

# DNA sequencing reveals unexpected Recent diversity and an ancient dichotomy in the American marsupial genus *Marmosops* (Didelphidae: Thylamyini)

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To assess species-level diversity in the didelphid marsupial genus *Marmosops*, we obtained sequence data from the mitochondrial *cytochrome b* (*CYTB*) gene from > 200 specimens, including exemplars of every currently recognized species together with multiple specimens of all geographically widespread forms. Analyses of these data using the general mixed Yule coalescent (GMYC) model suggest that the genus could be twice as speciose as currently recognized, but putative species identified by the GMYC criterion require careful evaluation using other data. To assess phylogenetic relationships within *Marmosops*, we additionally sequenced a large fragment of the *breast cancer activating 1* (*BRCA1*) gene from one specimen each of the putative species identified by the GMYC analyses of *CYTB*. Maximum likelihood and Bayesian analyses of a concatenated gene (*CYTB* + *BRCA1*) matrix revealed a basal dichotomy between two ancient, morphologically diagnosable clades with apparently distinct distributions and adaptive phenotypes. We describe those clades as subgenera and assign 12 nominal taxa to ***Sciophanes* subgen. nov.** (with type species *Marmosops parvidens*) and 27 nominal taxa to the nominotypical subgenus (with type species *Marmosops incanus*).

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ADDITIONAL KEYWORDS: *BRCA1* – *cytochrome b* – Didelphimorphia – GMYC – species delimitation – taxonomy.

## INTRODUCTION

American marsupials of the genus *Marmosops* Matschie, 1916, are small (< 200 g) opossums distributed from Panama to southern Bolivia and south-eastern 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 & Creighton, 2008; Voss *et al.*, 2013). Most

of these areas are now recognized as important biodiversity hotspots owing 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 fully understand the species limits or phylogenetic relationships within the genus.

The current usage of *Marmosops* as a valid genus dates from Gardner & Creighton (1989), and the morphological diagnosis and phylogenetic position of the genus within the family Didelphidae were recently assessed by Voss & Jansa (2009). Although 39 nominal

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

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

taxa have been referred to *Marmosops*, many of these names are thought to be synonyms of just 17 currently recognized species (Voss & Jansa, 2009; Voss *et al.*, 2013; García, Sánchez-Hernández & Semedo, 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 & Creighton, 1989; Gardner, 2005), descriptions of new

taxa (Handley & Gordon, 1979; Pine, 1981; Gardner, 1990; Voss *et al.*, 2013; García *et al.*, 2014), re-descriptions based on newly collected material (Díaz-N, Gómez-Laverde & Sánchez-Giraldo, 2011), revisions of locally co-occurring species (Patton, da Silva & Malcolm, 2000; Voss, Lunde & Simmons, 2001; Voss, Tarifa & Yensen, 2004), phylogeographical studies (Musttrangi & Patton, 1997; Steiner & Catzeffis, 2004), and phylogenetic analyses based on a few exemplar species (Patton, dos Reis & Da Silva, 1996; Jansa & Voss, 2000; Voss & 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 the improbably wide geographical distributions of some species, high levels of intraspecific molecular variation in others, and numerous specimens that cannot be assigned to any currently recognized taxon.

In this study, we assessed 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, George & Wilson, 1979; Moore, 1995), mitochondrial DNA (mtDNA) is the most widely used marker for assessing species limits of didelphid marsupials (Musttrangi & Patton, 1997; Patton *et al.*, 2000; Giarla, Voss & Jansa, 2010; Gutiérrez, Jansa & Voss, 2010; Solari, 2010; de la Sancha, D'Elia & Teta, 2012). We sequenced *CYTB* from holotypes, paratypes, or topotypical material of most of the 39 nominal taxa in the genus, and we sequenced numerous specimens from as many localities as possible of geographically widespread taxa. As preliminary analyses of mtDNA sequences suggested a basal dichotomy in the genus, and because we were unable to obtain *CYTB* sequence data from one species, we 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 our analyses of *CYTB*. Together, these molecular data provide important new perspectives on both Recent diversity and ancient-lineage membership. As a basis for future revisionary work, we name a new subgenus and discuss the probable application of names to the *CYTB* clades recovered in our analyses.

## MATERIAL AND METHODS

### TAXON SAMPLING AND SPECIMEN IDENTIFICATION

We 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

**Table 2.** Sequences of *Marmosops* and outgroups included in this report. Samples in bold font identify sequences used in general mixed Yule coalescent model 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). 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 (bp)	BRCA1 (bp)	Source
<i>bishopi</i> A	<b>MVZ 190283</b>	<b>JLP15826</b>	Brazil: Amazonas (20)	1149	–	This report
<i>bishopi</i> A	<b>MPEG 28041</b>	<b>JUR476</b>	Brazil: Amazonas (22)	1149	–	Patton <i>et al.</i> (2000)
<i>bishopi</i> A	<b>MVZ 191188</b>	<b>MNFS1757</b>	Brazil: Amazonas (22)	1149	–	This report
<i>bishopi</i> A	<b>FMNH 169800</b>	<b>SS1796</b>	Peru: Madre de Dios (110)	1149	–	This report
<i>bishopi</i> A	FMNH 169801	SS1856	Peru: Madre de Dios (110)	635	–	This report
<i>bishopi</i> A	FMNH 203328	PMV2365	Peru: San Martín (116)	1149	876	This report
<i>bishopi</i> A	<b>FMNH 203509</b>	<b>PMV2361</b>	Peru: San Martín (116)	1149	–	This report
<i>bishopi</i> B	<b>AMNH 268938</b>	<b>NK25679</b>	Bolivia: La Paz (6)	1149	–	This report
<i>bishopi</i> C	<b>ICN 18338</b>	–	Colombia: Amazonas (50)	629	–	This report
<i>bishopi</i> D	<b>CBF 7531</b>	<b>EY1909</b>	Bolivia: Cochabamba (2)	1149	–	This report
<i>bishopi</i> D	<b>MSB 55843</b>	<b>NK12946</b>	Bolivia: Santa Cruz (18)	1149	–	This report
<i>bishopi</i> E	<b>MNK</b>	<b>LHE1498</b>	Bolivia: Santa Cruz (14)	423	–	This report
<i>bishopi</i> E	USNM 584464	LHE1541	Bolivia: Santa Cruz (14)	1149	612	This report
<i>bishopi</i> F	<b>TTU 101239</b>	<b>TK75131</b>	Peru: Loreto (104)	1149	882	This report
<i>bishopi</i> F	<b>KU 157969</b>	<b>RMT4042</b>	Peru: Loreto (107)	391	–	This report
<i>bishopi</i> F	KU 157971	RMT4091	Peru: Loreto (108)	1149	–	This report
<i>carri</i>	<b>AMNH 188353</b>	–	Trinidad and Tobago: Trinidad (122)	379	–	This report
<i>carri</i>	<b>EBRG 27001</b>	<b>EGC137</b>	Venezuela: Aragua (124)	1149	885	This report
<i>carri</i>	<b>USNM 406931</b>	–	Venezuela: Monagas (129)	379	–	This report
<i>carri</i>	<b>USNM 372933</b>	–	Venezuela: Trujillo (131)	379	–	This report
<i>carri</i>	USNM 372934	–	Venezuela: Trujillo (131)	379	–	This report
<i>caucae</i> A	<b>FMNH 70939</b>	–	Colombia: Antioquia (53)	1149	–	This report
<i>caucae</i> A	<b>CTUA 427</b>	<b>JFD125</b>	Colombia: Antioquia (55)	1149	882	This report
<i>caucae</i> A	<b>ICN uncatalogued</b>	<b>BVG257</b>	Colombia: Caldas (58)	1149	–	This report
<i>caucae</i> A	ICN uncatalogued	BVG258	Colombia: Caldas (58)	1149	–	This report
<i>caucae</i> A	ICN uncatalogued	BVG272	Colombia: Caldas (58)	1149	–	This report
<i>caucae</i> A	<b>USNM 280889</b>	–	Colombia: Cesar (63)	1000	–	This report
<i>caucae</i> A	<b>FMNH 70930</b>	–	Colombia: Huila (64)	1000	–	This report
<i>caucae</i> A	<b>FMNH 70933</b>	–	Colombia: Huila (64)	1000	–	This report
<i>caucae</i> A	<b>FMNH 70938</b>	–	Colombia: Huila (65)	1000	–	This report
<i>caucae</i> A	FMNH 70944	–	Colombia: Huila (66)	1000	–	This report
<i>caucae</i> A	<b>AMNH 136157</b>	–	Colombia: Meta (67)	538	–	This report
<i>caucae</i> A	<b>AMNH 139226</b>	–	Colombia: Meta (67)	194	–	This report
<i>caucae</i> A	<b>QCAZ 8665</b>	<b>KMH2254</b>	Ecuador: Cotopaxi (70)	1149	–	This report
<i>caucae</i> A	<b>QCAZ 8666</b>	<b>MP59</b>	Ecuador: Cotopaxi (70)	1149	–	This report
<i>caucae</i> A	QCAZ 8667	MP73	Ecuador: Cotopaxi (70)	1149	–	This report
<i>caucae</i> A	QCAZ 8668	TK149092	Ecuador: Cotopaxi (70)	1149	–	This report
<i>caucae</i> A	<b>AMNH 47180</b>	–	Ecuador: El Oro (71)	878	–	This report
<i>caucae</i> A	<b>AMNH 47182</b>	–	Ecuador: Loja (72)	194	–	This report
<i>caucae</i> A	<b>QCAZ 8836</b>	<b>DFA413</b>	Ecuador: Morona-Santiago (73)	1149	–	This report
<i>caucae</i> A	<b>USNM 574501</b>	<b>JFJ668</b>	Ecuador: Pastaza (76)	1149	–	This report
<i>caucae</i> A	TTU 84898	TK104126	Ecuador: Pastaza (77)	1149	–	This report
<i>caucae</i> A	TTU 84923	TK104151	Ecuador: Pastaza (77)	1149	–	This report
<i>caucae</i> A	<b>USNM 513424</b>	–	Ecuador: Zamora-Chinchipe (78)	538	–	This report
<i>caucae</i> A	<b>ROM 116281</b>	<b>F-48823</b>	Panama: Darién (88)	1149	–	This report
<i>caucae</i> A	<b>AMNH 268099</b>	<b>DPL233</b>	Peru: Cajamarca (91)	1149	–	This report
<i>caucae</i> A	<b>UMMZ 176705</b>	<b>LLW1214</b>	Peru: Cajamarca (92)	1149	–	This report
<i>caucae</i> A	UMMZ 176576	LLW1079	Peru: Cajamarca (93)	1149	–	This report

Table 2. Continued

Putative species	Voucher	Tissue	Locality	CYTB (bp)	BRCA1 (bp)	Source
<i>cauceae</i> A	UMMZ	LHL111	Peru: Cajamarca (94)	1149	–	This report
<i>cauceae</i> A	UMMZ	RCO1031	Peru: Cajamarca (94)	1149	–	This report
<i>cauceae</i> A	UMMZ 176774	LLW991	Peru: Cajamarca (95)	1149	–	This report
<i>cauceae</i> A	FMNH 81444	–	Peru: Piura (112)	1000	–	This report
<i>cauceae</i> A	USNM 560732	ALG14410	Venezuela: Amazonas (123)	1149	–	This report
<i>cauceae</i> A	USNM 560735	ALG14436	Venezuela: Amazonas (123)	1149	–	This report
<i>cauceae</i> A	USNM 418507	–	Venezuela: Táchira (130)	383	–	This report
<i>cauceae</i> A	USNM 418509	–	Venezuela: Táchira (130)	362	–	This report
<i>cauceae</i> B	MVZ 190270	MNFS1067	Brazil: Acre (19)	1149	–	This report
<i>cauceae</i> B	MVZ 190272	JLP15450	Brazil: Amazonas (21)	1149	882	This report
<i>cauceae</i> B	FMNH 203324	PMV2408	Peru: San Martín (115)	1149	–	This report
<i>cauceae</i> B	FMNH 203325	RCO1009	Peru: San Martín (115)	1149	–	This report
<i>cauceae</i> 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
<i>creightoni</i>	CBF 7641	GVA314	Bolivia: La Paz (7)	1149	882	This report
<i>creightoni</i>	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
<i>fuscatus</i>	USNM 418503	–	Venezuela: Falcón (126)	619	–	This report
<i>fuscatus</i>	USNM 442719	–	Venezuela: Falcón (126)	579	–	This report
<i>fuscatus</i>	AMNH 276509	JOG4531	Venezuela: Falcón (127)	1149	885	This report
<i>fuscatus</i>	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
<i>handleyi</i>	FMNH 69823	–	Colombia: Antioquia (54)	208	–	This report
<i>handleyi</i>	CTUA 413	JFD122	Colombia: Antioquia (55)	1149	–	This report
<i>handleyi</i>	CTUA 415	JFD162	Colombia: Antioquia (56)	1149	879	This report
<i>incanus</i> A	MZUSP 29173	MAM186	Brazil: Rio de Janeiro (42)	1149	882	Voss <i>et al.</i> (2013)
<i>incanus</i> A	MZUSP 29174	MAM188	Brazil: Rio de Janeiro (42)	400	–	Mustrangi & Patton (1997)
<i>incanus</i> B	MZUSP 29186	MAM5	Brazil: São Paulo (45)	777	–	Mustrangi & Patton (1997)
<i>incanus</i> B	MZUSP 29170	MAM137	Brazil: São Paulo (46)	397	–	Mustrangi & Patton (1997)
<i>incanus</i> B	MVZ 182061	MAM71	Brazil: São Paulo (47)	718	–	Mustrangi & Patton (1997)
<i>incanus</i> B	Not catalogued	CRS279	Brazil: São Paulo (48)	1149	705	This report
<i>incanus</i> B	MVZ 192502	JLP16299	Brazil: São Paulo (49)	400	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	MF26	Brazil: Espírito Santo (27)	398	–	Mustrangi & Patton (1997)
<i>incanus</i> C	MZUSP 29175	MAM192	Brazil: Espírito Santo (27)	400	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	LPC1080	Brazil: Espírito Santo (28)	801	–	Agrizzi <i>et al.</i> (2012)
<i>incanus</i> C	–	MF34	Brazil: Espírito Santo (29)	801	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	MF35	Brazil: Espírito Santo (29)	400	–	Mustrangi & Patton (1997)
<i>incanus</i> C	MZUSP 29176	MAM194	Brazil: Espírito Santo (29)	1149	879	This report
<i>incanus</i> C	–	YL444	Brazil: Espírito Santo (30)	798	–	Agrizzi <i>et al.</i> (2012)
<i>incanus</i> C	–	MAM203	Brazil: Minas Gerais (32)	384	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	MAM204	Brazil: Minas Gerais (32)	801	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	MAM206	Brazil: Minas Gerais (32)	270	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	MAM207	Brazil: Minas Gerais (32)	335	–	Mustrangi & Patton (1997)
<i>incanus</i> C	MVZ 182768	MAM201	Brazil: Minas Gerais (32)	1149	–	This report
<i>incanus</i> C	MVZ 182769	MAM202	Brazil: Minas Gerais (32)	1149	–	This report



**Table 2.** *Continued*

Putative species	Voucher	Tissue	Locality	CYTB (bp)	BRCA1 (bp)	Source
<i>incanus</i> C	–	<b>GM3</b>	Brazil: Minas Gerais (33)	335	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	<b>LC22</b>	Brazil: Minas Gerais (33)	398	–	Agrizzi <i>et al.</i> (2012)
<i>incanus</i> C	–	<b>LC49</b>	Brazil: Minas Gerais (36)	797	–	Agrizzi <i>et al.</i> (2012)
<i>incanus</i> C	–	<b>AL3035</b>	Brazil: Minas Gerais (37)	386	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	<b>JCN893</b>	Brazil: Minas Gerais (37)	400	–	Mustrangi & Patton (1997)
<i>incanus</i> C	–	<b>LC81</b>	Brazil: Minas Gerais (38)	801	–	Agrizzi <i>et al.</i> (2012)
<i>incanus</i> D	<b>MVZ 197435</b>	<b>LPC231</b>	Brazil: Bahia (26)	1149	879	This report
<i>incanus</i> D	<b>MVZ 197761</b>	<b>LPC201</b>	Brazil: Bahia (26)	781	–	Agrizzi <i>et al.</i> (2012)
<i>invictus</i>	<b>USNM 337962</b>	–	Panama: Darién (89)	483	388	This report
<i>juninensis</i>	AMNH 230016	–	Peru: Junín (102)	–	882	This report
'Juruá'	<b>MSB 57002</b>	<b>NK14140</b>	Bolivia: Pando (10)	1149	–	This report
'Juruá'	<b>MVZ 190269</b>	<b>MNFS1319</b>	Brazil: Acre (19)	1149	–	This report
'Juruá'	<b>MVZ 190268</b>	<b>MNFS760</b>	Brazil: Amazonas (20)	1149	–	This report
'Juruá'	<b>MVZ 190267</b>	<b>JLP15633</b>	Brazil: Amazonas (25)	1149	–	This report
'Juruá'	<b>UMMZ 176449</b>	<b>LLW869</b>	Peru: San Martín (113)	1149	–	This report
'Juruá'	UMMZ 176464	LLW884	Peru: San Martín (113)	1149	882	This report
<i>noctivagus</i> A	<b>FMNH 70946</b>	–	Colombia: Caquetá (62)	362	–	This report
<i>noctivagus</i> A	<b>QCAZ 8833</b>	<b>DFA410</b>	Ecuador: Morona-Santiago (74)	1149	888	This report
<i>noctivagus</i> A	<b>ROM 105316</b>	<b>F37644</b>	Ecuador: Napo (75)	1149	–	This report
<i>noctivagus</i> A	TTU 98590	TK73933	Peru: Loreto (103)	1149	–	This report
<i>noctivagus</i> A	<b>TTU 100924</b>	<b>TK73278</b>	Peru: Loreto (104)	1149	–	This report
<i>noctivagus</i> A	<b>LSU 28016</b>	<b>LJB2318</b>	Peru: Loreto (105)	1149	–	This report
<i>noctivagus</i> A	<b>KU 157961</b>	<b>RMT4047</b>	Peru: Loreto (107)	1149	–	This report
<i>noctivagus</i> A	KU 157967	RMT4068	Peru: Loreto (108)	1149	–	This report
<i>noctivagus</i> B	<b>UMMZ 176459</b>	<b>LLW879</b>	Peru: San Martín (113)	1149	–	This report
<i>noctivagus</i> B	UMMZ 176497	LLW917	Peru: San Martín (114)	1149	–	This report
<i>noctivagus</i> B	<b>FMNH 203327</b>	<b>PMV2353</b>	Peru: San Martín (116)	1149	882	This report
<i>noctivagus</i> C	AMNH 262402	NK14139	Bolivia: Pando (10)	1149	–	This report
<i>noctivagus</i> C	<b>AMNH 262404</b>	<b>NK13990</b>	Bolivia: Pando (11)	202	–	This report
<i>noctivagus</i> C	<b>MVZ 191194</b>	<b>JRM251</b>	Brazil: Amazonas (23)	1149	–	This report
<i>noctivagus</i> C	INPA 2931	MNFS381	Brazil: Amazonas (24)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	<b>MVZ 190275</b>	<b>JLP15353</b>	Brazil: Amazonas (24)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	<b>MVZ 190277</b>	<b>JLP15566</b>	Brazil: Amazonas (25)	1149	–	This report
<i>noctivagus</i> C	<b>USNM 545537</b>	–	Brazil: Mato Grosso (31)	1149	–	This report
<i>noctivagus</i> C	USNM 545538	–	Brazil: Mato Grosso (31)	1149	–	This report
<i>noctivagus</i> C	<b>USNM 545540</b>	–	Brazil: Pará (41)	416	–	This report
<i>noctivagus</i> C	USNM 588014	LHE1482	Peru: Cuzco (100)	1149	–	This report
<i>noctivagus</i> C	<b>FMNH 169786</b>	<b>BDP3775</b>	Peru: Cuzco (101)	424	–	This report
<i>noctivagus</i> C	<b>MVZ 173930</b>	<b>JLP13887</b>	Peru: Cuzco (96)	1149	–	This report
<i>noctivagus</i> C	<b>MVZ 173931</b>	<b>JLP13888</b>	Peru: Cuzco (96)	783	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	<b>MVZ 171408</b>	<b>JLP11895</b>	Peru: Cuzco (97)	1149	–	This report
<i>noctivagus</i> C	UMMZ 160470	PM4804	Peru: Cuzco (97)	791	–	This report
<i>noctivagus</i> C	MVZ 173932	JLP13905	Peru: Cuzco (98)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	MVZ 173933	JLP13906	Peru: Cuzco (98)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	MVZ 173934	JLP13947	Peru: Cuzco (98)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	MVZ 173935	JLP13948	Peru: Cuzco (98)	1149	–	Mustrangi & Patton (1997)
<i>noctivagus</i> C	<b>USNM 588013</b>	<b>LHE1473</b>	Peru: Cuzco (99)	1149	–	This report
<i>noctivagus</i> C	AMNH 272775	RSV2225	Peru: Loreto (106)	1149	–	This report
<i>noctivagus</i> C	AMNH 272782	RSV2242	Peru: Loreto (106)	1149	–	This report
<i>noctivagus</i> C	AMNH 272809	RSV2294	Peru: Loreto (106)	1149	–	This report
<i>noctivagus</i> C	MUSM 13289	RSV2224	Peru: Loreto (106)	1149	–	This report
<i>noctivagus</i> C	<b>MUSM 13292</b>	<b>RSV2131</b>	Peru: Loreto (106)	1149	882	This report
<i>noctivagus</i> C	<b>KU 144070</b>	<b>NW518</b>	Peru: Madre de Dios (109)	1149	–	This report
<i>noctivagus</i> C	KU 144085	NW737	Peru: Madre de Dios (109)	1149	–	This report

Table 2. Continued

Putative species	Voucher	Tissue	Locality	CYTB (bp)	BRCA1 (bp)	Source
<i>noctivagus</i> D	<b>AMNH 275451</b>	<b>NK30258</b>	Bolivia: Cochabamba (3)	1149	882	This report
<i>noctivagus</i> D	AMNH 275458	NK30333	Bolivia: Cochabamba (4)	414	–	This report
<i>noctivagus</i> D	<b>CBF 7527</b>	<b>CBF7527</b>	Bolivia: Cochabamba (2)	538	–	This report
<i>noctivagus</i> D	CBF 7560	TTS715	Bolivia: Cochabamba (2)	401	–	This report
<i>noctivagus</i> D	CBF 7573	CBF7573	Bolivia: Cochabamba (2)	1149	–	This report
<i>noctivagus</i> D	CBF 7577	TTS718	Bolivia: Cochabamba (2)	420	–	This report
<i>noctivagus</i> D	AMNH 268936	NK25272	Bolivia: La Paz (5)	551	–	Mustrangi & Patton (1997)
<i>noctivagus</i> D	AMNH 268937	NK25274	Bolivia: La Paz (5)	1149	–	This report
<i>noctivagus</i> D	<b>AMNH 275459</b>	<b>NK25203</b>	Bolivia: La Paz (5)	551	–	This report
<i>noctivagus</i> D	<b>AMNH 72561</b>	–	Bolivia: La Paz (8)	394	–	This report
<i>ocellatus</i>	<b>MSB 63275</b>	<b>NK21845</b>	Bolivia: Chuquisaca (1)	1149	–	This report
<i>ocellatus</i>	<b>MSB 58511</b>	<b>NK15126</b>	Bolivia: Santa Cruz (12)	764	–	Mustrangi & Patton (1997)
<i>ocellatus</i>	AMNH 261265	NK13053	Bolivia: Santa Cruz (13)	1149	–	This report
<i>ocellatus</i>	USNM 584467	LHE1573	Bolivia: Santa Cruz (14)	1149	–	This report
<i>ocellatus</i>	AMNH 275462	NK23270	Bolivia: Santa Cruz (15)	1149	–	This report
<i>ocellatus</i>	<b>USNM 581979</b>	<b>ECH7</b>	Bolivia: Santa Cruz (16)	1149	882	This report
<i>ocellatus</i>	<b>MSB 67021</b>	<b>NK22947</b>	Bolivia: Santa Cruz (17)	1149	–	This report
<i>ojastii</i>	<b>USNM 371299</b>	–	Venezuela: Falcón (125)	635	882	This report
<i>pakaraimae</i>	ROM 115129	F-46739	Guyana: Cuyuni-Mazaruni (82)	1149	–	Voss <i>et al.</i> (2013)
<i>pakaraimae</i>	<b>ROM 114698</b>	<b>F-46454</b>	Guyana: Potaro-Siparuni (85)	1149	–	Voss <i>et al.</i> (2013)
<i>pakaraimae</i>	ROM 115841	F-47080	Guyana: Potaro-Siparuni (86)	1149	882	Voss <i>et al.</i> (2013)
<i>parvidens</i>	ISEM V-1633	ISEM T-3832	French Guiana: Les Nouragues (79)	800	–	This report
<i>parvidens</i>	AMNH 267817	LHE1161	French Guiana: Paracou (80)	800	–	This report
<i>parvidens</i>	<b>ISEM V-1399</b>	–	French Guiana: Paracou (80)	799	–	Steiner & Catzefflis, 2004
<i>parvidens</i>	ISEM V-1581	–	French Guiana: Paracou (80)	1149	–	Steiner & Catzefflis, 2004
<i>parvidens</i>	MNHN1998-1830	–	French Guiana: Saint-Eugène (81)	645	–	Steiner & Catzefflis, 2004
<i>parvidens</i>	<b>ROM 97938</b>	<b>FN-33439</b>	Guyana: Upper Takutu-Upper Essequibo (87)	645	882	This report
<i>parvidens</i>	<b>ROM 114144</b>	<b>F-41219</b>	Surinam: Brokopondo (118)	1149	–	Voss <i>et al.</i> (2013)
<i>parvidens</i>	ROM 114299	F-41329	Surinam: Brokopondo (118)	755	–	Steiner & Catzefflis, 2004
<i>parvidens</i>	ROM 114322	F-41352	Surinam: Brokopondo (118)	773	–	Steiner & Catzefflis, 2004
<i>parvidens</i>	<b>ROM 117348</b>	<b>F-54669</b>	Surinam: Sipaliwini (121)	1149	–	This report
<i>paulensis</i> A	–	<b>MP405</b>	Brazil: Minas Gerais (34)	1149	882	This report
<i>paulensis</i> A	–	<b>YL19</b>	Brazil: Minas Gerais (35)	782	–	Mustrangi & Patton (1997)
<i>paulensis</i> B	<b>MZUSP 29184</b>	<b>MAM475</b>	Brazil: Rio de Janeiro (43)	371	–	Mustrangi & Patton (1997)
<i>paulensis</i> B	<b>MZUSP 29185</b>	<b>MAM481</b>	Brazil: Rio de Janeiro (43)	1139	–	Mustrangi & Patton (1997)
<i>paulensis</i> B	<b>Uncatalogued</b>	<b>EEB1021</b>	Brazil: São Paulo (44)	247	705	This report
<i>paulensis</i> C	MVZ 182059	MAM25	Brazil: São Paulo (45)	1149	–	This report
<i>paulensis</i> C	<b>MVZ 183243</b>	<b>JLP16216</b>	Brazil: São Paulo (45)	1149	–	Voss <i>et al.</i> (2013)
<i>paulensis</i> C	<b>MVZ 183244</b>	<b>JLP16217</b>	Brazil: São Paulo (45)	1149	882	This report
<i>paulensis</i> C	<b>MZUSP 29166</b>	<b>MAM20</b>	Brazil: São Paulo (45)	376	–	Mustrangi & Patton (1997)
<i>paulensis</i> C	MZUSP 29167	MAM31	Brazil: São Paulo (45)	787	–	Mustrangi & Patton (1997)
<i>paulensis</i> C	MZUSP 29168	MAM32	Brazil: São Paulo (45)	399	–	Mustrangi & Patton (1997)
<i>paulensis</i> C	MZUSP 29169	MAM33	Brazil: São Paulo (45)	385	–	Mustrangi & Patton (1997)
<i>pinheiroi</i>	–	<b>ISEM V-955</b>	French Guiana: Les Nouragues (79)	800	–	Steiner & Catzefflis, 2004
<i>pinheiroi</i>	<b>ROM 108920</b>	<b>F-43900</b>	Guyana: Potaro-Siparuni (83)	1149	–	Voss <i>et al.</i> (2013)
<i>pinheiroi</i>	<b>ROM 111558</b>	<b>F-44687</b>	Guyana: Potaro-Siparuni (84)	799	–	Steiner & Catzefflis, 2004
<i>pinheiroi</i>	<b>ROM 114318</b>	<b>F-41348</b>	Surinam: Brokopondo (118)	800	–	Steiner & Catzefflis, 2004
<i>pinheiroi</i>	<b>CM 63506</b>	<b>TK10169</b>	Surinam: Nickerie (119)	1149	882	Voss <i>et al.</i> (2013)
<i>pinheiroi</i>	ROM 116974	F-54337	Surinam: Sipaliwini (120)	1149	–	Voss <i>et al.</i> (2013)
<i>ucayaliensis</i>	<b>KU 144088</b>	<b>NW509</b>	Peru: Madre de Dios (109)	1149	882	This report

**Table 2.** *Continued*

Putative species	Voucher	Tissue	Locality	<i>CYTB</i> (bp)	<i>BRCA1</i> (bp)	Source
<i>ucayaliensis</i>	KU 144090	RMT3920	Peru: Madre de Dios (109)	1149	–	This report
<i>ucayaliensis</i>	<b>AMNH 230025</b>	–	Peru: Pasco (111)	362	–	This report
<i>ucayaliensis</i>	AMNH 230027	–	Peru: Pasco (111)	362	–	This report
<i>ucayaliensis</i>	AMNH 76532	–	Peru: Ucayali (117)	194	–	This report
'West Magdalena'	<b>CTUA 434</b>	<b>CACE004</b>	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
<i>woodalli</i>	<b>USNM 549294</b>	<b>MDC589</b>	Brazil: Pará (39)	1149	882	Voss <i>et al.</i> (2013)
<i>woodalli</i>	<b>USNM 545543</b>	–	Brazil: Pará (40)	421	–	Voss <i>et al.</i> (2013)
<b>Outgroups</b>						
<i>Cryptonanus unduaviensis</i>	AMNH 262401	NK14234	Bolivia: Pando, Independencia	1149	888	This report
<i>Didelphis marsupialis</i>	USNM 578138	FMG2573	Panama: Bocas Del Toro, Peninsula Valiente, Punta Alegre	1149	879	This report
<i>Gracilinanus microtarsus</i>	MVZ 182055	MAM38	Brazil: São Paulo, Fazenda Intervalles, Capao Bonito	1149	888	This report
<i>Lestodelphis halli</i>	CNP 889	CNP889		1149	887	Giarla <i>et al.</i> (2010)
<i>Marmosa murina</i>	USNM 549291	LHE503	Brazil: Pará, 52 km SSW Altamira, E Bank Rio Xingu	1146	885	This report
<i>Metachirus nudicaudatus</i>	MUSM 13293	RSV2329	Peru: Loreto, Rio Gálvez	1149	882	Giarla & Jansa (2014)
<i>Monodelphis arlindoi</i>	CM 68359	TK17069	Surinam: Nickerie, Kayserberg Airstrip	1146	882	This report
<i>Thylamys pallidior</i>	OMNH 23482	ARG43	Argentina: Mendoza	1149	884	This report

*BRCA1*, breast cancer activating 1; *CYTB*, cytochrome *b*.

species, we sequenced multiple specimens, and we 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, we 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, we obtained partial or complete *CYTB* sequences for 31 nominal forms of *Marmosops*: five sequences from holotypes, one from a paratype, and 25 from topotypical material (see below). To further increase our ingroup geographical sampling, we downloaded an additional 62 *CYTB* sequences from GenBank and other sources to create a total mtDNA data set of 213 sequences. We 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 we also obtained a *BRCA1* sequence from *Marmosops juninensis*, a species from which we were unable to amplify *CYTB*. For all of our

phylogenetic analyses, we obtained *CYTB* and/or *BRCA1* sequences from other members of the tribe Thylamyini and more distantly related didelphids for use as outgroups (Table 2).

In order to associate haplogroups (putative species; see below) with named taxa, we 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 & Jansa (2009), and Díaz-Nieto *et al.* (2011). Haplogroups that could not be confidently associated with Latin epithets were provisionally labelled with geographical or alphabetical designations.

#### LABORATORY METHODS AND SEQUENCE ALIGNMENT

Methods for DNA extraction from preserved tissue and dried museum specimens followed Voss & Jansa (2009) and Giarla *et al.* (2010), respectively. For DNA of high molecular weight (extracted from preserved tissue), we 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), we developed internal primers to sequence *CYTB* as six overlapping fragments (c. 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 (c. 500 bp each). Primers for all loci are listed in Table S1. For *CYTB* we 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 v. 4.8 (Gene Codes Inc.) and aligned using the default settings of MUSCLE (Edgar, 2004) in GENEIOUS PRO v. 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 (Table S2).

#### PUTATIVE SPECIES DELIMITATION BASED ON *CYTB* SEQUENCES

We 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). We conducted four independent ML searches in GARLI 2.0 (Zwickl, 2006) and evaluated nodal support based on bootstrap analyses of 1000 pseudoreplicated data sets with the same parameters as the initial searches. Bootstrap support (BS) values were summarized on the ML tree using SUMTREES v. 3.3.1 (Sukumaran & Holder, 2010). BI was implemented in MrBayes v. 3.2 (Ronquist *et al.*, 2012) by running two independent Markov chain Monte Carlo (MCMC) analyses for 50 000 000 generations each, sampling every 5000 generations and including one cold chain and three heated chains. To ensure convergence, the results of the MCMC runs were inspected in TRACER v. 1.5 (Rambaut & Drummond, 2007) and AWTY (Nylander *et al.*, 2008). We discarded the first 50% of trees of each run as burn-in and combined the remaining trees into a final set of 10 000 trees. Tree topology, mean log-likelihood value, nodal support (posterior probability, PP), and remaining parameters were summarized in a maximum-clade-credibility tree with TreeAnnotator v. 1.7.2 (Drummond *et al.*, 2012).

To identify putative species, we 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 & Carstens, 2012). To avoid confusion, we refer to the general model developed by Pons *et al.* (2006) as GMYC, we use 'LGMYC' for its likelihood implementation in SPLITS, and we use 'BGMYC' for the Bayesian version. GMYC methods delimit putative species by estimating the point of transition between intra- and interspecific 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 MCMC simulation to account for error in phylogenetic estimation and uncertainty of model parameters (e.g. tree topology and branch lengths; Pons *et al.*, 2006; Reid & Carstens, 2012). For the purposes of this report, we 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. We associate species names with these putative species based on routine taxonomic criteria (genetic or morphological similarity with type material) whenever possible.

As it has been shown that the accuracy of GMYC methods is compromised by the presence of duplicate haplotypes (Monaghan *et al.*, 2009; Fujisawa & Barraclough, 2013) we only used unique haplotypes across the aligned region (129 terminals; Table 2). All of our 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 intralinear haplotype dynamics) (Pons *et al.*, 2006). We did not implement the LGMYC analyses allowing multiple shifts across the phylogeny because – based on empirical and simulated data sets – it has been demonstrated that such analyses have a strong tendency to overestimate the diversity of a clade (Fujisawa & Barraclough, 2013). For BGMYC we first evaluated the MCMC parameters and appropriate burn-in value by checking the likelihood plots of the 'single.phy' option (Reid & Carstens, 2012) using the maximum clade credibility tree from BEAST v. 1.7.2 (Drummond *et al.*, 2012; see below). Subsequently we obtained 100 random trees from the posterior distribution of the BEAST analyses using the R (R Core Team, 2015) package APE (Paradis, Claude & Strimmer, 2004) and ran the program for 50 000 generations, sampling every 100 generations and discarding the first 40 000 trees as burn-in, giving a total of 10 000 retained trees.

To implement the LGMYC and BGMYC analyses we constructed an ultrametric tree in BEAST using a log-normal 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). We ran two independent MCMC analyses



**Table 3.** Optimal partitioning scheme and substitution models for the two-gene concatenated data set (*BRCA1* + *CYTB*). Parameters = 119, aligned sites = 2046, Bayesian information criterion = 34290.67

Partition	Best model	Characters
1	HKY + $\Gamma$	<i>BRCA1</i> position 1, <i>BRCA1</i> position 2
2	HKY	<i>BRCA1</i> position 3
3	SYM + I + $\Gamma$	<i>CYTB</i> position 1
4	HKY + I + $\Gamma$	<i>CYTB</i> position 2
5	GTR + I + $\Gamma$	<i>CYTB</i> position 3

*BRCA1*, breast cancer activating 1; *CYTB*, cytochrome b; GTR, generalized time reversible model; HKY, Hasegawa-Kishino-Yano model; I, proportion of invariant sites; SYM, symmetrical model;  $\Gamma$ , gamma-distributed rate variation.

for 50 000 000 generations each, sampling every 5000 generations. Analyses of convergence, burn-in, 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, Pfeiffer & Schwartz, 2010). We estimated uncorrected (*p*-) and model-corrected genetic distances within and amongst putative species using MEGA5 (Tamura *et al.*, 2011).

#### PHYLOGENETIC ANALYSES OF *BRCA1* AND *BRCA1* + *CYTB*

We analysed two additional matrices to reconstruct phylogenetic relationships amongst putative species of *Marmosops*, one that included only *BRCA1* sequences and another that added *CYTB* sequences from the same taxa. The nuclear exon *BRCA1* was analysed using ML and BI methods as previously described for the *CYTB* data set (see above), with the exception that each of the two independent MCMC analyses were run for 1 000 000 generations, sampling every 100 generations. We 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 v. 3.2 (Ronquist *et al.*, 2012), respectively. We estimated the best data-partitioning scheme and substitution model(s) using the BIC as implemented in PartitionFinder v. 1.0 (Lanfear *et al.*, 2012) with unlinked branch lengths and the greedy algorithm search strategy (Table 3). For MrBayes we ran two independent MCMC analyses for 20 000 000 generations each, sampling every 2000 generations, including one cold chain and three heated chains. All subsequent steps of the BI analyses (i.e. convergence, burn-in, and summarization) followed those previously described for the *CYTB* dataset.

## RESULTS

### PHYLOGENETIC ANALYSES AND SPECIES DELIMITATION BASED ON *CYTB* SEQUENCE DATA

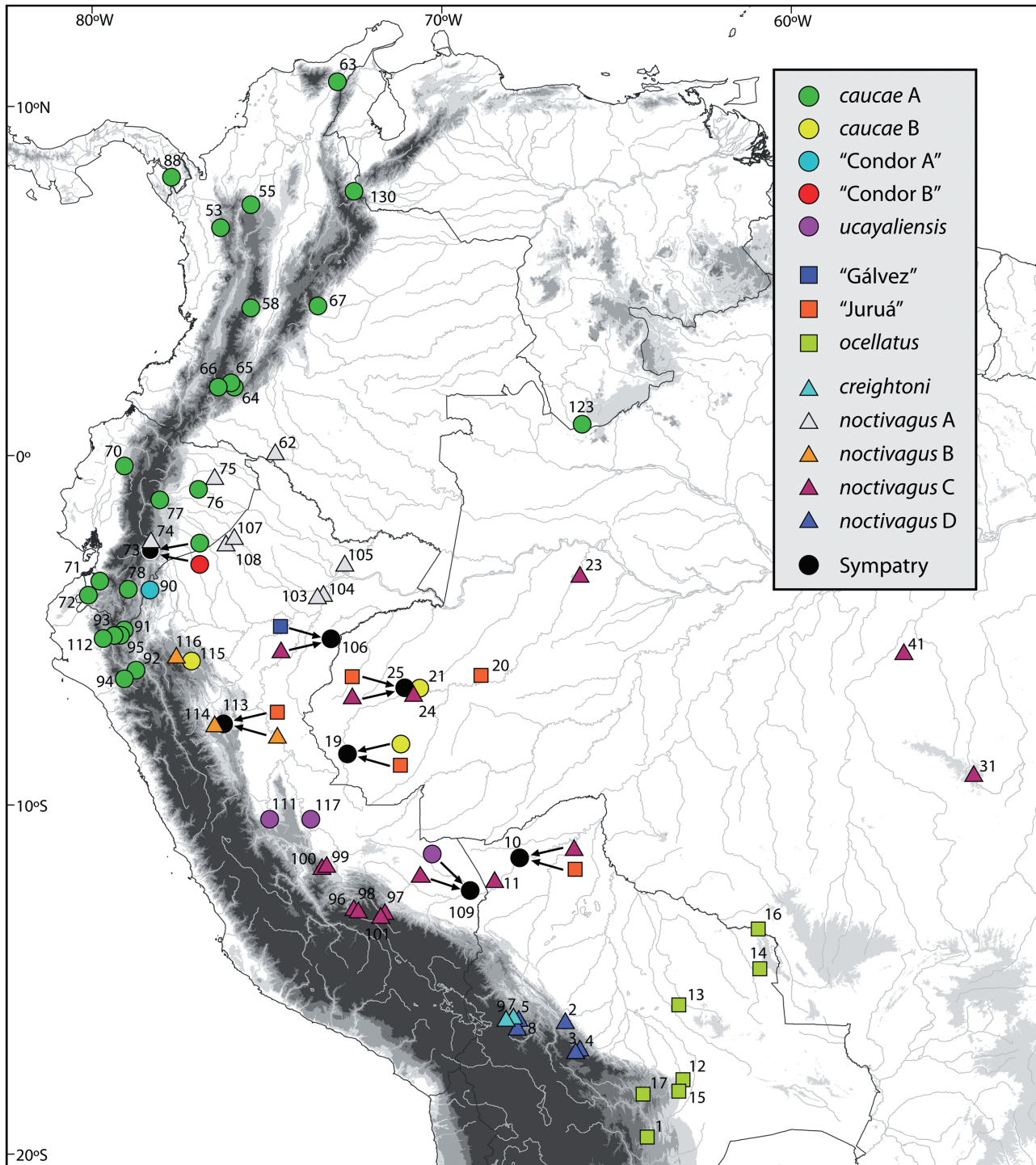
Our final *CYTB* matrix contained 213 *Marmosops* sequences from 131 localities plus eight outgroup sequences; analysed *CYTB* sequences ranged in length from 194 to 1149 bp, representing 77.2% nucleotide coverage overall (Figs 1–3, Table 2). We were unable to obtain any *CYTB* sequence from *M. juninensis* because we consistently co-amplified a nuclear pseudogene from our only available sample (a scrap of dried skin). The best-fit nucleotide substitution model for all of our mitochondrial analyses was a generalized time reversible model with gamma-distributed rate variation and a proportion of invariant sites.

Salient features of our *CYTB* analyses (Figs 4, S1, S2) are (1) strong support for the monophyly of *Marmosops*, and (2) a basal dichotomy within the genus between two robustly supported clades that we 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 Fig. 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 amongst the sequences referable to *Marmosops paulensis* of current usage, whereas only two such clades were recovered by BGMYC.

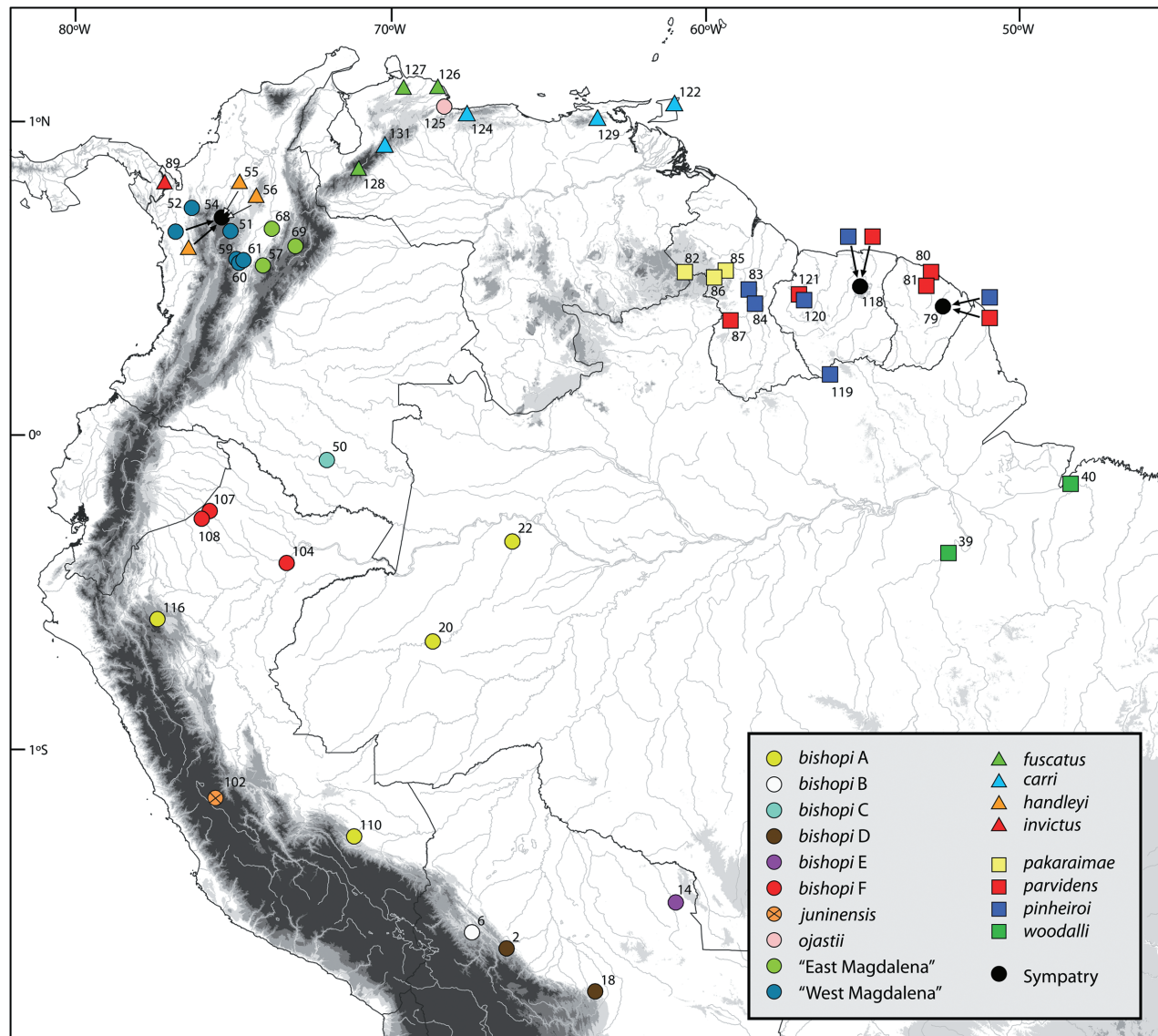
Although many of the taxa recognized by recent authors (e.g. Gardner & Creighton, 2008; Voss & Jansa, 2009; Voss *et al.*, 2013) were recovered as well-supported (PP  $\geq$  0.95; BS  $\geq$  75%), reciprocally monophyletic groups that correspond to putative species according to the LGMYC and BGMYC analyses, there are important exceptions. *Marmosops 'impavidus'* (*sensu* Gardner & Creighton, 2008; Voss & Jansa, 2009), for example, includes five putative species (*cauca* A, *cauca* B, *ucayaliensis*, 'Gálvez,' and 'Juruá') that do not form a monophyletic group. Other currently recognized species (e.g. *Marmosops bishopi* and *Marmosops 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 (labelled by geographical descriptors in Fig. 4) lack available names.

### PHYLOGENETIC RELATIONSHIPS

Both the ML and BI analyses of *CYTB* sequences recovered a monophyletic *Marmosops*, and most nodes



**Figure 1.** Collection localities for sequenced specimens of subgenus II of *Marmosops*. Progressively darker shading indicates the following elevations: pale grey  $\geq 500$  m, medium grey  $\geq 1000$  m, dark grey  $\geq 2000$  m, and darkest grey  $\geq 3000$  m.

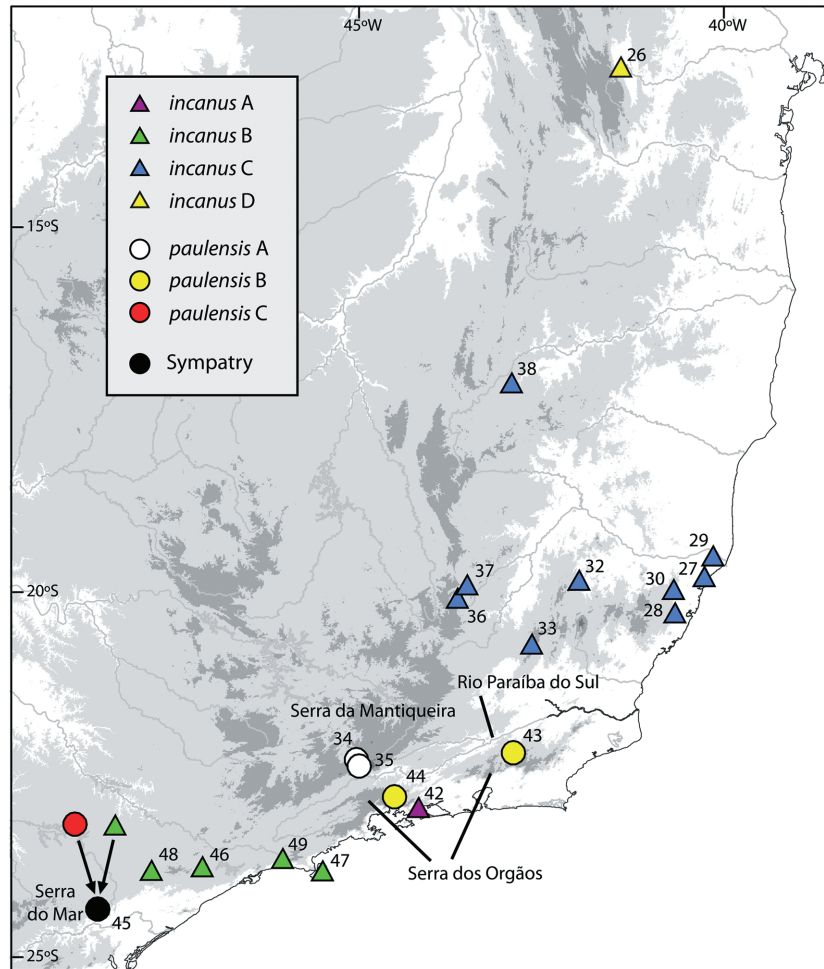


**Figure 2.** Collection localities for sequenced specimens of subgenus I of *Marmosops*. Progressively darker shading indicates the following elevations: pale grey  $\geq 500$  m, medium grey  $\geq 1000$  m, dark grey  $\geq 2000$  m, and darkest grey  $\geq 3000$  m.

representing phylogenetic relationships amongst 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 multispecies 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 biogeographical analyses. To corroborate and extend these results, additional sequence data from other loci are clearly needed.

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 we obtained from our analyses of *CYTB* (Fig. 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). We were 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





**Figure 3.** Collection localities for sequenced specimens of Atlantic Forest species included in subgenus II of *Marmosops*. Progressively darker shading indicates the following elevations: pale grey  $\geq 500$  m, medium grey  $\geq 1000$  m, and dark grey  $\geq 2000$  m.

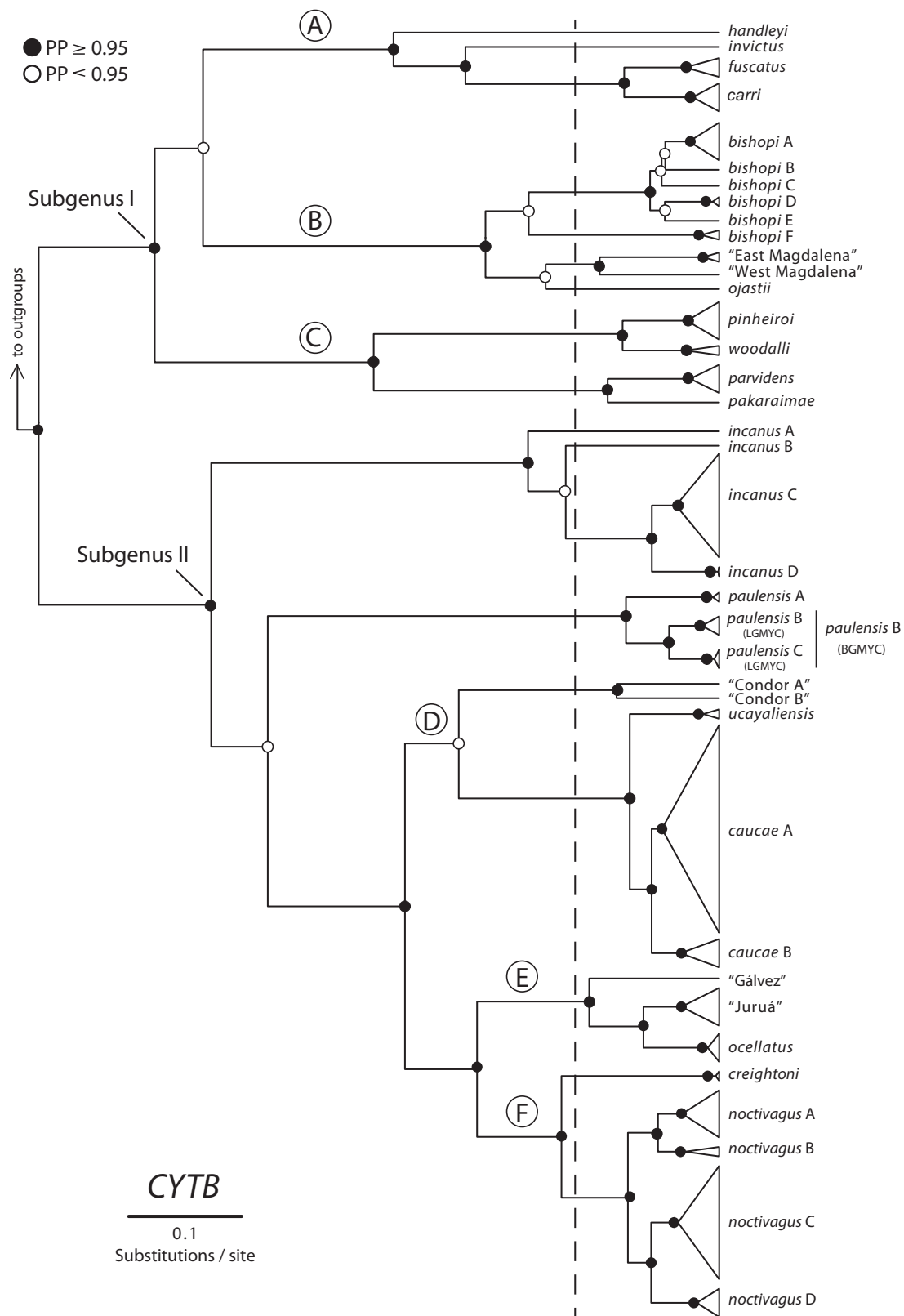
**Figure 4.** BEAST ultrametric tree based on *cytochrome b* (CYTB) sequences with putative species (as cartooned terminals). Dashed vertical line shows the threshold between Yule and coalescent branching processes as estimated by the likelihood implementation of the general mixed Yule coalescent model (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 [posterior probability (PP)  $\geq 0.95$ ]. Abbreviation: BGMYC, Bayesian implementation of the GMYC.

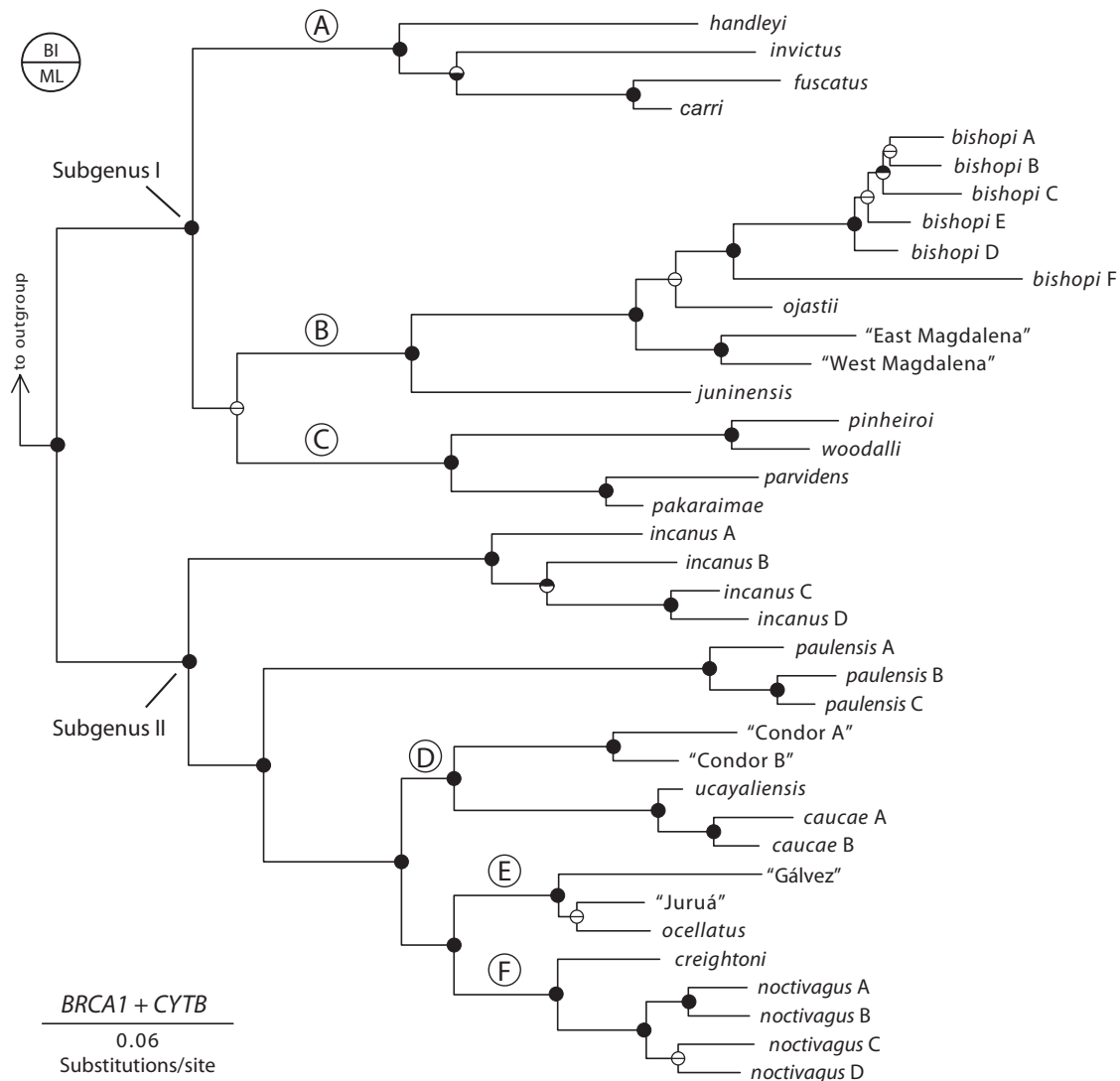
of these three groups (Clades A, B, and C) is strongly supported, the relationships amongst them are not. Additionally, the relationships of *ojastii* and relationships within the *bishopi* complex cannot be convincingly resolved with these data, and the position of *invictus* within Clade A is only 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 [cytochrome *b* + breast cancer activating 1 (*CYTB* + *BRCA1*)] data set. Terminals are putative species recovered by general mixed Yule coalescent model analyses of *CYTB* plus *Marmosops juninensis* (uniquely represented by a *BRCA1* sequence). Filled semicircles at internal nodes indicate high support (posterior probability  $\geq 0.95$ , bootstrap  $\geq 75\%$ ). Abbreviations: BI, Bayesian inference; ML, maximum likelihood.

## DISCUSSION

### ASSESSMENT OF SPECIES-LEVEL DIVERSITY AND PHYLOGENETICS IN *MARMOSOPS*

A recent overview of opossum systematics (Voss & 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 & 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'. The present study is the first to assess intra- and interspecific variation for *Marmosops* by sequencing representatives of all currently recognized species and by including multiple individuals from many widespread taxa. Our 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 phy-

logeny shifts from interspecific (Yule) to intraspecific (coalescent) processes; therefore, 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 & 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 & Barraclough, 2013). When implementing the likelihood version of GMYC with our 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 & Carstens, 2012). By contrast, the Bayesian implementation of GMYC takes uncertainty of the parameters and phylogenetic error into account. Additionally, in our application, BGMYC suggests that the coalescent branching rate is substantially larger than the Yule rate: the mean values that we 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 (Fig. 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 & 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 & Barraclough, 2013). Although our current data set does not include relevant genetic data from other loci, we consider morphology and geographical distributions in the following taxonomic accounts, which discuss the possibility that some putative species delimited by GMYC methods might actually be evolutionarily independ-

ent lineages (valid species). In effect, our 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.

Our 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 geographical distributions. Based just on the samples analysed for this report (Figs 1–3), members of subgenera I and 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 south-eastern Brazil. These distributions, together with an estimated divergence age of about 9 000 000 years – based on the time tree in Jansa, Barker & Voss (2014) – and a consistent difference in mean body size between members of the two subgenera where they occur sympatrically (e.g. Patton *et al.*, 2000; Díaz-N *et al.*, 2011; Hice & Velazco, 2012), suggest a long independent history of geographical 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 we provide a new name below.

Additionally, these accounts justify our assignment of nominal taxa to each subgenus based on morphological, geographical, and/or molecular criteria. Although we 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.

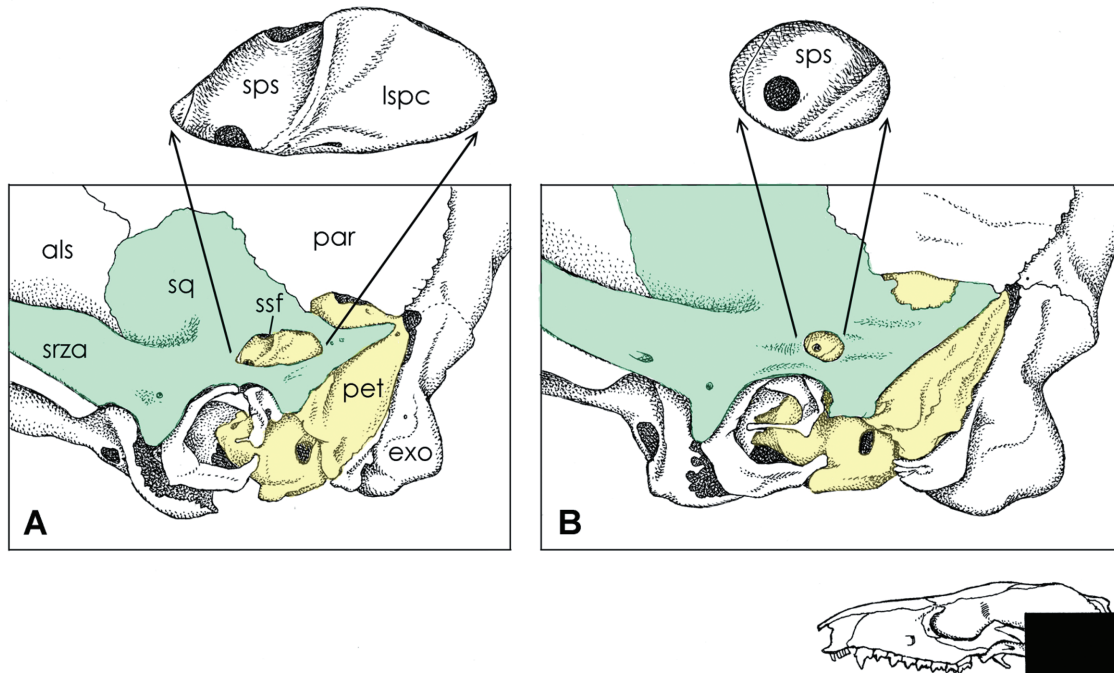
### *SCIOPHANES* SUBGEN. NOV.

#### *Type species*

*Marmosops parvidens* (Tate, 1931).

#### *Included taxa*

We refer 12 nominal taxa to *Sciophanes*: *bishopi* Pine, 1981; *carri* Allen & Chapman, 1897; *cracens* Handley



**Figure 6.** Lateral view of posterior braincase of *Marmosops (Sciophanes) pinheiroi* (A, AMNH 267345) and *Marmosops (Marmosops) 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 canicularis (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.

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 & Creighton, 2008), but our examination of the holotype suggests that this name is a junior synonym of *Marmosops cauae* (a member of the nominotypical subgenus, see below).

#### Diagnosis

Specimens that we refer to the subgenus *Sciophanes* can be distinguished morphologically from those that we refer to the nominotypical subgenus by their shared possession of an anteroposteriorly elongated subsquamosal foramen, accessory upper canine cusps, and two antibrachial 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 (Fig. 6). In *Sciophanes*, the subsquamosal foramen 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 canicularis behind that groove. [See Wible (2003) for a detailed description and illustrations of didelphid petrosal morphology.] By contrast, the subsquamosal foramen 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 amongst the tissue vouchers and examined type material that we refer to *Sciophanes* on the one hand and to the subgenus *Marmosops* on the other.

All species of *Sciophanes* also have accessory upper canine (C1) 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 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: fig. 23). Although the 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. [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, amongst them LSU 25902 (a juvenile male) and two young adult females described by (Peralta & Pacheco, 2014), all have distinct posterior accessory cusps on C1.] Based on the material that we 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 antibrachial vibrissae, long tactile hairs on the dorsolateral surface of the forearm, by contrast with the single antibrachial vibrissa normally found in most species of the subgenus *Marmosops* (Díaz-N *et al.*, 2011: fig. 5). The only exceptional species of the latter clade known to us is *Marmosops (Marmosops) ocellatus*, most examined specimens of which appear to have two antibrachial 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; amongst other material unambiguously referable to this species, the validity of which is clearly supported by our analyses, we sequenced a paratype (FMNH 69823). Our unique sequence of *invictus*, one of only two species of *Marmosops* known to occur in Panama, was obtained from a specimen that we compared directly with Goldman's (1912) type material, which it closely resembles in all relevant external and craniodental details; the very large *CYTB* distances between 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 we sequenced both the holotype (USNM 418503) and a paratype (USNM 442719) of *cracens* from the Caribbean coast of northern Venezuela, we 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). We use *carri* (previously considered to be a synonym of *fuscatus*; e.g. by Gardner & Creighton, 2008) for sequences that we obtained from Trinidad (the type locality of *carri*) and from the adjacent Venezuelan mainland. The *CYTB* sequences that we refer to *fuscatus* (including *cracens*) and *carri* are substantially divergent (4.9%, uncorrected), and relevant voucher material is unambiguously distinguishable by dental measurements, so we 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. Our unique *BRCA1* sequence of *juninensis* was obtained from a specimen collected near the Peruvian type locality (in Junín department), and which we compared directly with the holotype (AMNH 63864). We have not personally examined type material of *ojastii*, but the sequence that we 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 *M. bishopi*. These taxonomically problematic lineages differ from one another by 3.5 to 11.3% in mean uncorrected *CYTB* sequence comparisons (Table S3) and, in default of available names, we distinguish them by alphabetical labels. *Marmosops bishopi* is based on a specimen from central Brazil that closely resembles voucher material of 'bishopi E', the haplogroup to which the epithet might apply 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 zoogeographical 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 (J. F. Díaz-Nieto, R. S. Voss & S. A. Jansa, unpubl. data), we regard them as valid species.

Clade C has received some revisionary attention, most recently from Voss *et al.* (2013), who analysed morphological data and *CYTB* sequences to establish *pakaraimae*, *parvidens*, and *pinheiroi* as valid species. Our samples from this clade are identical to theirs, and include several sequences from the type series of *pakaraimae*. Identifications of sequences that we 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 we 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 we are not aware of any consistent phenotypic character by which these nominal taxa can be distinguished. We are, therefore, inclined to regard *pinheiroi* and *woodalli* as conspecific.

### Etymology

From the ancient Greek (σκιοφανής) for shadowy or phantom-like, in reference to the elusive habits of these small forest creatures.

### SUBGENUS *MARMOSOPS* MATSCHIE, 1916

#### Type species

*Marmosops incanus* (Lund, 1840).

#### Included taxa

We refer 25 nominal taxa to the subgenus *Marmosops*: *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 definitely 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 north-eastern Peru is inconsistent with Tschudi's type locality. In our opinion, *impavidus* is best regarded as a *nomen dubium* and should be retired from taxonomic service.

#### Remarks

The sequences that we identify as *incanus* are from south-eastern Brazilian material that exhibits the diagnostic morphological traits of *M. incanus* as described and illustrated by Mustrangi & Patton (1997). As in their study, we found substantial geographically structured *CYTB* sequence divergence amongst *incanus*-like specimens, which GMYC analysis suggests represent four putative species (differing by 4.2–10.8%, on average, in uncorrected pairwise comparisons). Although we use alphabetical designations for these haplogroups, the type locality of *incanus* (Lagoa Santa, in Minas Gerais) falls within the geographical 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) seem 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, we apply the name *paulensis* to specimens from south-eastern Brazil that share the diagnostic morphological traits of *M. 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 Orgãos, '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 Orgãos, 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 we 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 north-eastern Peru and from the immediately adjacent Cordillera Oriental of southern Ecuador. No name is available for either putative species, which we distinguish alphabetically. Sequenced specimens of 'Condor A' and 'Condor B' were collected over 1700 m a.s.l. on opposite sides of the Río Zamora, and their *CYTB* sequences differ by about 7.5% (uncorrected) – an impressive difference for material obtained only 98 km apart on a straight line – but we 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 our analyses. Our 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 S4) putative species. The name *caucae* is based on a Colombian specimen that morphologi-

cally resembles all of the referred material that we 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 we 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 on a straight line distance to our material of ‘*caucae* B’ (e.g. locality 115, Fig. S3) but the type was collected at a much higher elevation. [The type locality of *madescens* is in the highlands at approximately 2700 m a.s.l., whereas geographically adjacent material of ‘*caucae* B’ was collected in the lowlands (below 815 m).] Consequently, we are 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 south-eastern 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; Fig. S3) might be a senior synonym. The average pairwise uncorrected difference between *CYTB* sequences of *caucae* (including haplogroups A and B) and *ucayaliensis* is just 3.9%, and we are not aware of any consistent morphological differences amongst relevant voucher specimens. In effect, there is, as yet, no compelling evidence that these are distinct species.

Clade E consists of two putative species that lack available names (‘Gálvez’ and ‘Juruá’) and a third that corresponds to *M. 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 that they called *Marmosops impavidus*), which might be valid species despite modest sequence divergence (4.2%, uncorrected). ‘Juruá’ and ‘Gálvez’ differ by an average pairwise *CYTB* 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 we 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 four putative species that collectively correspond to *Marmosops noctivagus* of current usage (*sensu* Gardner & Creighton, 2008). We use alphabetical 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 geographical ranges of ‘*noctivagus* B’ and ‘*noctivagus* C’. As we 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 geographical 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. Our 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).

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## APPENDIX

This gazetteer includes all localities from which we analysed 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). Geographical coordinates (decimal degrees) and elevation (m a.s.l., m) are provided in parentheses with a cited source for these data. The elevations given in bold 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, pers. comm.).
8. *La Paz*, Río Unduavi, Pitiguaya, La Florida (c. –16.3500, –67.7833, 1785 m; Anderson, 1997).
9. *La Paz*, Saynani hydroelectric plant, on south-east 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, c. 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, c. 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, c. **250 m**; Patton *et al.*, 2000).
20. *Amazonas*, Barro Vermelho, left bank Rio Juruá (–6.4667, –68.7667, c. **117 m**; Patton *et al.*, 2000).
21. *Amazonas*, Igarapé Nova Empresa, left bank Rio Juruá (–6.8000, –70.7333, c. **150 m**; Patton *et al.*, 2000).
22. *Amazonas*, Ilhazinha, left bank Rio Juruá on Igarapé Arabidi, affluent of Paran  Breu (–3.2833, –66.2333, c. **76 m**; Patton *et al.*, 2000).



23. *Amazonas*, Lago Vai-Quem-Quer, right bank Rio Juruá (−3.3167, −66.0167, c. **55 m**; Patton *et al.*, 2000).
24. *Amazonas*, Penedo, right bank Rio Juruá (−6.8333, −70.7500, c. **150 m**; Patton *et al.*, 2000).
25. *Amazonas*, Seringal Condor, left bank Rio Juruá (−6.7500, −70.8500, c. **190 m**; Patton *et al.*, 2000).
26. *Bahia*, Fazenda Santa Rita, 8 km E Andaraí (−12.8017, −41.2614, 399 m; MVZ database, accessed April 2013).
27. *Espírito Santo*, Forest fragments of Aracruz Celulose Company, Santa Cruz, Município 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*, Estação Biológica de Santa Lucia, Santa Teresa (−19.9600, −40.5400, 650 m; Agrizzi *et al.*, 2012).
31. *Mato Grosso*, Aripuanã (−9.1700, −54.7000, c. **660 m**; USNM database, accessed April 2013).
32. *Minas Gerais*, Minas Gerais, Estação 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, c. **1160 m**; Edson Fiedler de Abreu Júnior, pers. comm.).
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*, Estação 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, c. **130 m**; USNM database, accessed April 2013).
40. *Pará*, Belém (−1.4500, −48.4833, c. **77 m**; Paynter & Traylor, 1991).
41. *Pará*, Itaituba, Transamazonica Hwy., Itaituba-Jacareacanga, km. 212 (−5.6700, −56.7500, c. **160 m**; USNM database, accessed April 2013).
42. *Rio de Janeiro*, private lands of Cia. Mineradoras Brasileiras Reunidas, Ibicui, Município 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, Município de Sumidouro (−22.2000, −42.7333, 1000 m; Mustrangi & Patton, 1997).
44. *São Paulo*, Estação Ecológica de Bananal, Bananal (−22.8056, −44.3639, 1200 m; Edson Fiedler de Abreu Júnior, pers. comm.).
45. *São Paulo*, Base do Carmo, Fazenda Intervalles, 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, c. **714 m**; Google Earth).
49. *São Paulo*, Estação Biológica de Boracéia, Museu Zoologia da USP, Município 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, pers. comm.).
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, 9 km 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, 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, c. **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, 1993).
72. *Loja*, Celica (-4.1167, -79.9833, 2103 m; Paynter, 1993).
73. *Morona-Santiago*, Agua Rica (-3.0093, -78.5030, 2050–2300 m; specimen label).
74. *Morona-Santiago*, Rosario (-2.9094, -78.3995, c. **1000 m**; specimen label).
75. *Orellana*, Parque Nacional Yasuní, Onkone Gare, 38 km S Pompeya Sur (-0.6500, -76.4500, c. **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, c. 45 m; Simmons & Voss, 1998).

81. Saint-Eugène (4.8500, -53.0667, c. **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, c. **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; Mustringi & Patton, 1997).

## PANAMA

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

## PERU

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, c. **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 Montesecco (-6.5593, -79.0017, c. 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*, 2 km NE Amaybamba (-13.0503, -72.4407, 2000 m; MVZ database, accessed April 2013).
97. *Cuzco*, 72 km 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; Mustringi & Patton, 1997).
99. *Cuzco*, La Convención Province, Tangoshiari (-11.7667, -73.3258, c. 500 m; Emmons, Luna & Romo, 2001).

100. *Cuzco*, La Convención Province, Tangoshiari 2 km SW (−11.7797, −73.3408, c. 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, 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, c. 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, pers. comm.).
114. *San Martín*, Bella Vista, Alto Biabo, Parque Nacional Cordillera Azul ‘Shushupe’ (−7.7474, −76.3591, 930 m; Lucia Luna, pers. comm.).
115. *San Martín*, Moyobamba, Tingana (−5.9107, −77.1120, 815 m; Paúl M. Velazco, pers. comm.).
116. *San Martín*, Rioja, Pardo Miguel, Naranjos, Caserio El Diamante (−5.7534, −77.5261, 1078 m; Paúl M. Velazco, pers. comm.).
117. *Ucayali*, Alto Ucayali, Lagarto (−10.5972, −73.8778, c. **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, c. **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, c. 14 km NW Maracay, Estación Biológica de Rancho Grande, El Portachuelo (10.3500, −67.6830, 1100–1150 m; Robert P. Anderson, pers. comm.).
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, pers. comm.).
128. *Mérida*, Mérida (8.600, −71.1333, 1600; Paynter, 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).

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Relationships amongst *cytochrome b* sequences of *Marmosops* subgenus I recovered by Bayesian inference (BI). Terminals are identified by country and state/department/province of origin, locality number (in

parentheses; see Appendix), and an alphanumeric specimen identifier (see Table 2). Values above branches correspond to nodal support recovered by independent BI and maximum likelihood analyses (posterior probability/bootstrap).

**Figure S2.** Relationships amongst *cytochrome b* sequences of *Marmosops* subgenus II recovered by Bayesian inference (BI). Terminals are identified by country and state/department/province of origin, locality number (in parentheses; see Appendix), and an alphanumeric specimen identifier (see Table 2). Values above branches correspond to nodal support recovered by independent BI and maximum likelihood analyses (posterior probability/bootstrap).

**Figure S3.** Map of collecting localities for specimens of *Marmosops* from which we 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).

**Table S1.** Primers used to amplify and sequence the mitochondrial gene *cytochrome b* and a fragment of the nuclear exon *breast cancer activating 1* used in this study.

**Table S2.** GenBank accession numbers for all the sequences included in our analyses.

**Table S3.** Per cent pairwise *cytochrome b* sequence divergence amongst putative species of subgenus I (*Sciophanes*). 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).

**Table S4.** Per cent pairwise *cytochrome b* sequence divergence amongst putative species of subgenus II (*Marmosops*). 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).