579249), La Reserva (AMNH 268938); *Santa Cruz,* El Refugio (USNM 584464, 584465), San Rafael de Amboró (MSB 55843). **Brazil—***Amazonas,* Barro Vermelho (MVZ 190283), Vai-Quem-Quer (MVZ 190284); *Mato Grosso,* 264 km N Xavantina (USNM 393535 [holotype]). **Colombia—***Amazonas*, Vereda Peña Roja (ICN 18338). **Ecuador—***Morona Santiago*, Wisui (EPN 11947); *Napo*, Ituamani (EPN 127), Río Hollín (EPN 129); *Orellana*, Parque Nacional Yasuní (EPN 10706; QCAZ 8168, 8169, 11004); *Pastaza*, Arajuno (QCAZ 9954, 10074, 10308, 10606, 10608, 10661, 10758); *Sucumbíos*, Cantón Shushufindi (EPN 11686), El Reventador (QCAZ 316). **Peru—***Amazonas***,** Puerto Tunduza (MUSM 16237, 16240, 16241, 16243); *Cuzco*, Camisea

(MUSM 14857), Cosñipata (FMNH 84251); *Huánuco,* Puerto Márquez (AMNH 67243); *Loreto,* Cocha Coconilla (MUSM 17691, 17723), Collpa Salvador (MUSM 17661), El Triunfo km 48 carretera Iquitos-Nauta (MUSM 33445, 33487), Estación Biológica Allpahuayo (LACM 96113; TTU 98653, 98702, 98857, 98964, 99031, 99032, 100941, 101238, 101239, 101155, 101257), Jenaro Herrera (AMNH 276697, 276700, 276705, 276718, 276723; MUSM 15978–15981, 23799–23803), La Habana km 52 carretera Iquitos-Nauta (MUSM 33446), Nuevo San Juan (MUSM 13287), Quebrada Agua Negra (MUSM 24432), San Jacinto (KU 157969), San Lucas km 44 carretera Iquitos-Nauta (MUSM 33448, 33450, 33451), San Pedro (UF 30454), Teniente López (KU 157970, 157971), Trece de Febrero km 31.5 carretera Iquitos-Nauta (MUSM 33452); *Madre de Dios*, 2.75 km E Shintuya (FMNH 169802; MUSM 16803, 16804), 12 km E Puerto Maldonado (MVZ 168966), Blanquillo (MUSM 8396), Reserva Cuzco Amazónico (MUSM 6060, 6061), Río La Torre (MUSM 20087), S.N. Pampas del Heath (MUSM 11652); *San Martín*, Caserío El Diamante (FMNH 203328, 203509); *Ucayali*, Cerros de Canchaguaya (MUSM 17902, 17930, 17952).

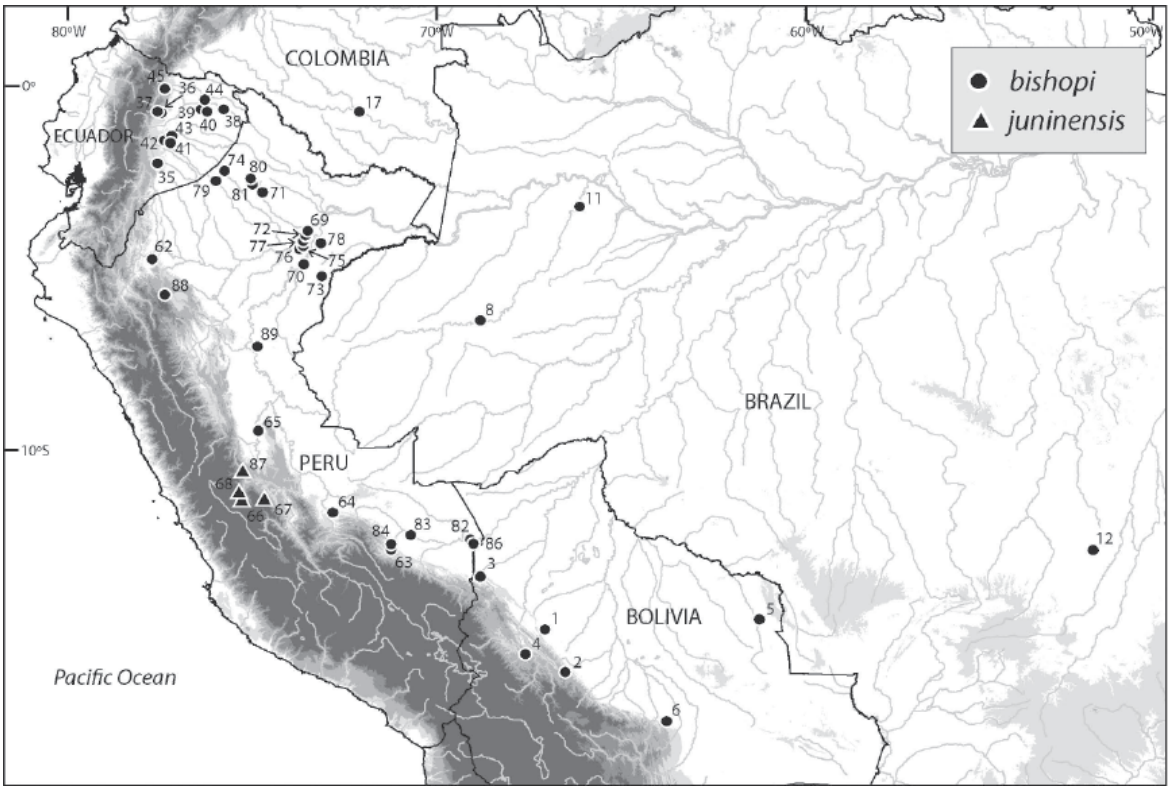

Figure 29. Collecting localities of examined specimens of *Marmosops bishopi* and *M. juninensis*. Numbers are keyed to entries in the gazetteer (appendix 6). Progressively darker shading indicates higher elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, dark gray ≥ 2000 m, darkest gray ≥ 3000 m.

Marmosops juninensis (Tate, 1931)

Figures 11, 26–28

Marmosa juninensis Tate, 1931: 13 (original description).

Marmosa parvidens juninensis: Pine, 1981: 64 (name combination).

Marmosops parvidens juninensis: Gardner, 1993: 20 (name combination).

Marmosops juninensis: Emmons, 1990: 22 (first use of current binomial).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of a young adult female (AMNH 63864) collected by H. Watkins on 25 February 1929 at Utcuyacu (figure 29: locality 68), between Tarma and Chanchamayo, in Junín department, Peru, at an altitude of 4800 feet (1463 m).

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens suggest that *Marmosops juninensis* has a restricted distribution in premontane and montane rain forest on the eastern slopes of the Peruvian Andes in the departments of Junín and Pasco between 1387 and 2316 m above sea level. According to Peralta and Pacheco (2014), at the lower limit of its elevational range *M. juninensis* occurs sympatrically with *M. bishopi*, where at least two species of the nominotypical subgenus (*M. noctivagus* and a member of the *M. caucae* complex) could also be expected to occur.

DESCRIPTION: Body pelage reddish-brown (near Prout's Brown) middorsally, indistinctly paler laterally, and about 7–9 mm long at mid-back; ventral pelage superficially whitish, but hairs extensively gray-based on throat, chest, and abdomen (including the insides of the fore- and hindlimbs), with or without a narrow, discontinuous midventral streak of self-white fur.[15] Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles blade-like. Mammary formula unknown (no female specimens with visible teats were examined). Tail substantially longer than combined length of head

[15] Voss et al. (2001: 48) described the ventral fur as "entirely gray-based," corresponding to the phenotype seen in AMNH specimens, but Peralta and Pacheco (2014) described and illustrated recently collected material with a midventral streak of self-white fur.

and body (mean LT/HBL × 100 = 126–137%); dorsal caudal surface dark (perhaps brownish in life), ventral surface indistinctly paler.

Nasals long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; apex of zygomatic process of squamosal distinctively rounded anteriorly and not (or only slightly) overlapped dorsally by jugal. Palatine fenestrae consistently present, but sometimes irregular in size and shape. Dorsolateral margin of ethmoid foramen formed by the frontal.

Upper canine (C1) with only posterior accessory cusp in both sexes. Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp usually present but very small. First lower molar (m1) entoconid shorter than m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: Comparisons of *Marmosops juninensis* with *M. bishopi* are provided in the preceding account.

Marmosops juninensis seems to be about the same size as *M. ojastii* (table 13), but with the very small samples available for both species, morphometric inference is problematic. In side-by-side comparisons of skins these species are most readily distinguished by ventral pelage coloration: whereas the ventral pelage of *M. juninensis* is extensively gray-based (with only a discontinuous midventral streak of self-white fur), the ventral pelage of *M. ojastii* is almost entirely self-white with no trace of gray-based

hairs. *Marmosops juninensis* can also be unambiguously distinguished from *M. ojastii* by several craniodental characters including dorsal overlap between the squamosal and jugal (shallow or absent in *M. juninensis* versus extensive in *M. ojastii*), the dorsolateral margin of the ethmoid foramen (usually formed by the frontal in *M. juninensis* versus by the orbitosphenoid in *M. ojastii*), palatine fenestrae (consistently present in *M. juninensis* versus absent in *M. ojastii*), and a lingual accessory cusp on c1 (present in *M. juninensis* but absent in M. *ojastii*).

Insofar as can be judged from my very small samples, *Marmosops juninensis* and *M. chucha* are about the same size. Skins of these species are distinguishable by ventral pelage coloration, which is extensively gray-based in *M. juninensis* (notably on the throat and inside surfaces of the fore- and hindlimbs) but broadly self-white in *M. chucha* (in which the throat is always self-white and the inside surfaces of the limbs usually have some self-white markings). In qualitative cranial comparisons, these species can be readily distinguished based on squamosal-jugal overlap (the jugal does not dorsally overlap the zygomatic process of the squamosal bone in *M. juninensis*, whereas dorsal overlap between the jugal and squamosal bone is broad in *M. chucha*), palatine fenestration (palatine fenestrae are consistently present and large in *M. juninensis* whereas palatine fenestrae are minute or absent in *M. chucha*), and the lingual accessory cusp of c1 (usually present in *M. juninensis* versus usually absent in *M. chucha*).

Marmosops juninensis is likewise similar in size to *M. magdalenae*, from which it cannot confidently be distinguished based on measurement data alone. However, these species are distinguishable by ventral pelage coloration (extensively gray based in *M.*

juninensis versus extensively self-white in *M. magdalenae*), dorsal overlap between the jugal and squamosal zygomatic process (shallow or absent in *M. juninensis* versus extensive in *M. magdalenae*), the lingual accessory cusp on c1 (usually present in *M. juninensis* versus usually absent in *M. magdalenae*), and the number of m4 talonid cusps (three in *M. juninensis* versus two in *M. magdalenae*).

REMARKS: The Pasco specimen (LSU 25902) is a juvenile male, but it is a good match in pelage and dental traits with other material referred to this species. In particular, the ventral fur of LSU 25902 is entirely gray-based, C1 has a distinct posterior accessory cusp, and the combined length of M1–M2 is 3.5 mm (versus 3.4–3.6 mm in AMNH specimens, including the holotype).

SPECIMENS EXAMINED ($N = 7$): **Peru—***Junín,* San Antonio (MUSM 40616, 40617), 22 mi E Tarma (AMNH 230014–230016), Utcuyacu (AMNH 63864); *Pasco,* Santa Cruz (LSU 25902).

Marmosops ojastii **(García et al., 2014)**
Figures 30–32

Marmosops ojastii García et al., 2014: 704 (original description).

TYPE MATERIAL: The holotype (by original designation) consists of a fluid preserved body and skull of an adult male (EBRG 27474) said to have been collected by Frank Steines on 27 February 1996 at Pico Guacamaya (figure 33: locality A), Parque

Nacional Henri Pittier, Cordillera de la Costa, Aragua, Venezuela. Additionally, García et al. (2014: 705) designated one paratype (EBRG 29540), but excluded four other examined specimens (EBRG 27475, 27476, 29566, 29587) from the type series.

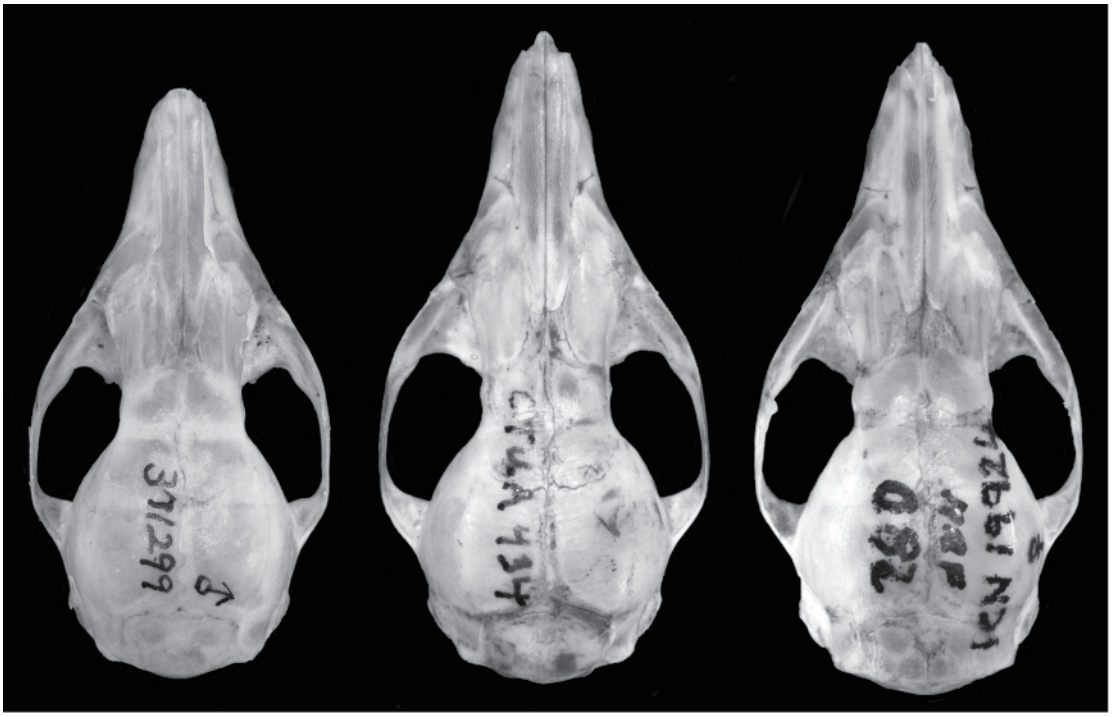

Figure 30. Dorsal views of skulls of *Marmosops ojastii* (left, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (right, ICN 19924). All views about ×3.

DISTRIBUTION, HABITATS, AND SYMPATRY: *Marmosops ojastii* occurs in the Cordillera de la Costa and adjacent lowlands of northern Venezuela and in the Cordillera de Mérida of western Venezuela (figure 33) from near sea level to at least 1850 m. Habitats within this elevational range include lowland rain forest (e.g., near Urama; Handley, 1976: 84) and premontane rainforest (e.g., at Pico Guacamayo; García et al., 2014: 713, figure 7). This species apparently occurs sympatrically with *M. fuscatus* at

Rancho Grande (appendix 6: locality 103) and may do so throughout its geographic range.

DESCRIPTION: Dorsal body pelage pale reddish brown and about 8–10 mm long at mid-back;[16] ventral pelage self-white from chin to groin (including the inside surfaces of the fore- and hindlimbs), without lateral zones of gray-based hairs. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercle blade-like, not spoon-shaped. Mammary formula unknown (no adult female specimens examined by us or by García et al., 2014). Tail considerably longer than combined length of head and body (mean LT/HBL × 100 = 143%) and indistinctly bicolored.

Nasals apparently not very long (not extending posteriorly much behind the lacrimals) and wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of the squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canines short and apparently not sexually dimorphic; males and females with posterior accessory cusp only.[17] Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1)

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[16] Near Buffy Brown middorsally and somewhat paler laterally in USNM 371299, "marrón rojizo" in specimens examined by García et al. (2014: 707). The dorsal fur is a little shorter in USNM 371299 (collected near sea level) than in the material measured by García et al. (2014) from higher elevations.

[17] I have not examined any female specimens, but García et al. (2014) described two juvenile females with a posterior accessory cusp on C1.

premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

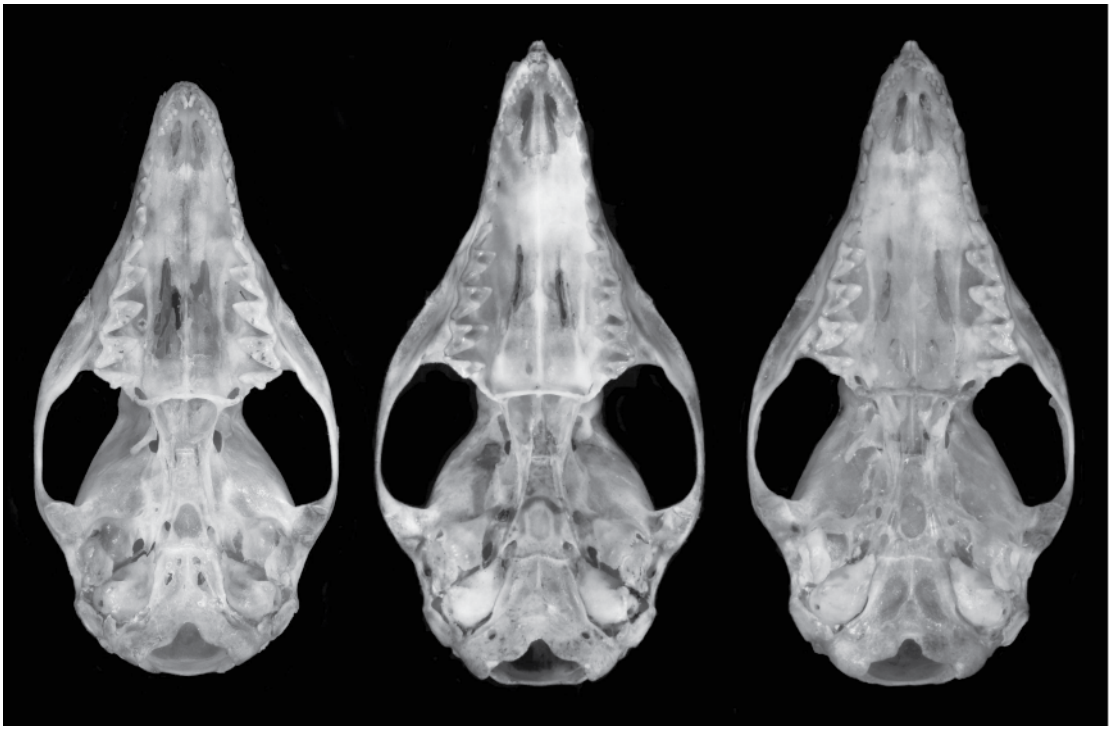

Figure 31. Ventral views of skulls of *Marmosops ojastii* (left, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (right, ICN 19924). All views about ×3.

COMPARISONS: Comparisons of *Marmosops ojastii* with *M. bishopi* and *M. juninensis* have already been provided in the preceding species accounts (above).

Marmosops ojastii appears to be smaller, on average, than *M. chucha* (table 13). In fact, males of these allopatric species exhibit nonoverlapping variation in several external and craniodental dimensions (e.g., HBL, NB, LIB, PL, PB, MTR, LM), although the diagnostic value of these data is compromised by small sample sizes. The single skin

of *M. ojastii* available for side-by-side comparisons with skins of *M. chucha* is conspicuously paler than any of the latter species, and it has more extensively self-white underparts than most skins of *M. chucha* (which often have lateral zones of gray-based ventral fur). Additionally, *M. ojastii* appears to have a relatively longer tail (about 140% of head-and-body length) by comparison with *M. chucha* (about 130% of head-and-body length). Skulls of the two species are qualitatively similar, but (in addition to the aforementioned size difference), the nasal bones of *M. ojastii* are visibly narrower in proportion to interorbital breadth than are those of *M. chucha* (NB/LIB = ca. 0.57 versus 0.70, respectively, for males). Whereas males and females of *M. ojastii* have only a posterior accessory cusp on C1, most female specimens of *M. chucha* have both anterior and posterior C1 accessory cusps.

Marmosops ojastii appears to differ from *M. magdalenae* in many of the same traits that apparently distinguish it from *M. chucha*, including smaller size, paler dorsal pelage, more extensively self-white ventral pelage, longer tail (relative to head-and-body), and narrower nasals (relative to interorbital breadth). Additionally, palatine fenestrae are absent in both intact adult skulls of *M. ojastii* (figure 31; García et al., 2014: figure 2B), whereas these openings are consistently present in examined specimens of *M. magdalenae* (figures 11C, 31). Other possibly diagnostic characters include the dorsolateral margin of the ethmoid foramen (formed by the orbitosphenoid in USNM 371299, but by the frontal in examined specimens of *M. magdalenae*), and the number of m4 talonid cusps (three in USNM 371299, usually two in *M. magdalenae*).

REMARKS: The single specimen of *Marmosops ojastii* that I examined (USNM 371299) was not part of García et al.'s (2014) type material, but it agrees with their morphological description in all important respects, its measurements correspond closely to their measurements of the holotype skull and paratype skin, and it was collected within the geographic range of their material (figure 33). Those authors did not analyze any genetic data, so it is relevant to note that the cytochrome-*b* sequence I obtained from USNM 371299 is highly divergent (by 9–15% in average pairwise uncorrected comparisons; table 4) from those of previously described taxa in the subgenus *Sciophanes* and tends to support the conclusion that *M. ojastii* is a valid species. This specimen was previously identified as *M. parvidens* by Pine (1981) and Voss et al. (2001: 48–49), although the latter authors remarked several of the traits that I now recognize as diagnosing the Bishopi Group (e.g., its bladelike carpal tubercle and lack of an anterior C1 accessory cusp).[18]

A single specimen from the Maracaibo Basin of western Venezuela (UMMZ 53222), a fluid-preserved adult male with an extracted skull, might also represent this species. Like other members of the Bishopi Group, it has blade-like carpal tubercles, and the anterior cingulum of M3 is narrowly continuous. Like *M. ojastii*, it has completely self-white underparts, lacks palatine fenestrae, and has narrow nasals relative to interorbital breadth (LB/LIB = 0.54). Unlike *M. ojastii*, however, C1 has well-developed anterior and posterior accessory cusps. Unfortunately, I was unable to amplify DNA from this old specimen (collected in 1914; see appendix 6: locality 118), and I am unaware of

[18] According to García et al. (2014: 715), USNM 371299 is a juvenile, but in fact it is a young adult.

any additional material from the Maracaibo lowlands, which are now extensively deforested.

In my phylogenetic analyses (figures 4, 5) I was not able to convincingly resolve the position of *M. ojastii*, which was either recovered as the sister taxon of *M. chucha* + *M. magdalenae* (using cytochrome-*b* sequences only) or as the sister species of *M. bishopi* (using sequences from cytochrome-*b* and the Breast Cancer Activating 1 nuclear gene).

SPECIMENS EXAMINED (*N* = 1): **Venezuela—***Carabobo/Falcón/Yaracuy,* 19 km NW Urama (USNM 371299).

***Marmosops chucha*, new species**
Figures 12, 30–32

HOLOTYPE: CTUA 434 (original number CACE004), consisting of the skin, skull, fluid-preserved carcass, and associated tissues of an adult female collected by Camilo A. Calderón-Acevedo on 15 July 2010 at Hacienda Vegas de La Clara (figure 33: locality 18), municipio Gómez Plata, Antioquia, Colombia.

DISTRIBUTION, HABITATS, AND SYMPATRY: Examined specimens of *Marmosops chucha* are from west of the Río Magdalena in northern Colombia between 130 m and 1400 m above sea level; known collection localities are in the foothills of the Serranía de Abibe (the northwestern terminus of the Cordillera Occidental), the northeastern part of the Cordillera Central, and the interandean valley of the Río Porce (figure 33). Recorded

capture habitats include premontane rain forest (Sánchez-Giraldo and Díaz-Nieto, 2015), premontane moist forest (Estrada-Pareja et al., 2007), and lowland rain forest (Castaño and Corrales, 2010), all of which now occur as fragments within an anthropogenic matrix of pastures and agricultural fields. At the upper limit of its known elevational range, *M. chucha* occurs sympatrically with *M. handleyi* (e.g., near Valdivia [appendix 6: locality 24]; see Díaz-N. et al., 2011).

DESCRIPTION: Body pelage brownish (near Prout's Brown in darker specimens, closer to Dresden Brown in others) middorsally, indistinctly paler laterally, and about 7–10 mm long at mid-back; ventral pelage continuously self-white from chin to groin (usually including the insides of the fore- and hindlimbs), but self-white fur narrowed by lateral zones of gray-based abdominal fur (tipped with brown) in some specimens.[19] Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercle blade-like, not spoon-shaped. Mammary formula 4–1–4 = 9 in all examined females with visible teats. Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 130%), usually indistinctly bicolored and sometimes indistinctly paler distally than basally.

Nasals not very long (usually not extending posteriorly behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin;

[19] This might be a sexually dimorphic trait. The midventral zone of self-white fur—measured across the sternum—seems to be wider in females (17–20 mm, $N = 3$) and narrower in males (7–12 mm, $N = 5$).

zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent or minute. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

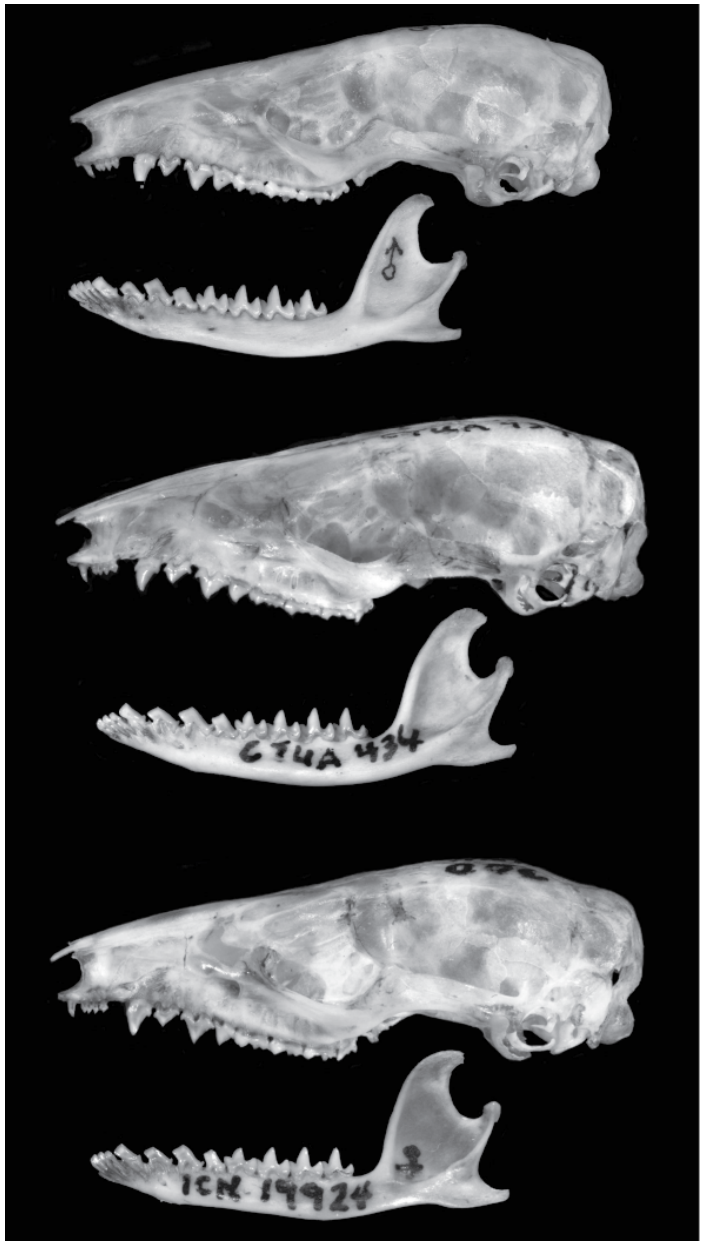

Figure 32. Lateral views of skulls of *Marmosops ojastii* (above, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (below, ICN 19924). All views about ×3.

Upper canines short in both sexes but apparently sexually dimorphic: males usually with only posterior accessory cusp and females usually with both anterior and posterior accessory cusps (MHNUC 986, a male with both anterior and posterior accessory cusps, and FMNH 698222, a female with just a posterior accessory cusp, are exceptions). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent in most examined material (but distinctly present in FMNH 70925). Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

COMPARISONS: Comparisons of *Marmosops chucha* with *M. bishopi*, *M. juninensis*, and *M. ojastii* have already been provided in the accounts for those species (above).

Marmosops chucha and *M. magdalenae* are similar in most qualitative and morphometric traits, but palatine fenestrae are consistently absent or indistinct in *M. chucha*, whereas these openings are consistently large in *M. magdalenae*. Additionally, the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid bone in *M. chucha* whereas the dorsolateral margin of this foramen is usually formed by the frontal in *M. magdalenae*. Lastly, there are apparent taxonomic differences in the presence of C1 accessory cusps: in *M. chucha* most males have only posterior accessory

cusps whereas most females have both anterior and posterior cusps, whereas in *M. magdalenae* both sexes have only posterior accessory cusps..

ETYMOLOGY: From *chucha*, a colloquial term for "opossum" in Colombian Spanish (Comisión de Lingüística de la Academia Colombiana, 2012), here treated as a noun in apposition.

REMARKS: The known geographic ranges of *Marmosops chucha* and *M. magdalenae* are separated by the Río Magdalena, an important geographic barrier (Chapman, 1917; Gutérrez-Pinto, 2012), and they differ from one another by about 5.9% in average uncorrected pairwise comparisons of partial cytochrome-*b* sequences. Although additional phenotypic and genetic evidence that these are fully differentiated species would be welcome, the results at hand seem sufficient to justify their recognition as such in the context of this revision.

The material that I refer to *Marmosops chucha* was previously identified as *Marmosa parvidens* by Pine (1981), as *Marmosops parvidens* by Díaz-N. et al. (2011), and as *Marmosops* "West Magdalena" by Díaz-Nieto et al. (2016a).

SPECIMENS EXAMINED ($N = 10$): **Colombia**—*Antioquia*, Amalfi (CTUA 428), Gómez Plata (CTUA 434), Valdivia (FMNH 69822, 69825, 69826), Villa Arteaga (FMNH 69837); *Caldas*, Norcasia (MNHUC 750, 986), Samaná (FMNH 70925; MNHUC uncatalogued DCV69).

Marmosops magdalenae, new species
Figures 11, 30–32

HOLOTYPE: ICN 19924 (original number MRP82), consisting of the skin and skull of an adult female collected by Miguel E. Rodríguez-Posada on 18 July 2002 at Bosque de Roble Cerca de Torre, Reserva Biológica Cachalú (figure 33: locality 33), vereda Rionegro, municipio Encino, Santander, Colombia.

DISTRIBUTION AND SYMPATRY: Examined specimens of *Marmosops magdalenae* are from east of the Río Magdalena in northern Colombia, where it has been collected between 104 m and 1940 m above sea level (figure 33). Capture habitats include lowland rain forest along the right bank of the Río Magdalena (e.g., at Corregimiento Campo Capote [figure 33: locality 34]) and lower montane moist forest on the western slope of the Cordillera Oriental (e.g., at Reserva Biológica Cachalú [figure 33: locality 33]; Otálora Ardila, 2003; Ávila et al., 2010). This species is not known to occur sympatrically with any other congener, but at the upper limit of its elevational range it might co-occur with *M. caucae*, a member of the nominotypical subgenus that is widespread in Andean cloud forests (figure 1).

DESCRIPTION: Body pelage fuscous to reddish-brown (near Dresden Brown) middorsally, indistinctly paler laterally, and about 9 mm long at mid-back (based on FMNH 70926); ventral pelage self-white from chin to groin (including the inside surface of the forelimbs and sometimes also the hindlimbs), but midventral band of self-white fur narrowed by lateral zones of gray-based abdominal hairs (sometimes with brownish tips) on abdomen. Manus covered dorsally with uniformly pale fur, without pigmental contrast

between the metacarpal and digital pelage; lateral carpal tubercles blade-like in all examined adult males. Mammary formula unknown.[20] Tail longer than combined length of head and body (mean LT/HBL × 100 = 125–130%), indistinctly bicolored, and somewhat paler distally than proximally (but not distinctly particolored).

Nasals not very long (usually not extending posteriorly behind lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by jugal. Palatine fenestrae consistently present and large. Dorsolateral margin of ethmoid foramen usually formed by the frontal.

Upper canines short, with posterior accessory cusps in both sexes (anterior accessory cusps consistently absent in all examined material). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent or indistinct. Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid usually with only two distinct cusps.

COMPARISONS: Comparisons between *Marmosops magdalenae* and other species of the Bishopi Group have already been provided in the preceding accounts.

[20] The skin tag of ICN 19924 mentions the presence of "*6 mamas*," but no mammary formula was provided. I inspected the skin of this specimen and found 6 teats in the arrangement 3–1–2. Because no species of *Marmosops* is known to have unpaired lateral mammae it seems probable that additional mammae are normally present in this species.

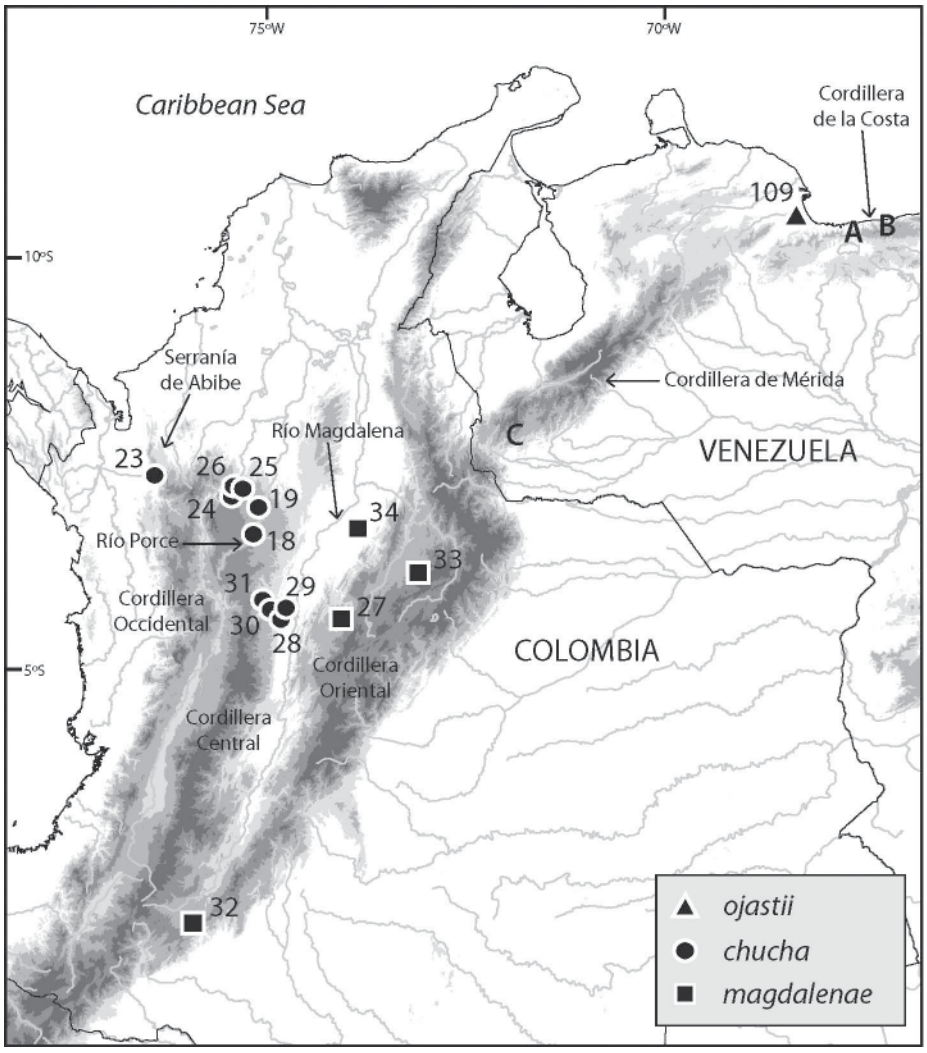

Figure 33. Collecting localities of *Marmosops ojastii*, *M. chucha*, and *M. magdalenae*. Numbers are keyed to entries in the gazetteer for material examined by us; letters indicate collection localities of unexamined material of *M. ojastii* reported by García et al. (2014): A, Pico Guacamaya, Parque Nacional Henri Pittier, Aragua, Venezuela (10°21′ N, 67°40′ W); B, Sector Buenos Aires, Monumento Nacional Pico Codazzi, Aragua, Venezuela (10°25′N, 67°21′W); C, Campamento La Trampita, Uribante-Caparo, Táchira, Venezuela (7°50′ N, 71°57′W). Progressively darker shading indicates higher elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, dark gray ≥ 2000 m, darkest gray ≥ 3000 m.

ETYMOLOGY: For the Río Magdalena, economically and culturally the most important river of Colombia, and a well-known dispersal barrier for the terrestrial vetebrate fauna of northwestern South America.

REMARKS: The material that I refer to *Marmosops magdalenae* was previously identified in the literature as *Marmosa parvidens* by Pine (1981), as *Marmosops parvidens* by Díaz-N. et al. (2011), and as *Marmosops* "East Magdalena" by Díaz-Nieto et al. (2016a).

SPECIMENS EXAMINED ($N = 3$): **Colombia**—*Boyacá,* Muzo (FMNH 70926); *Huila*, near San Adolfo (FMNH 70927, 70928); *Santander*, Encino (ICN 19924), Puerto Parra (ICN 18788).

DISCUSSION

Specimens of the subgenus *Sciophanes* are not common in museum collections. Although I examined all the material that I was able to locate in North American, Colombian, and Ecuadorean museums, the total available for this study of 12 species amounted to fewer than 300 specimens. By contrast, Rossi et al. (2010) were able to examine almost 1500 specimens for their revision of just seven species of *Marmosa*. This difference in specimen availability perhaps reflects the difficulty of trapping very small marsupials like *Sciophanes* with commercially available equipment. Pitfall trapping appears to be a more effective collecting method (Voss et al., 2001), but pitfalls have only recently come into routine use for Neotropical rainforest mammal inventory work (Umetsu et al., 2006; Ribeiro-Júnior et al., 2011). As pitfall trapping continues to gain in popularity, I predict a corresponding increase in numbers of fresh specimens of *Sciophanes*, which should provide abundant material for evaluating the taxonomic conclusions of my study.

Even a cursory examination of the maps in this report suggests where new discoveries are likely to be made. I have not seen any material of *Sciophanes* from vast Amazonian landscapes, including those drained by such major rivers as the Rio Negro, the Tapajos, the Madeira, and the upper Xingu. No specimens are known from the eastern slopes of the Colombian Andes, nor from the Chocó lowlands of western Colombia. Based on the distribution of other small didelphids that often co-occur with *Sciophanes*, it seems likely that the subgenus does occupy many regions from which specimens are currently unknown. Therefore, I confidently predict that future collecting will result either in significant geographic range extensions of currently recognized taxa, or in the discovery of new species. In effect, this report is no more than a preliminary assessment of the species-level diversity of *Sciophanes* based on the material now at hand.

Future research might also profitably focus on assessing the genetic independence of several mtDNA haplogroups that I am currently unable to distinguish by phenotypic criteria. In particular, coalescent analyses of nuclear markers could help determine whether any of the several haplogroups of *M. bishopi* (figure 4, table 16) are cryptic species. On the other hand, morphological analyses would be welcome in any future attempt to evaluate the taxonomic status of populations with *M. pinheiroi*-like mtDNA sequences from savanna landscapes in Maranhão (Nascimento et al., 2015), and larger sample sizes would certainly be helpful for testing the statistical significance of morphometric differences inferred from small numbers of specimens in this study.

There is still much to learn.

CHAPTER 3
PHYLOGENETIC RELATIONSHIPS OF *CHACODELPHYS* (MARSUPIALIA: DIDELPHIDAE: DIDELPHINAE) BASED ON "ANCIENT" DNA SEQUENCES

INTRODUCTION

The didelphid species *Chacodelphys formosa* has remained a phylogenetic enigma for more than a decade since the genus *Chacodelphys* was proposed by Voss et al. (2004) for "*Marmosa*" *formosa* Shamel, 1930. At that time, *C. formosa* was known from a single specimen collected in the Chaco of northern Argentina in 1920 by the ornithologist Alexander Wetmore. Phylogenetic analyses of morphological character data that Voss et al. (2004) obtained from the holotype skin and skull suggested that *C. formosa* belonged to the subfamily Didelphinae, but different sets of characters tended to place this taxon either with *Lestodelphys* and *Thylamys* (tribe Thylamyini) or with *Monodelphis* (tribe Marmosini). Although subsequent analyses of larger datasets suggested that *Chacodelphys* was a thylamyine rather than a marmosine, this result was not consistently strongly supported, and different analytic permutations placed the genus either as the sister taxon of *Lestodelphys* + *Thylamys* or in an unresolved polytomy with other thylamyine genera (Voss and Jansa, 2009). As discussed by Voss et al. (2004), this phylogenetic uncertainty resulted from conflicting patterns of morphological homoplasy and from the absence of relevant molecular sequence data.

Chacodelphys formosa was rediscovered by Argentinean mammalogists in 2006, but the phylogenetic situation was unimproved because none of the new material was suitable for DNA sequencing. Most of the recently collected specimens are partial skulls recovered from owl pellets, and one is a skull extracted from a formalin-preserved head (Teta et al., 2006; Teta and Pardiñas, 2007). Therefore, the 95-year-old holotype currently remains the only potential source of molecular data.

Here I report the results of phylogenetic analyses of mitochondrial and nuclear sequences that I obtained by nondestructive sampling of dried soft tissue from the almost completely cleaned holotype skull of *Cryptonanus formosa*. Although sparse, these data are sufficient to identify the sister taxon of *Chacodelphys* with high confidence, and they underscore the potential usefulness of old osteological material for molecular systematics when other sources of crucial sequence data are unavailable. Additionally, these results provide a more densely taxon-sampled thylamyine phylogeny than any previously available in the literature, and they raise interesting questions about morphological trait evolution in this still-poorly understood didelphid tribe.

MATERIALS AND METHODS

Source of "ancient" DNA

I was not allowed to remove integumental fragments from the holotype skin of *Chacodelphys formosa*, a specimen in the National Museum of Natural History (USNM 236330), but permission was given to place the holotype skull in distilled water for

several minutes and then to use jewelers' forceps to remove small amounts of rehydrated soft tissue adhering to cranial bones. Although the skull (figure 34) appeared to be completely clean, microscopic examination revealed loose periosteum (membranous connective tissue) covering many surfaces as well as small fragments of muscle in various places and relatively abundant alveolar epithelium surrounding the teeth. This material was carefully harvested, preserved in 95% ethanol, and subsequently stored at -20ºC prior to DNA extraction.

Figure 34. Dorsal and ventral views of the holotype skull of *Chacodelphys formosa* (USNM 236330) before tissue harvesting. The condylobasal length of this specimen is 20.6 mm.

Sources of other material

All other voucher specimens and associated tissues sampled for this study are preserved in the following collections: AMNH, American Museum of Natural History (New York); CBF, Colección Boliviana de Fauna (La Paz); CM, Carnegie Museum of Natural History (Pittsburg); CNP, Centro Nacional Patagónico (Puerto Madryn); CTUA, Colección Teriológica Universidad de Antioquia (Medellín); EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay); FMNH, Field Museum of Natural History (Chicago); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); MZUSP, Museu de Zoologia Universidade de São Paulo (São Paulo); OMNH, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, (Norman); ROM, Royal Ontario Museum (Toronto); UMMZ, University of Michigan, Museum of Zoology (Ann Arbor); UMSNH, Universidad Michoacana de San Nicolas de Hidalgo (Morelia); USNM, United States National Museum of Natural History (Washington); UWZ, University of Wisconsin Zoological Museum (Madison).

Taxon and gene sampling

The designated ingroup for my analyses included 57 representatives of the didelphid subfamily Didelphinae (table 17). Within Didelphinae my sampling for the tribes Didelphini, Marmosini, and Metachirini was the same as in Voss et al. (2004), but I followed subsequent taxonomic revisions in using *Monodelphis peruviana* for the

material that Voss et al. (2004) called *M. adusta* (see Solari, 2007), in using *M. scalops* for the species they called *M. theresa* (see Pavan et al., 2014), and in using *Marmosa* in binomial combinations with the epithets they referred to *Micoureus* (Voss and Jansa, 2009). My sampling for the tribe Thylamyini is the most complete yet achieved in any published phylogenetic analysis; notably, it includes nearly all of the currently recognized valid species of *Cryptonanus*, *Gracilinanus*, *Marmosops*, and *Thylamys*. However, samples of *Cryptonanus agricolai* were unavailable for this study, and I omitted *C. ignitus* and *Gracilianus dryas* because I was unable to resolve these nominal taxa as lineages distinct from *C. chacoensis* and *G. marica*, respectively, based on *Cytb* sequence data. My use of *Marmosops fuscatus* (for *M. cracens*), my use of *M. caucae* (for *M. neblina*), and my omission of *M.* "*impavidus*" follow the results obtained in chapter 1. I used two species of *Caluromys* (subfamily Caluromyinae) as outgroups.

I compiled a multi-locus matrix with sequence data from one mitochondrial gene (cytochrome-*b*, CYTB) and 5 nuclear markers: a fragment of exon 11 from the Breast Cancer type 1 susceptibility gene (BRCA1), exon 1 from the gene encoding the Interphotoreceptor Retinoid Binding Protein (IRBP), intron 14 of the X chromosome-linked O-linked N-acetylglucosamine transferase (OGT), intron 7 from the autosomal gene sodium-coupled neutral amino acid transporter 2 (SLC38), and an anonymous locus (Anon128, corresponding to a marker originally recovered for the genus *Thylamys*; Giarla et al., 2014). Some of these data (the unshaded cells in table 17) were downloaded from Genbank, where they had previously been archived following earlier studies (Jansa and Voss, 2000; Voss and Jansa, 2003, 2009; Voss et al., 2005, 2013, 2014; Giarla et al.,

2010, 2014; Gutiérrez et al., 2010; Giarla and Jansa, 2014), but I also generated many new sequences for this work (the shaded cells in table 17).

Table 17. List of taxa and loci included in the present analyses. Unshaded cells represent sequences obtained from Genbank (see text) and highlighted cells are new sequences obtained for this work.

Species	Voucher	*Cytb*	*BRCA1*	*IRBP*	*Anon128*	*OGT*	*SLC38*
Caluromys derbianus	USNM 578119	1140	948	1158	636	662	730
Caluromys lanatus	ROM 104570	1140	948	1158	636	666	730
Chacodelphys formosa	USNM 236330	237	376	—	—	—	—
Chironectes minimus	ROM 98855	1140	942	1158	638	591	620
Cryptonanus chacoensis	GD521 (to be catalogued at MNHNP)	1140	951	810	635	636	762
Cryptonanus guahybae	FQ23 (to be catalogued at FURB)	313	—	—	637	636	681
Cryptonanus unduaviensis	AMNH 260032	715	951	1158	637	632	530
Didelphis albiventris	UMMZ 134058	1140	942	1158	645	651	786
Didelphis marsupialis	chimera (see table S2)	1140	942	1158	646	651	540
Didelphis virginiana	ROM 96483	1140	942	1158	647	651	540
Gracilinanus aceramarcae	MUSM 13002	1133	951	1158	637	621	602
Gracilinanus agilis	MVZ 197439	1140	951	1158	557	625	745
Gracilinanus emiliae	MUSM 15292	1140	951	1158	636	626	356
Gracilinanus marica	EBRG 24864	1140	618	1158	533	626	628

Gracilinanus microtarsus	MVZ 182056	1140	951	1155	508	621	822
Gracilinanus peruanus	LHE1676a (to be catalogued at MNK)	692	909	547	635	626	750
Lestodelphys halli	chimera (appendix 7)	1140	353	1158	614	644	602
Lutreolina crassicaudata	UMMZ 134019	1140	942	1154	643	651	547
Marmosa demerarae	ROM 113431	1140	948	1158	637	645	—
Marmosa lepida	chimera (appendix 7)	1140	948	1158	637	645	639
Marmosa mexicana	chimera (appendix 7)	1140	881	1158	625	657	613
Marmosa murina	chimera (appendix 7)	1140	929	1158	617	644	642
Marmosa paraguayanus	MVZ 182065	1140	948	1158	637	645	632
Marmosa regina	MVZ 190332	1140	942	1158	594	637	709
Marmosa robinsoni	AMNH 276746	1132	884	1146	637	664	629
Marmosa rubra	chimera (appendix 7)	1140	948	1158	630	362	345
Marmosops bishopi	FMNH 203328	1140	880	1158	648	653	769
Marmosops caucae	MVZ 190272	1140	886	1158	600	667	521
Marmosops creightoni	CBF 7641	1140	886	1158	645	673	771
Marmosops fuscatus	AMNH 276509	1140	889	1149	582	657	782
Marmosops handleyi	CTUA 415	1140	883	1149	591	658	786
Marmosops incanus	chimera (appendix 7)	1140	883	1158	638	631	674
Marmosops invictus	USNM 337962	483	388	—	—	—	—
Marmosops juninensis	AMNH 230016	—	930	—	553	639	604
Marmosops noctivagus	MUSM 13292	1140	882	1158	527	670	—
Marmosops ocellatus	USNM 581979	1140	886	1158	554	669	745
Marmosops ojastii	USNM 371299	391	882	—	—	503	—
Marmosops pakaraimae	ROM 115841	645	886	1158	581	573	775

Marmosops parvidens	ROM 97938	645	945	1158	580	545	678
Marmosops paulensis	MVZ 183244	1140	886	1158	577	634	705
Marmosops pinheiroi	chimera (appendix 7)	1140	945	1158	641	574	763
Metachirus nudicaudatus	ROM 105345	1140	942	1158	641	523	759
Monodelphis brevicaudata	ROM 98909	1140	945	1158	637	650	876
Monodelphis emiliae	MUSM 13298	795	945	1158	634	650	865
Monodelphis peruviana	AMNH 272695	795	945	1158	636	649	854
Monodelphis scalops	MVZ 182776	1140	945	1158	626	644	875
Philander frenatus	MVZ 182067	1140	942	1158	538	641	783
Philander mcilhennyi	AMNH 272818	1140	942	1158	590	642	783
Philander opossum	CM 76743	1140	942	732	565	641	757
Thylamys elegans	MSB 87097	1140	951	1158	646	654	513
Thylamys karimii	MZUSP 32094	1140	954	548	581	653	470
Thylamys macrurus	MSB 70700	1140	951	1158	648	653	513
Thylamys pallidior	chimera (appendix 7)	1140	951	1134	643	645	513
Thylamys pusillus	MSB 67016	1140	951	1158	648	653	516
Thylamys sponsorius	FMNH 162505	1140	930	1158	648	653	756
Thylamys tatei	MVZ 135504	1140	—	—	—	—	—
Thylamys velutinus	OMNH 37216	1140	—	—	—	—	—
Thylamys venustus	AMNH 275428	1140	951	1102	648	653	513
Tlacuatzin canescens	UMSNH 2993	1140	948	1158	630	618	731

Laboratory methods and sequence alignment

I extracted DNA either from preserved tissue or from dried museum specimens following procedures explained in Voss and Jansa (2009) and Giarla et al. (2010), respectively. All the markers implemented in this study were amplified using PCR methods. To minimize the risk of contamination, ancient DNA extraction and corresponding PCR amplifications were carried out in a laboratory where mammalian DNA amplified from fresh tissue has never been present. Primers for the loci CYTB, BRCA1, IRBP, OGT, and SLC38 were described in Jansa and Voss (2009), Giarla et al. (2010), and Voss et al. (2014). The anonymous locus (Anon128) was obtained using primers modified from those in Giarla et al. (2014), and for thylamyine species I designed new primers for SLC38. Additionally, due to the highly degraded "ancient" DNA obtained from *Chacodelphys*, I obtained a small fragment each of CYTB and BRCA1 (in a single reaction for each gene) using internal primers. All the new primers designed for this study, including those used to amplify *Chacodelphys* sequences, can be found in appendix 2. Amplification protocols for CYTB, BRCA1, IRBP, OGT, and SLC38 closely resembled those described in Voss et al. (2014), and amplification protocols for Anon128 can be found in Giarla et al. (2014). The resulting PCR products were sequenced using amplification primers and dye-terminator chemistry on an ABI-3730xl automated sequencer. For the nuclear genes, heterozygous indels were detected and phased using the software Indelligent v.1.2 (Dmitriev and Rakitov 2008). Sequences were assembled using Sequencher ver. 4.8 (Gene Codes Inc.) and aligned using the default settings of MUSCLE (Edgar 2004) in Geneious Pro ver. 5.6.3 created by Biomatters (available from

http://www.geneious.com). The resulting alignments (of protein coding genes) were inspected with reference to translated amino acid sequences. All new sequences obtained for this study have been deposited in GenBank: Anon128 (KU171130–KU171171), BRCA1 (KU171172–KU171184), CYTB (KU171185–KU171199), IRBP (KU171200–KU171219), OGT (KU171220–KU171245), and SLC38 (KU171246–KU171275).

Table 18. Optimal partitioning schemes and substitution models for *Cytb*, *BRCA1*, *IRBP*, and two concatenated-gene datasets.

Name	Partition #	Characters	Model
CYTB	1	CYTB position 1	GTR+I+Γ
	2	CYTB position 2	HKY+I+Γ
	3	CYTB position 3	HKY+I+Γ
BRCA1	1	BRCA1 positions 1 and 2	HKY+Γ
	2	BRCA1 position 3	HKY+Γ
IRBP	1	IRBP position 1	HKY+I+Γ
	2	IRBP position 2	HKY+I
	3	IRBP position 3	K80+ Γ
CYTB+BRCA1	1	BRCA1 positions 1 and 2	HKY+Γ
	2	BRCA1 position3	HKY+Γ
	3	CYTB position 1	GTR+I+Γ
	4	CYTB position 2	HKY+I+Γ
	5	CYTB position 3	HKY+I+Γ
CYTB+nucDNA	1	BRCA1 positions 1 and 2	HKY+Γ
	2	BRCA1 position3	HKY+Γ
	3	CYTB position 1	GTR+I+Γ
	4	CYTB position 1, IRBP position 1	HKY+I+Γ
	5	CYTB position 3	GTR+I+Γ
	6	IRBP position 1	HKY+I
	7	IRBP position 3, OGT	K80+Γ
	8	Anon128	K80+Γ
	9	SLC38	SYM+Γ

Phylogenetic analyses

I generated gene trees from independent phylogenetic analyses of each of the six loci sampled for this study, and I also performed phylogenetic analyses on concatenated-gene datasets. For the latter analyses, I evaluated two different concatenations: one with just the two loci from which sequence data were obtained for *Chacodelphys* (CYTB +BRCA1) and a second including all of the mitochondrial and nuclear markers (CYTB +nucDNA). Unless noted otherwise, all phylogenetic analyses were implemented through the CIPRES Science Gateway (Miller et al., 2010). Each of the protein coding genes (CYTB, BRCA1, and IRBP) was partitioned by codon position, and the Bayesian Information Criterion (BIC) implemented in PartitionFinder (Lanfear et al., 2012) was used to determine the best partitioning scheme and substitution models (table 18). The nuclear introns and the anonymous locus were each analyzed as a single partition, and the best-fitting nucleotide substitution model was determined under the BIC in jModelTest 2 (Darriba et al., 2012). Gene trees were subsequently generated using Bayesian Inference (BI) and Maximum Likelihood (ML) searches. In all instances, Bayesian Inference was implemented in MrBayes v3.2 (Ronquist et al., 2012) by running two independent Markov Chain Monte Carlo (MCMC) analyses including one cold chain and three heated chains. For the non-coding genes the length of the chain was 2×10^6 generations, sampling every 200 generations, and implementing the optimal substitution model from jModelTest. Because initial runs for the protein coding genes did not converge after 2×10^6 generations, I increased the length of the chain to 4×10^6 generations, sampling every 400 generations, and implementing the optimal partitioning scheme and substitution

model from PartitionFinder. I evaluated convergence and appropriate burnin values by examining the results of the MCMC runs in Tracer v1.5 (Rambaut and Drummond, 2007). For each of the BI analyses all parameters were summarized in a maximum clade credibility tree with TreeAnnotator v1.7.2 (Drummond et al., 2012). Maximum-likelihood analyses for each locus were implemented in RAxML ver. 8.0 (Stamatakis, 2014). For the coding genes I implemented the optimal partition scheme from PartitionFinder and the GTRGAMMA as substitution model; each of the non-coding genes was analyzed as a single partition with the GTRGAMMA model. I implemented 20 independent searches from which I chose the topology with the best lnL score. Subsequently I evaluated nodal support by running 1000 bootstrap replicates using the GTRGAMMA model and the "thorough" optimization option. Bipartitions of the bootstrap searches were summarized on the best ML topology.

For the two concatenated-gene datasets, I determined the optimal partitioning scheme and substitution models using the *greedy* search algorithm and BIC implemented in PartitionFinder (Lanfear et al., 2012). For the two datasets I partitioned the protein coding genes by locus and by codon position, and used a single partition for each of the non-coding nuclear genes: 6 partitions were analyzed for the CYTB+BRCA1 dataset and 12 partitions for the CYTB+nucDNA dataset. Optimal partitioning schemes and substitution models can be found in table 18. Multilocus partitioned datasets were analyzed using Bayesian Inference (BI) and Maximum Likelihood (ML) searches implementing the best partition scheme from PartitionFinder and following the same strategies as described for the gene trees with a few exceptions. Bayesian analyses of the

CYTB+BRCA1 dataset were run for 2×10^7 generations, sampling every 2000 generations, whereas the length of the chain for the CYTB+nucDNA dataset was 4×10^7 generations, sampling every 4000 generations.

Hypotheses testing

Previous phylogenetic analyses have recovered *Chacodelphys* in two alternative positions within the subfamily Didelphinae: as the sister taxon of *Lestodelphys* + *Thylamys* in the tribe Thylamyini (Voss et al., 2004: figure. 3; Voss and Jansa, 2009: figure. 27) or as the sister taxon of *Monodelphis* in the tribe Marmosini (Voss et al., 2004: figure 4). To test these alternative hypotheses against my results, I used Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa, 1999) and the approximately unbiased (AU) test of Shimodaira (2002). Although both SH and AU tests are excellent in controlling for type-1 errors, the SH test is thought to be too conservative in some circumstances, and this bias is corrected for by the AU test (Shimodaira, 2002). I performed ML analyses in RAxML as described above for 4 different alignments (CYTB, BRCA1, Cytb+BRCA1, Cytb+nucDNA) with the only difference that I used topological constraints to infer the best tree that conformed to the alternative hypotheses (table 19). I implemented SH and AU tests in CONSEL v0.20 (Shimodaira and Hasegawa 2001); however, because CONSEL does not estimate the likelihoods for the topologies itself I first obtained the site-likelihoods of each alignment in TREE-PUZZLE 5.3 (Schmidt et al. 2002). Subsequently using CONSEL, the SH test was implemented

allowing 1000 resampling estimated log likelihoods (RELL) replicates, and for the AU test 10000 multiscale bootstraps were performed also using the RELL method.

Table 19. Shimodaira-Hasewaga (SH) and approximately unbiased (AU) topology tests for four different alignments. I tested the phylogenetic position of *Chacodelphys formosa* obtained in the present work (hypothesis 1) against two alternative hypotheses. Significance levels where hypothesis 2 or 3 are different from my results are denoted by asterisks: < 0.05 (*), < 0.01 (**), and < 0.001 (***).

Alternative hypotheses	CYTB		BRCA1		CYTB+BRCA1		CYTB+nucDNA	
	AU	SH	AU	SH	AU	SH	AU	SH
1. *Chacodelphys* + *Cryptonanus*	0.766	0.901	0.978	0.973	0.991	0.984	0.992	0.987
2. *Chacodelphys* + *Monodelphis*	0.044*	0.171	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
3. *Chacodelphys* + (*Lestodelphys*+*Thylamys*)	0.328	0.408	0.022*	0.235	0.010**	0.202	0.008**	0.149

RESULTS

Taxon/gene coverage and sequence description

My multi-locus dataset contains 179 newly generated sequences, 175 sequences downloaded from Genbank, and 26 missing sequences for a total of 92.7% sequence coverage (table 17). I obtained CYTB sequences for all taxa except *Marmosops juninensis*, a species for which I consistently co-amplified a nuclear pseudogene from my only available sample (a scrap of dried skin). Only two species (*Thylamys tatei* and *T. velutinus*) completely lack nuclear sequence data (because the DNA I obtained from dried skins of these taxa was highly degraded). Although I tested several combinations of primers for *Chacodelphys formosa* to amplify as much sequence as possible from as many loci as possible, I could only successfully amplify and sequence short fragments of

CYTB and BRCA1 from this taxon. Finally, for nine species (identified as chimeras in column 2 of table 17) it was necessary to combine sequences from different voucher specimens to maximize gene coverage (appendix 7).

My concatenated-gene alignments contained 2097 base pairs (bp) for CYTB+BRCA1, and 5893 bp for CYTB+nucDNA (CYTB: 1140 bp; BRCA1: 957 bp; IRBP: 1158 bp; OGT: 840 bp; SLC38: 1124 bp; Anon128: 674 bp). Base-compositional heterogeneity tests were not significant for the individual gene alignments BRCA1, IRBP, OGT, SLC38, and Anon128, but significant heterogeneity was found for CYTB and for my two concatenated datasets (table 20). However, critical values of the "g1" skewness test statistic (Hillis and Huelsenbeck 1992) suggest that the observed base frequencies are nonrandom and that there is significant ($p < 0.01$) phylogenetic signal in all of the single-gene and concatenated alignments.

Table 20. Chi-square tests for base-compositional stationarity and g_1 skewness test statistic (Hillis and Huelsenbeck, 1992).

Alignment	Chi-square test			Skewness test g_1 ($p < 0.01$)		
	X^2	*d.f.*	*p*-value	N variable characters	N taxa	g_1
CYTB	230.157	171	0.002	557	58	-0.491
BRCA1	14.369	165	1	338	56	-0.526
IRBP	21.656	153	1	218	52	-0.599
OGT	52.726	162	1	406	55	-0.593
SLC38	170.963	153	0.152	540	53	-0.473
Anon128	17.216	159	1	211	54	-0.891
CYTB+BRCA1	314.163	174	0	895	59	-0.51
CYTB+nucDNA	350.095	174	0	2333	59	-0.573

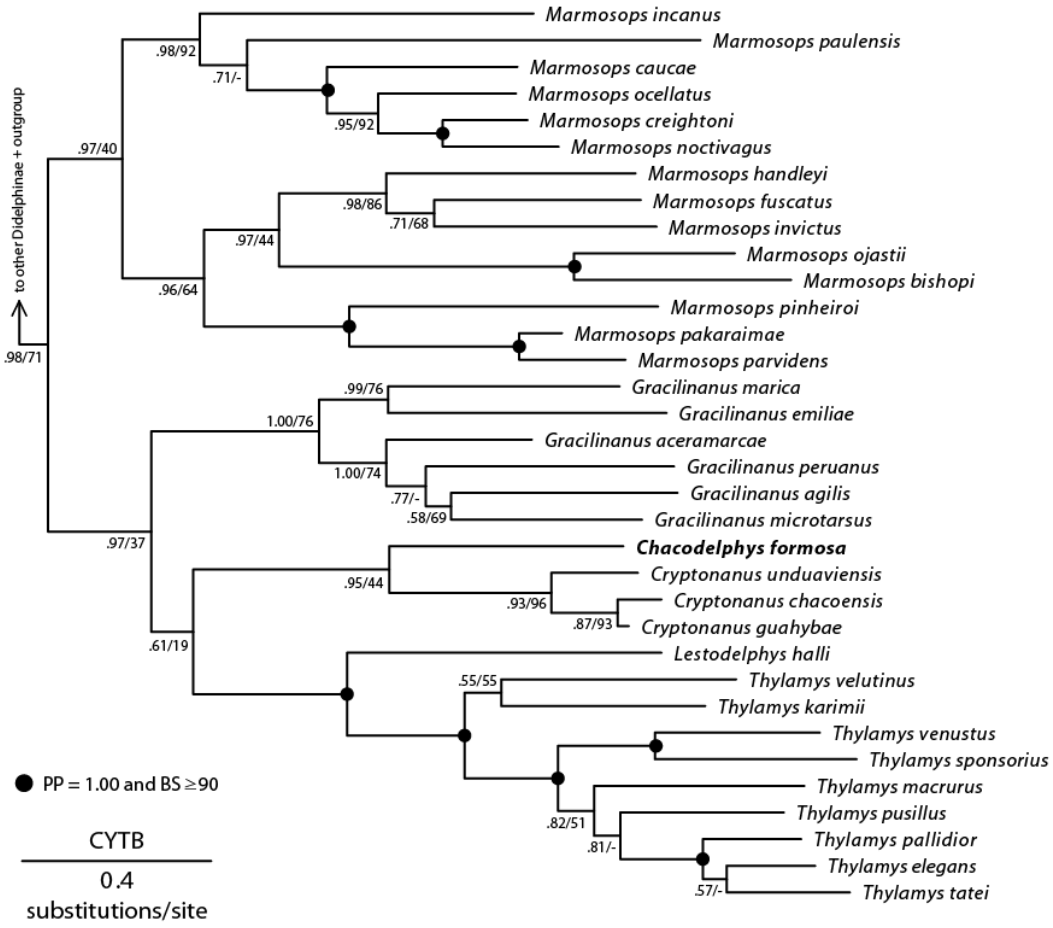

Figure 35. Bayesian Inference topology detailing the phylogenetic relationships of *Chacodelphys formosa* within the Thylamyini using CYTB sequences. Posterior Probabilities below 1.00 and bootstrap values below 90% are shown along branches (PP/BS), whereas PP of 1.00 and BS ≥ 90% are indicated with filled circles at relevant nodes. Outgroup and other non-thylamyine didelphines are not shown.

Phylogenetic results

Gene trees that were obtained from phylogenetic analyses of CYTB (figure 35) and BRCA1 (figure 36) both recovered *Chacodelphys* as a member of the tribe Thylamyini, to which I restrict my attention hereafter. Within Thylamyini, *Chacodelphys*

was consistently recovered in a clade that also included *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, and *Thylamys*. Within the latter group, both genes also recovered *Chacodelphys* as the sister taxon of *Cryptonanus*, a previously unsuspected relationship that is strongly supported by BRCA1 and less so by CYTB. This new clade (*Chacodelphys*+*Cryptonanus*) was recovered as the sister taxon of *Lestodelphys*+*Thylamys* in the analyses of CYTB sequences, whereas analyses of BRCA1 recovered *Chacodelphys*+*Cryptonanus* as the sister taxon of a group that also included *Gracilinanus.* Although the two gene trees differ in this and other respects, it is noteworthy that no strongly supported node in one topology is incompatible with any strongly supported node in the other, so it seems reasonable to analyze the concatenated sequences obtained from these largely congruent loci. Analyses of this two-gene dataset (figure 37) resulted in strong support for many thylamyine nodes that were only weakly supported in the individual gene trees, and they recovered *Chacodelphys*+*Cryptonanus* as the sister taxon of *Lestodelphys*+*Thylamys* (as in the CYTB tree), but without strong support.

Despite the fact that I was unable to amplify and sequence *Chacodelphys* for the other four loci I sampled (IRBP, OGT, SLC38, Anon128), it seemed plausible that those genes might help resolve its relationships by constraining the position of *Cryptonanus* (for which I have much more extensive sequence data). Inspection of individual gene trees for those loci (appendix 8) revealed no strong incongruence among them, nor is there any strong incongruence between this set of trees and the results I obtained from separate and concatenated analyses of CYTB and BRCA1. The results of analyzing a

matrix of concatenated sequence data from all six loci (CYTB+nucDNA; figure 38) are not essentially different from those obtained from the concatenated two-gene analyses insofar as the relationships of *Chacodelphys* are concerned, but several thylamyine nodes that were only weakly supported by CYTB+BRCA1 are strongly supported by this much larger dataset. Unfortunately, the sister-group relationship between *Chacodelphys*+*Cryptonanus* and *Lestodelphys*+*Thylamys* remains present but weakly supported.

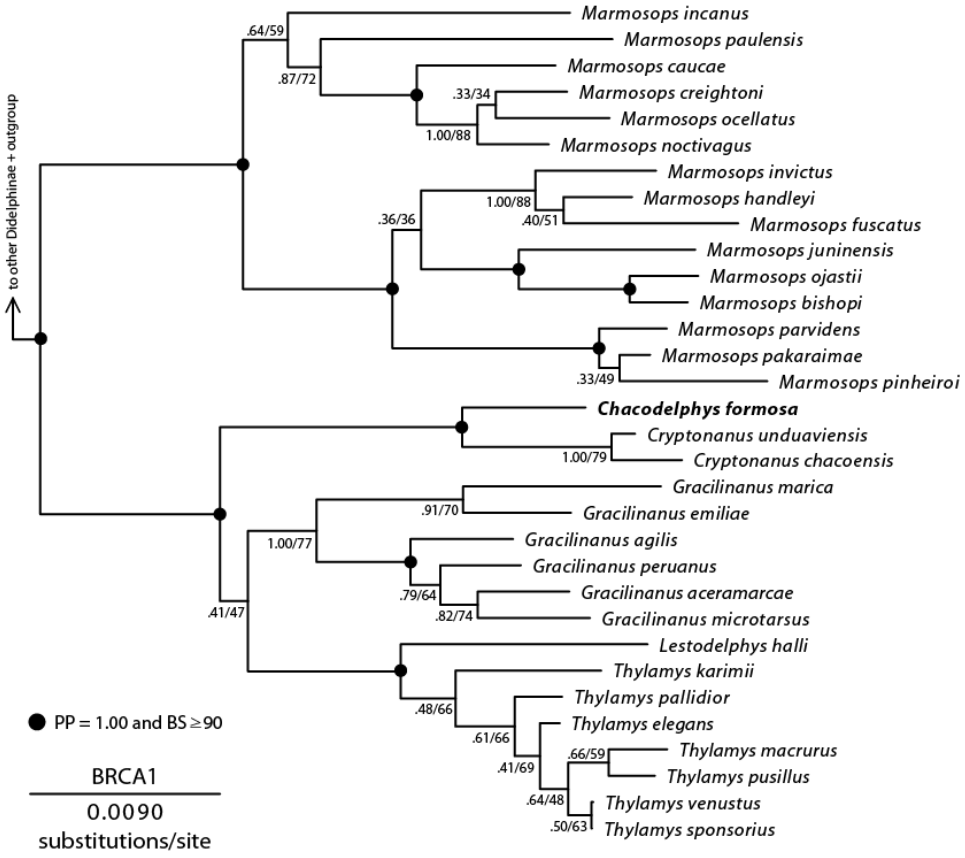

Figure 36. Bayesian Inference topology detailing the phylogenetic relationships of *Chacodelphys formosa* within the Thylamyini using BRCA1 sequences. Posterior Probabilities below 1.00 and bootstrap values below 90% are shown along branches (PP/BS), whereas PP of 1.00 and BS ≥ 90% are indicated with filled circles at relevant nodes. Outgroup and other non-thylamyine didelphines are not shown.

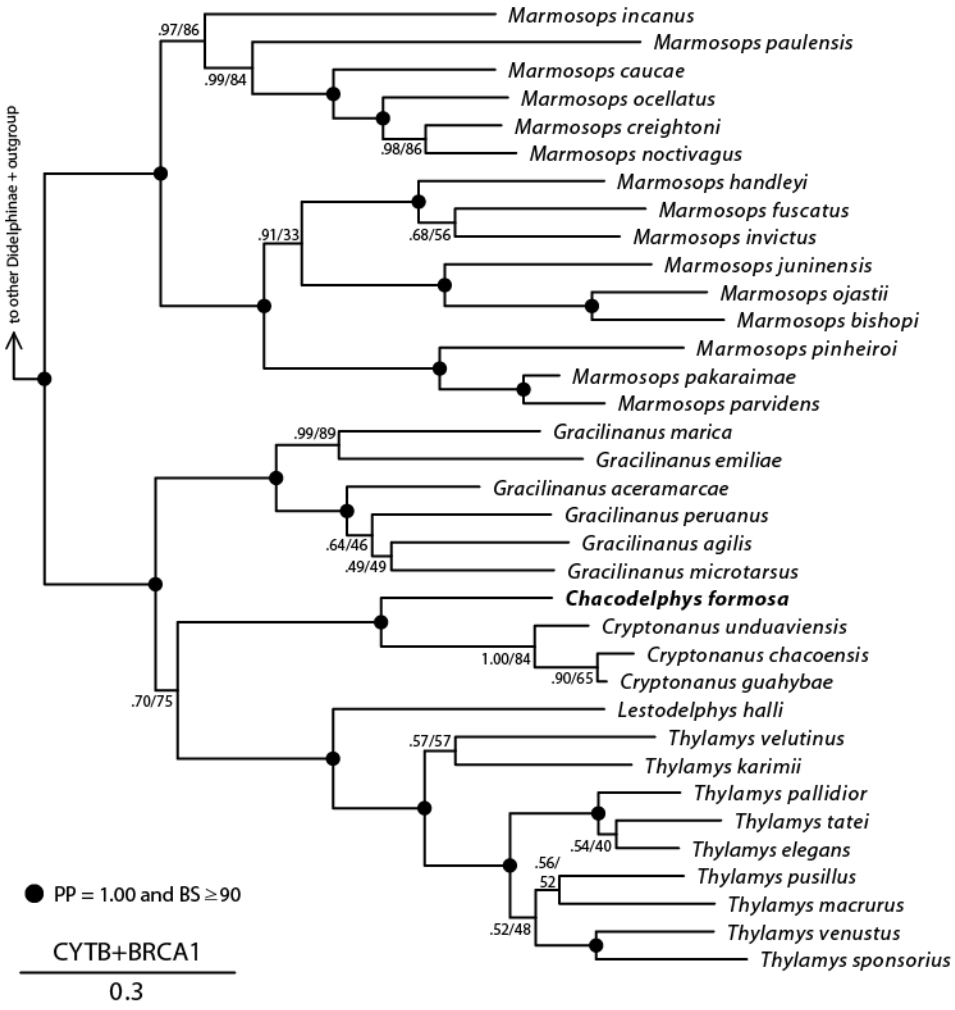

Figure 37. Bayesian Inference analysis of the concatenated dataset CYTB+BRCA1 detailing the phylogenetic relationships of *Chacodelphys formosa* within the Thylamyini. Posterior Probabilities below 1.00 and bootstrap values below 90% are shown along branches (PP/BS), whereas PP of 1.00 and BS ≥ 90% are indicated with filled circles at relevant nodes. Outgroup and other non-thylamyine didelphines are not shown.

The topology tests that I performed (table 19) almost uniformly reject the hypothesis that *Chacodelphys* is the sister taxon of *Monodelphis* (the unique exception is the SH test for CYTB). The hypothesis that *Chacodelphys* is the sister taxon of

Lestodelphys+Thylamys is rejected for most datasets by the AU test (the unique exception, again, is CYTB), but not by the more conservative SH test.

Although the focus of this report concerns *Chacodelphys*, my results include several other noteworthy contributions to didelphid phylogenetics including (1) strong support for most polytypic thylamyine genera, several of which are here represented by more species than in earlier studies; (2) strong support for a basal dichotomy in *Marmosops*; (3) strong support for numerous relationships among previously unsequenced species of *Marmosops*; (4) strong support for a sister-group relationship between *Gracilinanus marica* (previously unsequenced) and *G. emiliae*; and (5) strong support for the monophyly of the nominotypical subgenus of *Thylamys*.

DISCUSSION

Although sparse, the sequence data obtained from *Chacodelphys* (613 bp from two loci) seem sufficient to confidently reject at least two previously published hypotheses. In particular, the suggestion that *Chacodelphys* might be a marmosine closely related to *Monodelphis* (Voss et al., 2004) now seems highly improbable based on nodal statistics computed from my concatenated six-gene dataset (figure 38) and from the results of topology tests (table 19). Because CYTB sequences are saturated (and therefore phylogenetically uninformative) at deeper levels of didelphid phylogeny (Jansa and Voss, 2000: figure 12), the non-significant SH test result and the only marginally significant AU test result from this locus by comparison with those obtained from the more slowly

evolving nuclear loci are not surprising. In effect, it now seems reasonably certain that *Chacodelphys* belongs in the tribe Thylamyini.

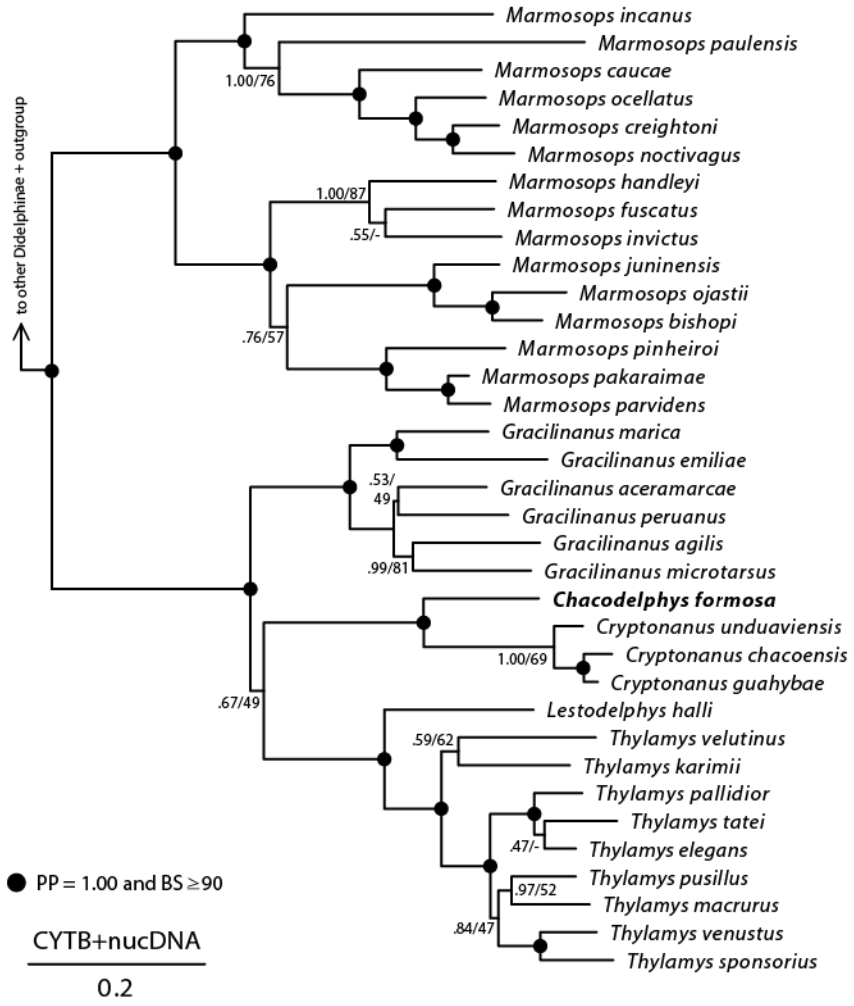

Figure 38. Bayesian Inference analysis of the concatenated dataset CYTB+nucDNA detailing the phylogenetic relationships of *Chacodelphys formosa* within the Thylamyini. Posterior Probabilities below 1.00 and bootstrap values below 90% are shown along branches (PP/BS), whereas PP of 1.00 and BS ≥ 90% are indicated with filled circles at relevant nodes. Outgroup and other non-thylamyine didelphines are not shown.

Within the tribe Thylamyini, nodal statistics (Bayesian posterior probabilities and likelihood bootstrap values) strongly constrain the plausible relationships of

Chacodelphys to a rather small set of alternatives hypotheses. That *Chacodelphys* appears to be the sister taxon of *Cryptonanus*, although unexpected, is not hard to reconcile with the results of earlier analyses. *Cryptonanus* was not included in the morphology-based phylogenetic study that previously associated *Chacodelphys* with *Lestodelphys+Thylamys* or with *Monodelphis* (Voss et al., 2004) because *Cryptonanus* had yet to be recognized as generically distinct from *Gracilinanus* (which was represented in those analyses only by *G. microtarsus*). In subsequent analyses that included *Cryptonanus*, none of the nodes that separated that genus from *Chacodelphys* were strongly supported (Voss and Jansa, 2009: figures 27, 36). Therefore, the sister-group relationship reported here is not strongly contradicted by those results.

Nodal statistics likewise exclude *Marmosops* from any close relationship with *Chacodelphys+Cryptonanus*, which, instead, belongs to a strongly supported clade with the other three thylamyine genera. Thus, what remains for future research to resolve is whether *Chacodelphys+Cryptonanus* is more closely related to *Gracilinanus* (the genus that previously included species that are now placed in *Chacodelphys* and *Cryptonanus*; Voss et al. 2004, 2005) or with *Lestodelphys+Thylamys*, another well-supported generic pairing. Extensive missing sequence data from *Chacodelphys* might be part of the reason why these relationships are still in question, but I note that the relationships of *Cryptonanus* with respect to *Gracilinanus* and *Lestodelphys+Thylamys* are not convincingly resolved by nuclear-sequence datasets that exclude *Chacodelphys* (e.g., in Voss and Jansa, 2009), so it is possible that the essential problem is short evolutionary intervals between successive speciation events rather than missing data.

Tabla 21. Qualitative morphological differences between *Chacodelphys* and *Cryptonanus*. (See Voss and Jansa [2009] for explanations of character-state descriptors.)

Character	*Chacodelphys*	*Cryptonanus*
Relative tail length:[a]	81%	117–136%
Manus:	mesaxonic[b]	paraxonic[c]
Central palmar surface of manus:	densely tubercular	sparsely tubercular
Caudal prehensile surface:	absent	present
Nasal bones:	uniformly narrow	widened posteriorly
Maxillary fenestrae:	present	absent
C1:	w/o accessory cusps	usually w/accessory cusp(s)
P2, P3 heights:	P2 = P3	P2 < P3
Hypoconid on m3:	lingual to protoconid	labially salient
Entoconid, hypoconulid heights:	entoconid ≈ hypoconulid	entoconid >> hypoconulid

[a] Length of tail divided by length of head-and-body, expressed as a percentage (based on measurement data in Voss et al. 2004, 2005).

[b] Digit III longest.

[c] Digit III = digit IV.

Because *Chacodelphys* and *Cryptonanus* have not previously been recognized as sister taxa, it seems useful to list the phenotypic differences that support their recognition as distinct genera and which suggest that each is adapted to a different ecological niche (table 21). Judging from its short tail, lack of a caudal prehensile surface, and mesaxonic forefeet, for example, I expect that *Chacodelphys* is almost exclusively terrestrial, whereas a contrasting set of traits (longer tail, caudal prehensile surface present, paraxonic forefeet) lead me to expect that *Cryptonanus* is scansorial. Testing for such behavioral differences, which might be correlated with habitat occupancy at localities where these taxa are sympatric (e.g., those mapped by Teta et al., 2006), should be a priority for future field research.

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APPENDICES

Appendix 1. Gazetteer including all localities from which I analyzed sequences of *Marmosops* for this study.

This gazetteer includes all localities from which I analyzed sequences of *Marmosops* for this study. Italicized place names are those of the largest administrative units (states, departments, etc.) within each country (but note that "French Guiana" is an overseas department of France). Geographic coordinates (decimal degrees) and elevation (meters above sea level, m) are provided in parentheses with a cited source for these data. Bolded elevations were extracted from Google Earth at the referenced coordinates. Collection localities are mapped in figures 1–3.

BOLIVIA

1. *Chuquisaca*, Río Limón (-19.5500, -64.1333, 1300 m; Voss *et al.*, 2004).
2. *Cochabamba*, Cordillera de Mosetenes (-16.2333, -66.4167, 1300–1600 m; Voss *et al.*, 2004).
3. *Cochabamba*, Tablas Monte, 4.4 km by road N (-17.0667, -66.0167, 1833–2100 m; Voss *et al.*, 2004).
4. *Cochabamba*, Tablas Monte, 9.5 km by road NE (-17.0333, -65.9833, 1500 m; Voss *et al.*, 2004)
5. *La Paz*, Chijchijpa, 20 km by road from Coroico (-16.1500, -67.7500, 1114–1400 m; Voss *et al.*, 2004).
6. *La Paz*, La Reserva (-15.7167, -67.5167, 940 m; Voss *et al.*, 2004).
7. *La Paz*, Provincia Sud Yungas, Parque Nacional Cotapata, Mina Sueño (-16.1942, -67.8937, 2610 m; Teresa Tarifa, personal commun.).
8. *La Paz*, Río Unduavi, Pitiguaya, La Florida (ca. -16.3500, -67.7833, 1785 m; Anderson, 1997).
9. *La Paz*, Saynani hydroelectric plant, on southeast side of the Zongo Valley (-16.1167, -68.0833, 2500 m; Voss *et al.*, 2004).
10. *Pando*, Palmira (-11.7000, -67.9333, 170 m; Voss *et al.*, 2004).
11. *Pando*, Santa Rosa (-12.2167, -68.4000, 180 m; Voss *et al.*, 2004).
12. *Santa Cruz*, 15 km S Santa Cruz (-17.8833, -63.1167, 400 m; Voss *et al.*, 2004).
13. *Santa Cruz*, 6 km by road W Ascención (-15.7167, -63.1500, 240 m; Voss *et al.*, 2004).
14. *Santa Cruz*, El Refugio, Parque Nacional Noel Kempff Mercado (-14.7667, -61.0333, ca. 200 m; Voss *et al.*, 2004).
15. *Santa Cruz*, Hacienda El Pelicano, 3 km N Zanja Honda (-18.2667, -63.1833, 500 m; Voss *et al.*, 2004)
16. *Santa Cruz*, Lago Caimán, Parque Nacional Noel Kempff Mercado (-13.5967, -60.9147, ca. 200 m; Killeen & Schulenberg, 1998).
17. *Santa Cruz*, Río Ariruma, 7 km by road SE Ariruma (-18.3333, -64.2167, 1750 m; Voss *et al.*, 2004).

18. *Santa Cruz*, San Rafael de Amboró (-17.6000, -63.6000, 400 m; Voss *et al.*, 2004).

BRAZIL

19. *Acre*, Igarapé Porongaba, right bank Rio Juruá (-8.6667, -72.7833, **ca. 250 m**; Patton *et al.*, 2000).
20. *Amazonas*, Barro Vermelho, left bank Rio Juruá (-6.4667, -68.7667, **ca. 117 m**; Patton *et al.*, 2000).
21. *Amazonas*, Igarapé Nova Empresa, left bank Rio Juruá (-6.8000, -70.7333, **ca. 150 m**; Patton *et al.*, 2000).
22. *Amazonas*, Ilhazinha, left bank Rio Juruá on Igarapé Arabidi, afluent of Paraná Breu (-3.2833, -66.2333, **ca. 76 m**; Patton *et al.*, 2000).
23. *Amazonas*, Lago Vai-Quem-Quer, right bank Rio Juruá (-3.3167, -66.0167, **ca. 55 m**; Patton *et al.*, 2000).
24. *Amazonas*, Penedo, right bank Rio Juruá (-6.8333, -70.7500, **ca. 150 m**; Patton *et al.*, 2000).
25. *Amazonas*, Seringal Condor, left bank Rio Juruá (-6.7500, -70.8500, **ca. 190 m**; Patton *et al.*, 2000).
26. *Bahia*, Fazenda Santa Rita, 8 km E Andarai (-12.8017, -41.2614, 399 m; MVZ database, accessed April 2013).
27. *Espírito Santo*, Forest fragments of Aracruz Cellulose Company, Santa Cruz, Municipio de Aracruz (-19.7833, -40.1167, 50 m; Mustrangi & Patton, 1997).
28. *Espírito Santo*, Reserva Biológica de Duas Bocas, Alto Alegre, Cariacica (-20.2800, -40.5200, 550 m; (Agrizzi *et al.*, 2012).
29. *Espírito Santo*, Reserva Florestal da Companhia Vale do Rio Doce, 30 km by road N of Linhares (-19.5000, -40.0000, 50 m; Mustrangi & Patton, 1997).
30. *Espírito Santo*, Estaçao Biológica de Santa Lucia, Santa Teresa (-19.9600, -40.5400, 650 m; Agrizzi *et al.*, 2012).
31. *Mato Grosso*, Aripuanã (-9.1700, -54.7000, **ca. 660 m**; USNM database, accessed April 2013).
32. *Minas Gerais*, Minas Gerais, Estaçao Biológica de Caratinga, 890 ha, in the Fazenda Montes Claros, 54 km E Caratinga (-19.8333, -41.8333, 400-700 m; Mustrangi & Patton, 1997).
33. *Minas Gerais*, Fervedouro, Fazenda Neblina (-20.7100, -42.4800, 1300 m; Mustrangi & Patton, 1997).
34. *Minas Gerais*, Itamonte (-22.2931, -44.8861, **ca. 1160 m**; Edson Fiedler de Abreu Júnior, personal commun.).
35. *Minas Gerais*, Itanhandu (-22.3833, -44.8500, 1400 m; Mustrangi & Patton, 1997).
36. *Minas Gerais*, Santa Barbara, Parque do Caraça (-20.0800, -43.5000, 1300 m; Agrizzi *et al.*, 2012)
37. *Minas Gerais*, Estaçao de Pesquisas de Peti (CEMIG), São Gonçalo do Rio Abaixo (-19.8992, -43.3686, 630–806 m; Paglia *et al.*, 2005).
38. *Minas Gerais*, Estação Ecológica de Acauã, 17 km N of Turmalina (-17.1300, -42.7600, 800 m; Agrizzi *et al.*, 2012).

39. *Pará*, 52 km SSW Altamira, east bank Rio Xingu (-3.6500, -52.3667, **ca. 130 m**; USNM database, accessed April 2013).
40. *Pará*, Belém (-1.4500, -48.4833, **ca. 77 m**; Paynter Jr & Traylor Jr, 1991).
41. *Pará*, Itaituba, Transamazonica Hwy., Itaituba-Jacareacanga, km. 212 (-5.6700, -56.7500, **ca. 160 m**; USNM database, accessed April 2013).
42. *Rio de Janeiro*, Private lands of Cia. Mineradoras Brasileiras Reunidas, Ibicui, Municipio de Mangaratiba (-22.9500, -44.0333, 50 m; Mustrangi & Patton, 1997).
43. *Rio de Janeiro*, Sitio São José da Serra, 9.2 km N and 6 km E by road Bonsucesso, Serra de Paquequé, Municipio de Sumidouro (-22.2000, -42.7333, 1000 m; Mustrangi & Patton, 1997).
44. *São Paulo*, Estaçao Ecológica de Bananal, Bananal (-22.8056, -44.3639, 1200 m; Edson Fiedler de Abreu Júnior, personal commun.).
45. *São Paulo*, Base do Carmo, Fazenda Intervales, Município de Capão Bonito, Serra de Paranapiacaba (-24.3333, -48.4167, 100–900 m; Mustrangi & Patton, 1997).
46. *São Paulo*, Caucaia do Alto, Município de Cotia (-23.7600, -47.0000, 1000 m; coordinates from Costa et al., 2007; altitude from Mustrangi & Patton, 1997).
47. *São Paulo*, Fazenda da Toca, Ilha de São Sebastião (-23.8167, -45.3500, 150 m; MVZ database, accessed April 2013).
48. *São Paulo*, Pilar do Sul (-23.8097, -47.6983, **ca. 714 m**; Google Earth).
49. *São Paulo*, Estação Biológica de Boracéia, Museu Zoologia da USP, Municipio de Salesópolis (-23.6500, -45.9000, 850 m; Mustrangi & Patton, 1997).

COLOMBIA

50. *Amazonas*, Leticia, Vereda Peña Roja (-0.6883, -72.1333, 300 m; Díaz-N, 2012).
51. *Antioquia*, Gómez Plata, Vegas de La Clara (6.5895, -75.1970, 1100 m; Camilo A. Calderón, personal commun.).
52. *Antioquia*, Urabá, Villa Arteaga (7.3333, -76.4333, 130 m; Anderson, 1999).
53. *Antioquia*, Urrao, Santa Barbara (6.4167, -76.2500, 2800 m; FMNH database, accessed April 2013).
54. *Antioquia*, Valdivia, 9km S (7.0944, -75.4604, 1400 m; Díaz-N *et al.*, 2011).
55. *Antioquia*, Yarumal, Corregimiento El Cedro, Vereda Corcovado, Finca El Bosque, Bosque San Andres (7.0727, -75.4213, 1676 m; Díaz-N *et al.*, 2011).
56. *Antioquia*, Yarumal, Vereda El Rosario, Alto de Ventanas, Finca Villa Nueva (7.0836, -75.4448, 1950 m; Díaz-N *et al.*, 2011).
57. *Boyacá*, Muzo (5.5000, -74.1667, 1300 m; Gardner, 2008).
58. *Caldas*, Manizalez, Las Palomas, Viveros (4.0830, -75.4178, 2500 m; specimen label).
59. *Caldas*, Samaná, Río Hondo (5.7000, -75.0167, 1200 m; Anderson, 1999).
60. *Caldas,* Norcasia, Vereda Montebello, entre las fincas el Horizonte y la Albania, Quebrada La Albania (5.5801, -74.9296, 817 m; specimen label).
61. *Caldas,* Norcasia, Vereda San Roque, Reserva Natural Río Manso (5.6690, -74.7882, 200 m; specimen label).
62. *Caquetá*, Río Caquetá, La Tagua, Tres Troncos (0.1333, -74.6833, 150 m; Díaz-N, 2012).

63. *Cesar*, Sierra Negra, Villanueva, Valledupar (10.6000, -72.9167, 1500 m; Anderson, 1999).
64. *Huila*, Acevedo, San Adolfo (1.8167, -75.8667, 1400 m; Paynter Jr, 1997).
65. *Huila*, Pitalito (1.8500, -76.0333, 1250 m; Gardner, 2008).
66. *Huila*, San Agustín, Río Magdalena (1.8508, -76.3440, 2300 m; FMNH database, accessed April 2013).
67. *Meta*, Villavicencio (4.1667, -73.5167, 500 m; Bugher *et al.*, 1940).
68. *Santander,* Puerto Parra, Vereda India Baja, Corregimiento Campo Capote (6.6682, -73.8901, **ca. 104 m**; Instituto Geográfico Agustín Codazzi, 2015).
69. *Santander*, Encino, Vereda Rionegro, Reserva Biológica Cachalú, Bosque de Roble cerca de Torre (6.1138, -73.1360, 1940 m; specimen label).

ECUADOR

70. *Cotopaxi*, Otonga (-0.4167, -79.0033, 2080 m; specimen label)
71. *El Oro*, Portovelo (-3.7167, -79.6500, 610 m; Paynter Jr, 1993).
72. *Loja*, Celica (-4.1167, -79.9833, 2103 m; Paynter Jr, 1993).
73. *Morona-Santiago*, Agua Rica (-3.0093, -78.5030, 2050–2300 m; specimen label).
74. *Morona-Santiago*, Rosario (-2.9094, -78.3995, **ca. 1000 m**; specimen label).
75. *Orellana*, Parque Nacional Yasuní, Onkone Gare, 38 km S Pompeya Sur (-0.6500, -76.4500, **ca. 255 m**; Gardner, 2008).
76. *Pastaza*, Tiguino, 130 km S Coca (-1.1167, -76.9500, 300 m; Gardner, 2008)
77. *Pastaza*, 5 km E Puyo, Safari Hosteria Park (-1.4426, -77.9955, 964 m; Haynie *et al.*, 2006).
78. Zamora-Chinchipe, 4 km E Sabanilla (-4.0167, -78.9500, 1585 m; Gardner, 2008).

FRENCH GUIANA

79. Les Nouragues (4.0833, -52.6667, 210 m; Voss & Emmons, 1996).
80. Paracou, near Sinnamary (5.2833, -52.9167, ca. 45 m; Simmons & Voss, 1998).
81. Saint-Eugène (4.8500, -53.0667, **ca. 100 m**; Cosson *et al.*, 1999).

GUYANA

82. *Cuyuni-Mazaruni,* Mount Roraima, "Second Camp" (5.2833, -60.7500, 800 m; Voss *et al.*, 2013).
83. *Potaro-Siparuni,* Iwokrama Forest, Turtle Mountain, 10 km NW Kurupukari (4.7333, -58.7167, 50 m; Voss *et al.*, 2013).
84. *Potaro-Siparuni,* Iwokrama Forest, Kabukalli Landing (4.2833, -58.5167, **ca. 100 m**; Voss *et al.*, 2013).
85. *Potaro-Siparuni,* Mount Ayanganna, First Plateau Camp (5.3333, -59.4500, 1100 m; (Lim *et al.*, 2010).
86. *Potaro-Siparuni,* Mount Wokomung, First Plateau Camp (5.1167, -59.8167, 1130 m; Voss *et al.*, 2013).
87. *Upper Takutu-Upper Essequibo*, Karanambo (3.7500, -59.3000, 100 m; Mustrangi & Patton, 1997).

PANAMÁ

88. *Darién*, Cerro Pirré (7.8500, -77.7333, 1570 m; Fairchild & Handley Jr, 1966).
89. *Darién*, Cerro Tacarcuna (8.1667, -77.3000, 1470 m; Anderson, 1999).

PERÚ

90. *Amazonas*, Cordillera del Condor (-3.8850, -78.4328, 1738 m; based on flanking localities from Schulenberg & Awbrey, 1997).
91. *Cajamarca*, Tabaconas, 4 km W El Chaupe (-5.2053, -79.0606, **ca. 1700 m**; Rengifo, Pacheco, & Salas, 2011).
92. *Cajamarca*, Cutervo, San Andrés de Cutervo (-6.2355, -78.7189, 2135 m; specimen label).
93. *Cajamarca*, San Ignacio, Tabaconas, C. la Viuda (-5.2844, -79.3217, 1897 m; specimen label).
94. *Cajamarca*, Santa Cruz, Catache, 3.81 km NE Monteseco (-6.5593, -79.0017, ca.1800 m; specimen label).
95. *Cajamarca*, Tabaconas, Piedra Cueva in Cerro Coyona, Tabaconas-Namballe National Sanctuary (-5.2798, -79.2740, 2587 m; specimen label).
96. *Cuzco*, 2km NE Amaybamba (-13.0503, -72.4407, 2000 m; MVZ database, accessed April 2013).
97. *Cuzco*, 72km NE (by road) Paucartambo, km 152 (-13.0667, -71.5333, 1400–1550 m; Patterson, Stotz, & Solari, 2006).
98. *Cuzco*, Amaybamba, 3 km E Amaybamba (-13.0631, -72.4260, 2200 m; Mustrangi & Patton, 1997).
99. *Cuzco*, La Convención Province, Tangoshiari (-11.7667, -73.3258, ca. 500 m; Emmons, Luna, & Romo, 2001).
100. *Cuzco*, La Convención Province, Tangoshiari 2 km SW (-11.7797, -73.3408, ca. 1000 m; Emmons *et al.*, 2001).
101. *Cuzco*, Paucartambo, Suecia, km 138.5 Carretera Shintuy (-13.1005, -71.5675, 1920 m; Patterson *et al.*, 2006).
102. *Junín*, 22 mi E Tarma (-11.4167, -75.7000, 2316 m; Stephens & Traylor Jr, 1983).
103. *Loreto*, 21 km S Iquitos, Otorongo Army Base (-3.9500, -73.3667, 110–180 m; Hice, 2003).
104. *Loreto*, 25 km S Iquitos, Estación Biológica Allpahuayo (-3.9667, -73.4167, 110–180 m; Hice, 2003).
105. *Loreto*, Quebrada Oran, ~5 km N Río Amazonas, 85 km NE Iquitos (-3.1422, -72.7211, 110 m; Burney & Brumfield, 2009).
106. *Loreto*, Río Gálvez, Nuevo San Juan (-5.2500, -73.1667, 150 m; Voss & Fleck, 2011).
107. *Loreto*, San Jacinto (-2.3124, -75.8628, 175 m; Duellman & Mendelson III, 1995).
108. *Loreto*, Teniente López (-2.5579, -76.1167, 175 m; KU database, accessed April 2013).
109. *Madre de Dios*, Reserva Cuzco Amazónico (-12.5500, -69.0500, 200 m; Voss & Emmons, 1996).

110. *Madre de Dios,* Manu, Quebrada Aguas Calientes, left bank, Río Alto Madre de Dios, 2.75 km E Shintuya (-12.6683, -71.2690, 450 m; Patterson *et al.*, 2006).
111. *Pasco*, Oxapampa, San Pablo (-10.4500, -74.8667, ca. 275; Stephens & Traylor, 1983).
112. *Piura*, Huancabamba, Canchaqua (-5.4000, -79.6000, 1198 m; Stephens & Traylor, 1983).
113. *San Martín*, Bella Vista, Alto Biabo, Parque Nacional Cordillera Azul (-7.7467, -76.3750, 1395 m; Lucia Luna, personal commun.).
114. *San Martín*, Bella Vista, Alto Biabo, Parque Nacional Cordillera Azul "Shushupe" (-7.7474, -76.3591, 930 m; Lucia Luna, personal commun.).
115. *San Martín*, Moyobamba, Tingana (-5.9107, -77.1120, 815 m; Paúl M. Velazco, personal commun.).
116. *San Martín*, Rioja, Pardo Miguel, Naranjos, Caserio El Diamante (-5.7534, -77.5261, 1078 m; Paúl M. Velazco, personal commun.).
117. *Ucayali*, Alto Ucayali, Lagarto (-10.5972, -73.8778, **ca. 222 m**; Wiley, 2010).

SURINAM
118. *Brokopondo,* Brownsberg Nature Park, Jeep Trail (4.9333, -55.2000, 500 m; Voss *et al.*, 2013).
119. *Nickerie,* Sipaliwini Airstrip (2.0333, -56.1333**, ca. 280 m**; Voss *et al.*, 2013).
120. *Sipaliwini,* Bakhuis Transect 9 (4.4781, -57.0417, 170 m; Voss *et al.*, 2013).
121. *Sipaliwini,* Bakhuis Transect 13 (4.5461, -57.0628, 175 m; Voss *et al.*, 2013).

TRINIDAD AND TOBAGO
122. *Trinidad*, Sangre Grande, Rio Grande Forest (10.6667, -61.0833, 61 m; Anderson & Gutiérrez, 2009).

VENEZUELA
123. *Amazonas*, Cerro Neblina, Camp VII (0.8444, -66.4194, 1800 m; Gardner, 1990).
124. *Aragua*, Parque Nacional Henri Pittier, ca. 14 km NW Maracay, Estación Biológica de Rancho Grande, El Portachuelo (10.3500, -67.6830, 1100–1150 m; Robert P. Anderson, personal commun.).
125. *Falcón*, 19 km N Urama, km 40 (10.5500, -68.4000, **6 m**; Gardner, 2008).
126. *Falcón*, near La Pastora, 14 km ENE Mirimire (11.2000, -68.6167, 125-170 m; Handley & Gordon, 1979).
127. *Falcón*, Serranía de San Luis, ~10 km W and 4 km N Cabure (11.1833, -69.7000, 1300 m; Robert P. Anderson, personal commun.).
128. *Mérida,* Mérida (8.600, -71.1333, 1600; Paynter Jr, 1982).
129. *Monagas*, 2 km N and 4 km W of Caripe (La Laguna) (10.2000, -63.5300, 1325 m; USNM database, accessed April 2013).
130. *Táchira*, Buena Vista, 41 km SW San Cristobal, near Páramo de Tamá (7.4500, -72.4300, 2395 m; Gardner, 2008).
131. *Trujillo*, Hacienda Misisí, 14 km E Trujillo (9.3500, -70.3000, 2210 m; USNM database, accessed April 2013).

Appendix 2. Primers used to amplify and sequence the loci used in this study.

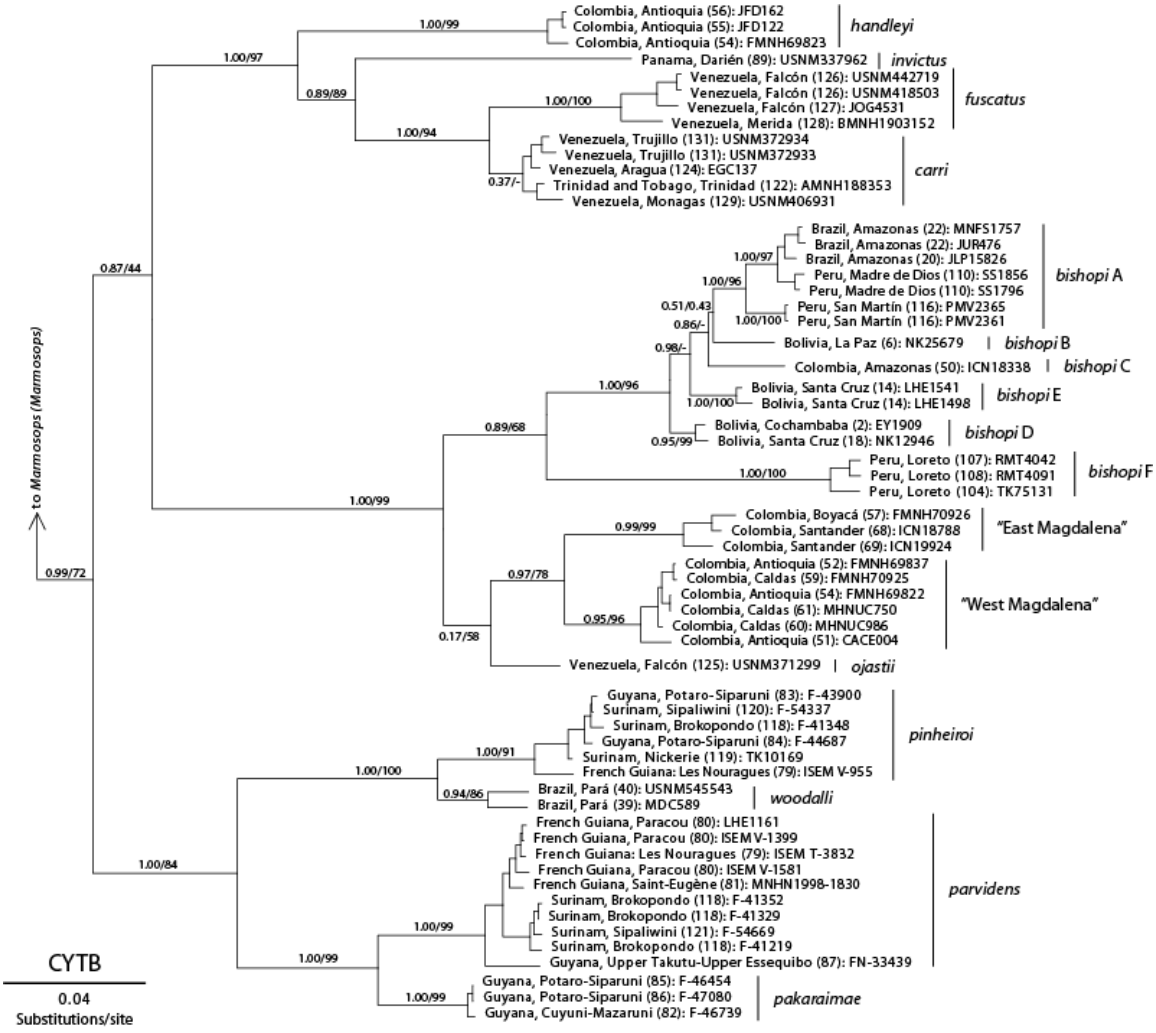
Name [a]	Sequence (5'-3')
Cytochrome-*b*	
CYTB-F1-Didelphidae[b]	ATAACCTATGGCATGAAAAACCATTGTTG
CYTB-100F-SubgenusI	TTCGGCTCTCTACTAGGAA
CYTB-125F-*fuscatus*	TTACTAGGAATCTGCCTAATCATCC
CYTB-300F-SubgenusI	ACGAGGRATCTACTACGGAT
CYTB-400F-*Marmosops*	CCATGAGGACAAATATCATTCTGAGG
CYTB-420F-*Marmosops*	TGAGGACAGATATCATTTTGAG
CYTB-421F-*parvidens*	GAGGGGCTACAGTTATTACCAACC
CYTB-500F-SubgenusI	AATCTGAGGCGGRTTTTCCG
CYTB-566F-*parvidens*	CTAAGCCTTAGTCATCGTTCACC
CYTB-750F-SubgenusI	TCTCTAGTCYTATTCTCTCCTGACA
CYTB-870F-SubgenusI	CAAAYAAACTCGGAGGAGTC
CYTB-R1-Didelphidae[b]	GCCTTGTAAGCCAGCAATGAAGG
CYTB-R2-Didelphidae	GGACTAACACCCTACCATCAACACCCA
CYTB-200R-SubgenusI	CTCGGCAGATATGGGCGACT
CYTB-260R-elegans[b]	GCTCCATTAGCGTGAATGTTTCG
CYTB-374R-*fuscatus*	GGATGACTCCAATGTTTCAGG
CYTB-399R-*fuscatus*	RAGAACGTAYCCGACGAATG
CYTB-399R-*fuscatus*	RAGAACGTAYCCGACGAATG
CYTB-400R-SubgenusI	ATGCGGTTGCTATTACTGTT
CYTB-411R-*bishopi*	ATGTTCTTCCATGAGGGCAG
CYTB-421R-*parvidens*	GAGGGGCTACAGTTATTACCAACC
CYTB-580R-SubgenusI	CGGTAGGATGAAATGGAAGG
CYTB-610R-*Marmosops*	GTCCACCTCTTATTCCTCCATGAAAC
CYTB-620R-*Marmosops*	TATTCCTACATGAAACAGGATC
CYTB-640R-*bishopi*	GAGTTTGGATTAATTCCTGTTG
CYTB-655R-*bishopi*	GGATTTTGTCTGGGTTTGGA
CYTB-670R-*Marmosops*	GACAAAATCCCATTCCATCCTTACTA
CYTB-800R-SubgenusI	TGGGTTTGCAGGAGTGAART
CYTB-1020R-SubgenusI	CCTTAACATGAATCGGAGGC
Breast Cancer Activating 1	
BRCA1-F1163a[c]	AATGAGACTGAACTACAGATCGAT
BRCA1-F1697[c]	TTWGATGRTTGTTCATCYRAAAACAC
BRCA1-R1780[c]	TAAATAYTGGGTRTCRAGTTCACT
BRCA1-R2151[c]	TCCTTTTGATYAGGAACTTGTGAAATT
Autosomal gene sodium-coupled neutral amino acid transporter 2 (intron 7)	

SLC38-F2	TTCTTCCTTTGTCATTGCTGAG
SLC38-R3	AGTTGAAGATAAAGTACCGGGG
Anonymous locus 128	
Anon128-F2	TGAAGTGAGAGGGAAATGAACAGAAGC
Anon128-R2	AGGTGGGCAGAACCAGAGAGAAGC

[a] Name of each primer follows the nomenclature given by Giarla et al. (2010), unless it has been designed by other author. In the latter case I provide the original name and reference.
[b] Primers designed by Giarla et al. (2010).
[c] Primers designed by Voss et al. (2014).

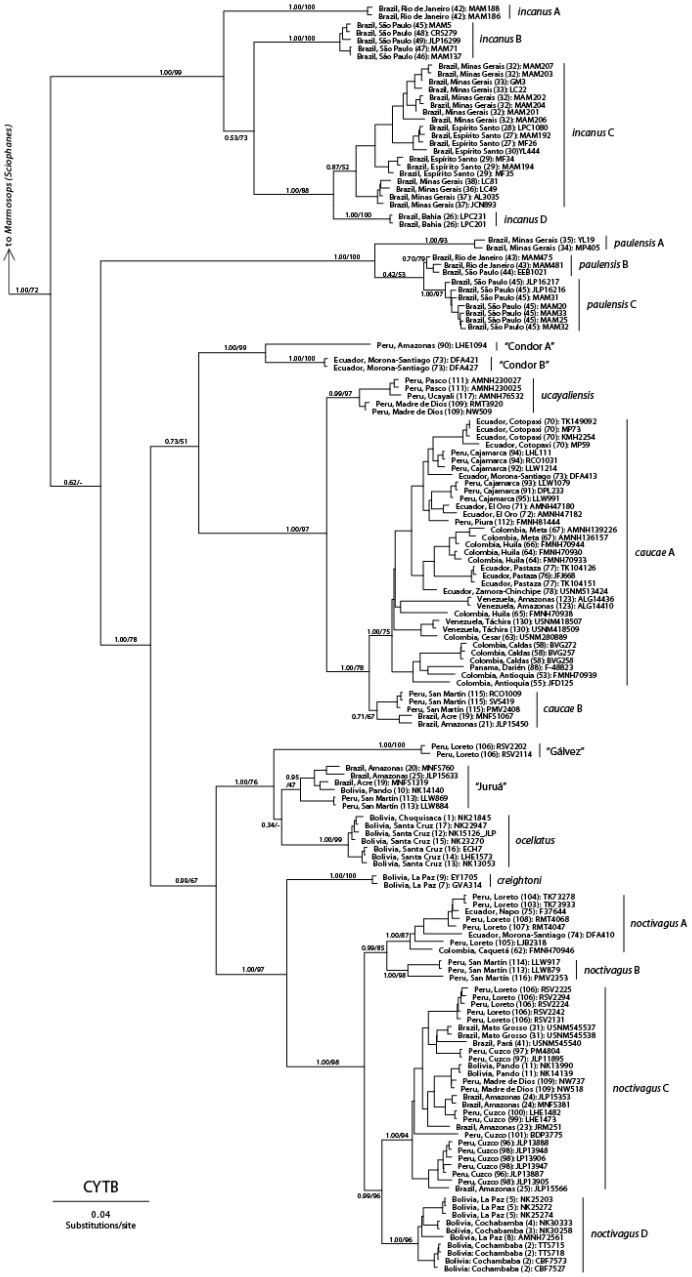
Appendix 3. Relationships among CYTB sequences of *Marmosops* Subgenus I.

Relationships among CYTB sequences of *Marmosops* Subgenus I recovered by BI. Terminals are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 2). Values above branches correspond to nodal support recovered by independent BI and ML analyses (Posterior Probability/Bootstrap).



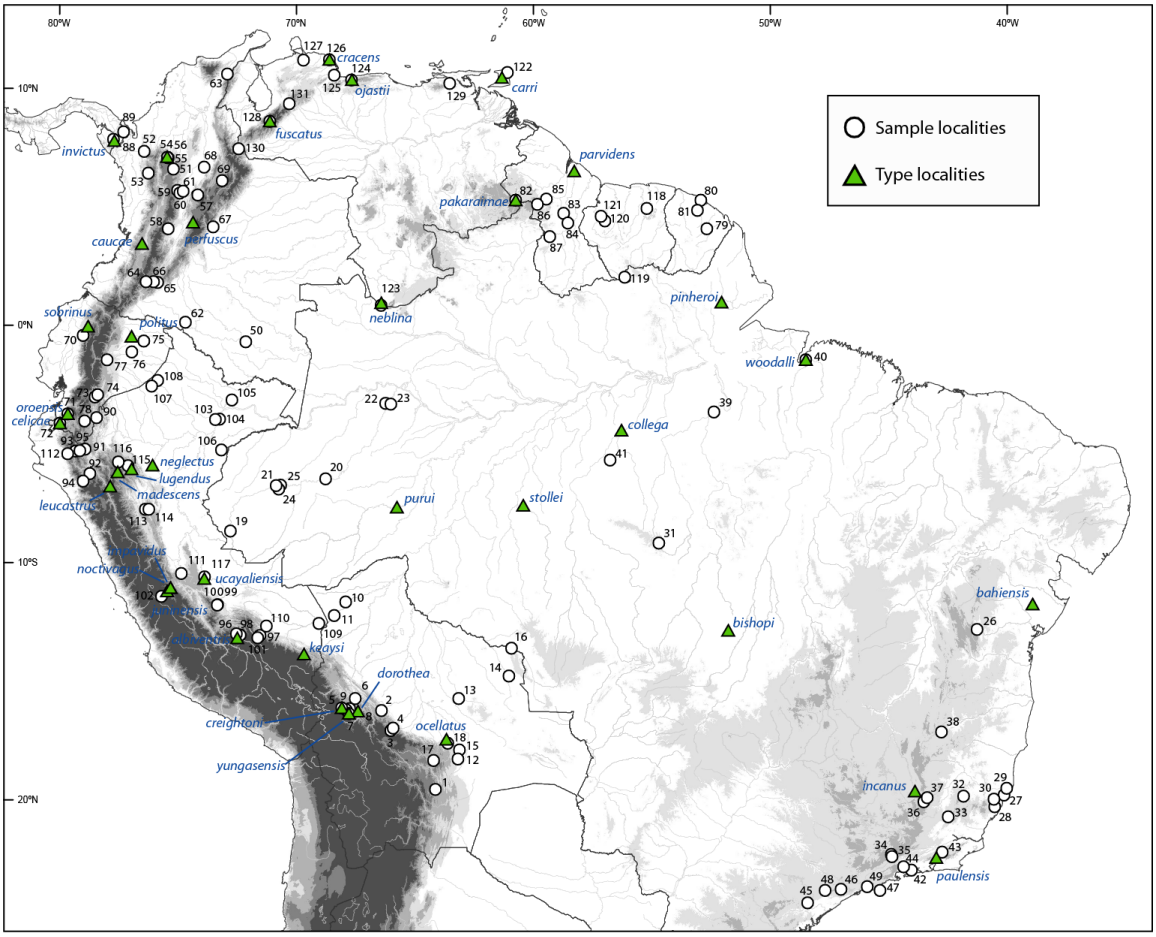
Appendix 4. Relationships among CYTB sequences of *Marmosops* Subgenus II.

Relationships among CYTB sequences of *Marmosops* Subgenus II recovered by BI. Terminals are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 2). Values above branches correspond to nodal support recovered by independent BI and ML analyses (Posterior Probability/Bootstrap).



Appendix 5. Collecting localities for specimens of *Marmosops* and type localities of nominal forms of *Marmosops*.

Map of collecting localities for specimens of *Marmosops* from which I obtained sequences for this study (circles) and type localities of nominal forms of *Marmosops* after Voss et al. (2004), Voss et al. (2013) and García et al. (2014) (triangles). Numbers are keyed to entries in the gazetteer (appendix 1).



Appendix 6. Gazetteer including all localities from which I examined specimens of *Marmosops* for this study.

This gazetteer includes all localities from which I personally examined specimens of *Marmosops* (*Sciophanes*) for this report. Numbers correspond to specimen records plotted on maps in the text. Italicized place names are those of the largest political divisions (state, department, province, etc) within each country. Boldface identifies collection localities as they appear in the text of this report. For each entry I provide geographic coordinates and elevation above sea level (in parentheses if recorded by the collector, otherwise in square brackets), name(s) of the species collected there, name(s) of the collector(s), and date(s) of collection. Units of distance (kilometers [km] or miles [mi]) are those recorded by the collector(s), as are units of elevation above sea level (meters [m] or feet [ft]).

BOLIVIA

1. *Beni,* **1 km E La Emboscada** [= La Embocada at 15°03′S, 66°58′W, 600 m; Anderson, 1997], Estancia La Cabaña: *Marmosops bishopi* (G.K. Creighton, 13 November 1979).
2. *Cochabamba,* **Serranía Mosetenes** (16°14′S, 66°25′W, 1300 m): *Marmosops bishopi* (E. Yensen, 3 September 2003).
3. *La Paz,* Iturraldi, **Alto Río Madidi** [13°35′S, 68°46′W, 270 m; Anderson, 1997]: *Marmosops bishopi* (L.H. Emmons, 27 May 1990).
4. *La Paz,* **La Reserva** (15°44′S, 67°31′W, 840 m): *Marmosops bishopi* (T. Tiurina, 22 July 1992).
5. *Santa Cruz,* **El Refugio** (14°46′S, 61°02′W, ca. 200 m): *Marmosops bishopi* (L.H. Emmons, 6–15 November 1998).
6. *Santa Cruz,* **San Rafael de Amboró** (17°36′S, 63°36′W, 400 m): *Marmosops bishopi* (B.R. Riddle, 31 July 1985).

BRAZIL

7. *Amapá,* **Serra do Navio** (including sublocalities "Rio Amapari" and "Km 190 EFA") [ca. 0°59′N, 52°03′W, 100 m; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (F. de P. Pinheiro, 16 September 1969–8 May 1970).
8. *Amazonas,* **Barro Vermelho**, left bank Rio Juruá (6°28′S, 68°46′W): *Marmosops bishopi* (J.L. Patton, 25 October 1991).
9. *Amazonas,* Faro, **Boca Rio Paratucu** [= Rio Piratucu, mouth at 1°59′N, 56°58′W; Paynter and Traylor, 1991]: *Marmosops parvidens* (A.M. Olalla, 21 December 1930).
10. *Amazonas,* MCSE Reserves, **80 km N Manaus** (2°25′S, 59°50′W): *Marmosops parvidens* (J.R. Malcolm, 7 October 1983–4 September 1985).
11. *Amazonas,* **Vai-Quem-Quer**, right bank Rio Juruá [3°19′S, 66°01′W; Patton et al., 2000]: *Marmosops bishopi* (J.R. Malcolm, 14 May 1992).

12. *Mato Grosso,* **264 km N (by road) Xavantina**, Serra do Roncador [12°51′S, 51°46′W, 1750 ft; Pine, 1981]: *Marmosops bishopi* (R.H. Pine, 5 July 1968).
13. *Pará,* **52 km SSW Altamira** (3°39′S, 52°22′W), east bank Rio Xingu: *Marmosops pinheiroi* (M.D. Carleton, 15 September 1986).
14. *Pará,* **Belém** [1°27′S, 48°29′W; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (collector unknown, 25 May 1970).
15. *Pará,* Rio Tocantins, **Ilha do Taiuna** [ca. 2°15′S, 49°30′W]: *Marmosa parvidens* (A.M. Olalla, 2 November 1931).
16. *Pará,* **Utinga** [near Belém, ca. 1°27′S, 48°29′W (see above); including sublocalities "Agua Preta", "Nova Area Experimental", and "Trapping Area 1"]: *Marmosops pinheiroi* (R.H. Pine, 10–14 June 1968; A.P. Souza, 18 February–25 June 1965 and 3 August 1967).

COLOMBIA

17. *Amazonas*, Leticia, **Vereda Peña Roja** [0°41′S, 72°08′W, 300m; Díaz-N., 2012]: *Marmosops bishopi* (P. Rivas P, 31 March 2004).
18. *Antioquia*, Gómez Plata, **Hacienda Vegas de la Clara** (6°35′22″N, 75°11′49″W, 1120 m): *Marmosops chucha* (C.A. Calderón-Acevedo, 16 July 2014).
19. *Antioquia,* Municipio Amalfi, **Porce Tres** [6°56′N, 75°08′W, 660 m; Google Earth at the crest of the wall of the dam]: *Marmosops chucha* (M. Bernal, 6 September 2004).
20. *Antioquia,* Municipio Amalfi, Vereda Guayabito, **Finca Costa Rica**, Bosque Caracolí (6°52′N, 75°06′W, 1840 m): *Marmosops handleyi* (C. Sánchez-Giraldo, J.F. Díaz-Nieto, D. Marín-C, November 2004–February 2008).
21. *Antioquia,* Municipio Yarumal, Corregimiento El Cedro, Vereda Corcovado, **Finca El Bosque**, Bosque San Andrés (7°04′N, 75°25′W, 1760 m): *Marmosops handleyi* (C. Sánchez-Giraldo, J.F. Díaz-Nieto, 1–2 October 2005).
22. *Antioquia,* Municipio Yarumal, Corregimiento El Cedro, Vereda El Rosario, sitio Alto de Ventanas, **Finca Villa Nueva** (7°05′N, 75°27′W, 1950 m): *Marmosops handleyi* (C. Sánchez-Giraldo, J.F. Díaz-Nieto, 9–11 January 2006).
23. *Antioquia,* Urabá, **Villa Arteaga** ([7°20′N, 76°26′W; Hershkovitz, 1977], 130 m): *Marmosops chucha* (P. Hershkovitz, 28 January 1950).
24. *Antioquia,* Valdivia, **9 km S Valdivia** ([7°06′N, 75°28′W; Anderson, 1999], 1400 m): *Marmosops handleyi* (P. Hershkovitz, 16–18 June 1950), *M. chucha* (P. Hershkovitz, 17 June 1950).
25. *Antioquia,* Valdivia, **La Cabaña** [ca. 7°10′N, 75°25′W; based on P. Hershkovitz field notes]: *Marmosops chucha* (P. Hershkovitz, 22 June 1950).
26. *Antioquia,* Valdivia, **Quebrada Valdivia** ([7°10′N, 75°26′W; Anderson, 1999], 900 m): *Marmosops chucha* (P. Hershkovitz, 30 June 1950).
27. *Boyacá,* **Muzo** [5°32′N, 74°06′W, 1300 m; Paynter, 1997]: *Marmosops magdalenae* (P. Hershkovitz, 15 August 1952).
28. *Caldas*, Norcasia, **Vereda Montebello**, entre las fincas El Horizonte y La Albania, quebrada La Albania (5°34′48″N, 74°55′46″W, 817 m): *Marmosops chucha* (J.H. Castaño, 6 April 2014).

29. *Caldas*, Norcasia, Vereda San Roque, **Reserva Natural Río Manso** (05°40′08″N, 74°47′17″W, 200 m): *Marmosops chucha* (J.H. Castaño, 26 November 2009).
30. *Caldas*, Samaná, Corregimiento San Diego, **Vereda La Sonrisa** [5°37′N, 74°57′W, 900 m; Google Earth at "Vereda La Sonrisa"], Finca La Sonrisa: *Marmosops chucha* (D.C. Villanueva-C., 1 April 2014).
31. *Caldas,* Samaná, **Río Honda** ([5°42′N, 75°01′W; Hershkovitz, 1997], 1200 m): *Marmosops chucha* (P. Hershkovitz, 26 February 1951).
32. *Huila,* Acevedo, Río Aguas Claras, **near San Adolfo** ([ca. 1°37′N, 75°59′W; Paynter, 1997], 1400–1700 m): *Marmosops magdalenae*. (P. Hershkovitz, 21–28 June 1951).
33. *Santander*, Encino, Vereda Rionegro, **Reserva Biológica Cachalú**, Bosque de Roble Cerca de Torre (6°6′50″N, 73°8′10″W, 1940 m): *Marmosops magdalenae* (M.E. Rodríguez-Posada, 18 July 2002).
34. *Santander*, Puerto Parra, Vereda India Baja, **Corregimiento Campo Capote** [6°40′N, 73°53′W, ca. 104 m; Instituto Geográfico Agustín Codazzi, 2015]: *Marmosops magdalenae* (Y. Muñoz-Saba, 11 March 2012).

ECUADOR

35. *Morona Santiago*, Parroquia Macuma, **Wisui** [2°07′N, 77°44′W, 650 m; Arguero et al., 2012]: *Marmosops bishopi* (A. Arguero, and F. Sánchez, 21 July 2013).
36. *Napo*, **Huamaní** [0°43′S, 77°37′W, 1250 m; Gardner, 2008]: *Marmosops bishopi* (R. Mena, 27 August 1992).
37. *Napo*, parroquia Cotundo, **Río Hollín** [0°41′S, 77°44′W, 1105 m; Moreno and Albuja, 2005]: *Marmosops bishopi* (R. Mena, 23 February 1993).
38. *Orellana*, Aguarico, **Campamento Chiruisla**, Área de Amortiguamiento del Parque Nacional Yasuní (0°37′S, 75°53′W): *Marmosops bishopi* (A. Molina, G. Toscano, A. Camacho, 10 November 2009).
39. *Orellana*, Aguarico, Parque Nacional Yasuní, Río Tiputini, **Comunidad Guiyero**, Bosque de Nambay [0°36′35″ S, 76°27′52″ W, 237 m; Albuja and Arguero, 2011]: *Marmosops bishopi* (L. Albuja, and A. Arguero, 19 May 2012). This locality was originally reported in the UTM coordinate system by Albuja and Arguero (2011: 30).
40. *Orellana*, Parque Nacional Yasuní, **Estación Científica Yasuní** (0°40′38″S, 76°24′05″W): *Marmosops bishopi* (A. Pérez, 4 May 2011).
41. *Pastaza*, Arajuno, área operación AGIP, Bloque 10. Comunidad de Paparahua. Cercanías **Río Villano** (1°29′S, 77°25′W): *Marmosops bishopi* (C. Boada, 26 June 2012).
42. *Pastaza*, Arajuno, Curaray, área operación AGIP, Bloque 10, cercanías **Río Lliquino** (including "Helipuerto K4" at 1°28′S, 77°29′W; and "Helipuerto K10" at 1°28′, 77°31′W): *Marmosops bishopi* (C. Boada, 2–18 February 2012 and 11 October 2012).
43. *Pastaza*, Arajuno, Curaray, área operación AGIP, Bloque 10. Comunidad de Tarangaro, Cercanías **Río Manderocayu** (1°24′02″S, 77°22′59″W): *Marmosops bishopi* (C. Boada, 22–24 August 2012, and 5 November 2012).

44. *Sucumbíos*, Cantón Shushufindi, Parroquia Pañacocha, **Río Pañayaku** [0°21′S, 76°25′W, 230 m; Tirira, 2012]: *Marmosops bishopi* (Collector not recorded, 28 February 2014).
45. *Sucumbíos*, **El Reventador** [0°02′S, 77°31′W, Google Earth at "El Reventador"]: *Marmosops bishopi* (Collector and date not recorded).

FRENCH GUIANA (FRANCE)

46. **Les Nouragues** [4°05′N, 52°40′W, 210 m; Voss and Emmons, 1996]: *Marmosops parvidens* (F. Catzeflis, 3 August 2002) and *M. pinheiroi* (J.-F. Mauffrey, 15 May 1999).
47. **Paracou** [5°17′N, 52°55′W, ca. 45 m; Simmons and Voss, 1998], near Sinnamary: *Marmosops parvidens* and *M. pinheiroi* (L.H. Emmons, R.W. Kays, D.P. Lunde, and R.S. Voss, 1991–1994).
48. **River Arataye** (4°00′N, 52°40′W, 30 m): *Marmosops parvidens* (L.H. Emmons, 2 October 1984).

GUYANA

49. *Cuyuni-Mazaruni,* **Mount Roraima** (including "Second Camp" at 5°17′N, 60°45′W, 800 m; and "Third Camp" at 5°16′N, 60°44′W, 1000 m): *Marmosops pakaraimae* (B.K. Lim and D.M. Jafferally, 26 February–8 March 2003).
50. *Demerara-Mahaica,* **Hyde Park**, 30 mi [up the] Demerara R[iver] [6°30′N, 58°16′W, ca. 100 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (S.B. Warren, 8 September 1906).
51. *Potaro-Siparuni,* Iwokrama Forest, **Canopy Walkway** (4°15′N, 58°55′W, 70 m): *Marmosops pinheiroi* (B.K. Lim et al., 19 August 2008).
52. *Potaro-Siparuni,* Iwokrama Forest, **Kabukalli Landing** (4°17′N, 58°31′W): *Marmosops pinheiroi* (B.K. Lim et al., 13–18 October 1999).
53. *Potaro-Siparuni,* Iwokrama Forest, Turtle Mountain, **10 km NW Kurupukari** (4°44′N, 58°43′W, 50 m): *Marmosops pinheiroi* (B.K. Lim et al., 31 October 1997).
54. *Potaro-Siparuni,* **Mount Ayanganna**, First Plateau Camp (5°20′N, 59°57′W, 1100 m; Lim et al., 2010): *Marmosops pakaraimae* (B.K. Lim, 27 October 2002).
55. *Potaro-Siparuni,* **Mount Wokomung**, First Plateau Camp (5°07′N, 59°49′W, 1130 m): *Marmosops pakaraimae* (B.K. Lim and W.P. Kilburn, 19–20 February 2003).
56. *Upper Takutu-Upper Essequibo,* **Karanambo** [3°45′N, 59°18′W; Lim et al., 2008]: *Marmosops parvidens* (M.D. Engstrom et al., 1 October 1990).

PANAMA

57. *Darién*, **Cana** (= Santa Cruz de Cana [7°47′N, 77°42′W; Fairchild and Handley, 1966], 2000 ft): *Marmosops invictus* (E.A. Goldman, 14–20 March 1912).
58. *Darién*, **Cerro Tacarcuna** ([8°10′N, 77°18′W; Fairchild and Handley, 1966], 4800 ft): *Marmosops invictus* (C.O. Handley, Jr., 5–11 March 1964).
59. *Darién*, **Tacarcuna Casita Camp** ([8°01′N, 77°22′W; Fairchild and Handley, 1966], 2700 ft): *Marmosops invictus* (C.O. Handley, Jr., 21 January 1959).

60. *Darién*, **Tacarcuna Laguna Camp** ([8°04′N, 77°19′W; Fairchild and Handley, 1966], 4000 ft): *Marmosops invictus* (C.O. Handley, Jr., 9–11 March 1959).
61. *Panamá,* **Cerro Azul** [9°14′N, 79°21′W, 850–3200 ft; Fairchild and Handley, 1966]: *Marmosops invictus* (C.O. Handley, Jr., 3 February 1958).

PERU

62. *Amazonas*, Condorcanqui, Nieva, **Puerto Tunduza** [4°46′55″S, 77°52′32″W; Ruelas and Pacheco, 2015]: *Marmosops bishopi* (L. Luna, 8 November 1997; E. Vivar, 9–16 November 1997).
63. *Cusco,* Cosñipata, **Hacienda Villa Carmen** [ca. 12°50′S, 71°15′W, 600 m; Stephens and Traylor, 1983]: *Marmosops bishopi* (C. Kalinowski, 20 September 1954).
64. *Cusco*, Distrito Echarate, La Convención, Camisea, **Konkariari** ([11°48′S, 72°52′W; Velazco and Simmons, 2011], 450 m): *Marmosops bishopi* (J.L. Mena, 27 October 1997).
65. *Huánuco,* Montealegre, **Puerto Márquez** [= San Márquez at 9°32′S, 74°56′W, ca. 100 m; Stephens and Traylor, 1983], Río Pachitea: *Marmosops bishopi* (G. Tessman, 16 November 1923).
66. *Junín,* **22 mi E Tarma** ([ca. 11°25′S, 75°23′W], 7000–7600 ft): *Marmosops juninensis* (A.L. Tuttle, 21–24 June 1964; E.L. Bush, 19 June 1964).
67. *Junín,* Provincia Satipo, Distrito Pampa Hermosa, **San Antonio**, near to río Pampa Hermosa [11°24′S, 74°46′W, 1387–1406 m; Peralta and Pacheco, 2014]: *Marmosops juninensis* (M.C. Peralta, 5–8 July 2011).
68. *Junín,* **Utcuyacu** ([ca. 11°12′S, 75°28′W; Stephens and Traylor, 1983], 1463 m): *Marmosops juninensis* (H. Watkins, 25 November 1929).
69. *Loreto,* 25 km S Iquitos, **Estación Biológica Allpahuayo** [3°58′S, 73°25′W; Hice and Velazco, 2012]: *Marmosops bishopi* (C.L. Hice, 11 October 1997–10 November 1998). This locality is equivalent to the "Reserva Nacional Allpahuayo-Mishana," which is said to be located 28 km SW of Iquitos on the Iquitos-Nauta highway (Hice and Velazco, 2012: 3).
70. *Loreto,* **Jenaro Herrera** [4°55′S, 73°40′W; Voss and Fleck, 2011]: *Marmosops bishopi* (D.P. Lunde, 6 June 2003; J.A. Amanzo, 14–20 March 1997, 13 June–3 July 2003; M. Villalobos, 9 June–27 July 2003).
71. *Loreto*, Maynas, **Alto Nanay**, Quebrada Agua Negra ([2°55′26″S, 74°49′01″W; Hurtado et al., 2014], 177 m): *Marmosops bishopi* (L. Huamaní, 25 October 2008).
72. *Loreto*, Maynas, San Juan Bautista, **Trece de Febrero,** km 31.5 carretera Iquitos-Nauta, Estación de Campo UNAP ([3°59′59″S, 73°26′31″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 22 April 2004).
73. *Loreto,* **Nuevo San Juan** [5°15′S, 73°10′W; Voss and Fleck, 2011]: *Marmosops bishopi* (R.S. Voss, 28 May 1998).
74. *Loreto,* **San Jacinto** [2°19′S, 75°52′W, 180 m; Duellman and Mendelson, 1995]: *Marmosops bishopi* (R.M. Timm, 4 July 1993).

75. *Loreto*, San Juan Bautista, **El Triunfo,** km 48 (including km 49) carretera Iquitos-Nauta ([4°09′02″S, 73°28′03″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 24 February 2004, 01 April 2005).
76. *Loreto*, San Juan Bautista, **La Habana,** km 52 carretera Iquitos-Nauta ([4°10′52″S 73°28′52″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 28 June 2004).
77. *Loreto*, San Juan Bautista, **San Lucas,** km 44 carretera Iquitos-Nauta, 1 km E del camino ([ca. 4°06′15″S, 73°27′48″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 4 February 2005). Coordinates here provided (obtained from Hurtado et al., 2014) were taken at "San Lucas km 43 carretera Iquitos-Nauta."
78. *Loreto,* **San Pedro** ("hills 0.5 to 1 km E and NE of San Pedro") [4°20′S, 73°12′W; Valqui, 2001]: *Marmosops bishopi* (M. Valqui, 20 May 1994).
79. *Loreto,* **Teniente López** (including "1½ km N of Teniente López") [2°36′S, 76°07′W, 200 m; Duellman and Mendelson, 1995]: *Marmosops bishopi* (N. Woodman, 25 July 1993; R.M. Timm, 26 July 1991).
80. *Loreto*, Tigre, margen izquierda del río Pucacuro, **Collpa Salvador** [2°37′55″S, 75°08′39″W; Watsa et al., 2012]: *Marmosops bishopi* (L. Arias, 10 July 2001).
81. *Loreto*, Tigre, río Pucacuro (including "margen derecha" and "margen izquierda"), **Cocha Coconilla** [2°42′17″S, 75°05′50″W; Watsa et al., 2012]: *Marmosops bishopi* (L. Arias; 19 July–5 August 2001).
82. *Madre de Dios,* Albergue Lodge, **Cuzco Amazónico** [12°33′S, 69°03′W, 200 m; Woodman et al., 1991] (including "ca. 12 km E Puerto Maldonado, Río Madre de Dios"): *Marmosops bishopi* (J.E. Cadle, 8 March 1984; V. Pacheco, 18 June 1989; R. Arana, 21 January 1990).
83. *Madre de Dios*, Manu, **Blanquillo** [12°25′37″S, 70°42′17″W, 273 m; S. Solari personal communication]: *Marmosops bishopi* (S. Solari, 11 March 1993).
84. *Madre de Dios*, Quebrada Aguas Calientes, **2.75 km E Shintuya** ([12°41′S, 71°15′W; Patterson et al., 2006], 450–520 m): *Marmosops bishopi* (B.D. Patterson, 10 September 1999; S. Solari, 30 August 1999 and 11 September 1999).
85. *Madre de Dios*, Tambopata, **Río La Torre** [coordinates not located]: *Marmosops bishopi* (C. Ascorra, 11 December 1995).
86. *Madre de Dios*, Tambopata, S.N. **Pampas del Heath**, P.C. Enahuipa (12°39′45″S, 68°57′30″W): *Marmosops bishopi* (A. Cornejo, 19 June 1996).
87. *Pasco,* **Santa Cruz** [10°37′S, 75°22′W, 2050 m; Cadena et al., 2007], ca. 9 km SSE Oxapampa: *Marmosops juninensis* (T. Schulenberg, S. Allen, D. Stotz; 24 February 1982).
88. *San Martín*, Rioja, Pardo Miguel, Naranjos, **Caserio El Diamante** (5°45′12″S, 77°31′34″W, 1078 m): *Marmosops bishopi* (P.M. Velazco, 16–17 May 2011).
89. *Ucayali*, Contamana, Sierra de Contamana, Cerros de Canchaguaya, **Aguas Calientes** ([07°11′20″S, 74°56′54″W; Hurtado et al., 2014] 320 m): *Marmosops bishopi* (U. Paredes, 15–20 November 2000).

SURINAM

90. *Brokopondo,* **Brownsberg Nature Park**, Jeep Trail (4°56′N, 55°12′W, 500 m): *Marmosops parvidens* (M.D. Engstrom et al., 13–19 April 2002).
91. *Brokopondo,* **Finisanti** [5°08′N, 55°29′W; Voss, 1991], Saramacca River: *Marmosops pinheiroi* (P. Hershkovitz, 31 December 1961).
92. *Nickerie,* **Kayser Gebergte Airstrip**, E of Zuid River [ca. 3°07′N, 56°27′W, ca. 278 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (H.A. Beatty, 30 December 1960).
93. *Nickerie,* **Sipaliwini Airstrip** (2°02′N, 56°08′W): *Marmosops pinheiroi* (S.L. Williams, 20 August 1979).
94. *Sipaliwini,* **Bakhuis Transect 9** (4°29′N, 57°02′W, 170 m): *Marmosops pinheiroi* (B.K. Lim and S.L. Peters, 3 November 2005).
95. *Sipaliwini,* **Bakhuis Transect 13** (4°33′N, 57°04′W, 175 m): *Marmosops parvidens* (B.K. Lim and A.V. Borisenko, 19 January 2006).

TRINIDAD AND TOBAGO

96. *Tobago,* **near Charlotteville** [11°19′N, 60°33′W; Voss, 1991]: *Marmosops carri* (M.E. Holden, 18–22 January 1989).
97. *Trinidad,* **Caparo** [10°27′N, 61°20′W; USBGN, 1955]: *Marmosops carri* (F.M. Chapman, 19 March–17 April 1894).
98. *Trinidad,* **Cedros** [ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961]: *Marmosops carri* (Trinidad Regional Virus Laboratory [TRVL] collectors, 7 March 1972).
99. *Trinidad,* **Cumaca** [10°42′N, 61°09′W; USBGN, 1955]: *Marmosops carri* (W.G. Downs, 20 July 1954).
100. *Trinidad,* Sangre Grande, **Rio Grande Forest** [ca. 10°41′N, 61°01′W, 200 ft; see note]: *Marmosops carri* (W.G. Downs, 21 June–19 July 1956). Note: coordinates estimated from those of Sangre Grande (USBGN, 1955) based on Goodwin and Greenhall's (1961: 296) statement that RGF is ca. 10 airline miles NE.
101. *Trinidad,* **St. Augustine** [10°39′N, 61°24′W; USBGN, 1955]: *Marmosops carri* (E. Friend, 2 October 1936).
102. *Trinidad,* **Turure Forest** [ca. 10°32′N, 61°07′W; Goodwin and Greenhall, 1961]: *Marmosops carri* (TRVL collectors, 1966–1969).

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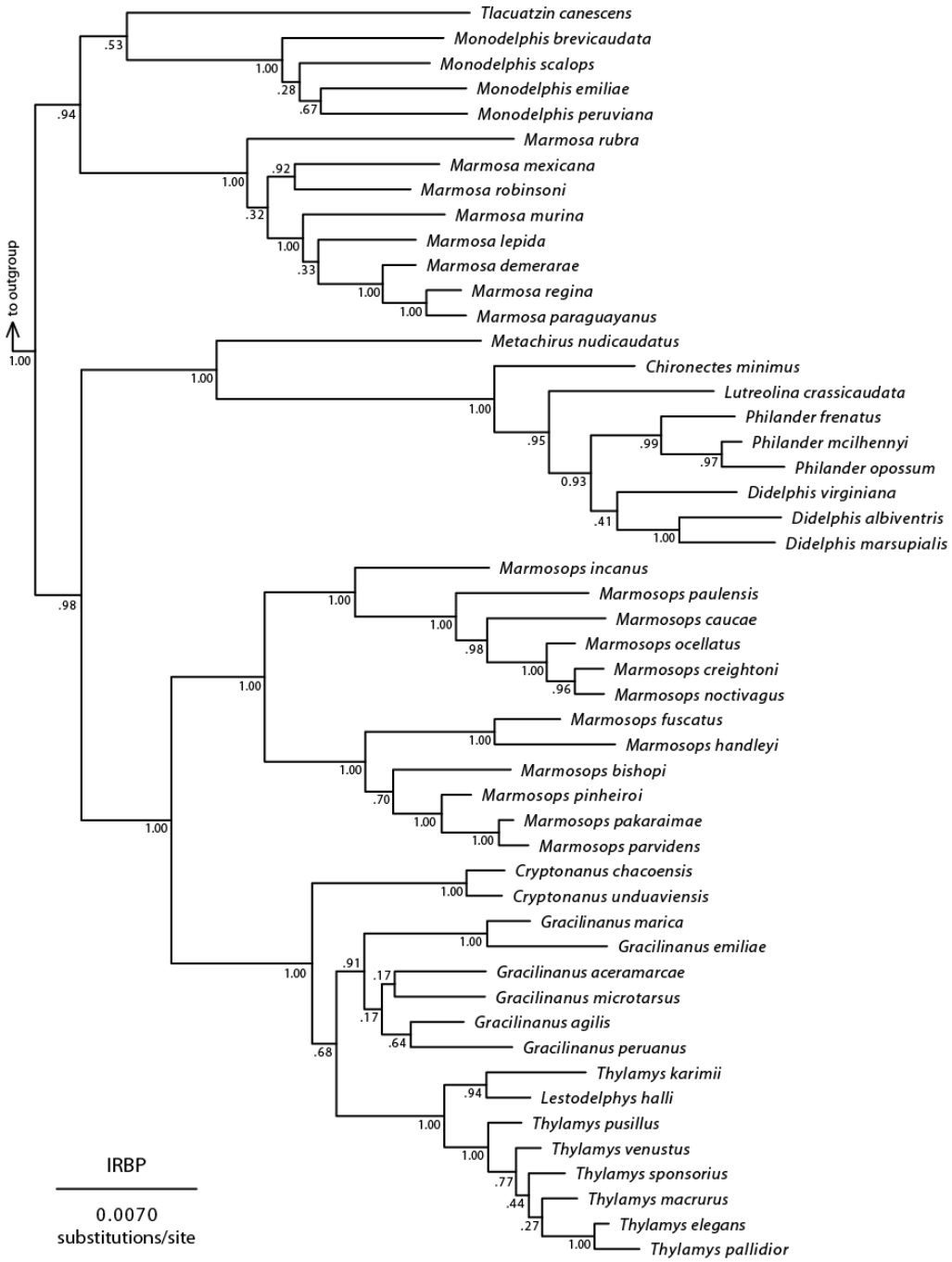
103. *Aragua*, **Rancho Grande** [10°21′N, 67°40′W, ca 1000 m; Handley, 1976]: *Marmosops carri* (W. Beebe, 29 June 1946; C.O. Handley and D.J. Rhymer, 27–31 March 1960). According to García et al. (2014: 721), *Marmosops ojastii* has also been taken at this locality.
104. *Bolívar,* **85 km SSE El Dorado**, Km 121 [= "Km 125" at 6°02′N, 61°22′W, 1032 m; Gardner, 2008]: *Marmosops pakaraimae* (M.D. Tuttle, 9 May 1966).
105. *Bolívar,* **Auyán-tepui** [ca. 5°55′N, 62°32′W; Paynter, 1982], 460 m: *Marmosops pinheiroi* (G.H.H. Tate, 9 March 1938). See Voss et al. (2013) for additional information about this locality.

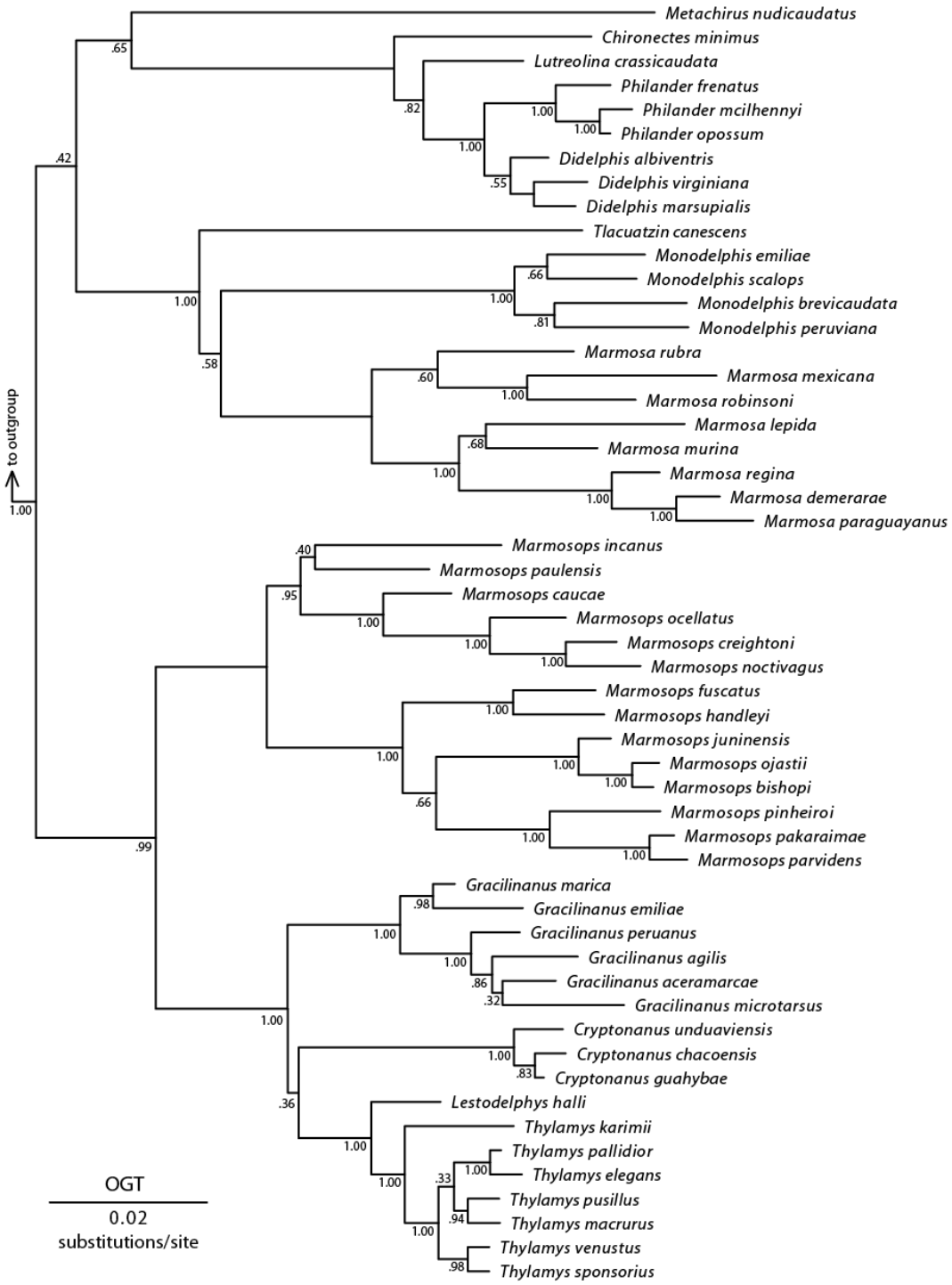
106. *Bolívar,* **Churi-tepui** [ca. 5°13′N, 61°54′W; McDiarmid and Donnelly, 2005], Camp 5 (4900 ft): *Marmosops pakaraimae* (E. McGuire, 13 January 1953).
107. *Carabobo,* **Cumbre de Valencia** [ca. 10°20′N, 68°00′W, 1700 m; Paynter, 1982]: *Marmosops carri* (M.A. Carriker, Jr., 20 October 1910).
108. *Carabobo,* La Copa, **4 km NW Montalbán** ([ca. 10°09′N, 68°21′W; Handley, 1976], 1513 m): *Marmosops carri* (A.L. Tuttle, 2–8 August 1968).
109. *Carabobo/Falcón/Yaracuy,* **19 km NW Urama** [ca. 10°37′N, 68°24′W, 25–60 m; Handley, 1976]: *Marmosops ojastii* (M.D. Tuttle, 19 October 1965).
110. *Distrito Federal,* 4 km N. Caracas, **Los Venados** (including locality 5 km N. Caracas [10°32′N, 66°54′W; Handley, 1976], 1443–1500 m): *Marmosops carri* (M.D. Tuttle, 10–11 August 1965).
111. *Falcón,* **near La Pastora** (including sublocalities 5 km N and 13 km E Mirimire, and 14 km ENE Mirimire; 11°12′N, 68°37′W, 122–125 m): *Marmosops fuscatus* (Smithsonian Venezuelan Project [SVP] team, 11–16 November 1967).
112. *Falcón,* **Serranía de San Luís**, Parque Nacional J.C. Falcón (including sublocalities in Sector Cerro Galícia, 10 km W and 4 km N Cabure [11°11′N, 69°42′W, ca. 1300 m; Anderson et al., 2012]; and in Sector Cumbres de Uria, ca. 9 km N Cabure [11°14′N, 69°37′W, 1320–1370 m; Anderson et al., 2012]): *Marmosops fuscatus* (J. Ochoa-G., 25 April 2006; R.P. Anderson, 12 August 2006).
113. *Mérida,* **La Azulita** [8°43′N, 71°27′S, 1135 m; Paynter, 1982]: *Marmosops fuscatus* (W.H. Osgood and H.B. Conover, 21 April 1920).
114. *Mérida,* **Mérida** (including sublocality "Rio Abbaregas" [ca. 8°36′N, 71°08′W; Paynter, 1982], 1600–1630 m): *Marmosops fuscatus* (S. Briceño, 1896–1902).
115. *Miranda/Vargas,* 9.4 km N Caracas, **Hotel Humboldt** ([10°33′N, 66°52′W; Handley, 1976], 2103–2230 m): *Marmosops carri* (M.D. Tuttle, 7 August–4 September 1965). Anderson and Gutiérrez (2009: 85) noted that SVP collections labeled "Hotel Humboldt" could have been collected either in the states of Miranda or Vargas contra Handley (1976: 79), who placed this locality on the border between the Distrito Federal and Miranda. One specimen from this locality (USNM 370035) has a recorded elevation of 1281 m, which I assume to be a lapsus for 2181 m.
116. *Monagas,* **San Augustín** (including sublocalities "2 km N and 4 km W Caripe" and "5 km NW Caripe"; 10°12′N, 63°32′W, 1150–1338 m): *Marmosops carri* (Smithsonian Venezuelan Project, 6 July 1967).
117. *Trujillo,* Hacienda Misisí, **13–14 km E Trujillo** ([9°21′N, 70°18′W; Handley, 1976], 2000–2210 m): *Marmosops carri* (SVP team, 28 January 1966; J.A.W. Kirsch, 21 June 1969).
118. *Zulia,* Pueblo Nuevo, **La Fría** [8°55′N, 71°25′W; DMA, 1993]: *Marmosops* sp. (H.B. Baker, 13 August 1914).

Appendix 7. Species for which sequences from different specimens were combined as chimeric terminals to improve gene coverage.

Species	*Cytb*	*BRCA1*	*IRBP*	*OGT*	*Anon128*	*SLC38*
Didelphis marsupialis	MUSM 13282	MUSM 13282	AMNH 272836	MUSM 13282	MUSM 13282	MUSM 13282
Lestodelphys halli	CNP 889	CNP 889	UWZ 22422	CNP 889	CNP 889	CNP 889
Marmosa lepida	ROM 107034	ROM 107034	ROM 107034	AMNH 273186	ROM 107034	AMNH 273186
Marmosa mexicana	ROM 96968	ROM 96968	ROM 99608	ROM 96968	ROM 96968	ROM 96968
Marmosa murina	ROM 113649	ROM 113649	CM 68346	ROM 113649	ROM 113649	ROM 113649
Marmosa rubra	ROM 118744	MVZ 153280	MVZ 153280	MVZ 153280	MVZ 153280	MVZ 153280
Marmosops incanus	MZUSP 29176	MZUSP 29176	MVZ 182769	MZUSP 29176	MZUSP 29176	MZUSP 29176
Marmosops pinheiroi	ROM 108920	ROM 108920	ROM 108920	CM 63506	ROM 108920	CM 63506
Thylamys pallidior	FMNH 162495	FMNH 162495	FMNH 162495	FMNH 162495	MSB 57003	FMNH 162495

Appendix 8. Individual genes trees obtained from MrBayes for loci *IRBP*, *OGT*, *SLC38*, and *Anon128*. Values on branches correspond to Posterior Probabilities.

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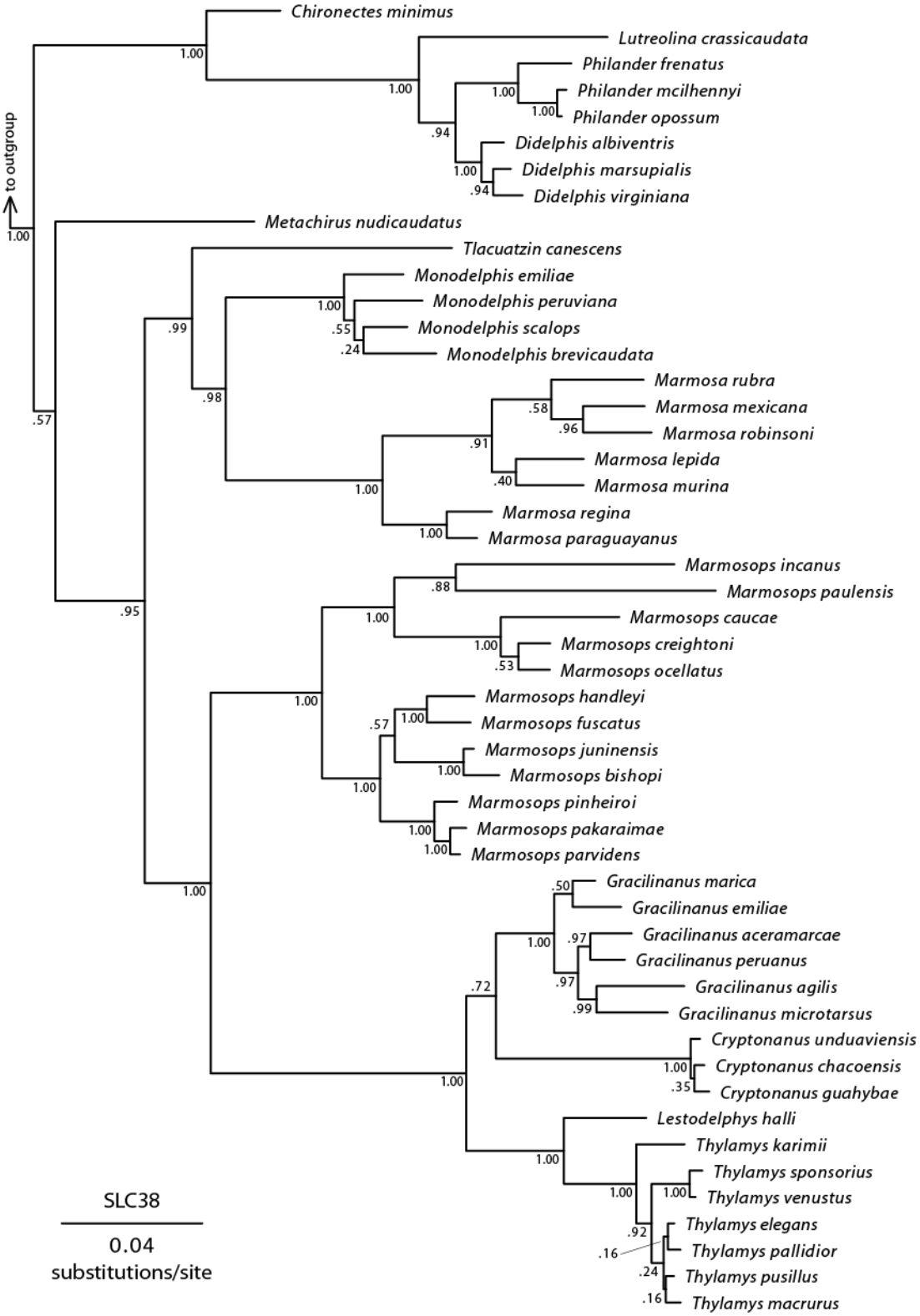
Chironectes minimus
Lutreolina crassicaudata
Philander frenatus
Philander mcilhennyi
Philander opossum
Didelphis albiventris
Didelphis virginiana
Didelphis marsupialis
Tlacuatzin canescens
Monodelphis emiliae
Monodelphis scalops
Monodelphis brevicaudata
Monodelphis peruviana
Marmosa rubra
Marmosa mexicana
Marmosa robinsoni
Marmosa lepida
Marmosa murina
Marmosa regina
Marmosa demerarae
Marmosa paraguayanus
Marmosops incanus
Marmosops paulensis
Marmosops caucae
Marmosops ocellatus
Marmosops creightoni
Marmosops noctivagus
Marmosops fuscatus
Marmosops handleyi
Marmosops juninensis
Marmosops ojastii
Marmosops bishopi
Marmosops pinheiroi
Marmosops pakaraimae
Marmosops parvidens
Gracilinanus marica
Gracilinanus emiliae
Gracilinanus peruanus
Gracilinanus agilis
Gracilinanus aceramarcae
Gracilinanus microtarsus
Cryptonanus unduaviensis
Cryptonanus chacoensis
Cryptonanus guahybae
Lestodelphys halli
Thylamys karimii
Thylamys pallidior
Thylamys elegans
Thylamys pusillus
Thylamys macrurus
Thylamys venustus
Thylamys sponsorius
to outgroup
OGT
0.02
substitutions/site


Chironectes minimus
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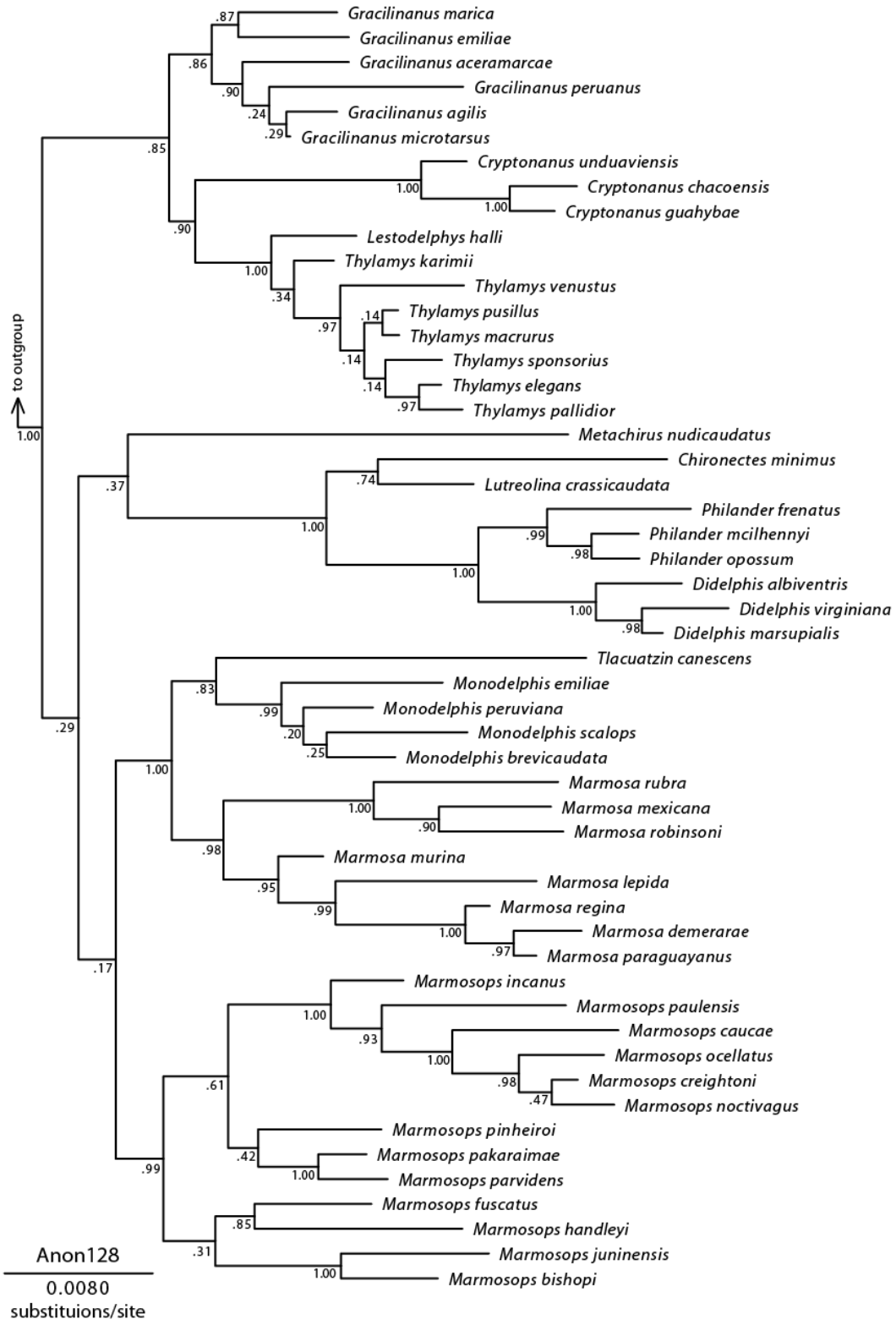
Thylamys karimii
Thylamys sponsorius
Thylamys venustus
Thylamys elegans
Thylamys pallidior
Thylamys pusillus
Thylamys macrurus
SLC38
0.04
substitutions/site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Marmosops pakaraimae
Marmosops parvidens
Marmosops fuscatus
Marmosops handleyi
Marmosops juninensis
Marmosops bishopi
Anon128
0.0080
substituions/site