A Revision of *Philander* (Marsupialia: Didelphidae), Part 1: *P. quica*, *P. canus*, and a New Species from Amazonia

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ABSTRACT

This is the first installment of a revision of the didelphid marsupial genus *Philander*, commonly known as gray four-eyed opossums. Although abundant and widespread in lowland tropical forests from southern Mexico to northern Argentina, species of *Philander* are not well understood taxonomically, and the current literature includes many examples of conflicting species definitions and nomenclatural usage. Our revision is based on coalescent analyses of mitochondrial gene sequences, phylogenetic analyses of mitochondrial and nuclear genes, morphometric analyses, and firsthand examination of relevant type material. Based on these results, we provisionally recognize eight species, of which three are formally treated in this report: *P. quica* (Temminck, 1824), an Atlantic Forest endemic formerly known as *P. frenatus* (Olfers, 1818); *P. canus* (Osgood, 1913), a widespread species formerly treated as a synonym or subspecies of *P. opossum* (Linnaeus, 1758); and *P. pebas*, a new species endemic to Amazonia. The remaining, possibly valid, species of *Philander* can be allocated to two clades. The first is a cis-Andean complex that includes *P. andersoni* (Osgood, 1913); *P. mcilhennyi* Gardner and Patton, 1972; and *P. opossum*. The second is a trans-Andean complex that includes *P. melanurus* (Thomas, 1899) and *P. pallidus* (Allen, 1901). Among other nomenclatural acts, we designate a neotype for the long-problematic nominal taxon *Didelphis superciliaris* Olfers, 1818, and (in an appendix coauthored by Renate Angermann), we establish that Olfers' coeval binomen *D. frenata* is based on an eastern Amazonian type and is a junior synonym of *P. opossum*.

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INTRODUCTION

Species of *Philander*, commonly known as "gray four-eyed opossums" or "pouched four-eyed opossums" (fig. 1), occur in lowland tropical and subtropical forests from Mexico to northern Argentina.[4] Closely related to other large didelphids with 22 chromosomes (tribe Didelphini: *Chironectes*, *Didelphis*, and *Lutreolina*), species of *Philander* are scansorial predators that eat a wide variety of invertebrates, small vertebrates, and fallen fruit (Charles-Dominique et al., 1981; Santori et al., 1997; Cáceres, 2004; Ceotto et al., 2009; Macedo et al., 2010). Because they are not reluctant to enter baited traps, species of *Philander* are abundant in museum collections, but their taxonomy has long been controversial.

Although 18 nominal taxa are currently referred to *Philander* (table 1), influential mid-20th century checklists (Cabrera, 1958; Hall and Kelson, 1959) recognized only a single widespread species, *Philander opossum*, with seven subspecies in South America and two in Central America. This hypothesis, implying reproductive continuity among populations spanning numerous zoogeographic barriers (mountains, rivers, open habitats) and many thousands of kilometers, persisted until Gardner and Patton (1972) reported sympatry between two phenotypically distinguishable species in western Amazonia. Subsequent publications have reported other examples of sympatry between two kinds of Amazonian *Philander* (Hutterer et al., 1995; Patton et al., 2000; Hice and Velazco, 2012), and DNA-sequencing studies have discovered deep genetic divergence—equivalent to that seen between sympatric Amazonian taxa—among allopatric forms that have long been considered synonyms or subspecies of *P. opossum* (see Patton and da Silva, 1997; Nunes et al., 2006; Chemisquy and Flores, 2012).

Although there is now broad consensus that multiple valid species of *Philander* merit recognition, authors disagree about what to call them (e.g., Patton and da Silva, 1997; Hershkovitz, 1997), and there are significant problems with the data currently available to test alternative taxonomic hypotheses. Among other difficulties, major geographic sampling gaps complicate the interpretation of phenotypic and genetic differences, morphological analyses of voucher specimens are often insufficient to support the application of names to haplotype groups, and nuclear-gene sequences are unavailable to assess whether mitochondrial haplogroups are really species. Additionally, no revision of the genus has been based on firsthand examination of relevant type material.

This is the first of several technical reports on the taxonomy of *Philander*. In this installment we analyze the most extensive set of mitochondrial DNA (mtDNA) sequences yet assembled for the genus. Additionally, we obtained sequence data from several nuclear markers that we use to test inferences about phylogenetic relationships previously based exclusively on mtDNA. Coalescent analyses of the mtDNA data, together with phenotypic information obtained from morphological vouchers, type material, and other specimens, support the provisional recognition of eight species, of which three are formally treated as valid in this report.

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[4] Both vernacular names distinguish species of *Philander* from superficially similar taxa referred to *Metachirus*, commonly known as "brown four-eyed opossums" or "pouchless four-eyed opossums."

FIG. 1. A member of the *Philander melanurus* complex attacking a large specimen of the venomous elapid snake *Micrurus nigrocinctus* (photo credit: Mario J. Gómez-Martínez). The pale supraocular spots and ashy dorsal coloration are diagnostic external traits of the genus *Philander*.

Materials and Methods

SOURCE OF MATERIAL: Except as noted, all specimens are preserved in the following collections: AMNH (American Museum of Natural History), New York; BMNH (Natural History Museum), London; CM (Carnegie Museum of Natural History), Pittsburgh; EBD (Estación Biológica Doñana), Seville; EBRG (Museo de la Estación Biológica de Rancho Grande), Maracay; FMNH (Field Museum), Chicago; INPA (Instituto Nacional de Pesquisas da Amazônia), Manaus; ISEM (Institut des Sciences de l'Evolution), Montpellier; KU (Biodiversity Research Center, University of Kansas), Lawrence; LSUMZ (Museum of Zoology, Louisiana State University), Baton Rouge; MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"), Buenos Aires; MCZ (Museum of Comparative Zoology, Harvard University), Cambridge; MHNLS (Museo de Historia Natural La Salle), Caracas; MN (Museu Nacional), Rio de Janeiro; MPEG (Museu Paraense Emílio Goeldi), Belém; MSB (Museum of Southwestern Biology, University of New Mexico), Albuquerque; MSU (Michigan State University Museum), East Lansing; MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos), Lima; MVZ (Museum of Vertebrate Zoology, University of California), Berkeley; MZUSP (Museu de Zoologia da Universidade de São Paulo), São Paulo; NMW (Naturhisorisches Museum Wien), Vienna; RMNH (Naturalis

TABLE 1. Nominal species-group taxa currently referred to *Philander*.[a]

	Type	Type locality
andersoni Osgood, 1913	FMNH19655[b]	Peru: Loreto, Yurimaguas
azaricus Thomas, 1923	BMNH 3.2.3.36[b]	Paraguay: Paraguarí, Sapucay
canus Osgood, 1913	FMNH 19347[b]	Peru: San Martín, Moyobamba
crucialis Thomas, 1923	BMNH 47.11.22.15[b]	Bolivia: Santa Cruz, Santa Cruz de la Sierra
deltae Lew et al., 2006	MHNLS 10679[b]	Venezuela: Monagas, Reserva Forestal de Guarapiche
frenatus Olfers, 1818	ZMB 2325[c]	Eastern Amazonian Brazil[d]
fuscogriseus J.A. Allen, 1900	AMNH 9920/8252[b]	Central America[e]
grisescens J.A. Allen, 1901	AMNH 15072[b]	Colombia: "Río Cauca"
mcilhennyi Gardner & Patton, 1972	LSU 16395[b]	Peru: Ucayali, Balta
melantho Thomas, 1923	BMNH 14.5.28.30[b]	Colombia: Chocó, Condoto
melanurus Thomas, 1899	BMNH 97.11.7.61[b]	Ecuador: Imbabura, Paramba
mondolfii Lew et al., 2006	EBRG 17513[b]	Venezuela: Bolívar, Reserva Forestal de Imataca
nigratus Thomas, 1923	BMNH 0.7.7.62[b]	Peru: Junín, Utcuyacu
olrogi Flores et al., 2008	CML 561[b]	Bolivia: Santa Cruz, 7 km N Santa Rosa
opossum Linnaeus, 1758	RMNH 25421[f]	Surinam
pallidus J.A. Allen, 1901	USNM 58158[b]	Mexico: Veracruz, Orizaba
quica Temminck, 1824	not located[g]	Brazil: Rio de Janeiro, Sepetiba
superciliaris Olfers, 1818	AMNH 203348[h]	Brazil: Pará, Capim[i]

[a] Only available names based on Recent type material are listed. Epithets originally published in combination with the genus *Didelphis* (often incorrectly spelled *Didelphys* in the older literature), feminine in gender, are here corrected to agree with *Philander* (masculine).

[b] Holotype by original designation.

[c] Holotype by monotypy (see appendix 5).

[d] Not "Bahia" (contra Hershkovitz, 1959, 1997; see appendix 5).

[e] The type of *fuscogriseus* was "found in a bunch of bananas in unloading a fruit steamer from a Central American port, most likely Colon, after its arrival alive in New York harbor" (Allen, 1900: 195). The type locality is, therefore, probably somewhere on the Caribbean coast of Panama. Allen's (1911) subsequent suggestion that the type locality be construed as Greytown, Nicaragua, is irrelevant because it was not based on new information about the geographic origin of the holotype. Hall and Kelson's (1959) statement that the type was from Greytown is unsubstantiated.

[f] Lectotype (designated by Hershkovitz, 1976; see Voss et al., 2001: 63).

[g] Lectotype (designated by Hershkovitz, 1959: 342) said to be in Vienna but no longer at the NMW (see text).

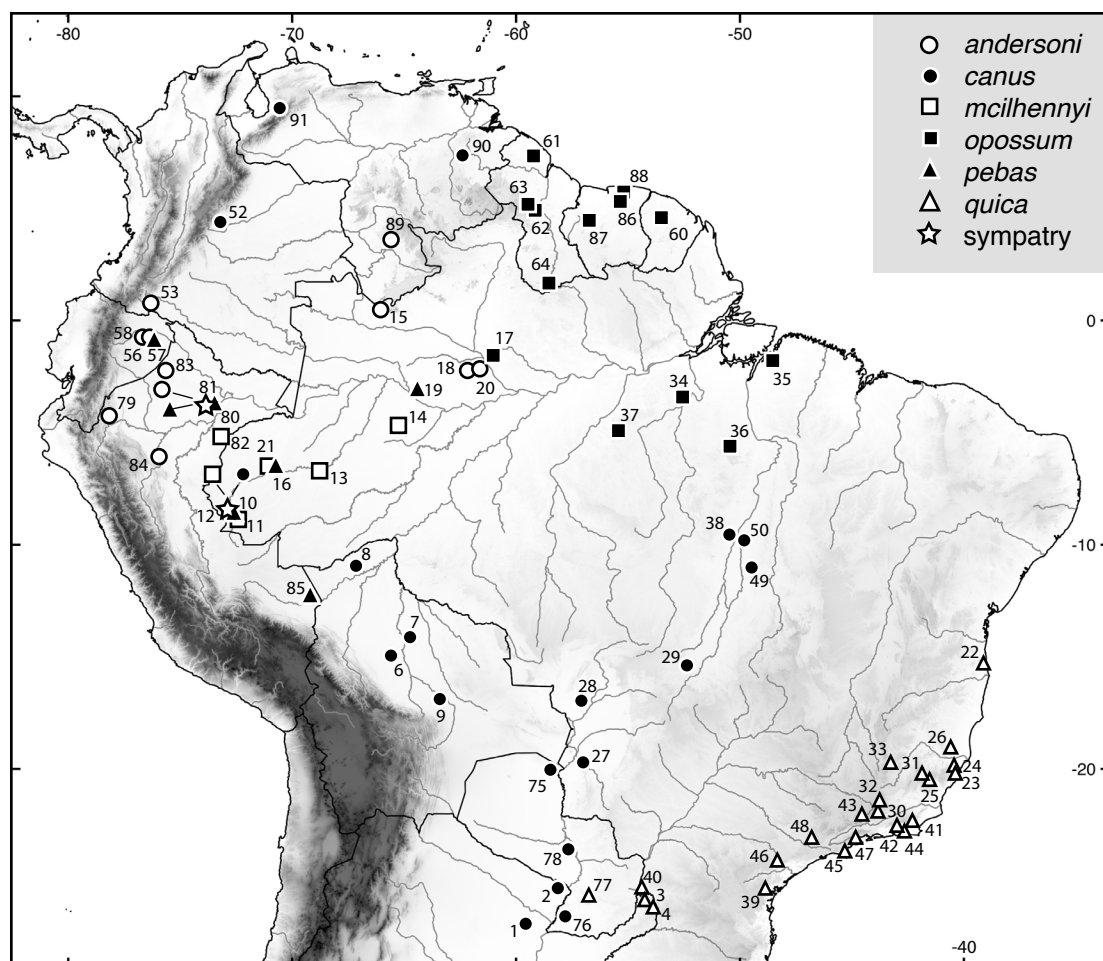[h] Neotype (designated in this report).

[i] Fixed by neotype selection.

FIG. 2. Cis-Andean collection localities for sequenced specimens of *Philander*. Numbers are keyed to localities listed in the gazetteer (appendix 1).

Biodiversity Center), Leiden; ROM (Royal Ontario Museum), Toronto; TTU (Museum of Texas Tech University), Lubbock; UFES (Universidade Federal do Espírito Santo), Vitória; UFMG (Universidade Federal de Minas Gerais), Belo Horizonte; USNM (National Museum of Natural History, Smithsonian Institution), Washington D.C.; ZMB (Museum für Naturkunde), Berlin.

TAXON SAMPLING AND LABORATORY METHODS: The sequences analyzed in this report were obtained from specimens representing most of the phenotypes that have previously been considered valid taxa of *Philander* (e.g., by Cabrera, 1958; Hall and Kelson, 1959; Patton and da Silva, 1997; Hershkovitz, 1997). Sequenced specimens include paratypes, topotypes, and otherwise geographically referable material of *andersoni*, *azaricus*, *canus*, *crucialis*, *frenatus*, *fuscogriseus*, *mcilhennyi*, *melantho*, *melanurus*, *mondolfii*, *olrogi, opossum*, *pallidus*, and *quica*. To the best of our knowledge, the only nominal taxa not represented by these molecular data are *deltae* (currently known only from a handful of specimens in Venezuelan museums) and *nigratus* (for which we were unable to obtain tissue).
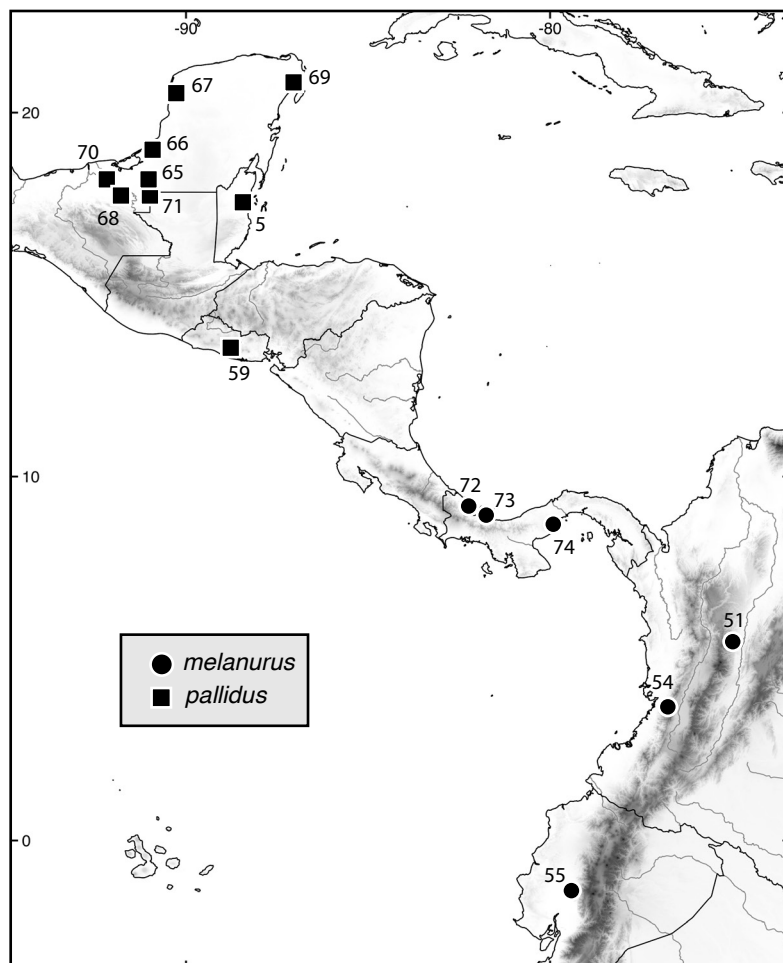
FIG. 3. Trans-Andean collection localities for sequenced specimens of *Philander*. Numbers are keyed to locali-ties listed in the gazetteer (appendix 1).

We extracted DNA from preserved tissue or from fragments of dried skin obtained from museum specimens as explained below. We also downloaded sequence data deposited in Gen-Bank by previous researchers, and several unpublished sequences were kindly made available to us by the Patton lab at the University of California at Berkeley. Careful checking of these data for provenance revealed that three pairs of GenBank accessions are duplicates (based on the same tissue/specimen; asterisks indicate the sequence used by us): JQ778972 and KT153576* were both obtained from MVZ 197405 (field number JLP 16968); GU112937 and U34679* were both obtained from a tissue with identifier "ORG 01," apparently corresponding to an uncataloged specimen at the Museu Nacional (Rio de Janeiro); and JQ778971 and JF281029* were both obtained from MZUSP 29212 (field number MAM 208). The sequences we analyzed are listed in tables 2 and 3 with voucher, tissue, and GenBank identifiers. Although we tried to examine mor-phological voucher material for every sequence analyzed in this report, we were not entirely

successful in doing so (examined voucher specimens are marked with asterisks in table 2). The collection localities of sequenced ingroup (*Philander*) specimens are mapped in figures 2 and 3.

Laboratory Methods: We extracted DNA from preserved tissues or dried museum specimens using methods described in Voss and Jansa (2009) and Giarla et al. (2010). To minimize risk of contamination, all extractions from museum specimens were performed in an isolated laboratory where mammalian polymerase chain reaction (PCR) products were not present. We PCR-amplified six loci for this study (CYTB, BRCA1, IRBP, OGT, SLC38, and Anon128) using the primers listed in appendix 2 and methods described in Voss and Jansa (2009), Giarla et al. (2010, 2014), Gutiérrez et al. (2010), and Pavan et al. (2014). The resulting PCR products were Sanger-sequenced on an ABI 3730xl automated sequencer. Sequences were edited and assembled in Geneious Pro ver. 7.0 (http://www.geneious.com; Kearse et al., 2012), and length heterozygotes in the nuclear loci were resolved using Indelligent v. 1.2 (Dmitriev and Rakitov, 2008). Individual genes were aligned using the default parameters of MUSCLE (Edgar, 2004), and alignments of all protein-coding genes were examined with reference to translated amino-acid sequences.

Phylogenetic and Coalescent Analyses: We performed maximum-likelihood and Bayesian phylogenetic analyses of a cytochrome-*b* (CYTB) matrix that included sequences obtained from 135 specimens of *Philander* together with several outgroup sequences (tables 2, 3). The best-fitting nucleotide substitution model for these data was determined under the corrected Akaike Information Criterion (AICc) in jModelTest (Posada, 2008). We conducted five independent maximum-likelihood (ML) searches in GARLI 2.0 (Zwickl, 2006) and evaluated nodal support based on bootstrap analyses of 1000 pseudoreplicated datasets with the same parameters as the initial searches. Bootstrap support (BS) values were summarized on the best ML tree using Sumtrees version 3.3.1 (Sukumaran and Holder, 2010). Bayesian inference (BI) 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 5000 generations and including one cold chain and three heated chains. To evaluate convergence, the results of the MCMC runs were inspected in Tracer v1.6 (Rambaut et al., 2014). We discarded the first 50% of trees from each run as burnin, combined the remaining trees into a final set of 10,000 trees, and summarized all parameters in a maximum-clade-credibility tree with TreeAnnotator v1.7.2 (Drummond et al., 2012). All phylogenetic analyses (including those described in subsequent paragraphs) were implemented in the CIPRES Science Gateway (Miller et al., 2010). We estimated uncorrected genetic distances (*p*-distances) within and among putative species using MEGA7 (Kumar et al., 2016).

To delimit putative species from our CYTB sequence data we first constructed an ultrametric tree in BEAST v1.7.2 (Drummond et al., 2012) including only unique haplotypes across the aligned region (125 terminals; table 2); we used 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). We ran two independent MCMC analyses for 50 million generations each, sampling every 5000 generations. Procedures for assessing convergence, fractions of trees discarded as burnin, and the summari-

TABLE 2. Specimens of *Philander* sequenced for cytochrome *b*.

Taxon	Voucher[a]	Tissue	Locality[b]	bp	GenBank no.[c]	Source
andersoni	INPA 2524	VCSV 85	Brazil: Amazonas (15)	660	**MG491889**	J.L. Patton lab
andersoni	INPA 4403	YL 139	Brazil: Amazonas (18)	660	**JF281033**	Rocha (2011)
andersoni	INPA 4222	MNFS 2088	Brazil: Amazonas (20)	660	**MG491890**	J.L. Patton lab
andersoni	KU 123950*	JAWK 417	Colombia: Putumayo (53)	498	**MG491891**	This study
andersoni	ROM 104029[d]	F 37126[c]	Ecuador: Orellana (56)	660	**JQ388602**	Nunes et al. (2006)
andersoni	ROM 106102*	F 40359	Ecuador: Orellana (58)	1149	**MG491892**	This study
andersoni	MVZ 153265*	JLP 6893	Peru: Amazonas (79)	1149	**MG491893**	This study
andersoni	TTU 101157*	TK 73847	Peru: Loreto (81)	831	**MG491894**	This study
andersoni	TTU 101246*	TK 75148	Peru: Loreto (81)	726	**MG491895**	This study
andersoni	KU 157979*	NW 844	Peru: Loreto (83)	1149	**MG491896**	This study
andersoni	FMNH 19657*		Peru: Loreto (84)	498	**MG491897**	This study
andersoni	USNM 388405*		Venezuela (89)	498	**MG491898**	This study
andersoni	USNM 388407*		Venezuela (89)	498	**MG491899**	This study
canus	MACN 20868		Argentina: Chaco (1)	721	**JQ778956**	Chemisquy & Flores (2012)
canus	MACN 20866		Argentina: Chaco (1)	704	**JQ778962**	Chemisquy & Flores (2012)
canus	MACN 20742[e]		Argentina: Formosa (2)	724	**JQ778957**	Chemisquy & Flores (2012)
canus	MACN 20740[e]		Argentina: Formosa (2)	732	**JQ778958**	Chemisquy & Flores (2012)
canus	AMNH 261271*	LAR 298	Bolivia: Beni (6)	498	**MG491900**	This study
canus	AMNH 261272*	LAR 299	Bolivia: Beni (6)	498	**MG491901**	This study
canus	MSB 56115*	NK 13171	Bolivia: Beni (7)	1149	**MG491902**	This study
canus	AMNH 261273*	NK 13172	Bolivia: Beni (7)	1149	**MG491903**	This study
canus	AMNH 262413*	NK 13894	Bolivia: Pando (8)	1149	**MG491904**	This study
canus	AMNH 260034*	NK 11830	Bolivia: Santa Cruz (9)	1149	**MG491905**	This study
canus	MVZ 190347*	MNFS 1453	Brazil: Acre (12)	1149	**MG491906**	This study
canus	MVZ 198013	LPC 584	Brazil: Mato Grosso (28)	829	**MG491907**	J.L. Patton lab
canus	MVZ 197403*	LPC 392	Brazil: Mato Grosso (29)	1149	**MG491908**	This study
canus	MVZ 197915	LPC 430	Brazil: Mato Grosso (29)	801	**KT153573**	Rocha et al (2015)
canus	MVZ 197402*	LPC 596	Brazil: Mato Grosso do Sul (27)	1149	**MG491909**	This study

TABLE 2. *continued*

Taxon	Voucher[a]	Tissue	Locality[b]	bp	GenBank no.[c]	Source
canus	MVZ 198017	LPC 597	Brazil: Mato Grosso do Sul (27)	660	**KT153574**	Rocha et al (2015)
canus	MVZ 197404	JLP 16967	Brazil: Mato Grosso do Sul (27)	660	**KT153575**	Rocha et al (2015)
canus	MVZ 197405	JLP 16968	Brazil: Mato Grosso do Sul (27)	660	**KT153576**	Rocha et al (2015)
canus	[UFES]	RGR 319	Brazil: Pará (38)	801	**JF281035**	Rocha et al (2015)
canus	[UFES]	RGR 338	Brazil: [Pará or Tocantins][g]	801	**JF281034**	Rocha et al (2015)
canus	[UFES]	RGR 31	Brazil: [Pará or Tocantins][g]	801	**JF281040**	Rocha et al (2015)
canus	[UFES]	RGR 489	Brazil: Tocantins (49)	801	**JF281036**	Rocha et al (2015)
canus	UFES 1286	RGR 13	Brazil: Tocantins (50)	801	**JF281039**	Rocha et al (2015)
canus	[UFES]	RGR 215	Brazil: Tocantins (50)	801	**JF281037**	Rocha et al (2015)
canus	UFES 1422	RGR 172	Brazil: Tocantins (50)	801	**JF281038**	Rocha et al (2015)
canus	KU 123943*	JAWK 402	Colombia: Meta (52)	498	**MG491910**	This study
canus	[unknown]	CZ 058	Paraguay: Alto Paraguay (75)	801	**KM188488**	de la Sancha and D'Elía (2015)
canus	UMMZ 174828*	GD 066	Paraguay: Ñeembucú (76)	1149	**MG491911**	This study
canus	[UMMZ?]	GD 151	Paraguay: Ñeembucú (76)	610	**KM188486**	de la Sancha and D'Elía (2015)
canus	TTU 80404*	TK 62049	Paraguay: Presidente Hayes (78)	801	**KM188487**	de la Sancha and D'Elía (2015)
canus	CMNH 78216*	TK 19152	Venezuela: Bolívar (90)	726	**MG491912**	This study
canus	KU 120245*	JAWK 281	Venezuela: Trujillo (91)	498	**MG491913**	This study
mcilhennyi	MVZ 190336	MNFS 1196	Brazil: Acre (11)	1149	**MG491914**	This study
mcilhennyi	MVZ 190337*	MNFS 1435	Brazil: Acre (12)	1149	**MG491915**	J.L. Patton lab
mcilhennyi	MVZ 190341	JLP 16069	Brazil: Amazonas (13)	765	**MG491916**	J.L. Patton lab
mcilhennyi	[MPEG?]	JLP 16057	Brazil: Amazonas (13)	801	**JF281031**	Rocha (2011)
mcilhennyi	[INPA?]	MNFS 146	Brazil: Amazonas (14)	1149	**MG491917**	J.L. Patton lab
mcilhennyi	MVZ 190339*	JLP 15677	Brazil: Amazonas (21)	1149	**MG491918**	This study
mcilhennyi	MVZ 190340	JLP 15702	Brazil: Amazonas (21)	660	**JQ388611**	Nunes et al. (2006)
mcilhennyi	AMNH 272818*	RSV 2310	Peru: Loreto (82)	1149	**MG491919**	This study
mcilhennyi	MUSM 13299*	RSV 2153	Peru: Loreto (82)	1149	**MG491920**	This study
mcilhennyi	AMNH 273055*	DWF 408	Peru: Loreto (82)	1149	**MG491921**	This study
mcilhennyi	AMNH 273089*	DWF 465	Peru: Loreto (82)	1149	**MG491922**	This study
melanurus	CTUA 500*	JFD 177	Colombia: Caldas (51)	1149	**MG491923**	This study

TABLE 2. *continued*

Taxon	Voucher[a]	Tissue	Locality[b]	bp	GenBank no.[c]	Source
melanurus	KU 123956*	JAWK 368	Colombia: Valle (54)	498	**MG491924**	This study
melanurus	USNM 534293*		Ecuador: Los Ríos (55)	498	**MG491925**	This study
melanurus	USNM 464248	J 200	Panama: Bocas del Toro (72)	660	**JQ778965**	Nunes et al. (2006)
melanurus	USNM 578125*	FMG 2562	Panama: Bocas del Toro (73)	1149	**MG491926**	This study
melanurus	USNM 578124*	FMG 2561	Panama: Bocas del Toro (73)	1149	**MG491927**	This study
melanurus	ROM 104260*	F 38101	Panama: Panamá (74)	1149	**MG491928**	This study
opossum	INPA 4527	JLP 16785	Brazil: Amazonas (17)	660	**JQ388608**	J.L. Patton lab
opossum	INPA 4342	LPC 164	Brazil: Amazonas (17)	660	**MG491929**	J.L. Patton lab
opossum	USNM 549297*	MDC 617	Brazil: Pará (34)	1149	**MG491930**	This study
opossum	USNM 549299*	LHE 583	Brazil: Pará (34)	1149	**MG491931**	This study
opossum	USNM 545592*	M22365	Brazil: Pará (35)	498	**MG491932**	This study
opossum	[INPA?]	CS4	Brazil: Pará (36)	653	**MG491933**	J.L. Patton lab
opossum	USNM 546225*	A2696	Brazil: Pará (37)	498	**MG491934**	This study
opossum	MNHN 2000.215	T 1819	France: French Guiana (60)	660	**MG491935**	J.L. Patton lab
opossum	MNHN 2000.216		France: French Guiana (60)	812	**AJ487009**	Steiner & Catzeflis (2003)
opossum	ROM 98910*	FN31732	Guyana: Barima-Waini (61)	660	**MG491936**	J.L. Patton lab
opossum	ROM 98045*	FN 31047	Guyana: Potaro-Siparuni (62)	660	**JQ388607**	J.L. Patton lab
opossum	ROM 111731*	F44860	Guyana: Potaro-Siparuni (63)	1149	**MG491937**	This study
opossum	ROM 106556*	F38553	Guyana: U. Takutu-U. Essequibo (64)	1149	**MG491938**	This study
opossum	CM 68365*	TK17015	Surinam: Para (86)	1149	**MG491939**	This study
opossum	ROM 117231*	F54552	Surinam: Sipaliwini (87)	1149	**MG491940**	This study
opossum	CM 76743*	TK17524	Surinam: Suriname (88)	1149	**MG491941**	This study
pallidus	AMNH 278388*	NBS 1046	Belize: Orange Walk (5)	1149	**MG491942**	This study
pallidus	AMNH 278387*	NBS 1045	Belize: Orange Walk (5)	1149	**MG491943**	This study
pallidus	AMNH 278390*	NBS 1048	Belize: Orange Walk (5)	1149	**MG491944**	This study
pallidus	TTU 63557*	TK34851	El Salvador: La Paz (59)	1149	**MG491945**	This study

TABLE 2. *continued*

Taxon	Voucher[a]	Tissue	Locality[b]	bp	GenBank no.[c]	Source
pallidus	TTU 63558*	TK34852	El Salvador: La Paz (59)	1149	**MG491946**	This study
pallidus	ASNHC 1284*	MDE 3589	Mexico: Campeche (65)	1149	**MG491947**	This study
pallidus	ROM 96402*	FN30219	Mexico: Campeche (66)	1149	**MG491948**	This study
pallidus	ASNHC 6436*	FN32779	Mexico: Campeche (67)	1149	**MG491949**	This study
pallidus	ASNHC 6437*	FN32807	Mexico: Campeche (67)	1149	**MG491950**	This study
pallidus	ASNHC 5648*	MDE 3489	Mexico: Chiapas (68)	1149	**MG491951**	This study
pallidus	ROM 97376*	FN29987	Mexico: Quintana Roo (69)	1149	**MG491952**	This study
pallidus	ROM 97377*	FN29988	Mexico: Quintana Roo (69)	1149	**MG491953**	This study
pallidus	ROM 96257*	FN30073	Mexico: Tabasco (70)	1149	**MG491954**	This study
pallidus	ASNHC 6438*	KLC 28	Mexico: Tabasco (71)	1149	**MG491955**	This study
pebas	MVZ 190345*	MNFS 1031	Brazil: Acre (10)	1149	**U34678**	Patton et al. (1996)
pebas	MVZ 190343*	JLP 15395	Brazil: Amazonas (16)	1149	**MG491956**	This study
pebas	MPEG 24571[f]	Mam1	Brazil: Amazonas (19)	418	**DQ236271**	Nunes et al. (2006)
pebas	MPEG 24572[f]	Mam6	Brazil: Amazonas (19)	426	**DQ236272**	Nunes et al. (2006)
pebas	MPEG 24573[f]	Mam4	Brazil: Amazonas (19)	418	**DQ236273**	Nunes et al. (2006)
pebas	MPEG 26340[f]	Mam2	Brazil: Amazonas (19)	399	**DQ236274**	Nunes et al. (2006)
pebas	MPEG 26342[f]	Mam7	Brazil: Amazonas (19)	418	DQ236275	Nunes et al. (2006)
pebas	MPEG 26343[f]	Mam3	Brazil: Amazonas (19)	418	**DQ236276**	Nunes et al. (2006)
pebas	MPEG 26346[f]	Mam5	Brazil: Amazonas (19)	285	**DQ236277**	Nunes et al. (2006)
pebas	ROM 106101*	F 40358	Ecuador: Orellana (57)	1149	**MG491957**	This study
pebas	TTU 98583*	TK 73919	Peru: Loreto (80)	1149	**MG491958**	This study
pebas	TTU 101192*	TK 73935	Peru: Loreto (80)	725	**MG491959**	This study
pebas	TTU 98953*	?	Peru: Loreto (81)	800	**KM188489**	de la Sancha and D'Elía (2015)
pebas	KU 144120*	NW 579	Peru: Madre de Dios (85)	1149	**MG491960**	This study
quica	MACN 51.127[e]		Argentina: Misiones (3)	745	**JQ778964**	Chemisquy & Flores (2012)
quica	MACN 51.18[e]		Argentina: Misiones (3)	749	**JQ778963**	Chemisquy & Flores (2012)
quica	MACN 49.376[e]		Argentina: Misiones (3)	743	**JQ778959**	Chemisquy & Flores (2012)
quica	MACN 52.19[e]		Argentina: Misiones (4)	683	**JQ778961**	Chemisquy & Flores (2012)
quica	UFMG 2661	YL 107	Brazil: Bahia (22)	621	**MG491961**	This study
quica	UFES 547	LPC 1127	Brazil: Espírito Santo (23)	801	**GU112942**	Agrizzi et al. (2012)
quica	MZUSP 29210	MAM 189	Brazil: Espírito Santo (24)	1149	**MG491962**	This study
quica	UFES 897	YL 573	Brazil: Espírito Santo (24)	801	**GU112940**	Agrizzi et al. (2012)
quica	UFES 984	LGA 1196	Brazil: Espírito Santo (25)	801	**GU112936**	Agrizzi et al. (2012)

TABLE 2. *continued*

Taxon	Voucher[a]	Tissue	Locality[b]	bp	GenBank no.[c]	Source
quica	UFES 253	LPC 944	Brazil: Espírito Santo (26)	801	**GU112941**	Agrizzi et al. (2012)
quica		YL 181	Brazil: Minas Gerais (31)	660	**MG491963**	J.L. Patton lab
quica	MZUSP 29212	MAM 208	Brazil: Minas Gerais (32)	660	**JF281029**	Rocha (2011)
quica		CEG 35	Brazil: Minas Gerais (33)	660	**JQ778966**	Chemisquy & Flores (2012)
quica	[UFMG]	LC 4	Brazil: Minas Gerais (30)	660	**MG491964**	J.L. Patton lab
quica		YL 225	Brazil: Paraná (39)	660	**MG491965**	J.L. Patton lab
quica		NC 14	Brazil: Paraná (39)	800	**JQ778969**	Chemisquy & Flores (2012)
quica	UFMG 2666	LPC 877	Brazil: Paraná (40)	801	**GU112939**	Agrizzi et al. (2012)
quica	MVZ 197401*	LPC 876	Brazil: Paraná (40)	1149	**MG491966**	This study
quica		LG 39	Brazil: Rio de Janeiro (41)	660	**JQ778970**	Chemisquy & Flores (2012)
quica	[MN]	ORG 01	Brazil: Rio de Janeiro (42)	1149	**U34679**	Patton et al. (1996)
quica	MZUSP 29209	MAM 183	Brazil: Rio de Janeiro (43)	660	**MG491967**	J.L. Patton lab
quica	MN 31479	MCL 137	Brazil: Rio de Janeiro (44)	1149	**MG491968**	This study
quica	MVZ 182067*	MAM 64	Brazil: São Paulo (45)	1149	**MG491969**	This study
quica	MVZ 182066*	MAM 41	Brazil: São Paulo (46)	510	**MG491970**	J.L. Patton lab
quica	MVZ 183247*	MAM 315	Brazil: São Paulo (46)	1149	**KJ868146**	Mitchell et al. 2014
quica	MZUSP 29213	MAM 74	Brazil: São Paulo (47)	510	**JQ778968**	Chemisquy & Flores (2012)
quica	MZUSP 29215	MAM 211	Brazil: São Paulo (48)	660	MG491971	J.L. Patton lab
quica	MACN 33.172		Paraguay: Paraguaí (77)	685	**JQ778960**	Chemisquy & Flores (2012)

[a] Asterisks indicate specimens personally examined by us. Square brackets enclose the assumed or conjectured museum repository of uncataloged specimens or specimens for which we were unable to determine catalog numbers.

[b] Country and next-largest administrative unit. Numbers in parentheses correspond to mapped localities (figs. 2, 3), for which additional information is provided in the gazetteer (appendix 1)

[c] Boldface identifies sequences used in the BEAST analysis.

[d] Correct catalog and field numbers for sequenced specimen originally reported as ROM 104030 (= *Mesophylla macconnelli*) by Nunes et al. (2006).

[e] Examined at our request by David Flores (personal commun., 10 March 2017).

[f] Examined at our request by Silvia Pavan (personal commun., 23 March 2017).

[g] According to Rocha et al. (2015: table S1), the haplotypes represented by these specimens were found on both sides of the Rio Araguaia, which separates the states of Pará and Tocantins; both were collected between 9.30 and 10.87° S and between 49.70 and 50.14° W.

zation process followed those described above for the MrBayes analysis. To estimate the threshold between interspecific and intraspecific branching processes we used the likelihood version of the General Mixed Yule Coalescent model (GMYC) as implemented in SPLITS (Pons et al., 2006). GMYC analyses were implemented on the ultrametric topology recovered by BEAST allowing only single shifts across the phylogeny (Fujisawa and Barraclough, 2013). For the purposes of this report, we recognize as putative species any CYTB

TABLE 3. Ingroup and outgroup specimens sequenced for multigene phylogenetic analyses.

	Voucher	Tissue/DNA	CYTB[a]	Nuclear loci[a]				
				Anon128	BRCA1	IRBP	OGT	SLC38
Chironectes minimus	ROM 98855	FN 31677	KJ129892	MG545082	FJ159280	AF257679	KJ129923	KJ129966
Didelphis albiventris	UMMZ 134058	GKC 816	MG491973	MG545083	FJ159283	AF257683	KM071232	MG554204
Didelphis aurita	MVZ 182995	MAM 396	MG491974	MG545084	MG545095	MG545105	MG554198	MG554205
Didelphis marsupialis	USNM 578138	FMG 2573	MG491975	MG545085	MG545096	MG545106	MG554199	MG554206
Didelphis virginiana	ROM 96483	FN 30300	KJ129896	MG545086	FJ159285	AF257678	KJ129927	KJ129965
Lutreolina crassicaudata	UMMZ 134019	GKC 849	KJ129893	KJ129863	FJ159292	AF257685	KJ129924	KJ129962
Philander andersoni	MVZ 153265	JLP 6893	MG491893	MG545087	MG545097	MG545107	MG554200	MG554207
Philander canus	MSB 56115	NK 13171	MG491902	MG545088	MG545098	—	MG554201	MG554208
Philander mcilhennyi	AMNH 272818	RSV 2310	MG491919	MG545089	MG545099	MG545108	KU171243	KU171271
Philander melanurus	CTUA 500	JFD 177	MG491923	MG545090	MG545100	MG545109	MG554202	MG554209
Philander opossum	CM 76743	TK 17524	MG491941	MG545091	MG545101	MG545110	KU171244	MG554210
Philander pallidus	ROM 96402	FN 30219	MG491948	MG545092	MG545102	MG545111	MG554203	MG554211
Philander pebas	TTU 98583	TK 73919	MG491958	MG545093	MG545103	—	—	MG554212
Philander quica	MVZ 182067	MAM 64	MG491969	MG545094	MG545104	MG545112	KU171242	MG554213

[a] Column entries are GenBank accession numbers.

lineage with strong support from either ML or BI that crosses the estimated threshold between cladogenetic and coalescent branching processes.

Lastly, we analyzed two concatenated-gene matrices that included a single representative from each putative species, the first matrix containing only the five nuclear loci, and the second containing the five nuclear loci plus cytochrome *b*. Both matrices were concatenated using Sequence Matrix 1.8 (Vaidya et al., 2011). We used the Bayesian information criterion and a greedy search algorithm (implemented in PartitionFinder; Lanfear et al., 2012) to identify the best partitioning scheme and substitution models. For each matrix, we partitioned protein-coding genes (BRCA1, CYTB, IRBP) by locus and codon position, whereas noncoding genes (Anon128, OGT, SLC38) were partitioned only by locus. We performed partitioned ML and BI phylogenetic analyses on each dataset following the methods and software described for the

CYTB analyses described above, with the unique exception that we ran 5 million generations sampling each 500 generations on each MCMC analysis of MrBayes.

Craniodental Measurements: 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 (fig. 4):

Condylobasal length (CBL): measured from the occipital condyles to the anteriormost point of the premaxillae.

Nasal length (NL): the anteroposterior dimension of the longest intact nasal 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 (anterior to the postorbital processes).

Least postorbital breadth (LPB): measured at the narrowest point across the frontals between the temporal fossae (behind the postorbital processes).

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

Palatal length (PL): measured from the 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.

Age Criteria: Unless otherwise noted below, we 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 was still in place; subadult if dP3 had been shed but P3 and/or M4 was still incompletely erupted (M4 is the last upper tooth to erupt in *Philander*); and adult if the entire permanent upper dentition (I1–5, C1, P1–3, M1–4) was fully erupted.

Morphometric Analyses: Adult male specimens of *Philander* are about 3% to 5% larger, on average, than conspecific adult females in most measured craniodental dimensions, so we tabulate descriptive sample statistics separately by sex. After the molar toothrow is fully erupted (in young adults), the measurement LM is ontogenetically invariant, so we often use LM as a univariate surrogate for size when comparing species. Estimates of central tendency and dispersion mentioned in these accounts (e.g., 12.4 ± 0.5 mm) are the sample mean plus or minus one sample standard deviation.
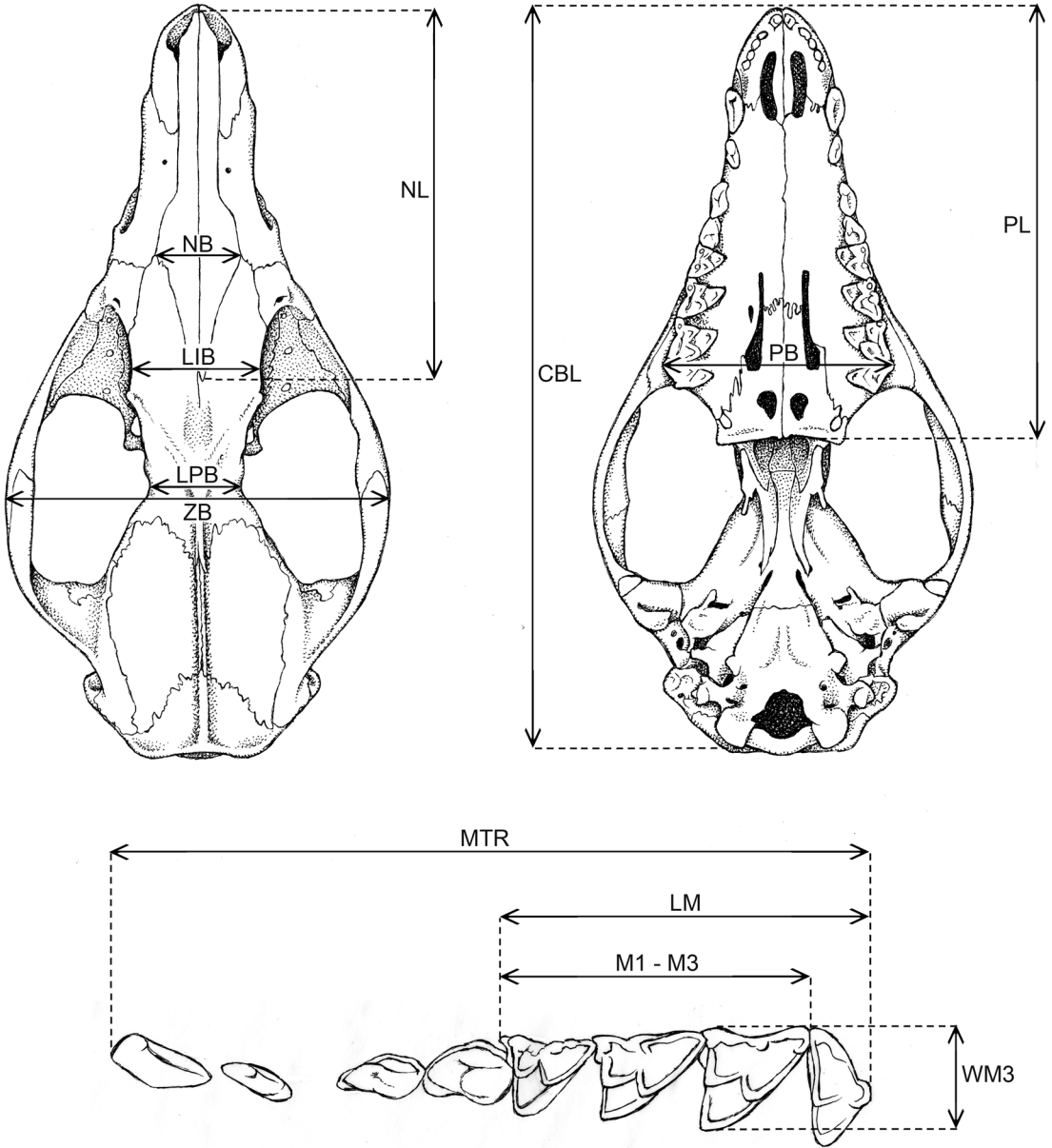
FIG. 4. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Philander opossum*, showing the anatomical limits of craniodental measurements defined in the text.

Because males are more numerous than females in our samples, we computed multivariate sample comparisons from adult male measurements. For the multivariate analyses reported below we deleted two measurements (MTR, M1–M3) that redundantly index variation along the same anterior-posterior dental axis as LM, we eliminated all specimens with missing values, and we log$_{10}$-transformed our data. We computed generalized (Mahalanobis)

distances among our samples and summarized the similarity structure of the resulting distance matrix using cluster analysis (with the Unweighted Pair-Group Method with Arithmetic Means, UPGMA).[5]

We extracted principal components from the variance-covariance matrix computed from log-transformed measurements for selected pairs of samples, and we inspected specimen scores in two-dimensional projections to assess sample overlap on the first several axes. On the assumption that the first eigenvector of the pooled within-group covariance matrix is an appropriate estimate of general size (growth, including ontogenetic allometry; Jolicoeur, 1963; Bookstein et al., 1985), we used Burnaby's (1996) method to obtain size and size-invariant shape factors for pairwise sample ordinations (Rohlf and Bookstein, 1987). All multivariate computations were made using NTSYS Version 2.2 (Exeter Software, Setauket, NY).

MOLECULAR RESULTS

Analyses of Cytochrome-*b* Sequence Data

The 135 cytochrome-*b* sequences we obtained from specimens of *Philander* ranged in length from 285 to 1149 bp (table 2), resulting in 74.6% overall nucleotide coverage for this matrix. The best-fitting nucleotide substitution model for these data was GTR+I+Γ, and the optimal topologies recovered from each of our independent analyses (ML, MrBayes, BEAST) were nearly identical, differing only with respect to weakly supported details. All three analyses provided strong support for the monophyly of *Philander* and for several groups that we interpret as multispecies clades (fig. 5). Nine lineages cross the GMYC species threshold, but two of these are not strongly supported by nodal statistics. For the purposes of this report, we recognize eight putative species, seven of which can be associated with available names based on phenotypic and geographic criteria.

Sister to all other putative species of *Philander* is a haplogroup from southeastern Brazil, for which the oldest available name is *P. quica*. The remaining putative species belong to a single strongly supported clade, but the two deepest nodes within this clade are not strongly supported. Among the robustly supported groups we recovered are: (1) a western Amazonian haplogroup that corresponds to *P. andersoni*, (2) a pair of trans-Andean haplogroups that we identify as *P. melanurus* and *P. pallidus*, (3) a pair of cis-Andean haplogroups that we identify as *P. mcilhennyi* and *P. opossum*, and (4) another pair of cis-Andean haplogroups that correspond to *P. canus* and a new species (*P. pebas*). Percent pairwise uncorrected sequence divergence among these putative species ranges from 1.8% (between *P. canus* and *P. pebas*) to 11.9% (between *P. pallidus* and *P. quica*; appendix 3).

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[5] The generalized distance (*D*) between two groups can be interpreted as the difference between group centroids scaled in units of within-group multivariate standard deviations; it is the appropriate metric for evolutionary inference from measurement data (Lerman, 1965).
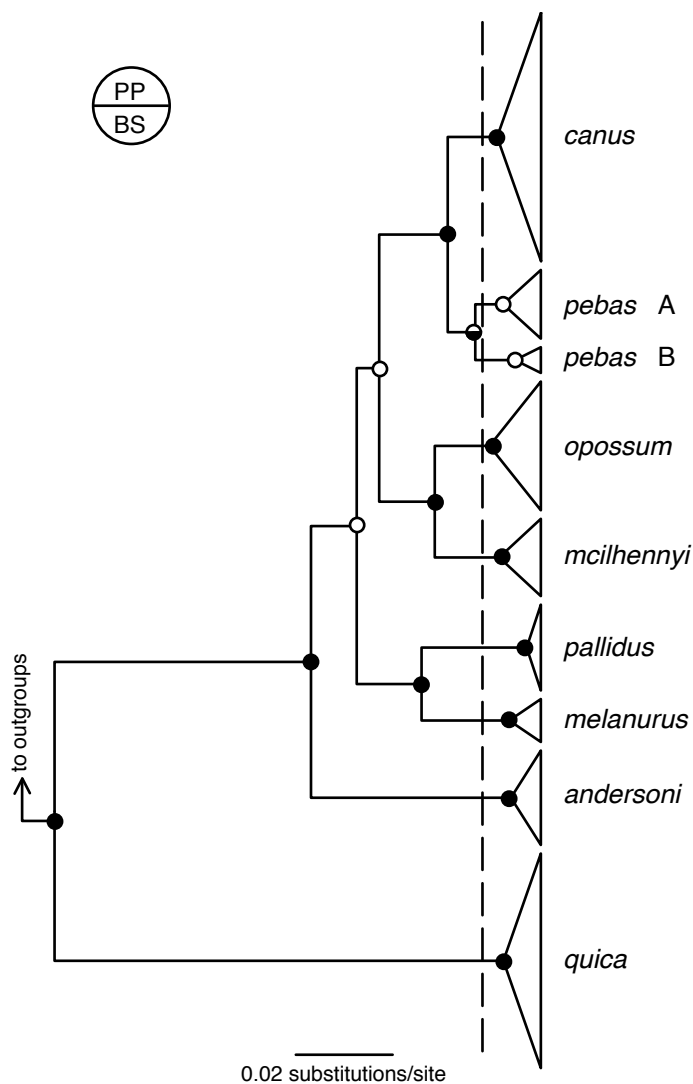
FIG. 5. Ultrametric tree from BEAST analysis of cytochrome-*b* sequences of *Philander* with putative species represented as cartooned terminals. Dashed vertical line indicates the threshold between Yule and coalescent processes as estimated by the likelihood implementation of the general mixed Yule coalescent model (GMYC). Bases of triangles at branch tips are proportional to the number of sequences belonging to each clade. Filled semicircles at each internal node indicate strong support from Bayesian (BEAST: PP) and maximum-likelihood (GARLI: BS) analyses of these data.

Analyses of Concatenated-gene Datasets

Our concatenated-gene alignments contained 4280 bp for the nuclear-gene (nucDNA) dataset and 5429 bp for the combined nuclear and mitochondrial dataset (CYTB+nucDNA); the nuclear sequence data in these alignments include 619 bp from Anon128, 946 bp from BRCA1, 1158 bp from IRBP, 653 bp from OGT, and 904 bp from SLC38. Each dataset was

TABLE 4. Optimal partitioning schemes and substitution models for two concatenated-gene datasets.

Dataset (partition)	Characters	Model
nucDNA (1)	Anon128, BRCA1 (position 3), IRBP (position 2)	HKY+I
nucDNA (2)	BRCA1 (positions 1 and 2)	HKY
nucDNA (3)	IRBP positions (1 and 3)	HKY
nucDNA (4)	OGT, SLC38	HKY+Γ
CYTB+nucDNA (1)	Anon128, BRCA1 (position 3)	K80+Γ
CYTB+nucDNA (2)	BRCA1 (positions 1 and 2)	HKY
CYTB+nucDNA (3)	CYTB (position 1)	SYM+I
CYTB+nucDNA (4)	CYTB (position 2), IRBP (position 2)	F81+I
CYTB+nucDNA (5)	CYTB (position 3)	HKY+I
CYTB+nucDNA (6)	IRBP (positions 1 and 3)	HKY+I
CYTB+nucDNA (7)	OGT, SLC38	HKY+I

analyzed using the partitions and DNA substitution models listed in table 4. Phylogenetic analyses of both datasets yielded identical topologies with differences observed exclusively in nodal support (fig. 6). *Philander quica* remains the first-diverging species of the genus, but relationships among the other species are rearranged from those previously observed from our CYTB analyses. Most importantly, *P. andersoni* is now recovered as the sister taxon of *P. mcilhennyi* + *P. opossum*, and this trio of Amazonian endemics is resolved as the sister group of the previously described trans-Andean lineage (*P. melanurus* + *P. pallidus*). Interestingly, although these relationships are robustly supported by the combined (nuclear + mitochondrial) data, some nodes are only weakly supported by the nuclear genes analyzed separately. However, the monophyly of *Philander* is strongly supported by both datasets, as is the *P. opossum* complex (*P. andersoni* + *P. mcilhennyi* + *P. opossum*), the *P. melanurus* complex (*P. melanurus* + *P. pallidus*), and the sister-group relationship between the two last-named clades.

Morphometric Analyses

Generalized distances (Mahalanobis *D* values) computed from craniodental measurements of adult male specimens representing the putative species identified by coalescent analysis of our molecular data range from about 1.7 to 7.4 (appendix 4). Notably higher values (mostly >5.0) were obtained for comparisons of *P. quica* and *P. canus* with other congeneric taxa, whereas lower values (mostly <4.0) were obtained for comparisons between *P. melanurus* and *P. pallidus* and among members of the *P. opossum* complex. This similarity structure can be heuristically summarized by cluster analysis, the results of which (fig. 7) clearly illustrate the wide divergence of *P. quica* and *P. canus* from other congeneric taxa. Principal-components analyses of selected pairs of taxa (see below) suggest that generalized distance values >4.5 are associated with nonoverlapping multivariate distributions.
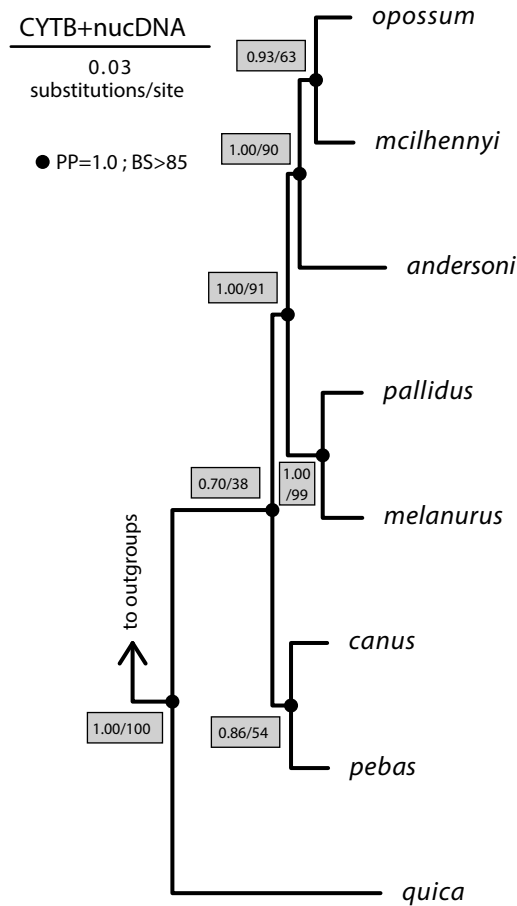
VOSS ET AL: REVISION OF *PHILANDER*

FIG. 6. Result of Bayesian analysis of concatenated sequence data from cytochrome *b* and five nuclear loci (Anon128, BRCA1, IRBP, OGT, SLC38) from exemplar specimens of each putative species (table 3). Gray boxes provide nodal support statistics (PP/BS) from analyses of nuclear genes only.

DISCUSSION

Like many other systematists (e.g., deQueiroz, 1998, 2007), we regard species as evolution-arily independent lineages. Widely accepted evidence for the evolutionary independence of candidate species includes—but is not limited to—reciprocal mtDNA monophyly, substantial sequence divergence, phenotypic diagnosability, ecological differences, and sympatry. In our opinion, none of these criteria is necessary or sufficient for recognizing species, but as such evidence accumulates, the case for species recognition becomes more compelling.

The putative species identified by the molecular analyses reported above correspond to reciprocally monophyletic mtDNA haplogroups that exhibit levels of sequence divergence equaling or exceeding the estimated threshold value between coalescent and branching pro-cesses. However, neither GMYC nor any other delimitation method based exclusively on genetic sequence data provides an infallible guide for recognizing species (Carstens et al., 2013;
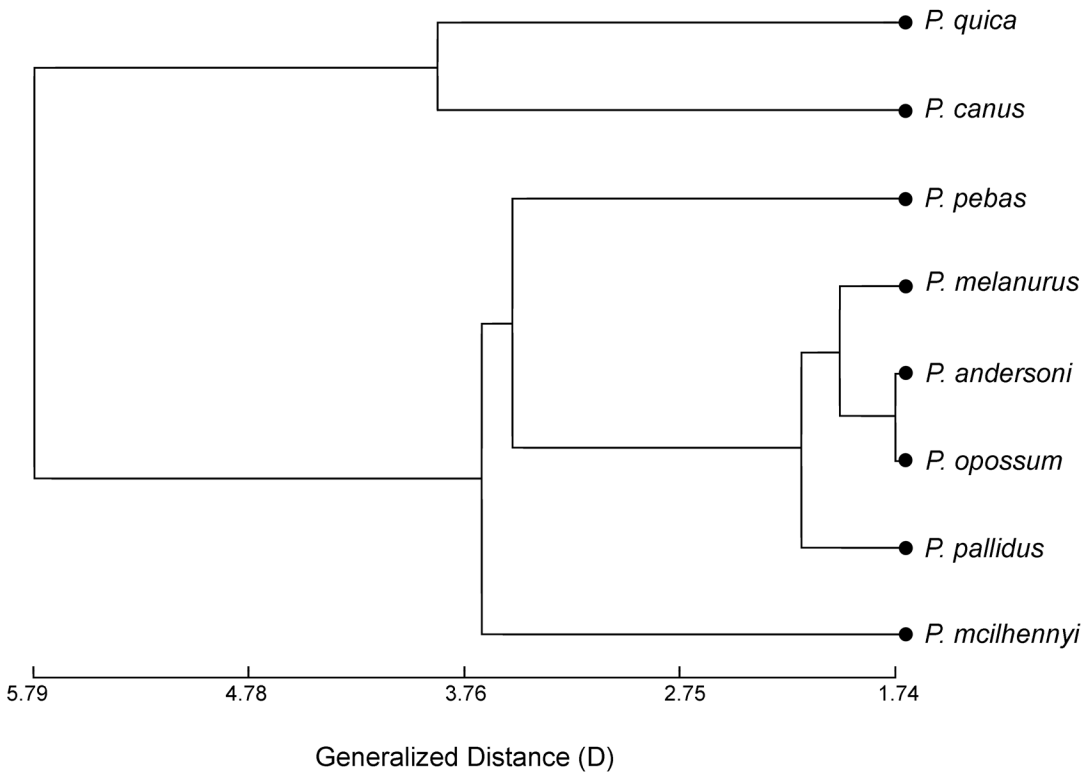
FIG. 7. Dendrogram resulting from UPGMA clustering of putative species of *Philander* using generalized distances computed from log-transformed craniodental measurement data (appendix 4).

Sukumaran and Knowles, 2017), so it is important to assess our molecular results for congruence with other lines of evidence. The nongenetic evidence at hand consists of morphology, geographic distributions, and ecology, which we briefly review here in advance of formal taxonomic treatment. Additionally, the following paragraphs serve to explain the synonymies implicit in our use of binomina for putative species.

Three Highly Corroborated Species

Three of the putative species identified by our interpretation of the GMYC results are strongly supported as independent evolutionary lineages by other types of evidence, and we are confident that they are valid species.

PHILANDER QUICA: In addition to its wide genetic divergence from other congeneric taxa (*p*-distances ≥9.9%; appendix 3), this species is morphologically and biogeographically distinctive. It is smaller than all other species with the exception of *P. canus*—from which it can be distinguished by qualitative craniodental traits (see below)—and it is the only species of *Philander* that occurs in the Atlantic Forest (Mata Atlântica), a well-known center of vertebrate endemism. It is not currently known to occur sympatrically with any other congener (table 5),

TABLE 5. Geographic relationships among putative species of *Philander*.

	quica	canus	pebas	andersoni	mcilhennyi	opossum	melanurus
quica	—						
canus	allopatric[a]	—					
pebas	allopatric	**sympatric**	—				
andersoni	allopatric	**sympatric**	**sympatric**	—			
mcilhennyi	allopatric	**sympatric**	**sympatric**	allopatric[a]	—		
opossum	allopatric[a]	allopatric[a]	allopatric[a]	allopatric[a]	allopatric[a]	—	
melanurus	allopatric	allopatric[a]	allopatric	allopatric	allopatric	allopatric	—
pallidus	allopatric	allopatric	allopatric	allopatric	allopatric	allopatric	allopatric[a]

[a] These species could occur sympatrically (or parapatrically) based on reasonable extrapolations of their known ecogeographic distributions (see text), but they are not currently known to do so.

but its geographic range must contact that of *P. canus* in eastern Brazil, eastern Paraguay, and northeastern Argentina and might historically have contacted that of *P. opossum* in northeastern Brazil. This species was formerly widely known as *P. frenatus* based on erroneous information about where the type of *frenatus* was collected (appendix 5). Thomas's (1923) name *azaricus* is a synonym, but Olfers' (1818) *superciliaris* is not.

PHILANDER CANUS: Long considered a subspecies of *P. opossum* (e.g., by Cabrera, 1958; Patton and da Silva, 1997, 2008; Gardner, 2005), these phylogenetically remote taxa are conspicuously divergent in molecular and morphometric traits. *Philander canus* is widely distributed across several cis-Andean biomes and is known to occur sympatrically with *P. andersoni*, *P. mcilhennyi*, and *P. pebas* (table 5). The names *crucialis*, *mondolfii*, and *olrogi* are junior synonyms.

PHILANDER PEBAS: This new Amazonian species is easily distinguished from all other species of *Philander* by dental morphology, and it additionally differs from its sister taxon, *P. canus*, in size and pelage pigmentation. It occurs sympatrically with *P. andersoni*, *P. canus*, and *P. mcilhennyi* (table 5). Whereas *P. pebas* apparently occurs in seasonally flooded habitats and secondary growth, sympatric congeners typically occur in upland (unflooded) primary forest.

Five Problematic Species

The remaining putative species form a clade of morphometrically similar allopatric taxa. Although pelage traits distinguish *P. mcilhennyi* and *P. andersoni* from each other and from *P. opossum*, morphological diagnoses of *P. opossum*, *P. melanurus*, and *P. pallidus* are difficult to formulate based on material examined to date. Given that *P. andersoni* and *P. mcilhennyi* are currently recognized as valid species (Patton and da Silva, 2008) and that we do not currently have any compelling evidence to suggest otherwise, there are only two nomenclatural options that merit consideration. One is to recognize a paraphyletic *P. opossum* with one subspecies in eastern Amazonia (*P. o. opossum*) and two others that only occur west of the Andes (*P. o. melanurus*, *P. o. pallidus*). To our knowledge, no other animal species shares this disjunct distribution. The second option, which we adopt below, is to treat all five putative species in this

complex as provisionally valid, with the caveat that three of them are not yet certainly distinguishable except by mtDNA sequence characteristics.

PHILANDER MELANURUS: This is the oldest available name for a robustly supported haplogroup that includes specimens from western Ecuador, western Colombia, and eastern Panama. By comparison with specimens from southern Mexico and northern Central America that we refer to *P. pallidus*, these are darker-furred animals with a marked tendency to have shorter white tail-tips; in fact, some specimens from northwestern Ecuador and southwestern Colombia are mostly blackish and have all-dark tails. The nominal taxa *fuscogriseus*, *grisescens*, and *melantho* are junior synonyms.

PHILANDER PALLIDUS: This is the only available name for a strongly supported haplogroup that occurs in southern Mexico, Belize, and El Salvador. As noted above, examined specimens from these regions (including those sequenced for this study) are paler-furred than specimens from Panama, western Colombia, and western Ecuador that we refer to *P. melanurus*, and most of them have longer white tail-tips (none has all-dark tails). Whether these phenotypes intergrade somewhere in the wide Central American hiatus from which we lack sequence data (Guatemala, Honduras, Nicaragua, and Costa Rica), and whether genetically intermediate haplogroups occur in the same region, are obvious topics for future research.

PHILANDER ANDERSONI: This is the only available name for a robustly supported haplogroup that occurs in northeastern Peru, eastern Ecuador, southeastern Colombia, southern Venezuela, and northwestern Brazil (north of the Amazon and west of the Rio Negro). It is known to occur sympatrically with *P. canus* and *P. pebas* in different pairwise combinations (all three species have yet to be found at the same locality). Sequenced specimens that we examined have a distinct middorsal stripe of blackish fur, pale preauricular spots, mostly black hind feet, and at least half-white tails, but other external and cranial traits are variable. Patton and da Silva (1997, 2008) listed *nigratus* (from southeastern Peru) as a synonym of *P. andersoni*, but specimens of *nigratus* are larger animals that (among other differences) lack a distinct middorsal blackish stripe and have only short white tail-tips.

PHILANDER MCILHENNYI: This is the only available name for a robustly supported haplogroup that is currently known to occur south of the Amazon in eastern Peru and western Brazil, where it is known to occur sympatrically with *P. canus* and *P. pebas*. Many sequenced specimens (and most other referred material) are phenotypically distinctive, with almost uniformly blackish pelage, but some sequenced specimens that we refer to *P. mcilhennyi* on the basis of haplogroup membership (e.g., AMNH 273055, 273089) resemble *P. andersoni* in pelage coloration, and the other external and craniodental characters by which Patton and da Silva (1997, 2008) diagnosed these taxa do not appear to consistently distinguish them.[6] Not unreasonably, Hershkovitz (1997) ranked *mcilhennyi* as a subspecies of *P. andersoni*, but

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[6] For example, Patton and da Silva (1997) described the middorsal fur as "ca. 10 mm long" in *P. andersoni* versus "ca. 18 mm in length" in *P. mcilhennyi*, a substantial difference. However, the middorsal fur of 21 specimens of *P. andersoni* that we measured from northern Peru (Amazonas) and eastern Ecuador was 13 ± 2 mm long with an observed range of 10–16 mm, whereas the middorsal fur of 21 *P. mcilhennyi* from south of the Amazon in Peru and Brazil was 16 ± 3 mm with an observed range of 12–22 mm.

as we did not recover *andersoni* and *mcilhennyi* as sister groups, we provisionally treat both as valid species.

PHILANDER OPOSSUM: By contrast with traditional usage, we restrict *P. opossum* to the large, uniformly gray form with a long white tail-tip that occurs throughout the Guianas (Guyana, Surinam, French Guiana) and the eastern part of Amazonian Brazil (Amapá, Pará, Roraima, and part of Amazonas). In terms of physical geography, Brazilian populations of this species occur east of the Rio Negro (along the north bank of the Amazon) and east of the Rio Madeira (along the south bank). As understood in this report (see Remarks under *P. quica* and appendix 5, below), *P. opossum* includes *frenatus* and *superciliaris* as junior synonyms.

TAXONOMIC ACCOUNTS

The following accounts include an emended description of the genus *Philander*, redescriptions of *P. quica* and *P. canus*, and a description of our new Amazonian species, *P. pebas*. Additionally, these accounts serve to summarize geographic distributions, comment on relevant issues of nomenclature and identification, and list the morphological specimens we examined. Our abbreviated synonymies include only original descriptions (subsequent name combinations can be found in Patton and da Silva, 2008). Qualitative morphological comparisons of *P. quica*, *P. canus*, and *P. pebas* are summarized in table 6, and descriptive statistics are summarized in tables 7 and 8. Morphological comparisons with other species are restricted to members of the cis-Andean *P. opossum* complex.

Philander Brisson, 1762

TYPE SPECIES: *Didelphis opossum* Linnaeus, 1758, by plenary action of the International Commission on Zoological Nomenclature (ICZN, 1998).

CONTENTS: Based on evidence summarized in this report, we tentatively recognize the following eight species as valid (synonyms in parentheses): **andersoni** Osgood, 1913; **canus** Osgood, 1913 (including *crucialis* Thomas, 1923; *mondolfii* Lew et al., 2006; and *olrogi* Flores et al., 2008); **mcilhennyi** Gardner and Patton, 1972; **melanurus** Thomas, 1899 (including *fuscogriseus* Allen, 1900; *grisescens* Allen, 1901; and *melantho* Thomas, 1923); **opossum** Linnaeus, 1758 (including *frenatus* Olfers, 1818; and *superciliaris* Olfers, 1818); **pallidus** Allen, 1901; **pebas,** new species (described below); and **quica** Temminck, 1824 (including *azaricus* Thomas, 1923).

In the absence of genetic information, we are currently unable to assess the validity of *deltae* Lew et al., 2006, and *nigratus* Thomas, 1923, either or both of which might also be good species.

DESCRIPTION:[7] Combined length of adult head and body ca. 250–350 mm; adult weight ca. 280–700 g. Rhinarium with one ventrolateral groove on each side of median sulcus; dark circumocular mask present, usually continuous with dark coronal fur; pale supraocular spots present; dark midrostral stripe absent; throat gland absent. Dorsal pelage unpatterned-

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[7] After Voss and Jansa (2009: 121–123), but including corrections and supplementary observations.
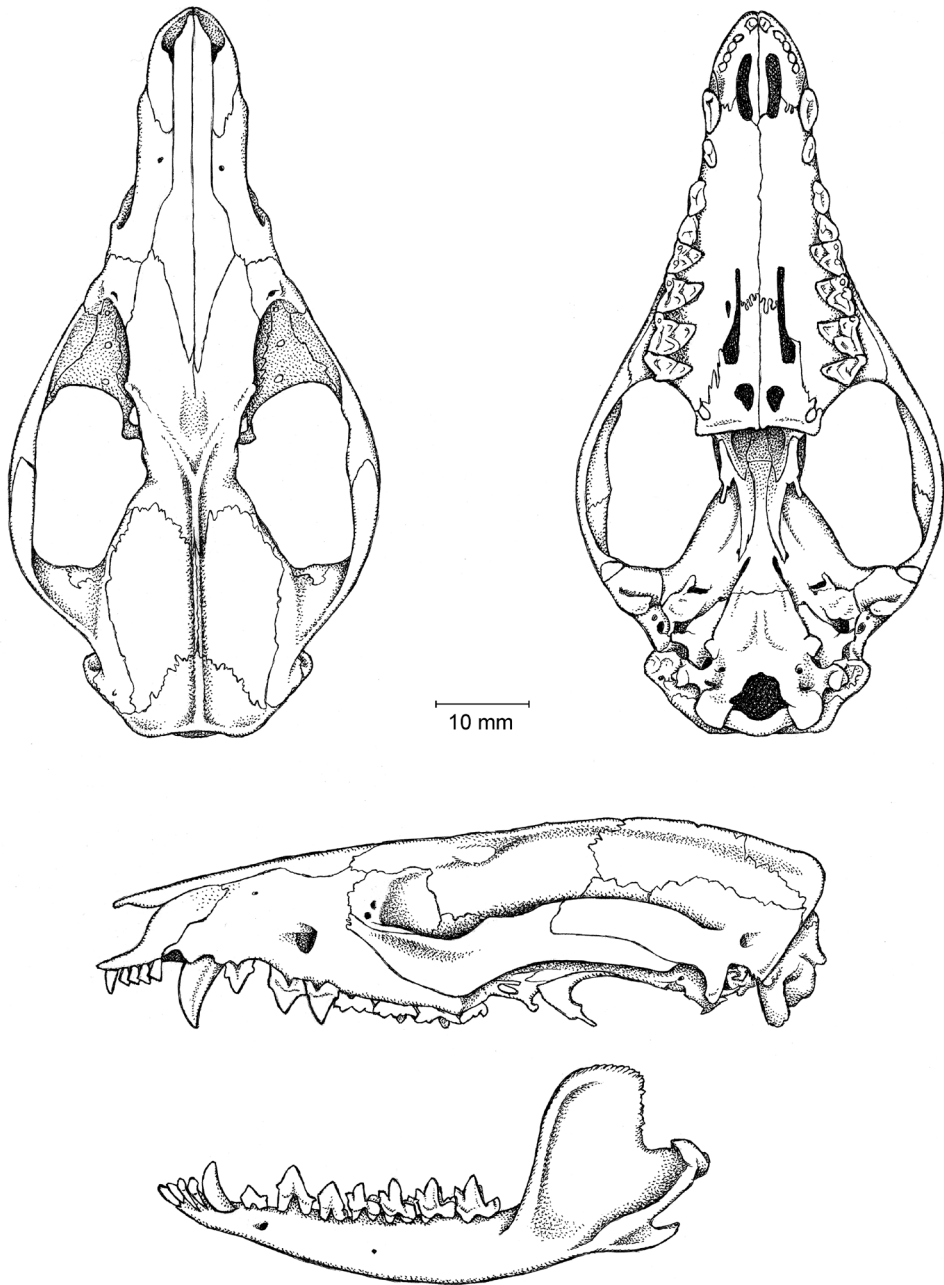
10 mm

FIG. 8. Dorsal, ventral, and lateral cranial views of *Philander opossum* (based primarily on AMNH 266387, an adult female from Paracou, French Guiana).
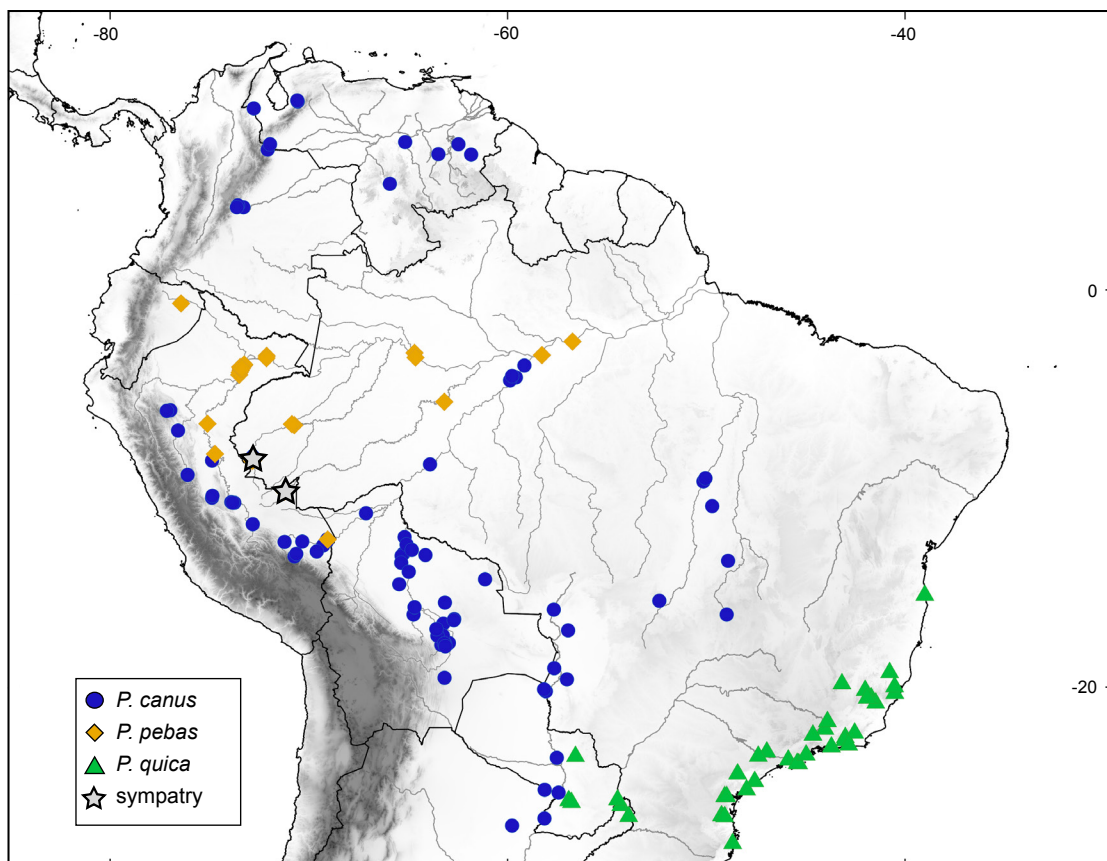
FIG. 9. Collection localities of examined specimens of *Philander quica*, *P. canus*, and *P. pebas*. The symbol for sympatry marks localities where *P. canus* and *P. pebas* have been collected together.

grayish or -blackish, or with grayish flanks and black middorsal stripe when fresh (foxing to brownish tones in old museum skins); dorsal underfur gray; dorsal guard hairs usually short (but sometimes much longer middorsally than along flanks in *P. mcilhennyi*); ventral fur variously pigmented (self-whitish or -buffy, gray-based buffy or cream, or entirely grayish; variable within and among species). Manus mesaxonic (dIII > dIV); manual claws about as long as fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch present, opening anteriorly; mammae usually 2–1–2 = 5 or 3–1–3 = 7; cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate); furred dorsally and ventrally to about the same extent at base; naked caudal integument blackish proximally and abruptly whitish distally (but a few specimens of some species have all-black tails); caudal scales in spiral series, each scale with 4–6 bristlelike hairs emerging from distal margin; ventral caudal surface modified for prehension distally, with apical pad bearing dermatoglyphs.

TABLE 6. Morphological and geographical comparisons among three species of *Philander*.

	P. quica	*P. canus*	*P. pebas*
Ventral pelage	self-whitish to -buffy	self-whitish to -buffy	mostly gray-based
White on tail[a]	usually ⅓ to ½	usually ⅓ to ½	usually <¼
P3 labial cingulum	incomplete	complete	complete
Protocone lingual enamel	smooth	smooth	crenulated when unworn
Pre- & postcingula[b]	absent	absent	present
Posterior cingulids[c]	absent	absent	present
Length upper molar row (LM)[d]	12.3 ± 0.4 mm	13.0 ± 0.4 mm	13.8 ± 0.5 mm
Distribution	Atlantic Forest	widespread	western & central Amazonia

[a] Proportion of unfurred (scaly) part of tail that is whitish distally.
[b] On upper molars.
[c] On lower molars.
[d] Mean plus or minus one standard deviation, sexes combined

Skull in general aspect (fig. 8) smaller and less robust than that of *Didelphis* (which it otherwise resembles). Premaxillary rostral process absent. Nasals short, usually not extending anteriorly above I1 (exposing nasal orifice in dorsal view), and widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina usually two on each side, exposed laterally on orbital margin or on face just anterior to orbit. Interorbital region smoothly rounded, without supraorbital beads or crests; short, blunt postorbital processes usually present in large adult specimens. Left and right frontals coossified (midfrontal suture incomplete or absent), but left and right parietals separated by persistent midparietal suture. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest present, well developed on parietals and extending anteriorly onto frontals. Petrosal not laterally exposed through fenestra in squamosal-parietal suture (fenestra absent). Parietal-mastoid contact absent (interparietal narrowly contacts squamosal).

Maxillopalatine and palatine fenestrae present; maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palate (behind toothrows) with prominent lateral corners, the choanae constricted behind. Maxillary and alisphenoid usually separated by palatine on floor of orbit (but maxillary-alisphenoid contact occurs unilaterally or bilaterally in a few specimens). Transverse canal foramen usually present. Alisphenoid tympanic process small and uninflated, usually with broad lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic indirectly suspended from basicranium (by malleus). Stapes usually triangular with large obturator foramen. Fenestra cochleae exposed (not concealed by rostral and caudal tympanic processes of petrosal). Paroccipital process large, erect, directed posteroventrally. Dorsal margin of foramen magnum bordered by exoccipitals only (incisura occipitalis absent).

TABLE 7. Summary statistics[a] for craniodental measurements (mm) of adult male specimens of *Philander quica*, *P. canus*, and *P. pebas*.

	P. quica[b]	*P. canus*[c]	*P. pebas*[d]
CBL	65.9 ± 4.1 (58.6–74.6) 22	64.0 ± 2.6 (60.0–70.7) 21	70.6 ± 2.8 (65.1–75.4) 27
NL	31.1 ± 1.8 (26.9–34.3) 21	29.4 ± 1.3 (26.8–31.4) 21	33.6 ± 1.7 (30.6–36.4) 22
NB	8.0 ± 0.9 (6.8–9.8) 23	7.4 ± 0.9 (5.8–9.0) 21	7.8 ± 0.8 (6.5–9.8) 27
LIB	11.7 ± 1.0 (10.1–14.1) 23	10.6 ± 0.6 (9.6–11.7) 21	12.2 ± 0.7 (11.0–13.9) 27
LPB	8.5 ± 0.3 (7.8–8.8) 23	7.9 ± 0.3 (7.4–8.5) 21	8.7 ± 0.3 (8.3–9.9) 27
ZB	35.0 ± 3.0 (30.1–40.2) 23	34.0 ± 1.7 (31.4–38.4) 21	35.8 ± 2.3 (32.0–40.5) 27
PL	38.7 ± 2.1 (34.5–43.4) 23	38.1 ± 1.4 (36.2–41.5) 21	43.7 ± 1.5 (40.5–46.3) 27
PB	19.4 ± 0.7 (18.1–20.9) 23	19.3 ± 0.7 (18.2–20.6) 21	20.0 ± 0.8 (18.5–21.9) 27
MTR	27.0 ± 1.1 (24.1–29.2) 23	27.4 ± 0.8 (26.4–29.5) 21	30.6 ± 0.8 (29.2–32.1) 27
LM	12.4 ± 0.5 (11.4–13.2) 23	13.2 ± 0.4 (12.4–13.7) 21	14.0 ± 0.5 (13.4–15.1) 27
M1–3	10.5 ± 0.4 (9.7–11.3) 23	11.1 ± 0.4 (10.4–11.7) 20	11.7 ± 0.5 (10.9–12.8) 27
WM3	4.0 ± 0.2 (3.4–4.4) 20	4.1 ± 0.2 (3.7–4.4) 21	4.2 ± 0.2 (3.9–4.5) 27

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size; see Materials and Methods for measurement abbreviations.
[b] AMNH 61852, 133107; BMNH 2.4.6.37, 2.4.6.38, 3.7.1.108, 3.7.1.109; FMNH 141590; MVZ 182066, 182067, 183246, 183247, 197401; NMW 2638, 2640; USNM 121412, 121414, 293133, 460503, 542920; ZMB 38063, 38069, 38091, 44285.
[c] AMNH 135887, 210402, 210410, 210411, 210413, 260037, 261269, 261271, 261272, 261278, 263966; FMNH 114707; MSB 55074, 55075 55854, 55856; USNM 390005, 390010–390012, 390562.
[d] LACM 91622; MUSM 33564, 33566, 33567, 33570, 33572, 33574, 33580, 33583, 33587, 33588, 33590, 33592, 33593, 33597–33600; MVZ 190343, 190344; TTU 98574, 98591, 98592, 98755, 101178, 101192, 101256.

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

Unworn crowns of I2–I5 with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars highly carnassialized (postmetacristae conspicuously longer than postprotocristae; relative widths M1 < M2 < M3 < M4; centrocrista only weakly inflected labially on M1–M3; ectoflexus usually distinct only on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista with carnassial notch. Last upper tooth to erupt is M4.

Lower incisors (i1–i4) without distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) much taller than p3; lower milk premolar (dp3) large and molariform with complete (tricuspid) trigonid. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

TABLE 8. Summary statistics[a] for craniodental measurements (mm) of adult female specimens of *Philander quica*, *P. canus*, and *P. pebas*.

	P. quica[b]	*P. canus*[c]	*P. pebas*[d]
CBL	62.0 ± 3.5 (56.1–68.5) 17	62.1 ± 3.0 (57.0–67.1) 22	68.5 ± 3.3 (61.0–75.8) 23
NL	29.1 ± 1.8 (25.9–33.4) 16	28.4 ± 1.6 (25.2–31.0) 21	32.3 ± 1.9 (29.2–35.1) 16
NB	7.4 ± 0.6 (6.5–8.3) 17	7.1 ± 0.6 (6.4–8.8) 22	7.3 ± 0.8 (5.7–8.9) 23
LIB	10.9 ± 0.6 (9.8–11.6) 17	10.1 ± 0.5 (9.3–11.1) 22	11.6 ± 1.0 (9.8–14.1) 22
LPB	8.5 ± 0.2 (8.1–8.9) 17	7.8 ± 0.3 (7.4–8.4) 22	8.8 ± 0.3 (8.3–9.5) 23
ZB	33.0 ± 2.3 (29.1–37.2) 15	32.4 ± 1.6 (29.8–35.7) 22	34.2 ± 1.9 (30.1–38.5) 23
PL	36.8 ± 2.0 (34.0–40.6) 17	37.2 ± 1.9 (33.8–40.1) 22	42.4 ± 2.2 (37.8–46.7) 23
PB	19.2 ± 0.6 (18.1–20.1) 16	19.0 ± 0.8 (17.8–20.5) 22	19.7 ± 0.7 (18.3–21.0) 22
MTR	26.0 ± 0.9 (25.0–28.0) 17	26.7 ± 1.0 (25.0–28.6) 22	29.4 ± 1.1 (27.4–30.9) 23
LM	12.2 ± 0.4 (11.7–12.8) 17	12.8 ± 0.4 (12.2–13.6) 22	13.7 ± 0.5 (12.7–14.5) 23
M1–3	10.5 ± 0.3 (10.0–11.1) 17	10.8 ± 0.3 (10.4–11.4) 22	11.4 ± 0.4 (10.7–12.3) 23
WM3	3.9 ± 0.2 (3.7–4.2) 16	4.0 ± 0.2 (3.6–4.4) 22	4.0 ± 0.2 (3.6–4.5) 23

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size; see Materials and Methods for measurement abbreviations.
[b] AMNH 133106; BMNH 2.11.7.48, 2.4.6.39, 2.4.6.40, 3.2.3.33–3.2.3.37; FMNH 141589; NMW 2636, B2529; USNM 121421, 121422; ZMB 38072, 38073, 38076.
[c] AMNH 210403, 210409, 210414, 210416, 260034, 261270, 261273, 261277, 263964; BMNH 47.11.22.15; FMNH 114685, 114694, 114701, 114714; MSB 55073, 55855, 58517, 59887, 67025; USNM 390009, 390564, 390565.
[d] AMNH 74388, 76448–76450, 98642; LACM 91621; MUSM 6074, 33569, 33576, 33586, 33594, 33602, 33603, 34892; MVZ 190345, 190346; TTU 98583, 98953, 100984, 101142, 101186, 101253, 101258.

Philander quica (Temminck, 1824)

Didelphis quica Temminck, 1824: 36; type locality (fixed by lectotype selection; Hershkovitz, 1959: 342) "Sapitibi" (= Sepetiba at 22°58′ S, 43°42′ W; Paynter and Traylor, 1991), Rio de Janeiro, Brazil.

Metachirus opossum azaricus Thomas, 1923: 604; type locality "Sapucay" (= Sapucaí at 25°41′ S, 56°57′ W; Paynter, 1989), Paraguarí, Paraguay.

Type Material: Temminck (1824: 36–38) based his description of *Didelphis quica* on an unknown number of specimens from various museums, presumably including one or more examples collected by Johann Natterer, whose information about the species was prominently acknowledged ("Nous devons à M. Natterer la connaissance plus exacte de cette espèce qu'il a envoyée au musée impérial de Vienne . . ."). In a published catalog of Natterer's mammals, Pelzeln (1883: 110–111) listed two specimens of *D. quica*, male and female, collected in 1818 at "Sapitiba" (= Sepetiba) near Rio de Janeiro. Of these, Hershkovitz (1959) designated the female as lectotype, apparently sight unseen. Unfortunately, this specimen is no longer in Vienna, where only the male topotype (NMW 7687/ST 1012) can now be found. The female may have been exchanged or gifted to Temminck, whose cabinet was subsequently transferred to the Leiden museum (formerly the Rijksmuseum van Natuurlijke Historie, now the Naturalis Biodiversity Center; S. Engelberger, personal commun., 26 November 2014), but no specimen

FIG. 10. Dorsal pelage of cis-Andean species of *Philander* compared in the text. From left to right: *P. quica* (MVZ 183246), *P. canus* (LACM 10086), *P. pebas* (MVZ 190343, holotype), *P. mcilhennyi* (LSU 16393), *P. andersoni* (LACM 91620), *P. opossum* (AMNH 266996). The dorsal fur of these species is always grayish or blackish in life, but museum skins often acquire brownish tones after long storage.

currently in Leiden can be positively identified as Hershkovitz's lectotype (S. van der Mije, 25 November 2014).

In the absence of any compelling evidence to the contrary, we accept Hershkovitz's (1959) lectotype designation as valid. Although the specimen in question appears to have been lost (or to be unidentifiable), the fixation of the type locality is sufficient for confident application of Temminck's epithet to the Atlantic Forest species of southeastern Brazil. The male topotype mentioned above (consisting of the mounted skin and extracted skull of a very old animal with much-faded pelage and teeth worn away almost to the roots) is not taxonomically informative, but other examined specimens of *Philander* from the Brazilian state of Rio de Janeiro (in the AMNH and ZMB; see below) exhibit all the diagnostic traits that we attribute to *P. quica* in the description that follows.

DISTRIBUTION AND SYMPATRY: Sequenced material and examined specimens that we assign to *Philander quica* are from rainforested tropical and subtropical landscapes in southeastern Brazil, northeastern Argentina (Misiones), and eastern Paraguay (fig. 9). Although *P. quica* is

FIG. 11. Ventral pelage of cis-Andean species of *Philander* compared in the text. From left to right: *P. quica* (MVZ 183246), *P. canus* (LACM 10086), *P. pebas* (MVZ 190343, holotype), *P. mcilhennyi* (LSU 16393), *P. andersoni* (LACM 91620), *P. opossum* (AMNH 266996).

the only species of *Philander* known to occur throughout this biome (the Mata Atlântica of Brazilian authors), it might occur sympatrically with *P. canus* along its margins, where Atlantic rainforests come into contact with (or grade into) the gallery formations and semideciduous forests apparently preferred by the latter species. Additionally, the range of *P. quica* might contact that of *P. opossum* somewhere along the coastline between Bahia and Rio Grande do Norte.[8] Published records of this species from the Cerrado, the Chaco, and western Amazonia (in Patton and da Silva, 1997, 2008; Hershkovitz, 1997) are based on misidentifications (see Remarks, below).

Description: Dorsal pelage short (usually <14 mm) and uniformly grayish, sometimes indistinctly darker along the midline but never with a distinctly blackish middorsal stripe (fig 10); fur of crown (between the ears) usually grizzled gray but sometimes blackish; pale preau-

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[8] We are told (D. Astúa, personal commun.) that this is unlikely. The southeasternmost record we have seen of *Philander opossum* is a specimen from Canudos, Rio Grande do Norte, Brazil, collected by F. Lima in 1920 (FMNH 24790).
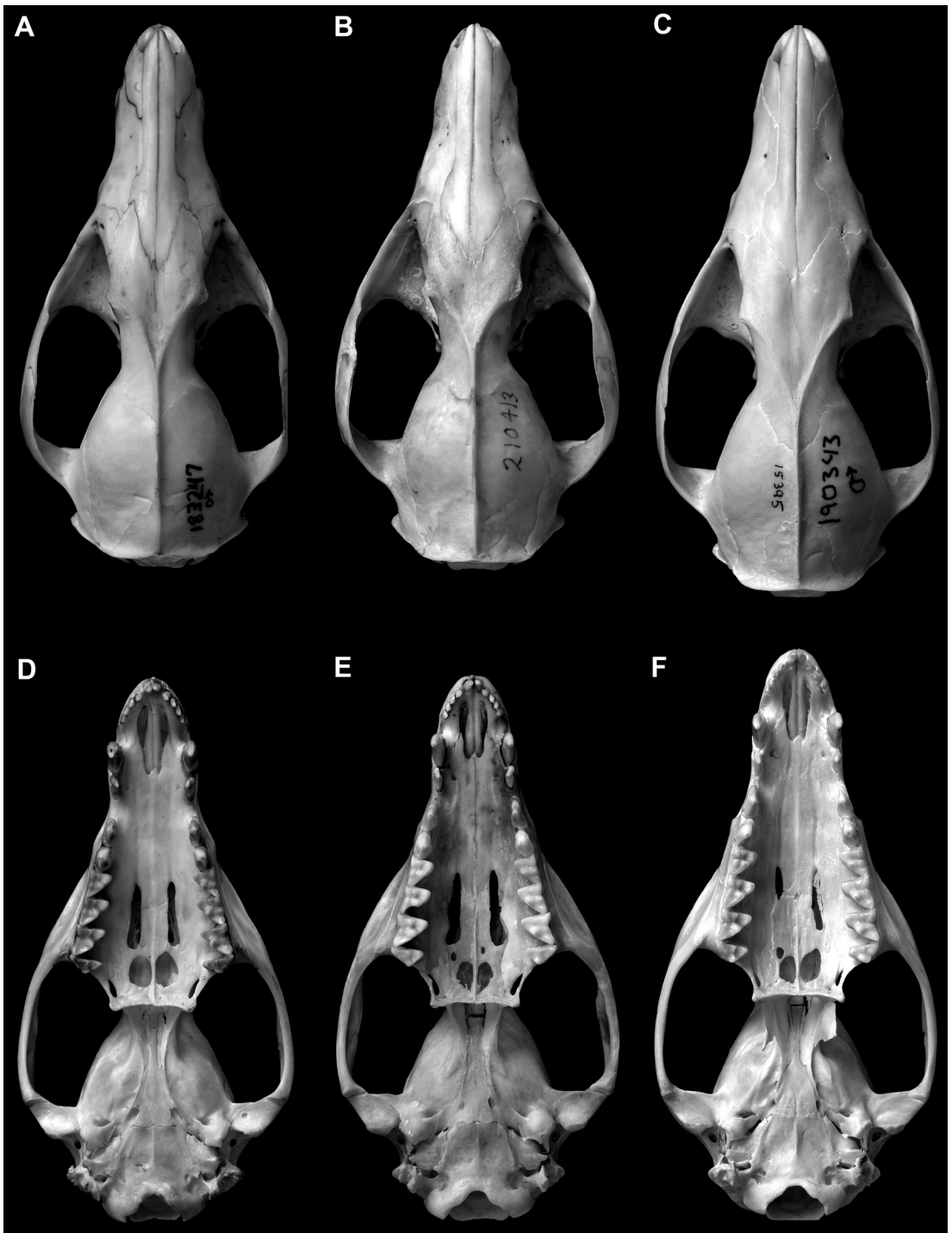
FIG. 12. Dorsal and ventral views of adult male crania of *Philander* species formally treated in this report: **A, D,** *P. quica* (MVZ 183247); **B, E,** *P. canus* (AMNH 210413); **C, F,** *P. pebas* (MVZ 190343, holotype). All views about ×1.3.
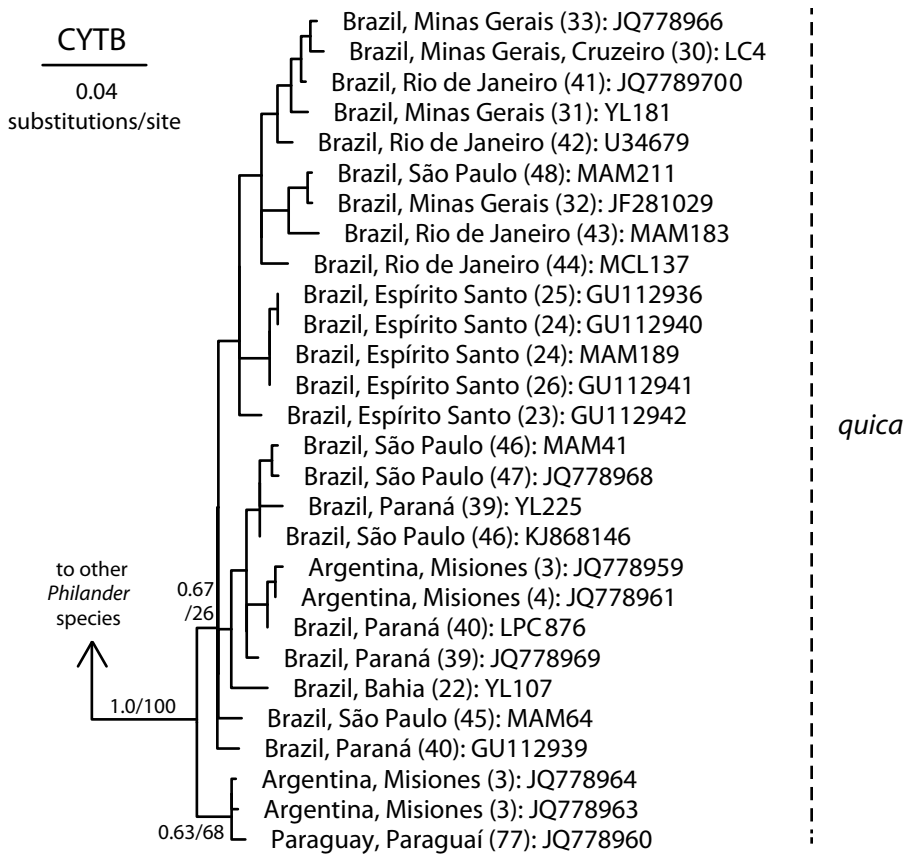
FIG. 13. Relationships among 28 cytochrome-*b* sequences of *Philander quica*. This subtree shows the full details of the cartooned clade labeled "*quica*" in figure 5.

ricular spot absent or indistinct; ventral fur pale, usually self-whitish or -yellowish, sometimes with broad lateral zones of gray-based hairs on the throat and between the fore- and hind legs, but apparently always self-colored in the midline (fig. 11); pinnae pale (unpigmented) basally, but abruptly blackish distally; dorsal pelage of hind feet often indistinctly darker laterally than medially, but never distinctly blackish or with blackish markings; scaly part of tail usually one-third to slightly less than one-half white distally. Skull (fig. 12A, D) substantially smaller than those of most congeneric species (except *P. canus*). Nasal bones neither conspicuously elongated nor very short (about 47% of condylobasal length on average), not extending posteriorly to or between postorbital processes. Third upper premolar (P3) labial cingulum incomplete, apparently never extending to anterior base of crown; crown length of upper molar series 12.3 ± 0.4 mm (sexes combined; observed range 11.4–13.2 mm, *N* = 40); enameled lingual surfaces of upper molars smooth, not crenulated; pre- and postcingula consistently absent; lower molar posterior cingulids absent.

PHYLOGEOGRAPHY AND GEOGRAPHIC VARIATION: Our phylogenetic analysis of 28 cytochrome-*b* sequences of *Philander quica* spanning some 10 degrees of latitude (from the Brazil-
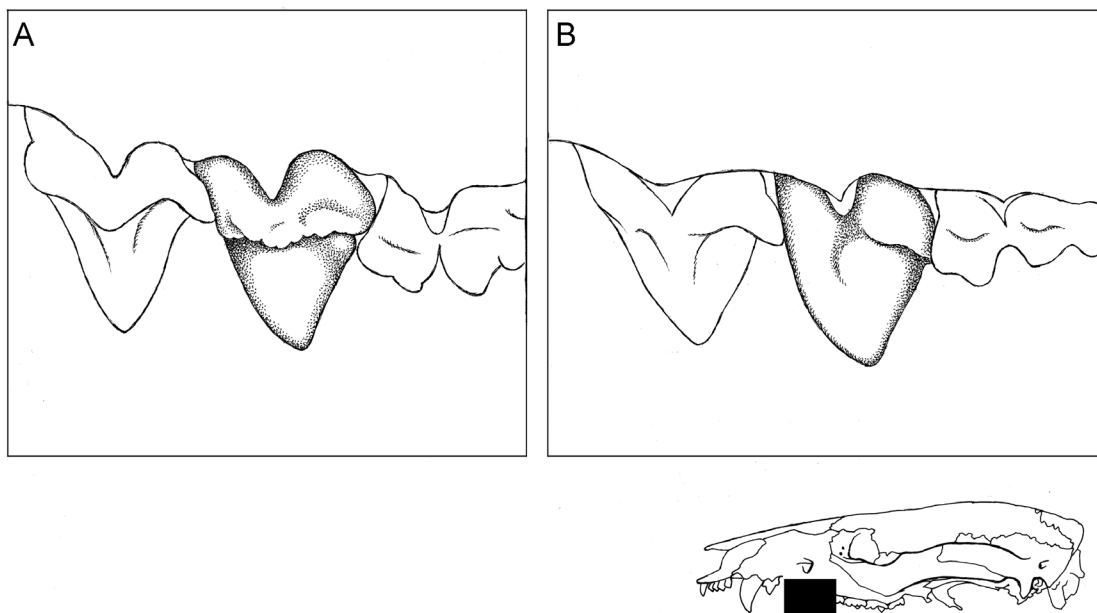
FIG. 14. Lateral view of P2–M1 of *Philander canus* (**A,** AMNH 210409) and *P. quica* (**B,** MVZ 182066). Whereas P3 has a complete labial cingulum that extends along the entire base of the tooth in *P. canus*, the labial cingulum of P3 is incomplete (extending only along the posterior part of that tooth) in *P. quica*.

ian state of Bahia in the north to the Argentinian province of Misiones in the south) provides scant evidence of phylogeographic structure (fig. 13). This lack of genetic differentiation with distance is accompanied by an absence of conspicuous geographic variation in morphology. In effect, this appears to be a genetically and phenotypically homogeneous taxon.

COMPARISONS: *Philander quica* closely resembles *P. canus*, which is similar in size (tables 7, 8); also has uniformly grayish dorsal pelage and self-whitish, -yellowish, or -buffy ventral fur (figs. 10, 11); and is not visually distinctive in any aspect of cranial appearance (fig. 12). Chemisquy and Flores (2012) suggested that these taxa could be distinguished by the width of the postorbital constriction (least postorbital breadth in our terminology), but the samples we measured exhibit broad overlap in this dimension (e.g., 7.8–8.8 mm in *P. quica* males versus 7.4–8.4 mm in *P. canus* males). *Philander quica* and *P. canus* also have broadly overlapping distributions in the plane of the first two principal components that we computed from craniodental measurements of both taxa (not shown), a result consistent with our impression that these species are metrically very similar. Instead, qualitative morphological comparisons are more informative.

In side-by-side comparisons, the molars of *Philander quica* appear to have somewhat less well-developed anterolabial cingula, narrower protocones, deeper ectoflexi (especially on M3), and longer postmetacristae than those of *P. canus*, but the single most useful dental trait that distinguishes these taxa is the morphology of P3. Whereas the third upper premolar of *P. canus* always has a complete labial cingulum that extends along the entire base of the tooth from anterior to posterior (fig. 14A), the labial cingulum of P3 is incomplete in *P. quica*, apparently

TABLE 9. Same-sex comparisons of summary statistics[a] for craniodental measurements of *Philander quica* and *P. opossum*.

	Males		Females	
	P. quica[b]	*P. opossum*[c]	*P. quica*[d]	*P. opossum*[e]
CBL	65.9 ± 4.1 (58.6–74.6) 22	71.0 ± 3.0 (65.7–77.4) 25	62.0 ± 3.5 (56.1–68.5) 17	68.7 ± 3.5 (64.6–75.4) 17
NL	31.1 ± 1.8 (26.9–34.3) 21	35.2 ± 1.9 (31.4–38.6) 25	29.1 ± 1.8 (25.9–33.4) 16	34.2 ± 2.2 (30.6–38.7) 17
NB	8.0 ± 0.9 (6.8–9.8) 23	8.3 ± 0.6 (7.2–10.0) 25	7.4 ± 0.6 (6.5–8.3) 17	8.0 ± 0.8 (6.6–10.0) 17
LIB	11.7 ± 1.0 (10.1–14.1) 23	12.4 ± 0.8 (11.1–14.8) 25	10.9 ± 0.6 (9.8–11.6) 17	11.8 ± 0.8 (10.8–13.6) 17
LPB	8.5 ± 0.3 (7.8–8.8) 23	8.8 ± 0.3 (8.2–9.5) 25	8.5 ± 0.2 (8.1–8.9) 17	8.7 ± 0.3 (8.1–9.1) 17
ZB	35.0 ± 3.0 (30.1–40.2) 23	36.3 ± 2.4 (32.8–42.4) 25	33.0 ± 2.3 (29.1–37.2) 15	34.6 ± 1.9 (32.1–38.5) 17
PL	38.7 ± 2.1 (34.5–43.4) 23	42.6 ± 1.5 (40.5–46.8) 25	36.8 ± 2.0 (34.0–40.6) 17	41.3 ± 1.8 (38.4–45.2) 17
PB	19.4 ± 0.7 (18.1–20.9) 23	20.7 ± 0.7 (19.7–22.2) 25	19.2 ± 0.6 (18.1–20.1) 16	20.5 ± 0.6 (19.4–21.5) 17
MTR	27.0 ± 1.1 (24.1–29.2) 23	29.7 ± 1.0 (28.8–33.2) 25	26.0 ± 0.9 (25.0–28.0) 17	28.7 ± 0.8 (27.6–30.0) 17
LM	12.4 ± 0.5 (11.4–13.2) 23	13.9 ± 0.5 (13.1–15.3) 25	12.2 ± 0.4 (11.7–12.8) 17	13.7 ± 0.3 (13.3–14.5) 17
M1–3	10.5 ± 0.4 (9.7–11.3) 23	11.6 ± 0.4 (10.9–12.8) 25	10.5 ± 0.3 (10.0–11.1) 17	11.5 ± 0.3 (11.1–12.1) 17
WM3	4.0 ± 0.2 (3.4–4.4) 20	4.2 ± 0.2 (3.9–4.8) 25	3.9 ± 0.2 (3.7–4.2) 16	4.1 ± 0.2 (3.9–4.4) 17

[a] Table entries include the sample mean plus or minus one sample standard deviation, the observed range (in parentheses), and the sample size.
[b] AMNH 61852, 133107; BMNH 2.4.6.37, 2.4.6.38, 3.7.1.108, 3.7.1.109; FMNH 141590; MVZ 182066, 182067, 183246, 183247, 197401; NMW 2638, 2640; USNM 121412, 121414, 293133, 460503, 542920; ZMB 38063, 38069, 38091, 44285.
[c] AMNH 96563, 96569, 96574, 96576, 96730, 96732, 96733, 96755, 203348, 203349; USNM 393606, 393607, 393610, 393612, 519732, 521434, 544496, 544497, 544499, 544503, 545588, 545591, 546226, 549297, 549298.
[d] AMNH 133106; BMNH 2.11.7.48, 2.4.6.39, 2.4.6.40, 3.2.3.33–3.2.3.37; FMNH 141589; NMW 2636, B2529; USNM 121421, 121422; ZMB 38072, 38073, 38076.
[e] AMNH 96556, 96561, 96571, 96579, 96620, 96738, 203347; USNM 393602, 393603, 393609, 519731, 544500, 545586, 545587, 545589, 545592, 549299

never extending anteriorly past the middle of that tooth (fig. 14B). Unfortunately, we have not found any external trait by which these species can be reliably identified in the field.

Close comparisons between *Philander quica* and our new species, *P. pebas*, seem unnecessary given their widely separated geographic distributions (fig. 9), large genetic and morphometric distances (appendices 3, 4), and salient qualitative differences (table 6).

By contrast, *Philander quica* and *P. opossum* merit comparison because they are externally similar (with uniformly grayish dorsal fur and mostly self-colored ventral fur) and might eventually be found to occur sympatrically in eastern Brazil (see above). Although

VOSS ET AL: REVISION OF *PHILANDER* 35

TABLE 10. Coefficients of principal components (PC1, PC2), general size (Size), and size-adjusted group differences (Shape) for multivariate analyses of *Philander quica* versus *P. opossum*[a]

	PC1	PC2	Size	Shape
CBL	0.338	0.056	0.303	0.161
NL	0.422	0.269	0.308	0.395
NB	0.388	-0.505	0.529	-0.357
LIB	0.409	-0.308	0.480	-0.158
LPB	0.064	0.111	0.010	0.136
ZB	0.374	-0.293	0.460	-0.168
PL	0.317	0.226	0.222	0.321
PB	0.232	0.119	0.181	0.187
LM	0.255	0.503	0.073	0.565
WM3	0.162	0.397	0.060	0.402

[a] See figure 15 for specimen projections on these axes. The first principal component accounts for 68.6% of the total variance in these data, whereas PC2 accounts for 17.7% (cumulative = 86.3%).

same-sex univariate comparisons (table 9) reveal some overlap in all measured craniodental dimensions, principal-components analysis indicates that these species have discrete multivariate distributions (fig. 15A). Because the axis of species discrimination is approximately perpendicular to the more or less parallel axes of within-species variation, and because these axes are oblique to PC1 and PC2, we computed size and size-independent shape factors to obtain vectors with more interpretable coefficients (fig. 15B; table 10). The latter suggest that, independent of general-size allometries, *P. opossum* has longer but narrower nasals, a longer palate, and much larger molars than *P. quica*.

Differences in nasal shape between *Philander quica* and *P. opossum* are subtle but useful for visual identification of skulls: expressed as a percentage, the ratio NB/NL is about 25% on average in *P. quica* versus about 22% in *P. opossum*. Additionally, the shorter/broader nasals of *P. quica* never extend posteriorly to or between the postorbital processes, whereas the longer nasals of *P. opossum* often (in about two-thirds of examined specimens) extend to or between the postorbital processes. Whereas *P. quica* always has an incomplete labial cingulum on P3 (fig. 14B), the labial cingulum of P3 is narrowly complete (ending along the entire base of the tooth when unworn) in about 28% of examined specimens of *P. opossum*. Externally, *P. opossum* has better-defined preauricular spots and more saturated (consistently buffy) underparts than *P. quica* (which usually has whitish or yellowish ventral fur), and *P. opossum* tends to have a more extensively white-tipped tail (over half the specimens we examined have tails that are about ⅔ white) than *P. quica* (in which most specimens have tails that are ≤ ½ white). In side-by-side comparisons, the furred basal portion of the tail is visibly longer in *P. opossum* than in *P. quica*; unfortunately, this trait is difficult to quantify due to the absence of a definite anterior landmark for relevant measurements.

REMARKS: Most recent authors have used the binomen *Philander frenatus* for this species following Patton and da Silva (1997), but the holotype of *frenatus* was collected in eastern Amazonia, and we treat that name as a junior synonym of *P. opossum* (see appendix 5).
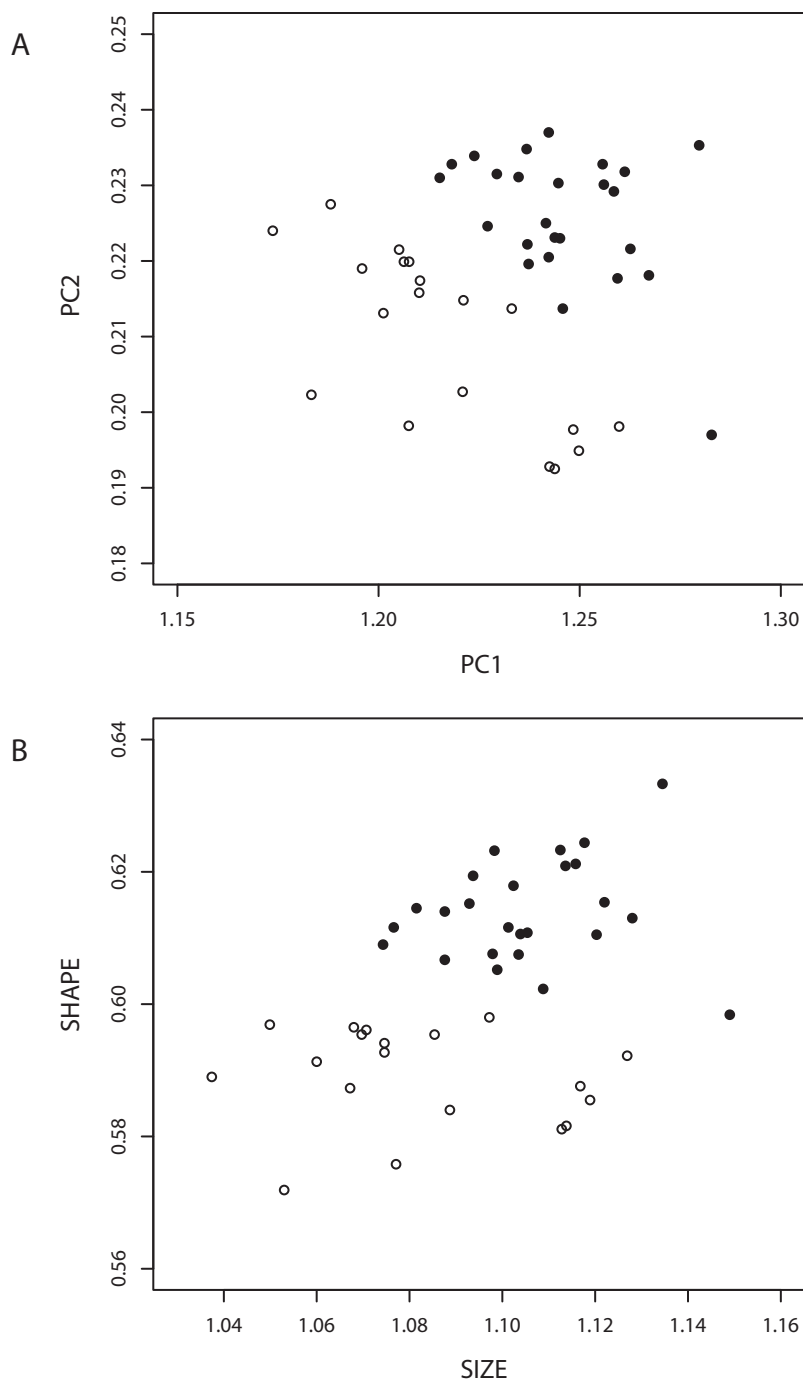
FIG. 15. Projections of specimen scores on the first two principal components (**A**) and on factors representing general size and size-invariant shape differences (**B**) from analyses of craniodental measurements of *Philander quica* (open circles) and *P. opossum* (filled circles). The coefficients of these axes are provided in table 10.

Hershkovitz (1997) used the trinomen *Philander opossum quica* for material that we refer to *P. quica, P. canus*, and *P. pebas*. He mapped the range of *P. o. quica* as including much of the Cerrado, Pantanal, and western Amazonia, but none of his material from Peru, Bolivia, or central Brazil corresponds to *P. quica* as recognized in this report. Hershkovitz (1997) regarded *Didelphis myosuros* Temminck, 1824, as a synonym of *P. o. quica* and designated a lectotype for this purpose, but his lectotype designation is invalid because Pohle (1927) had previously designated a lectotype for *D. myosuros*, which is currently recognized (e.g., by Gardner and Dagosto, 2008) as a subspecies of *Metachirus nudicaudatus* (Geoffroy, 1803).

According to Patton and da Silva (1997) this species—which they called *Philander frenatus* (see above)—occurs in the Brazilian state of Goiás, but they did not list any examined specimens from Goiás, and all the specimens of *Philander* that we examined from that state are unambiguously referable to *P. canus* (see below). Subsequently, Patton and da Silva (2008) mapped the range of *P. "frenatus"* as extending to the Chaco biome in the Argentinian province of Formosa, but the marginal record in question is based on AMNH 256980, a juvenile specimen that we reidentified as *P. canus*.

The status and relationships of Thomas's *azaricus* has long been unsettled. Whereas Cabrera (1958) and Patton and da Silva (1997) treated this nominal taxon as a valid subspecies of *P. opossum*, Hershkovitz (1997) assigned it to the synonymy of *P. o. quica*, and Patton and da Silva (2008) included it in their synonymy for *P. frenatus*. Recently, Chemisquy and Flores (2012) analyzed a cytochrome-*b* sequence from a topotype of *azaricus* and found that it belonged to the Atlantic Forest haplotype group that they called *P. frenatus*. We examined the type series of *azaricus* and an additional 13 topotypes for this report; all of these specimens (21 in total) are unambiguously assignable to *P. quica*, exhibiting the craniodental traits of that species as diagnosed above.

The identity of *Didelphys superciliaris* Olfers, 1818, which Patton and da Silva (1997, 2008) listed as a synonym of *Philander frenatus*, cannot now be determined. Both epithets were first published as nomina nuda by Illiger (1815), but their availability dates from Olfers (1818), who based his descriptions on material that he examined in Berlin (see appendix 5). However, whereas the application of *frenatus* can now be established based on an extant holotype, no type material of *superciliaris* is known to survive. Because the collections that Olfers examined in Berlin included specimens collected in both eastern Amazonia and southeastern Brazil, (Voss and Angermann, 1997; see also appendix 5), the lost type of *superciliaris* could have come from either place: if from the former region, the name would be a junior synonym of *P. opossum*; if from the latter, then it would be a senior synonym of *P. quica*. Because *superciliaris* has not, to our knowledge, been recognized as a valid taxon for almost two centuries, it would seem pointless to use this name to replace *quica*, the application of which is undisputed. Therefore, to fix the application of *Didelphys superciliaris* Olfers for the species that occurs in eastern Amazonia, we select as neotype a specimen in the American Museum of Natural History (AMNH 203348) consisting of the skin and skull of an adult male collected by personnel from the Instituto Oswaldo Cruz on 6 December 1960 near "Capim" (= São Domingos do Capim; 1°40′S, 47°47′W; Paynter and Traylor, 1991) at Km 92 on highway BR 14, Pará, Brazil.

Habitats: Within the Atlantic Forest biome or ecoregion (Mata Atlântica), *Philander quica* seems to be eurytopic, occurring in a wide range of vegetation types including mature lowland rainforest (formerly the dominant climax vegetation of southeastern Brazil; Por, 1992), sub-montane forest, secondary growth, agricultural fields, and coastal *restinga* scrub (Cerqueira et al., 1993; Bergallo, 1994; Bonvicino et al., 1997; Passamani et al., 2000; D'Andrea et al., 2007).

Specimens Examined (N = 66): **Brazil**—*Espírito Santo,* Engenheiro Reeve (BMNH 3.9.4.110); *Minas Gerais,* Serra de Caparaó (AMNH 8052–8053, 61851–61853); *Paraná,* Parque Nacional do Iguaçu (MVZ 197401), Roça Nova (BMNH 3.7.1.108–3.7.1.110); *Rio de Janeiro,* Barreira (ZMB 38069, 38072, 38073, 38076, 38091), Rio de Janeiro (AMNH 133106, 133107; ZMB 38063), Sepetiba (NMW 7687/ST 1012); *Rio Grande do Sul* (BMNH 84.2.8.29); *Santa Catarina,* Hansa (BMNH 29.6.6.71), Jaraguá (NMW B2529), Teresópolis (NMW 1671–1675); *São Paulo,* Boracéia (MVZ 182777; USNM 460503), Fazenda Intervales (MVZ 182066, 183246, 183247), Iguape (USNM 542920), Ilha de Sebastião (MVZ 182067), Ilha do Cardoso (FMNH 141589, 141590), São Sebastião (BMNH 2.4.6.37–2.4.6.40), Ypanema (NMW 2636, 2638, 2640). **Paraguay**—*Central,* "Caroreni Viejo" (not located; ZMB 44285); *Paraguarí,* Sapucaí (BMNH 2.11.7.14, 2.11.7.48, 3.2.3.32–3.2.3.37 [type series of *azaricus*]; USNM 121412–121422, 121457, 121458), "Ipitimi" (= Ybytymí; ZMB 91277); *San Pedro,* Tacuatí (USNM 293133).

Philander canus (Osgood, 1913)

Metachirus canus Osgood, 1913: 96; type locality Peru, San Martín, Moyobamba (6°03′ S, 76°58′ W; Stephens and Traylor, 1983).

Metachirus opossum crucialis Thomas, 1923: 604; type locality Bolivia, Santa Cruz, Santa Cruz de la Sierra (17°48′ S, 63°10′ W; Paynter, 1992).

Philander mondolfii Lew et al., 2006: 229; type locality Venezuela, Bolívar, Reserva Forestal de Imataca, Unidad V, between Tumeremo and Bochinche (8°00′ N, 61°30′ W).

Philander olrogi Flores et al., 2008: 17; type locality Bolivia, Santa Cruz, 7 km N Santa Rosa (17°03′ S, 63°35′ W).

Type Material: The holotype (by original designation, FMNH 19347) consists of the skin and skull of an adult male collected by W.H. Osgood and M.P. Anderson on 4 August 1912. Although the skin is well preserved, the skull is broken and incomplete (the left zygomatic arch, the left squamosal, and the left bulla are all missing).

Distribution and Sympatry: Sequenced specimens and other examined material that we refer to *Philander canus* have been collected in central and western Brazil, northern Argentina, Paraguay, eastern Bolivia, eastern Peru, northeastern Colombia, and Venezuela (fig. 9). Although we have not examined specimens from northeastern Peru (Loreto), eastern Ecuador, or southeastern Colombia (Caquetá, Putumayo), future collecting may eventually fill in this geographic hiatus. *Philander canus* occurs sympatrically with *P. andersoni* in southern Venezuela (at El Platanal in Amazonas state), with *P. mcilhennyi* in eastern Peru (e.g., at Balta, in Ucayali department) and western Brazil (at Sobral, in Acre state), and with *P. pebas* in eastern Peru (e.g., at Balta, in Ucayali department).
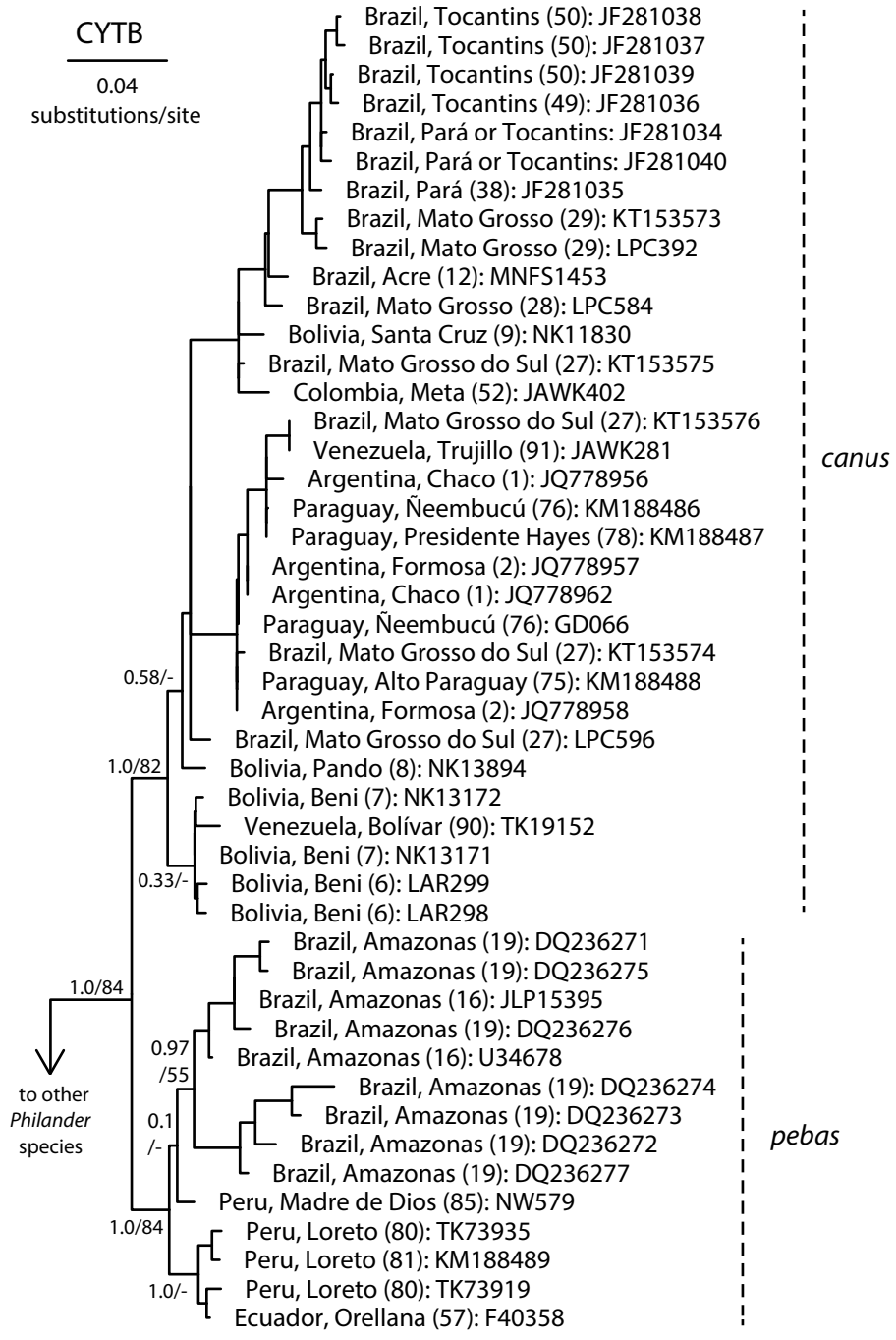
FIG. 16. Relationships among 46 cytochrome-*b* sequences of *Philander canus* and *P. pebas*. This subtree shows the full details of the cartooned clades labeled "*canus*" and "*pebas*" in figure 5.

Description: Dorsal pelage short (usually <14 mm) and uniformly grayish, usually without any trace of darker middorsal pigmentation; fur of crown (between the ears) usually grizzled gray; pale preauricular spot often present; ventral fur continuously self-whitish, -cream, or -buffy, at least along the midline, but sometimes with broad lateral zones of gray-based hairs; pinnae pale (unpigmented) basally, but blackish distally; dorsal pelage of hind feet usually pale, but sometimes indistinctly darker over lateral metatarsals (never distinctly marked with black); scaly part of tail usually <½ white distally but seldom <¼ white. Nasal bones short (about 46% of condylobasal length on average), never extending posteriorly to or between postorbital processes. Unworn third upper premolar (P3) apparently always with complete labial cingulum extending along entire base of tooth; crown length of upper molar series 13.0 ± 0.4 mm (sexes combined; observed range 12.2–14.1 mm, N = 99); enameled lingual surfaces of upper molars smooth, not crenulated; pre- and postcingula consistently absent; lower molar postcingulids absent.

Phylogeography and Geographic Variation: Our phylogenetic analysis of 32 sequences of *Philander canus* reveals no comprehensible phylogeographic structure, with haplotypes from northern populations (in Colombia and Venezuela) mixed in among those from central Brazil, Bolivia, Paraguay, and northern Argentina (fig. 16). Uncorrected sequence divergence at the cytochrome-*b* locus among haplotypes that we assign to *P. canus* is only about 0.8% despite the very wide geographic dispersion of collecting localities. Although we have not statistically tested for geographic variation in morphology among our samples, this appears to be another phenotypically rather uniform species despite modest sample differences in pelage pigmentation (some populations tending to have self-whitish or -cream underparts, whereas others have self-buffy ventral fur).

Comparisons: Morphological comparisons of *Philander canus* with *P. quica* have already been described (see above) and comparisons with *P. pebas* will be described subsequently (see below). It remains to compare this species with members of the *P. opossum* complex, which—as defined earlier in this report—includes *P. opossum*, *P. andersoni*, and *P. mcilhennyi*.

Philander canus is superficially similar to *P. opossum*, with which it has long been associated as a subspecies or synonym (e.g., by Cabrera, 1958; Patton and da Silva, 1997, 2008; Gardner, 2005; Chemisquy and Flores, 2012; Hice and Velazco, 2012). Although the geographic ranges of *P. canus* and *P. opossum* are not currently known to come into contact, it seems plausible that these species are sympatric or parapatric in the Brazilian states of Mato Grosso, Tocantins, and southern Pará, where Cerrado vegetation comes into contact with southeastern Amazonian rainforest. *Philander canus* is substantially smaller, on average, than *P. opossum* in several same-sex univariate comparisons (table 11), notably in condylobasal length (CBL), nasal length (NL), least interorbital breadth (LIB), least postorbital breadth (LPB), palatal length (PL), and maxillary toothrow (MTR). Despite some overlap in observed ranges for all dimensions, measured samples of these species have nonoverlapping multivariate distributions (fig. 17), and general-size-adjusted shape coefficients indicate that nasal morphology accounts for much of the observed divergence (table 12). Visual comparisons suggest that the posterior portion of the nasals of *P. canus* are typically much broader than those of *P. opossum*, do not

TABLE 11. Same-sex comparisons of summary statistics[a] for craniodental measurements of *Philander canus* and *P. opossum*.

	Males		Females	
	P. canus[b]	*P. opossum*[c]	*P. canus*[d]	*P. opossum*[e]
CBL	64.0 ± 2.6 (60.0–70.7) 21	71.0 ± 3.0 (65.7–77.4) 25	62.1 ± 3.0 (57.0–67.1) 22	68.7 ± 3.5 (64.6–75.4) 17
NL	29.4 ± 1.3 (26.8–31.4) 21	35.2 ± 1.9 (31.4–38.6) 25	28.4 ± 1.6 (25.2–31.0) 21	34.2 ± 2.2 (30.6–38.7) 17
NB	7.4 ± 0.9 (5.8–9.0) 21	8.3 ± 0.6 (7.2–10.0) 25	7.1 ± 0.6 (6.4–8.8) 22	8.0 ± 0.8 (6.6–10.0) 17
LIB	10.6 ± 0.6 (9.6–11.7) 21	12.4 ± 0.8 (11.1–14.8) 25	10.1 ± 0.5 (9.3–11.1) 22	11.8 ± 0.8 (10.8–13.6) 17
LPB	7.9 ± 0.3 (7.4–8.5) 21	8.8 ± 0.3 (8.2–9.5) 25	7.8 ± 0.3 (7.4–8.4) 22	8.7 ± 0.3 (8.1–9.1) 17
ZB	34.0 ± 1.7 (31.4–38.4) 21	36.3 ± 2.4 (32.8–42.4) 25	32.4 ± 1.6 (29.8–35.7) 22	34.6 ± 1.9 (32.1–38.5) 17
PL	38.1 ± 1.4 (36.2–41.5) 21	42.6 ± 1.5 (40.5–46.8) 25	37.2 ± 1.9 (33.8–40.1) 22	41.3 ± 1.8 (38.4–45.2) 17
PB	19.3 ± 0.7 (18.2–20.6) 21	20.7 ± 0.7 (19.7–22.2) 25	19.0 ± 0.8 (17.8–20.5) 22	20.5 ± 0.6 (19.4–21.5) 17
MTR	27.4 ± 0.8 (26.4–29.5) 21	29.7 ± 1.0 (28.8–33.2) 25	26.7 ± 1.0 (25.0–28.6) 22	28.7 ± 0.8 (27.6–30.0) 17
LM	13.2 ± 0.4 (12.4–13.7) 21	13.9 ± 0.5 (13.1–15.3) 25	12.8 ± 0.4 (12.2–13.6) 22	13.7 ± 0.3 (13.3–14.5) 17
M1–3	11.1 ± 0.4 (10.4–11.7) 20	11.6 ± 0.4 (10.9–12.8) 25	10.8 ± 0.3 (10.4–11.4) 22	11.5 ± 0.3 (11.1–12.1) 17
WM3	4.1 ± 0.2 (3.7–4.4) 21	4.2 ± 0.2 (3.9–4.8) 25	4.0 ± 0.2 (3.6–4.4) 22	4.1 ± 0.2 (3.9–4.4) 17

[a] Table entries include the sample mean plus or minus one sample standard deviation, the observed range (in parentheses), and the sample size.
[b] AMNH 135887, 210402, 210410, 210411, 210413, 260037, 261269, 261271, 261272, 261278, 263966; FMNH 114707; MSB 55074, 55075 55854, 55856; USNM 390005, 390010–390012, 390562.
[c] AMNH 96563, 96569, 96574, 96576, 96730, 96732, 96733, 96755, 203348, 203349; USNM 393606, 393607, 393610, 393612, 519732, 521434, 544496, 544497, 544499, 544503, 545588, 545591, 546226, 549297, 549298.
[d] AMNH 210403, 210409, 210414, 210416, 260034, 261270, 261273, 261277, 263964; BMNH 47.11.22.15; FMNH 114685, 114694, 114701, 114714; MSB 55073, 55855, 58517, 59887, 67025; USNM 390009, 390564, 390565.
[e] AMNH 96556, 96561, 96571, 96579, 96620, 96738, 203347; USNM 393602, 393603, 393609, 519731, 544500, 545586, 545587, 545589, 545592, 549299.

extend as far posteriorly, and lack the deep posterolateral notches that are often present in the latter species (fig. 18). *Philander canus* and *P. opossum* both have uniformly grayish dorsal fur, mostly pale hind feet, and self-colored ventral fur, but tail pigmentation might be useful for field identification. Whereas the scaly part of the tail is almost always <½ white in specimens of *P. canus*, the scaly part of the tail is typically ≥½ white in specimens of *P. opossum*, and this modal difference might be expected to become even more pronounced in sympatry.[9]

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[9] We suspect (although there is no behavioral evidence to support our conjecture) that the black-and-white tail markings of Didelphini have some social-signaling function that might be coopted for species recognition in sympatry.

TABLE 12. Coefficients of principal components (PC1, PC2), general size (Size), and size-adjusted group differences (Shape) for multivariate analyses of *Philander canus* versus *P. opossum*[a]

	PC1	PC2	Size	Shape
CBL	0.300	0.151	0.268	0.186
NL	0.461	0.325	0.307	0.503
NB	0.463	-0.845	0.663	-0.573
LIB	0.457	0.056	0.404	0.207
LPB	0.221	0.258	0.065	0.436
ZB	0.256	0.001	0.355	-0.121
PL	0.297	0.207	0.219	0.285
PB	0.206	0.110	0.189	0.118
LM	0.133	0.170	0.081	0.191
WM3	0.112	0.059	0.106	0.064

[a] See figure 17 for specimen projections on these axes. The first principal component accounts for 78.9% of the total variance in these data, whereas PC2 accounts for 8.2% (cumulative = 87.2%).

Philander canus is much smaller, on average, than either *P. andersoni* or *P. mcilhennyi*, from which it also differs in nasal shape as described and illustrated above (all members of the *P. opossum* complex have long, narrow nasals that are often laterally notched and often extend posteriorly to or between the postorbital processes). Large generalized distances (appendix 4) suggest that multivariate ordinations of *P. canus* with either *P. andersoni* or *P. mcilhennyi* would show nonoverlapping distributions, but we have not performed those analyses because these species are easy to tell apart by other characters. The dorsal pelage pigmentation of *P. canus* (uniformly gray; fig. 10) is quite unlike that of *P. andersoni* (with a distinctly blackish middorsal stripe) and *P. mcilhennyi* (some specimens of which are completely blackish). The self-whitish, -cream, or -buffy underparts of *P. canus* likewise contrast with the mostly gray-based ventral pelage of *P. andersoni* and the almost-blackish ventral fur of *P. mcilhennyi* (fig. 11). Whereas the hind feet of *P. canus* are covered dorsally with pale fur, the hind feet of *P. andersoni* and *P. mcilhennyi* are either completely blackish or have black metatarsals and abruptly whitish digits. Lastly, the scaly part of the tail is almost always <½ white in *P. canus* but apparently always ≥ ½ white in *P. andersoni* and *P. mcilhennyi*.

REMARKS: As understood herein, *Philander canus* includes the nominal taxa *crucialis*, *mondolfii*, and *olrogi*. The latter are represented in our molecular analyses by: (1) a CYTB sequence we obtained from a Bolivian specimen (AMNH 260034) that was collected near the type locality of *crucialis* and that resembles the holotype of *crucialis* in qualitative and morphometric traits; (2) two CYTB sequences, one from a Colombian specimen (KU 123943) and another from a Venezuelan specimen (KU 120245) that were part of Lew et al.'s (2006) original material of *mondolfii*; and (3) CYTB sequences that we obtained from two specimens (AMNH 261271, 261272) that were part of Flores et al.'s (2008) original material of *olrogi*. All these specimens conform to our morphological diagnosis of *P. canus*, so the conclusion that the nominal taxa in question are conspecific seems straightforward, but brief comments on each synonym are appropriate.
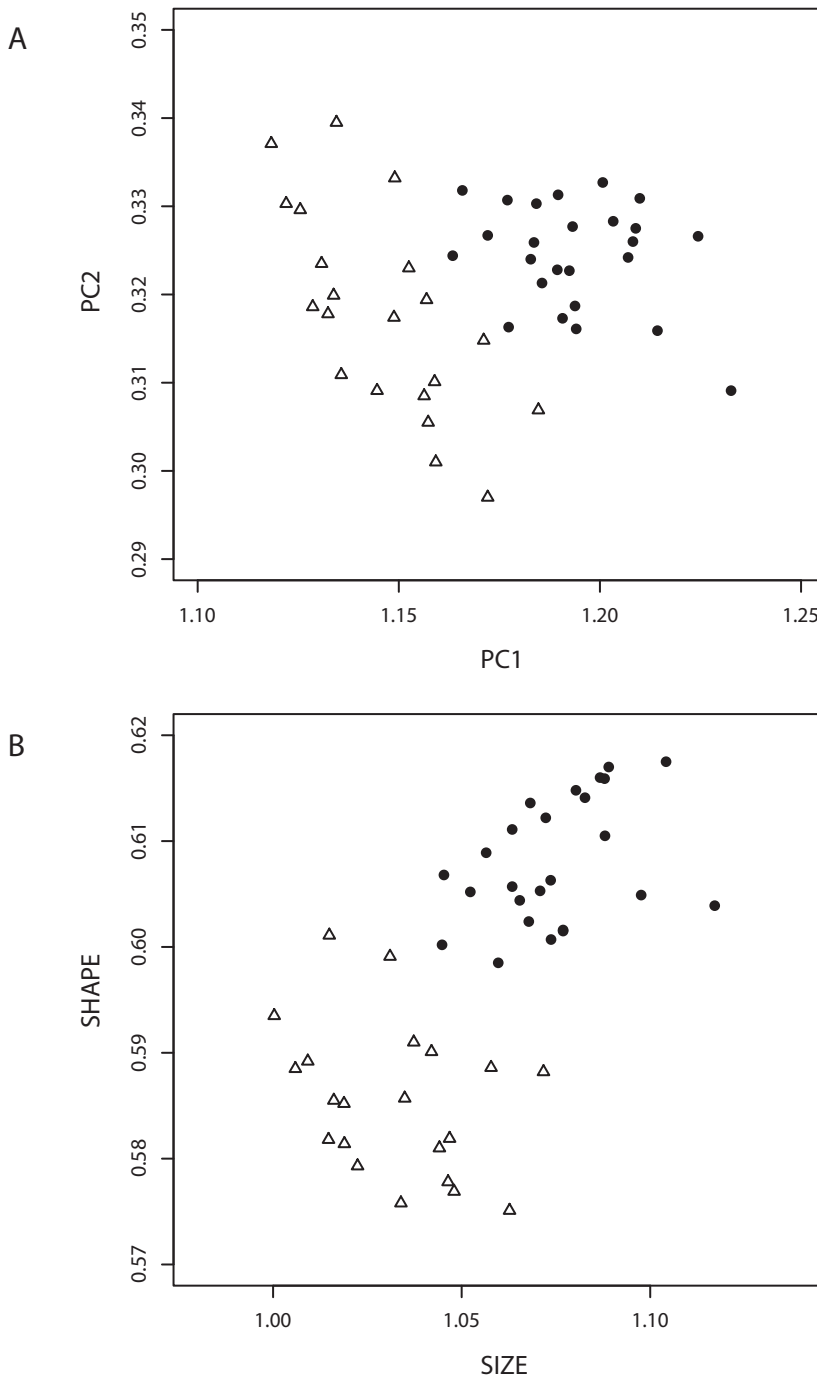
FIG. 17. Projections of specimen scores on the first two principal components (**A**) and on factors representing general size and size-invariant shape differences (**B**) from analyses of craniodental measurements of *Philander canus* (open triangles) and *P. opossum* (filled circles). The coefficients of these axes are provided in table 12.
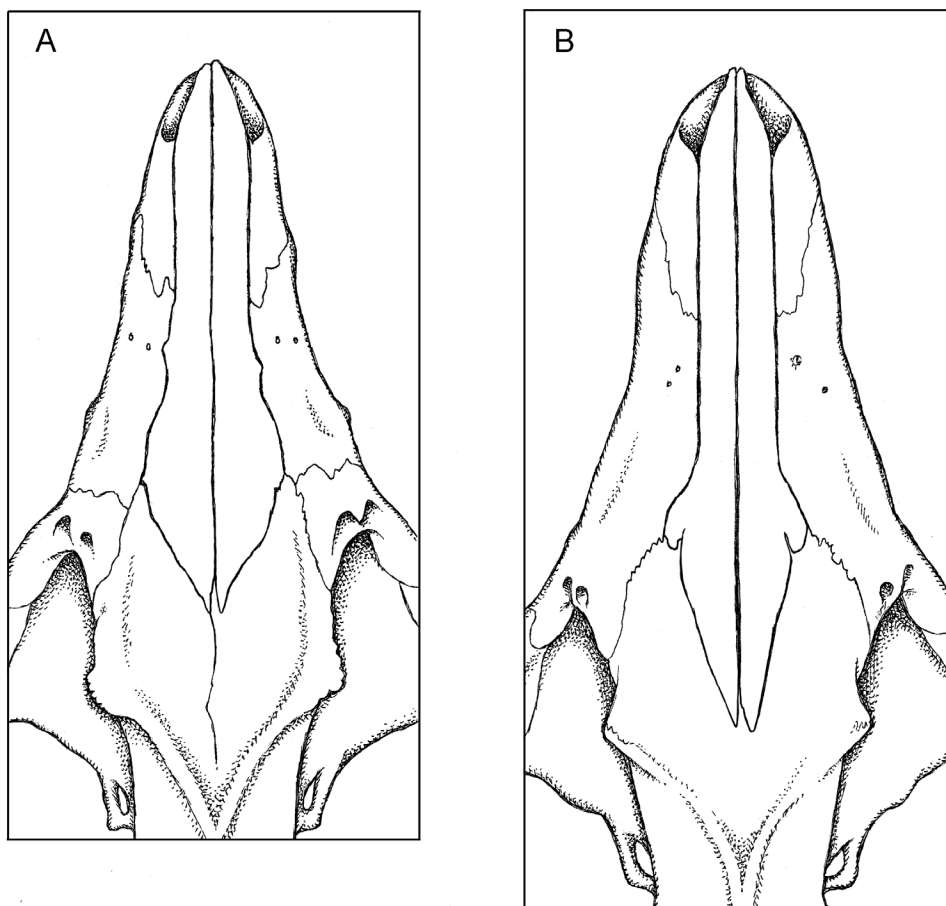
FIG. 18. Dorsal view of the rostrum in *Philander canus* (**A,** AMNH 133096) and *P. opossum* (**B,** AMNH 96608), illustrating differences in nasal morphology.

Thomas (1923) described *crucialis* on the basis of a single specimen, which he compared only with *azaricus* (= *P. quica*; see above). Later, with more Bolivian material at hand for comparison with topotypical specimens of Osgood's species, he (Thomas, 1928) judged *crucialis* and *canus* to be indistinguishable. We agree.

Lew et al. (2006) described *mondolfii* based on several dozen specimens from Colombia and Venezuela that the authors compared carefully with other species of *Philander* known to occur in or near those countries, including *P. andersoni*, *P. deltae*, *P. "fuscogriseus"* (= *P. melanurus*), and *P. opossum*, but they did not compare *mondolfii* with *P. canus*. Although we have not examined the holotype or paratypes of *mondolfii*—all currently inaccessible in Venezuelan museums—we did examine 16 specimens that were part of Lew et al's (2006) original material. These specimens (AMNH 16951, 30709, 30711–30714, 133119, 133120, 136163, 136167–136169, 139221; KU 120233, 120245, 123943) so closely resemble the type of *P. canus* and other referred material from eastern Peru that we could not find any phenotypic basis for retaining *mondolfii* even as a subspecies.

Flores et al. (2008) described *olrogi* on the basis of seven specimens from Bolivia and Peru. Although we have not seen the holotype, we examined the skull of a paratype (AMNH 246441) as well as several other specimens that were part of Flores et al.'s (2008) original material (AMNH 261269–261272). Despite careful study, we confess ourselves unable to consistently distinguish these specimens from material that the authors referred to *P. opossum canus*. Although they reported a principal-components analysis that was said to support the recognition of *olrogi* as a distinct taxon, *canus* and *olrogi* have overlapping distributions in their illustrated results (Flores et al., 2008: fig. 5). In the absence of compelling evidence for the phenotypic distinctness of these genetically indistinguishable nominal taxa, we interpret the allegedly diagnostic traits of *olrogi* to be aspects of intraspecific morphological variation within *P. canus*.

Cabrera (1958: 35) listed *nigratus* as a synonym of *canus* (which he ranked as a subspecies of *P. opossum*), but the holotype (BMNH 0.7.7.62) and other material that we refer to *nigratus*[10] are larger animals (LM = 14.7–16.4 mm) with much darker dorsal fur, completely gray-based ventral fur, blackish feet, shorter white tail-tips (less than ¼ of the tail is unpigmented in most specimens), and an incomplete labial cingulum on P3. Although we do not know whether *nigratus* is a valid species, its phenotype more closely resembles those of species in the *P. opossum* complex than that of *P. canus*.

Hershkovitz (1997) used the name *Philander opossum quica* for many specimens that we refer to *P. canus*, including all the material he listed from central Brazil (Goiás, Mato Grosso) and Bolivia; among the material that he listed from eastern Peru are specimens that we refer to both *P. canus* and *P. pebas*. The "dichromatism" that he (Hershkovitz, 1997: 49) noted among specimens of "*P. o. quica*" from Balta (in the Peruvian department of Ucayali) is the result of sympatry rather than polymorphism: of the six specimens in question that we examined, three (LSUMZ 12006, 12008, 12009) are *P. canus* and the others (LSUMZ 12007, 12010, 14011) are *P. pebas* (see Specimens Examined for both taxa, below; a third congener, *P. mcilhennyi*, also occurs at Balta).

The western Amazonian specimens that Patton et al. (2000) referred to *Philander opossum canus* include examples of both *P. canus* and *P. pebas*. Of the five that we were able to examine—the others having been returned to Brazil—four (MVZ 190343–190346) are *P. pebas*; only one (MVZ 190347, from the state of Acre, near the Peruvian border) is actually *P. canus*. The central Amazonian specimens that Nunes et al. (2006) identified as *P. canus* are also examples of *P. pebas*.[11] The only other material of *P. canus* that we have seen from the Brazilian Amazon (besides the MVZ specimen from Acre) is a small series collected many years ago along the lower Rio Madeira (in Amazonas state) and a single specimen from the upper Madeira (in Rondônia).

HABITATS: The geographic range of *Philander canus* extends over a wide range of biomes or ecoregions (including the Cerrado, Chaco, Pantanal, Llanos, and Amazonia), and it is possible that the species occurs in a corresponding variety of habitats, but definite ecological information associated with collected specimens is hard to find. Other species of *Philander* are

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[10] From the eastern Andean foothills of Junín and Ayacucho departments, Peru: BMNH 94.10.1.16, 94.10.1.17, 28.5.1.20; FMNH 65782; LSUMZ 16398, 16399; MUSM 71.

[11] We are indebted to S.E. Pavan, who kindly examined the MPEG voucher specimens from Nunes et al.'s (2006) study at our request.

known to live in rainforest, so collection records from biomes dominated by savanna vegetation and/or dry forest (e.g., the Cerrado, Chaco, and Llanos) seem anomalous, but the literature on Cerrado mammals provides a few relevant observations.

In the Cerrado landscapes of eastern Bolivia, *Philander canus* is apparently restricted to tall evergreen gallery forests and does not seem to occur in the savannas and dry forests that cover much of the landscape (Emmons et al., 2006). In the Cerrado of central Brazil, *P. "opossum"* (presumably *P. canus*) is also said to be a gallery-forest species (Mello and Moojen, 1979; Redford and Fonseca, 1986; Alho, 2005), but in one report of a multiyear trapping study *P. "opossum"* was said to prefer gallery forest but to occur frequently in other local habitats, including open grassland, shrub savanna, and dry forest (Alho et al., 1986). Following Pulliam's (1988) ecological terminology, we conjecture that gallery forests are probably the source habitat for *P. canus* in Cerrado landscapes, whereas open formations (including dry forests) are likely to be sink habitats. In the Chaco of northern Argentina, *Philander "opossum"* (presumably *P. canus*) is also said to occur in gallery forests (Huck et al., 2017).

Information about the habitat distribution of *Philander canus* appears to be unavailable from trapping studies in the Pantanal and Llanos, but we suspect that it is largely restricted to gallery forests in those ecoregions as well. Nevertheless, Lew et al.'s (2006) summary of macrohabitats where *Philander "mondolfii"* (= *P. canus*) has been collected in Venezuela (including lowland and submontane rainforest, semideciduous forest, and tree savannas) suggest that it has broad ecological tolerances, at least where other sympatric congeners are not known to occur.

We have not found any published accounts of where specimens that can definitely be identified as *Philander canus* have been collected in Amazonia. Although the natural climax vegetation throughout this enormous ecoregion can be broadly characterized as lowland rainforest, local disturbance (e.g., from lateral migration of rivers within their meander belts) and edaphic factors can result in a surprising diversity of natural vegetation types at many Amazonian localities (Pires and Prance, 1985; Puhakka and Kalliola, 1995), and anthropogenic habitats are also scattered throughout the region. The geographic distribution of Amazonian collection localities for *P. canus* provides no habitat clues, because these localities are not clustered around savanna enclaves, human settlements, or other obvious landscape features. The known Amazonian range of *P. canus* broadly overlaps those of *P. andersoni*, *P. mcilhennyi*, and *P. pebas*, so it would be reasonable to suppose that competitive interactions with sympatric congeners might restrict the habitat occupancy of this species to some extent, but the information compiled for this report is entirely inadequate even for conjecture.

Specimens Examined (N = 154): **Bolivia**—*Beni,* Arruda (FMNH 114701), Camiaco (AMNH 210402), Casarabe (AMNH 261269–261272; MSB 55854), 8 km N Exaltación (AMNH 210403), Magdalena (FMNH 114714), Mamore River (AMNH 210409), 4 km SE Palacios (210410), Puerto Caballo (AMNH 210411), Puerto Siles (AMNH 210413, 210414), Río Tijamuchi (AMNH 261273), San Joaquin (FMNH 114685, 114694, 114707); *Pando,* Bella Vista (MSB 57006, AMNH 262413); *Santa Cruz,* 7 km E aserradero Moira (EBD 8736), 6 km W Asención (MSB 55855), Ayacucho (USNM 390564), Becerra (390565), 2 km N Chapare River mouth (AMNH 210416), 2 km SE Cotoca (MSB 59887), Estancia Cachuela Esperanza (AMNH 260034,

MSB 55073), Hamecas (AMNH 135887), La Laguna (MSB 55856), 3 km SE Montero (AMNH 263964, MSB 67025), Palmar (USNM 390562), San Miguel Rincón (AMNH 260037, MSB 55074, 55075), 10 km N San Ramón (AMNH 261277, 261278), Santa Cruz de la Sierra (BMNH 47.11.22.15 [holotype of *crucialis*]), 15 km S Santa Cruz (AMNH 263966, MSB 58517), 7 km N Santa Rosa (AMNH 246441 [paratype of *olrogi*]), near Warnes (USNM 390005, 390009–390012). **Brazil**—*Acre,* Sobral on Rio Juruá (MVZ 190347); *Amazonas,* Auara Igarapé on Rio Madeira (AMNH 91749, 91750), Borba on Rio Madeira (AMNH 91748), Lago Sampaio on Rio Madeira (AMNH 92761, 92762), "Santo Antonio de Uayara" on Rio Madeira (= Santo Antonio de Guajará; AMNH 92293); *Goiás,* Anápolis (AMNH 133043, 133046, 133047, 133055, 133056, 133062, 133064, 133068–133070, 133073–133075, 133082, 133084–133086, 133091–133094, 133096–133101, 133123, 133172, 133171, 133182, 133192, 133195), 24 km SE Formoso (LACM 10086–10088); *Mato Grosso,* Caceres (USNM 390014), Fazenda São Luis (MVZ 197403); *Mato Grosso do Sul,* Corumba (USNM 390013), Passo do Lontra (MVZ 197402); *Rondônia,* Porto Velho (USNM 390001). **Colombia**—*Boyacá,* Río Cobaría (FMNH 92297); *Meta,* Finca El Capricho (KU 123943), Restrepo (AMNH 133119), Villavicencio (AMNH 136168, 136169, 139221). **Paraguay**—*Alto Paraguay,* Estancia Doña Julia (TTU 79753); *Central,* 17 km E Luque (MVZ 144304); *Presidente Hayes,* Estancia Loma Porá (TTU 80404). **Peru**—*Cusco,* Camisea (MUSM 14150), Hacienda Cadena (FMNH 66412, 68332), Quincemil (FMNH 75094–75096); *Huánuco,* Moyuna (MUSM 83); *Madre de Dios,* "Albergue Lodge Cuzco Amazonico" (= Cusco Amazónico; MVZ 157613, 165927), Boca Río Colorado (FMNH 84247), Lago Sandoval (MVZ 157614), mouth of Río La Torre (LSUMZ 24591), 6 km W Río Tambopata (USNM 39002); 2.75 km E Shintuya (FMNH 169815); *Pasco,* San Pablo (AMNH 230034), Nevati (AMNH 230028, 230030, 230031, 254509); *San Martín,* Bellavista (MUSM 92), Moyobamba (FMNH 19347 [holotype of *canus*]), Rioja (MUSM 88); *Ucayali,* Balta (LSUMZ 12006, 12008, 12009), 59 km SW Pucallpa (USNM 499001, 499002), Boca Río Urubamba (AMNH 75906–75908), Lagarto (AMNH 76636), Santa Rosa (AMNH 75909). **Venezuela**—*Amazonas*, El Platanal (EBD 8954, 8956); *Apure,* 29 km SSW Santo Domingo (USNM 418545, 418546); *Bolívar,* 20 km W La Paragua (USNM 388403), Maripa (AMNH 16951), Río Yuruán (AMNH 30709–30714); *Trujillo,* 9.8 km NNE Motatán (KU 120233, 120245, 120246, 120251), 19 km W Valera (USNM 371322); *Zulia,* 60 km WNW Encontrados (USNM 418548).

Philander pebas, new species

Type Material: The holotype, MVZ 190343, consists of the skin, skull, and frozen tissues of an adult male collected by J.L. Patton (original number 15395) on 1 September 1991 at Igarapé Nova Empresa, on the left bank of the Rio Juruá, Amazonas, Brazil (6°48′S, 70°44′W). A complete (1149 bp) cytochrome-*b* sequence that we obtained from this specimen is archived in GenBank with accession number MG491956.

Distribution and Sympatry: Sequenced specimens and other referred material of *Philander pebas* are from eastern Ecuador, eastern Peru, and Amazonian Brazil (fig. 9). Based on specimens we examined, *P. pebas* occurs sympatrically with *P. andersoni* in northeastern Peru
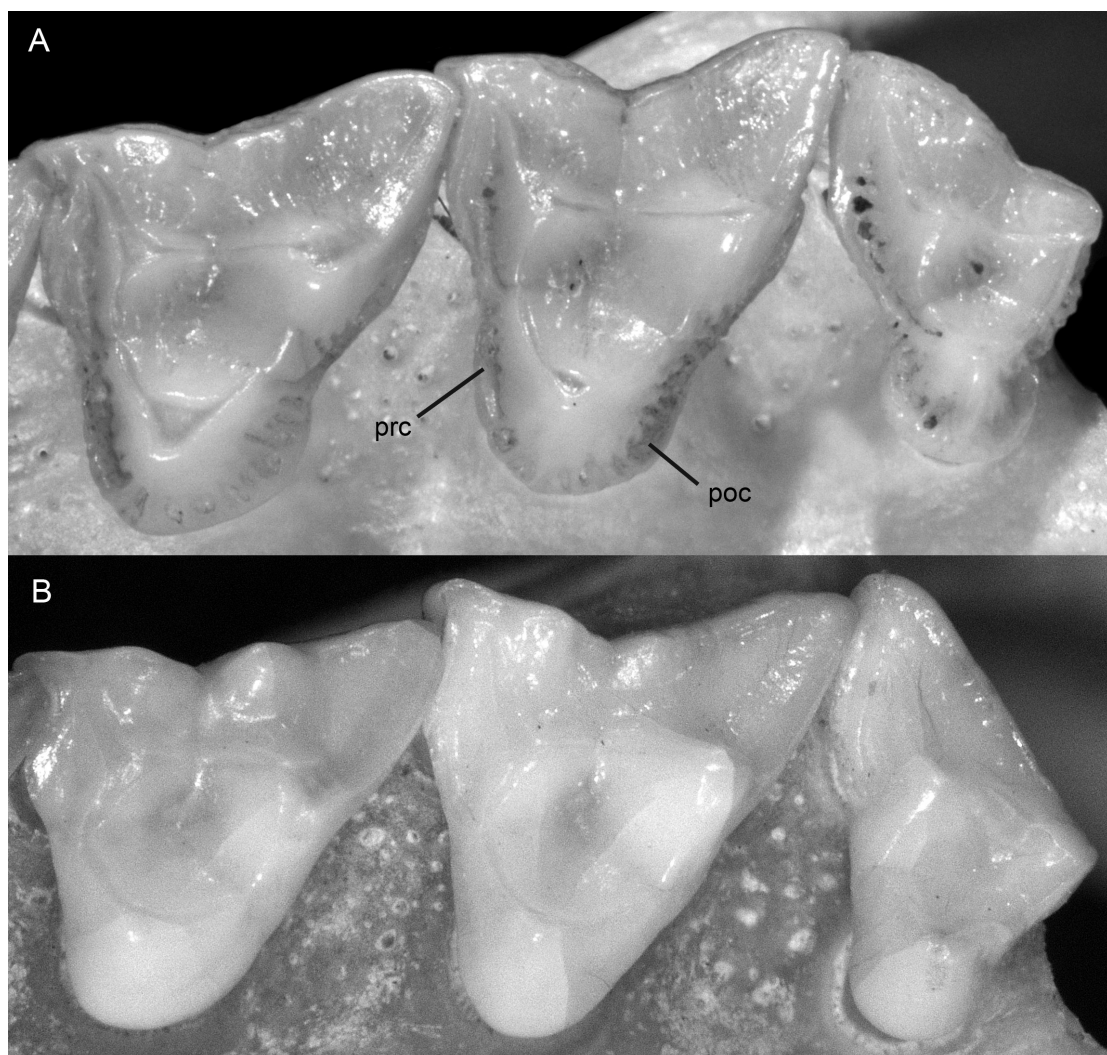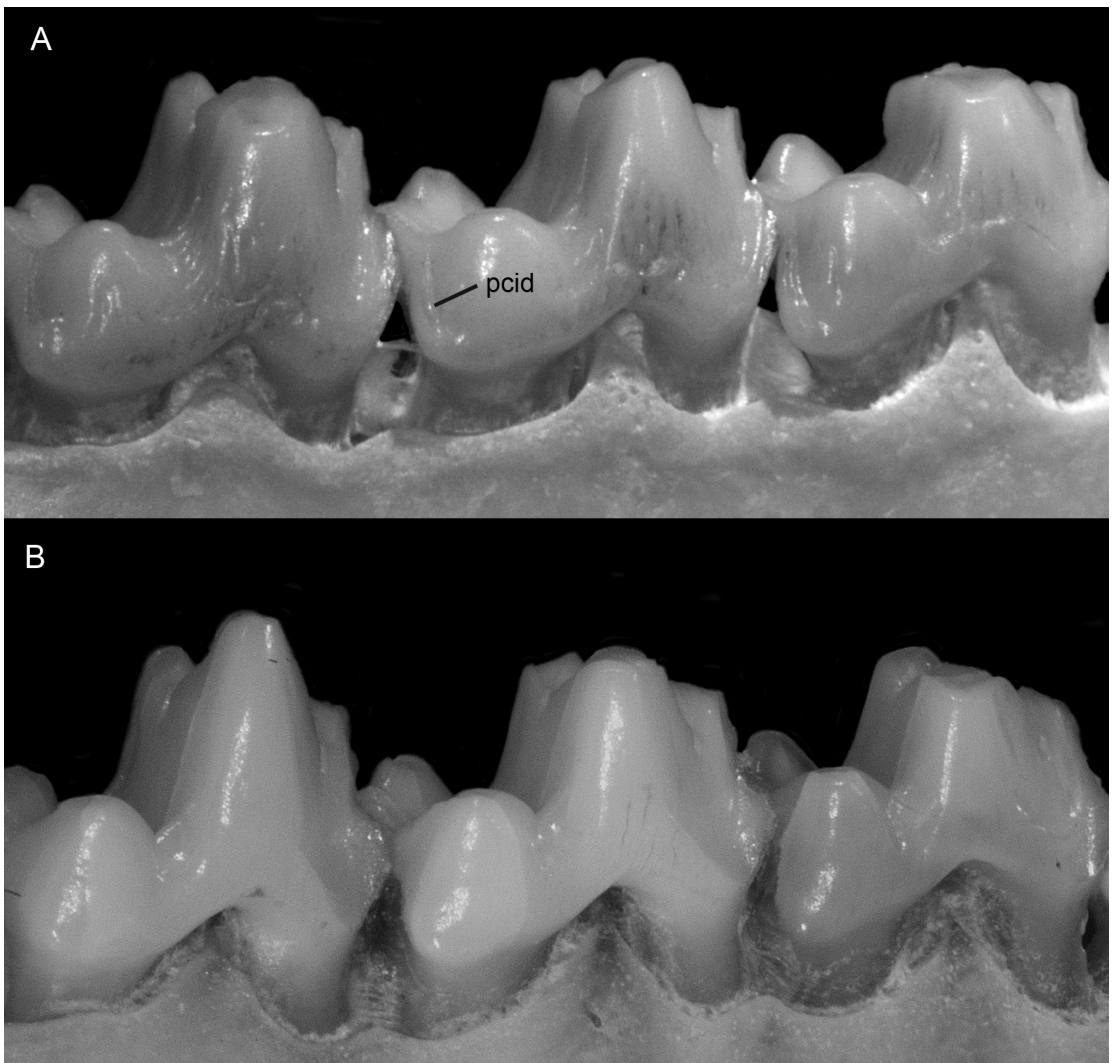
FIG. 19. Upper molar differences between *Philander pebas* and *P. canus* (see text for explanation). **A,** Occlusal view of left M2–M4 of *P. pebas* (MVZ 190343, holotype); **B,** occlusal view of left M2–M4 of *P. canus* (AMNH 210413). Abbreviations: **poc,** postcingulum; **prc,** precingulum.

(e.g., near Iquitos, in Loreto department) and with *P. canus* and *P. mcilhennyi* in southeastern Peru (e.g., at Balta in Ucayali department).

DESCRIPTION: Dorsal pelage very short (usually ≤12 mm) and uniformly grayish (sometimes darker middorsally than on the flanks but never with a distinct middorsal blackish stripe; fig. 10); fur of crown (between the ears) grizzled-grayish, often quite dark but apparently never clear black (at least some hairs frosted, with pale tips); pale preauricular spot absent or indistinct; ventral fur mostly gray-based (fig. 11), often self-cream or -buffy in the inguinal region but apparently never continuously self-colored along the abdominal and thoracic midline; pinnae sometimes entirely blackish but often indistinctly paler basally; hind feet often with dark

FIG. 20. Lower molar differences between *Philander pebas* and *P. canus* (see text for explanation). **A,** Labial view of right m1–m3 of *P. pebas* (MVZ 190343, holotype); **B,** labial view of right m1–m3 of *P. canus* (AMNH 210413). Abbreviations: **pcid,** postcingulid.

metatarsals and pale digits, but not blackish or with distinctly blackish markings; scaly part of tail usually <¼ white distally. Nasal bones neither very short nor unusually elongated (about 47% of condylobasal length on average), sometimes extending posteriorly to (but apparently never between) postorbital processes. Unworn third upper premolar (P3) with complete labial cingulum; crown length of upper molar series 13.8 ± 0.5 mm (sexes combined; observed range 12.7–15.1 mm, N = 50); unworn molar enamel distinctly crenulated, especially on lingual surfaces of protocones (fig. 19A); pre- and postcingula usually present on one or more upper molars (more frequently retained on M4 than on M1–3 in older specimens with worn teeth; fig. 19A); posterior cingulids apparently always present on one or more lower molars (fig. 20A).

PHYLOGEOGRAPHY AND GEOGRAPHIC VARIATION: Some phylogeographic structure is apparent among the 14 haplotypes that we assign to *Philander pebas*, with partial separation of Brazilian sequences on the one hand from Peruvian and Ecuadorean sequences on the other (fig. 16), but neither haplogroup received consistently strong support in our analyses. The only phenotypic evidence of geographic variation we observed was the caudal pigmentation of the easternmost specimens (from central Amazonia), most of which have ⅓ to ½ white tails, whereas those from western Amazonia usually have tails that are ≤¼ white.

COMPARISONS: *Philander pebas* is the only species in the genus with distinctly crenulated (folded and grooved) molar enamel, a trait that is most clearly visible on unworn teeth, but which persists on the lingual surfaces of the protocones even in old adults. Additionally distinctive traits, apparently unique among didelphids, are narrow enamel shelves along the anterolingual and posterolingual bases of the protocones; we refer to these shelves as the precingulum and postcingulum, respectively.[12] These shelves tend to wear away with age, but they often persist on M4 even in old adults. Another distinctive trait, only rarely observed as a polymorphism among other didelphids, is a narrow shelf along the posterolabial surface of the hypoconid; following standard tribosphenic terminology, this shelf is called the posterior cingulid or postcingulid.

Philander pebas can be distinguished from its sister species, *P. canus*, by additional characters. Among others, it is substantially larger than *P. canus* (tables 7, 8), and specimen scores on the first two principal components that we computed from craniodental measurements of both taxa illustrate nonoverlapping multivariate distributions (fig. 21A). Coefficients of general-size-invariant shape differences computed from these data suggest that *P. pebas* has longer but narrower nasals, wider interorbital and postorbital dimensions, and longer palates than *P. canus* (fig. 21B, table 13). The two species can also be reliably identified by external traits, of which ventral pelage coloration is the most consistently useful. Whereas the ventral fur of *P. canus* is continuously self-whitish, -cream, or -buffy from chin to groin, the ventral fur of *P. pebas* is extensively gray-based. Some specimens of *P. pebas* have self-whitish or -buffy fur on the chin, throat, and/or groin, but none of the specimens we examined has a continuous midventral streak of self-colored fur over the chest and upper abdomen. The two species also seem to be reliably identifiable by tail markings in Ecuador, Peru, and Acre (Brazil), where specimens of *P. canus* have tails that are at least ⅓ to almost ½ white, but where specimens of *P. pebas* have tails that are ≤¼ white.

Close comparisons of *Philander pebas* and *P. quica* seem unnecessary given their widely disjunct geographic distributions (fig. 9), large genetic and morphometric distances (appendices 3, 4), and salient qualitative differences (table 6).

Philander pebas differs from members of the *P. opossum* complex, with which it is broadly sympatric (*P. andersoni*, *P. mcilhennyi*) or potentially sympatric (*P. opossum*), by the unique dental traits described above and by external morphology. By comparison with *P. andersoni*—

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[12] There appears to be no standard terminology for these structures, despite their essential similarity among the tribosphenic taxa that exhibit them. Simpson (1936: 5), for example, used "anterior cingulum" and "posterior cingulum," and the postcingulum is sometimes called the "talon" (Bown and Kraus, 1979: 173).

TABLE 13. Coefficients of principal components (PC1, PC2), general size (Size), and size-adjusted group differences (Shape) for multivariate analyses of *Philander pebas* versus *P. canus*.[a]

	PC1	PC2	Size	Shape
CBL	0.310	0.154	0.216	0.270
NL	0.394	0.256	0.236	0.405
NB	0.486	-0.815	0.788	-0.480
LIB	0.469	0.101	0.355	0.319
LPB	0.219	0.300	0.033	0.388
ZB	0.253	-0.045	0.305	0.025
PL	0.367	0.320	0.167	0.462
PB	0.145	-0.012	0.164	0.030
LM	0.140	0.200	0.023	0.249
WM3	0.067	0.040	0.046	0.063

[a] See figure 21 for specimen projections on these axes. The first principal component accounts for 68.0% of the total variance in these data, whereas PC2 accounts for 16.7% (cumulative = 84.7%).

with its distinctly blackish middorsal stripe (fig. 10)—the dorsal fur of *P. pebas* is uniformly grayish, although it can be indistinctly darker (sometimes almost blackish) middorsally. Additionally, where the ranges of *P. andersoni* and *P. pebas* overlap, they can readily be distinguished by tail markings (the scaly part of the tail of *P. andersoni* is ≥ ½ white, whereas the tail of sympatric *P. pebas* is ≤¼ white). By comparison with *P. mcilhennyi* (which is sometimes almost entirely blackish), *P. pebas* is uniformly grayish, and these species also differ in fur length: although observed ranges narrowly overlap, the middorsal fur of *P. mcilhennyi* is much longer on average (16 ± 3 mm) than the middorsal fur of *P. pebas* (10 ± 2 mm), and the latter species never has the typically shaggy appearance of *P. mcilhennyi*. As in *P. andersoni*, the scaly portion of the tail is at least ½ white in *P. mcilhennyi*, whereas the tail is mostly black in *P. pebas*. By comparison with *P. opossum* (which has mostly self-buffy underparts), the ventral fur of *P. pebas* is extensively gray-based (and is never buffy in the specimens we examined).

REMARKS: Specimens that we refer to *Philander pebas* were among those previously identified as *P. opossum quica* by Hershkovitz (1997), as *P. opossum canus* by Patton et al. (2000), as *P. opossum* by Woodman et al. (1991) and Hice and Velazco (2012), and as *P. canus* by Nunes et al. (2006). Although we were unable to examine any of the specimens from northeastern Peru identified as *P. opossum* by Díaz (2014), we suspect that most of them are *P. pebas*.

We have not examined specimens of *Philander deltae* (known only from northeastern Venezuela), but Lew et al.'s (2006) description of that species includes several external traits (including brownish dorsal fur, a broad strip of "uniformly cream" ventral fur, very small and poorly defined supraorbital spots, and sparsely pigmented ears) that are quite unlike the corresponding attributes of *P. pebas*. Because Lew et al. (2006) did not publish measurement data for *P. deltae*, no morphometric comparisons with *P. pebas* are possible.

HABITATS: All examined specimens of *Philander pebas* are from western and central Amazonian landscapes where the natural climax vegetation is lowland rainforest, but many localities in this region support a wide range of habitats. The floodplains of white-water rivers, in par-
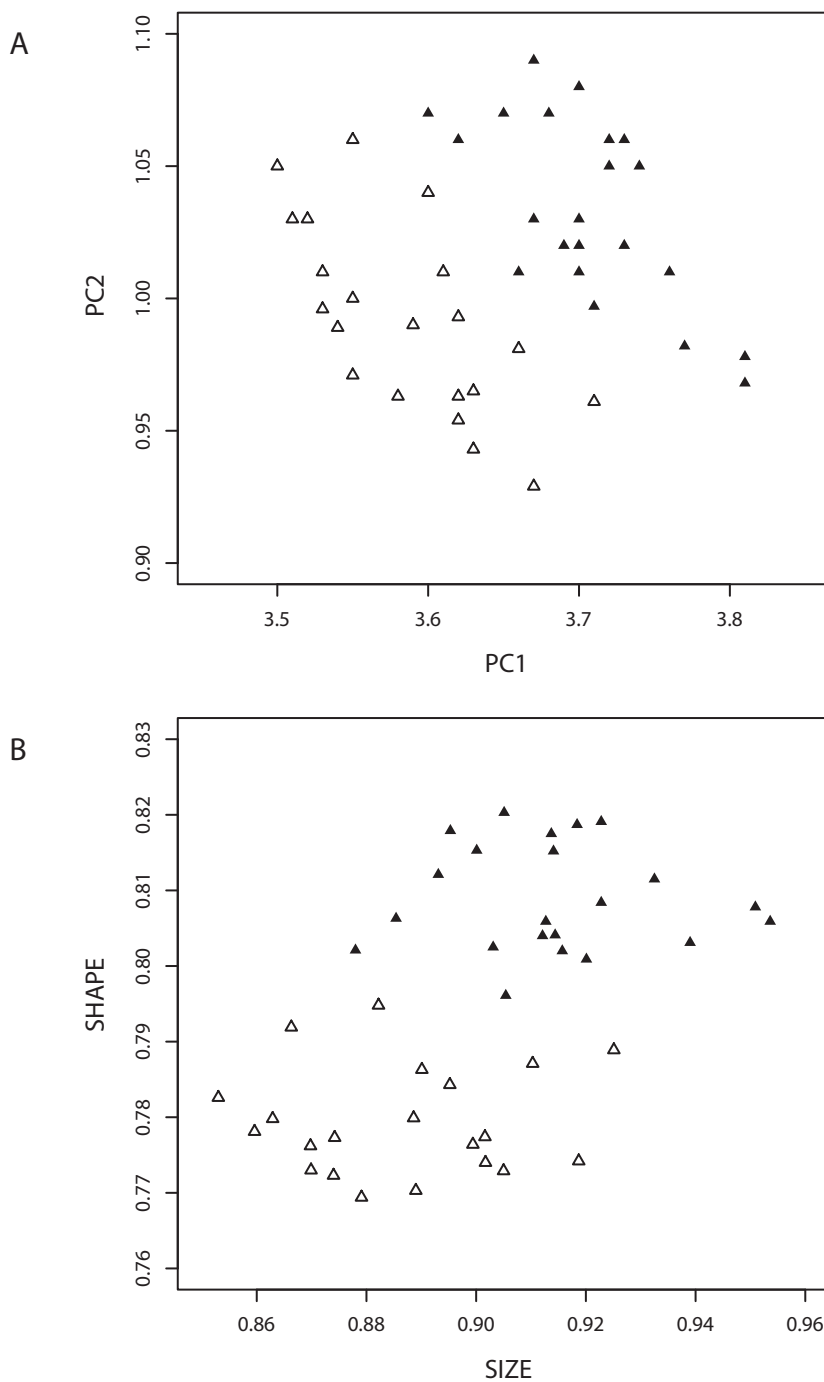
FIG. 21. Projections of specimen scores on the first two principal components (**A**) and on factors representing general size and size-invariant shape differences (**B**) from analyses of craniodental measurements of *Philander canus* (open triangles) and *P. pebas* (filled triangles). The coefficients of these axes are provided in table 13.

ticular, typically include a mosaic of successional stages and edaphic formations (Salo et al., 1986; Puhakka and Kalliola, 1995), and they are interdigitated with floristically distinct upland forests that grow on well-drained terraces and hillsides. Although fragmentary and incomplete, available ecological information from several localities suggest that *P. pebas* occupies a distinctive suite of natural and anthropogenic habitats within this diverse ecological matrix.

According to Patton et al. (2000), who trapped in both upland (*terra firme*) forest and seasonally flooded (*várzea*) forest along the Rio Juruá, *Philander* "*opossum*" was taken only in flooded forest, except in the headwaters region, where one specimen was trapped in upland forest. Of the 15 specimens of *P.* "*opossum*" they collected, we were able to examine only five, of which four were *P. pebas* and one was *P. canus*. All four specimens of *P. pebas* were taken at localities where the trapping habitat was described as várzea, by contrast with specimens of sympatric *P. mcilhennyi*, which the authors trapped in both terra firme and várzea habitats.

Another record of *Philander pebas* from seasonally flooded forest is based on the specimens of *Philander* "*canus*" analyzed by Nunes et al. (2006). These specimens, which we reidentified as *P. pebas*, were collected in the Mamirauá Sustainable Development Reserve, a protected area consisting entirely of várzea at the confluence of the Rio Japurá and the upper Amazon (Solimões). When the floodwaters are at their highest, virtually the entire reserve is flooded and only the forest canopy is visible above the water line (de Queiroz and Peralta, 2010). During the low-water season, emergent land is covered by tall forest growing on levees, shrubby vegetation in lower areas, and a variety of other floodplain habitats (Ayres, 1995). The specimens in question were trapped in seasonally flooded forest (C. Nunes, personal commun., 17 October 2017).

In addition to seasonally flooded riparian formations, this species has also been trapped in swamps (habitats with permanently waterlogged soils). Several specimens of *Philander* "*opossum*" have been collected in the vicinity of Cusco Amazónico, an ecotourist lodge on the Río Madre de Dios in southeastern Peru (Woodman et al., 1991). Although Cusco Amazónico is located within the meander belt of the Madre de Dios, the various habitats sampled by zoological collectors at this locality were not seasonally flooded by river water (Duellman, 2005). Of the two specimens of *P. pebas* that we examined from Cusco Amazónico—where *P. canus* also occurs—only one is accompanied by definite habitat information. This specimen (KU 1441209) was collected in a *Heliconia* swamp; judging from information provided by Duellman (2005), the capture site is probably seasonally inundated by accumulated rainwater in the wet season.

Lastly, this species has been collected in anthropogenic habitats on well-drained soils. According to Hice and Velazco (2012), who reported on material collected in the Reserva Nacional Allpahuayo-Mishana and at the nearby Fuerte Militar Otorongo in northeastern Peru, *Philander* "*opossum*" was collected only in secondary vegetation and agricultural fields, whereas *P. andersoni* occupied adjacent primary forest habitats. We examined 16 of the 39 specimens of *P.* "*opossum*" reported by these authors, and all were examples of *P. pebas*.

Based on these scant data, we hypothesize that *Philander pebas* is primarily a várzea species; that is, one that typically inhabits riparian formations seasonally flooded by white-water rivers (for Amazonian flooded-forest nomenclature, see Prance, 1979). In support of this conjecture, we note that the geographic distribution of the species (fig. 9) corresponds closely to the distribution of

white-water catchments in the Amazon Basin (Junk et al., 2011: fig. 1), and we boldly predict that *P. pebas* will eventually be found to inhabit the white-water Caquetá and Putumayo drainages of southeastern Colombia, from which we have yet to examine any material. Because várzea habitats are characterized by riverine flooding, terrestrial (nonaquatic and nonarboreal) species that inhabit such forests during the low-water season must periodically migrate to higher ground, and the ability to occupy temporary refugia may preadapt terrestrial várzea species to also utilize swampy habitats (seasonally flooded by accumulated rainwater), as well as to opportunistically invade secondary vegetation resulting from human activity on adjacent terraces and hillsides.

Etymology: After Lago Pebas, the vast Miocene lake complex (Wesselingh et al., 2001) or "mega-wetland" (Hoorn et al., 2010) that filled much of the Andean foreland basin, including almost the entire known geographic range of this morphologically distinctive species.

Specimens Examined (N = 58): **Brazil**—*Acre,* Fazenda Santa Fé (on Rio Juruá; MVZ 190345), opposite Ocidente (on Rio Juruá; MVZ 190346); *Amazonas,* Igarapé Nova Empresa (on Rio Juruá; MVZ 190343), Lago do Baptista (on S bank of Amazon; FMNH 51095), Sacado (on Rio Juruá; MVZ 190344), Santo Isidoro [near] Tefé (on S bank of Amazon; AMNH 78954), Parintins ("Villa Bella Imperatriz," on S bank of Amazon; AMNH 92880, 92881, 93526–93528, 93968), Tapauá (on Rio Purus; USNM 461374). **Ecuador**—*Orellana,* 42 km S Pompeya Sur (ROM 106101, 106139). **Peru**—*Loreto,* Apayacu (AMNH 74388), Avícola San Miguel (MUSM 33590, 33592, 33593), Cabo López (MUSM 33566, 33567, 33569, 33570, 33572), Carretera Iquitos-Nauta km 28.8 (MUSM 34892), Caserio Cahuide (MUSM 33564, 33574, 33576), El Paujil (MUSM 33580), El Triunfo (MUSM 33586, 33587, 33583), Iquitos (AMNH 98642), 19.7 km SW Iquitos (MUSM 33588), Mishana (MUSM 33597), Orosa (AMNH 73852), Otorongo Army Base (LACM 91621, 91622), Peña Negra (MUSM 33598), Picuro Yacu (MUSM 33594), Quistococha (FMNH 122745–122748; MUSM 33599, 33600), San Gerardo (MUSM 33602), Santo Tomas (MUSM 33603), Sarayacu (on Río Ucayali; AMNH 76448–76450); *Madre de Dios,* Cusco Amazónico (KU 144120, 144121; MUSM 6074); *Ucayali,* Balta (LSUMZ 12007, 12010, 14011), Yarinacocha (FMNH 55411).

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FIG. 22. Collecting specimens for this study (*Philander pallidus*, trapped at Lamanai Outpost Lodge, Orange Walk, Belize; 2012).

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APPENDIX 1

Gazetteer of Collection Localities for Sequenced Material

Below we list all the localities where sequenced specimens of *Philander* were collected, including those sequenced by us and others corresponding to sequences that we downloaded from GenBank (table 2). Italicized place names are those of the largest political units (states, departments, or provinces) within each country. Geographic coordinates (in decimal degrees) were obtained from specimen labels, field notes, or institutional databases except as noted otherwise (in square brackets, with a cited source). The name of the taxon collected at each locality (in boldface) together with the name of the collector(s) and year of collection (in parentheses) are also provided.

ARGENTINA

1. *Chaco,* Parque Nacional Chaco, Presidencia de la Plaza [ca. 26.93°S, 59.77°W; Lorea et al., 2008]: **canus** (coll. S. Heinonen, 1995).

2. *Formosa,* Pilcomayo, Parque Nacional Río Pilcomayo [ca. 25.13°S, 58.13°W; Pardiñas et al., 2004]: **canus** (coll. S. Heinonen, 1993).

3. *Misiones,* Iguazú, Río Urugua-í [ca. 25.92°S, 54.30°W; Pardiñas et al., 2003]: **quica** (coll. J.A. Crespo, 1949, 1951; W.H. Partridge, 1951). The Río Urugua-í, a left-bank tributary of the upper Río Paraná, is also known as the Arroyo Urugua-í (presumably to avoid confusion with the much larger Río Uruguay). It was the focus of much mid-20th-century collecting activity by various investigators, of whom those from the MACN seem to have worked at a site known as Yacú-poí (Massoia et al., 1987), about 30 km east of Puerto Libertad (= Puerto Bemberg; Baldo and Basso, 2004). Several MACN specimens from which Chemisquy and Flores (2012) obtained sequence data are assumed

to have been collected here, including those labeled "Río Urugua-í (curso medio)," "Río Urugua-í (curso medio) 30 km Puerto Bemberg," and "Arroyo Urugua-í."

4. *Misiones,* San Pedro, Tobuna [26.47°S, 53.90°W; Paynter, 1995]: ***quica*** (coll. J.A. Crespo, 1952).

BELIZE

5. *Orange Walk,* Lamanai Outpost Lodge (17.46°N, 88.39°W): ***pallidus*** (coll. N.S. Voss and N.B. Simmons, 2012).

BOLIVIA

6. *Beni,* Casarabe, 230 m (14.80°S, 65.45°W): ***canus*** (coll. L.A. Ruedas, 1985).

7. *Beni,* Río Tijamuchi, 240 m [14.17°S, 64.97°W; Anderson, 1997]: ***canus*** (coll. AMNH/MSB expedition, 1985).

8. *Pando,* Bella Vista, 170 m [11.23°S, 67.12°W; Anderson, 1997]: ***canus*** (coll. T.L. Yates, 1986).

9. *Santa Cruz,* Estancia Cachuela Esperanza [16.78°S, 63.23°W; Anderson, 1997]: ***canus*** (coll. N. Olds, 1984).

BRAZIL

10. *Acre,* Fazenda Santa Fé, left bank Rio Juruá [8.60°S, 72.85°W; Patton et al., 2000]: ***pebas*** (coll. M.N.F. da Silva, 1992).

11. *Acre,* Igarapé Porongaba, right bank Rio Juruá [8.67°S, 72.78°W; Patton et al., 2000]: ***mcilhennyi*** (coll. M.N.F. da Silva, 1992).

12. *Acre,* Sobral, left bank Rio Juruá [8.37°S, 72.82°W; Patton et al., 2000]: ***canus*** and ***mcilhennyi*** (coll. M.N.F. da Silva, 1992).

13. *Amazonas,* Altamira, right bank Rio Juruá (6.58°S, 68.90°W): ***mcilhennyi*** (coll. J.L. Patton, 1991).

14. *Amazonas,* alto Rio Urucu (4.85°S, 65.27°W): ***mcilhennyi*** (coll. M.N.F. da Silva, 1989).

15. *Amazonas,* Estrada Piçarreira, Parque Nacional do Pico da Neblina (0.61°N, 66.09°W): ***andersoni*** (coll. V.C.S. Vidigal [date unknown]).

16. *Amazonas,* Igarapé Nova Empresa, left bank Rio Juruá [6.80°S, 70.73°W; Patton et al., 2000]: ***pebas*** (coll. J.L. Patton, 1991).

17. *Amazonas,* Ilha das Onças, left bank Rio Negro (1.82°S, 61.37°W): ***opossum*** (coll. L.P. Costa and J.L. Patton, 2000). One sequenced specimen corresponding to this locality datum (INPA 4342/LPC 164) was erroneously reported to have been collected at Lago Meduiním (also on the left bank of the Rio Negro) by Patton et al. (2000: table 16; J.L. Patton, personal commun.).

18. *Amazonas,* Macaco, left bank Rio Jaú (2.08°S, 62.12°W): ***andersoni*** (coll. Y. Leite, 2000).

19. *Amazonas,* Mamirauá Reserve [3.17°S, 64.68°W; Nunes et al., 2006]: ***pebas*** (coll. C. Nunes, 1995–1997).

20. *Amazonas,* left bank Rio Jaú above mouth (1.96°S, 61.49°W): ***andersoni*** (coll. M.N.F. da Silva, 1996).

21. *Amazonas,* Seringal Condor, left bank Rio Juruá [6.75°S, 70.85°W; Patton et al., 2000]: ***mcilhennyi*** (coll. J.L. Patton, 1991).

22. *Bahia,* Fazenda Bolandeira, 10 km S Una [15.35°S, 39.00°W; Geise, et al., 2001]: ***quica*** (coll. Y. Leite, 1996).

23. *Espírito Santo,* Cariacica, Reserva Biológica de Duas Bocas, alto Alegre (20.28°S, 40.51°W; Y. Leite and L. Costa, personal commun.): ***quica*** (coll. L.P. Costa, 2007).

24. *Espírito Santo,* Estação Biológica de Santa Lúcia [ca. 19.95°S, 40.52°W; Y. Leite, and L. Costa, personal commun.]: ***quica*** (coll. M.A. Mustrangi, 1993; Y. Leite, 2007).

25. *Espírito Santo,* Ibitirama, Parque Nacional Caparaó, Posto Santa Maria (20.50°S, 41.70°W; Y. Leite, and L. Costa, personal commun.): *quica* (coll. V. Fagundes, 2006).

26. *Espírito Santo,* Pancas, Mata de Pedra do Camelo (19.24°S, 40.77°W; Y. Leite and L. Costa, personal com.): *quica* (coll. L.P. Costa, 2006).

27. *Mato Grosso do Sul,* Rio Miranda, above Passo do Lontra [19.58°S, 57.01°W; MVZ collection database]: *canus* (coll. L.P. Costa and J.L. Patton, 1998).

28. *Mato Grosso,* Base de Pesquisa do Pantanal CENEP/IBAMA, 110 km SSW Poconé (17.12°S, 56.95°W): *canus* (coll. L.P. Costa, 1998).

29. *Mato Grosso,* Fazenda São Luis, 30 km N Barra do Garças [15.63°S, 52.36°W; MVZ collection database]: *canus* (coll. L.P. Costa, 1998).

30. *Minas Gerais,* Cruzeiro, 8 km NE Santa Rita de Jacutinga (22.08°S, 44.03°W): *quica* (coll. L.P. Costa [date unknown]).

31. *Minas Gerais,* Estação Biológica Mata do Sossego, Simonésia (20.13°S, 42.00°W): *quica* (coll. Y. Leite [date unknown]).

32. *Minas Gerais,* Parque Estadual do Ibitipoca, 30 km N Lima Duarte (21.70°S, 43.90°W): *quica* (coll. M.A. Mustrangi, 29 October 1993).

33. *Minas Gerais,* RPPN Belgo Mineira, João Monlevade [19.80°S, 43.17°W; MVZ collection database]: *quica* (collector and date unknown).

34. *Pará,* 52 km SSW Altamira, east bank Rio Xingu (3.65°S, 52.37°W): *opossum* (coll. L.H. Emmons and M.D. Carleton, 1986).

35. *Pará,* Belém, IPEAN-APEG [ca. 1.45°S, 48.48°W; Paynter and Traylor, 1991]: *opossum* ([collector unknown] 1971).

36. *Pará,* Floresta Nacional Tapirapé-Aquiri, Município de Marabá (5.80°S, 50.52°W): *opossum* (collector and date unknown).

37. *Pará,* Itaituba, BR165 Santarém-Cuiabá zona sul [4.92°S, 55.60°W; USNM collection database]: *opossum* ([collector unknown] 1976).

38. *Pará,* Santana do Araguaia [9.63°S, 50.14°W; Rocha et al., 2015]: *canus* (coll. R.G. Rocha [date unknown]).

39. *Paraná,* Mananciais da Serra (SANEPAR), Piraquara (25.47°S, 49.07°W): *quica* (coll. Y. Leite [date unknown]; N. Caceres [date unknown]).

40. *Paraná,* Parque Nacional do Iguaçu (25.63°S, 54.46°W): *quica* (coll. L.P. Costa, 1998).

41. *Rio de Janeiro,* Debossan, Sítio Xitaca, Nova Friburgo (22.28°S, 42.53°W): **quica** (L. Geise [date unknown]).

42. *Rio de Janeiro,* Guapimirim, Garrafão, (22.45°S, 43.00°W; R. Cerqueira, personal commun.): *quica* (coll. L. Geise, 1991).

43. *Rio de Janeiro,* Parque Nacional de Itatiaia, Município de Itatiaia (22.38°S, 44.63°W): *quica* (coll. M.A. Mustrangi, 1993).

44. *Rio de Janeiro,* Restinga de Maricá, Barra de Maricá, Maricá (22.88°S, 42.83°W): *quica* (coll. M.C. Lara, 1992).

45. *São Paulo,* Fazenda da Toca, Ilha de São Sebastião, Ilhabela, 150 m (23.82°S, 45.35°W): *quica* (coll. M.A. Mustrangi, 1992).

46. *São Paulo,* Fazenda Intervales, Base do Carmo, 5.5 km S Capão Bonito (24.33°S, 48.42°W): *quica* (coll. M.A. Mustrangi, 1992).

47. *São Paulo,* Praia do Félix, Ubatuba (23.38°S, 44.97°W): *quica* (coll. M.A. Mustrangi [date unknown]).

48. *São Paulo,* Serra do Japí, 7 km W Jundiaí (23.23°S, 46.95°W): *quica* (coll. M.A. Mustrangi, 1993).

49. *Tocantins,* Lagoa da Confusão [10.87°S, 49.70°W; Rocha et al., 2015]: ***canus*** (coll. R.G. Rocha, [date unknown]).

50. *Tocantins,* near Pium, including sublocalities "Centro de Pesquisa Canguçu" (9.98°S, 50.03°W), "Parque Estadual do Cantão" (9.96°S, 50.12°W), and "N Pium" [9.47°S, 50.04°W; Rocha et al., 2015]: ***canus*** (coll. R.G. Rocha, 2007).

COLOMBIA

51. *Caldas,* Victoria, Vereda Canan, sitio La Esperanza (5.32°N, 74.93°W): ***melanurus*** (coll. J.F. Díaz-Nieto, 2006).

52. *Meta,* Finca El Capricho, 38 km E Villavicencio, 300 m [4.15°N, 73.29°W; KU collection database]: ***canus*** (coll. J.A.W. Kirsch, 1969).

53. *Putumayo,* 17 km N Puerto Asis [ca.0.67°N, 76.50°W; map estimate]: ***andersoni*** (coll. J.A.W. Kirsch, 1969).

54. *Valle,* 28 km NE Buenaventura, 150 m [3.60°N, 76.87°W; KU collection database]: ***melanurus*** (coll. J.A.W. Kirsch, 1969).

ECUADOR

55. *Los Ríos,* Lima Pareja, 4 km SW Puebloviejo (1.55°S, 79.47°W): ***melanurus*** (coll. R.G. McLean, 1975).

56. *Orellana,* Onkone Gare, 38 km S Pompeya Sur (0.65°S, 76.45°W): ***andersoni*** (coll. ROM expedition, 1995).

57. *Orellana,* Parque Nacional Yasuní, 42 km S, 1 km E Pompeya Sur [0.68°S, 76.43°W; Gregorin et al., 2006]: ***pebas*** (coll. ROM expedition, 1996).

58. *Orellana,* Parque Nacional Yasumí, 18 km S Pompeya Sur [ca. 0.60°S, 76.61°W; map estimate]: ***andersoni*** (coll. ROM expedition, 1996).

EL SALVADOR

59. *La Paz,* Zacatecoluca, Hacienda Escuintla [13.50°N, 88.87°W; TTU collection database]: ***pallidus*** (coll. J.G. Owen, 1990).

FRENCH GUIANA

60. Montagnes de la Trinité (4.62°N, 53.37°W): ***opossum*** (coll. F. Catzeflis, 1998).

GUYANA

61. *Barima-Waini,* Waikerebi (7.52°N, 59.38°W): ***opossum*** (coll. B.K. Lim and S.M. Woodward, 1991).

62. *Potaro-Siparuni,* 30 km NE Surama (4.33°N, 58.85°W): ***opossum*** (coll. ROM expedition, 1990).

63. *Potaro-Siparuni,* Iwokrama Forest, Sand Stone (4.38°N, 58.92°W): ***opossum*** (coll. ROM expedition, 1999).

64. *Upper Takutu-Upper Essequibo,* Chodikar River, 55 km SW Gunn's Strip (1.37°N, 58.77°W): ***opossum*** (coll. ROM expedition, 1996).

MEXICO

65. *Campeche,* 11 km by road S Candelaria [18.09°N, 91.07°W; ASNHC collection database]: ***pallidus*** (coll. M.D. Engstrom, 1984).

66. *Campeche,* 3.7 km SE Chekubul [18.80°N, 90.98°W; ROM collection database]: ***pallidus*** (coll. M.D. Engstrom and R.C. Dowler, 1989).

67. *Campeche,* El Remate, 14 km W Tancuche [20.51°N, 90.38°W; ASNHC collection database]: ***pallidus*** (coll. R. Dowler and B. Lim, 1990).

68. *Chiapas,* 19 km N Palenque [17.66°N, 92.00°W; ASNHC collection database]: ***pallidus*** (coll. M.D. Engstrom, 1984).

69. *Quintana Roo,* 1 km W Puerto Morelos [20.85°N, 86.90°W; ROM collection database]: ***pallidus*** (coll. M.D. Engstrom, 1990).

70. *Tabasco,* 5 km N Jonuta [18.13°N, 92.12°W; ROM collection database]: ***pallidus*** (coll. M.D. Engstrom and R.C. Dowler, 1989).

71. *Tabasco,* 27 km S and 14 km E El Triunfo [17.68°N, 91.04°W; ASNHC collection database]: ***pallidus*** (coll. K.L. Curran, 1986).

PANAMA

72. *Bocas del Toro,* Isla Bastimentos, Old Point [9.17°N, 82.05°W; Siegel and Olson, 2008): ***melanurus*** (J. Jacobs, 1987).

73. *Bocas del Toro,* Peninsula Valiente, Punta Alegre [9.09°N, 81.54°W; Siegel and Olson, 2008]: ***melanurus*** (coll. F.M. Greenwell, 1990).

74. *Panamá,* Parque Nacional Altos de Campana, 850 m (8.68°N, 79.93°W): ***melanurus*** (coll. ROM expedition, 1995).

PARAGUAY

75. *Alto Paraguay,* Bahia Negra, Tres Gigantes [20.08°S, 58.16°W; de la Sancha and D'Elía, 2015]: ***canus*** (collector and date unknown).

76. *Ñeembucú,* Estancia Santa Teresa, ca. 2 km S Puesto Anastacio (26.57°S, 58.14°W): ***canus*** (coll. G. D'Elía, 1999).

77. *Paraguarí,* Sapucay (= Sapucaí at 25.67°S, 56.92°W; Paynter, 1989): ***quica*** (coll. anonymous MACN personnel, 1933).

78. *Presidente Hayes,* Estancia Loma Porá [23.52°S, 57.52°W; de la Sancha and D'Elía, 2015]: ***canus*** (collector and date unknown).

PERU

79. *Amazonas,* vicinity of Huampami, Río Cenepa [4.47°S, 78.17°W; Patton et al., 1982]: ***andersoni*** (coll. J.L. Patton, 1977).

80. *Loreto,* 21 km S Iquitos, Otorongo Army Base [3.95°S, 73.37°W; C.L. Hice, personal commun.]: ***pebas*** (coll. C.L. Hice, 1998).

81. *Loreto,* 25 km S Iquitos, Estación Biológica Allpahuayo [3.97°S, 73.42°W; Hice et al., 2004]: ***andersoni*** and ***pebas*** (coll. C.L. Hice, 1998).

82. *Loreto,* Nuevo San Juan, right bank Río Gálvez [5.25°S, 73.17°W; Voss and Fleck, 2011]: ***mcilhennyi*** (coll. R.S. Voss, 1998; D.W. Fleck, 1999).

83. *Loreto,* San Jacinto [2.32°S, 75.87°W; Duellman and Mendelson, 1995]: ***andersoni*** (coll. N. Woodman, 1993).

84. *Loreto,* Yurimaguas [5.90°S, 76.08°W; Stephens and Traylor, 1983): ***andersoni*** (coll. M.P. Anderson, 1912).

85. *Madre de Dios,* Reserva Cuzco Amazónico [12.55°S, 69.05°W; Duellman and Koechlin, 1991]: ***pebas*** (coll. N. Woodman, 1989).

SURINAM

86. *Para,* Zanderij (5.45°N, 55.20°W): **opossum** (coll. L. Roberts, 1980).

87. *Sipaliwini,* Bakhuis, Transect 13 (4.55°N, 57.06°W): **opossum** (coll. ROM expedition, 2006).

88. *Suriname,* Plantation Clevia, 8 km NE Paramaribo [5.87°N, 55.13°W; CM database]: **opossum** (coll. S.L. Williams, 1981).

VENEZUELA

89. *Amazonas,* Belén, left bank Río Cunucunuma, 150 m [3.65°N, 65.77°W; Voss and Emmons, 1996]: **andersoni** (coll. USNM expedition, 1967).

90. *Bolívar,* 8 km S and 5 km E El Manteco [7.32°N, 62.47°W; Ochoa and Ibáñez, 1985]: **canus** (coll. L.W. Robbins, 1981).

91. *Trujillo,* 9.8 km NNE Motatán, 230 m [9.47°N, 70.56°W; KU collection database]: **canus** (coll. J.A.W. Kirsch, 1969).

APPENDIX 2

Primer Sequences Used for this Study

Gene	Primer Name	Sequence
CYTB	cytb-DidMVZ05	5′-ATAACCTATGGCATGAAAAACCATTGTTG
CYTB	cytb-Phil140F	5′-AATTTCGGTTCACTTCTAGGARTATGC
CYTB	cytb-Phil270F	5′-ATGRCTTATCCGAAAYATCCACG
CYTB	cytb-Mar650F	5′-CTATTCCTTCACGAAACAGGCTC
CYTB	cytb-Phil670F	5′-CCTAAATCCTGACGCAGATAAAATCC
CYTB	cytb-Mar690F	5′-CTCAGACAAAATCCCATTCAATCC
CYTB	cytb-Phil203R	5′-CAGATATGGGCTACTGATGAAAATGC
CYTB	cytb-Phil310R	5′-ATCCATARTAAATTCCTCGTCCTACG
CYTB	cytb-Phil518R	5′-TAGCTTTGTCAACGGAAAATCC
CYTB	cytb-Mar730R	5′-TCWCCTAATARRTCWGGTGARAATATTGC
CYTB	cytb-Did1260R	5′-CCTTCATTGCTGGCTTACAAGGC
BRCA	BRCA-F1163a	5′-AATGAGACTGAACTACAGATCGAT
BRCA	BRCA-R1780	5′-TAAATAYTGGGTRTCRAGTTCACT
BRCA	BRCA-F1697	5′-TTWGATGRTTGTTCATCYRAAAACAC
BRCA	BRCA-R2078	5′-GAAATTTCCTSGTTATTTCCAGCAA
IRBP	IRBP-A	5′-ATGGCCAAGGTCCTCTTGGATAACTACTGCTT
IRBP	IRBP-D1	5′-CATCATCAAACCGCAGATAGCCCA
SLC38	SLC38-F2	5′-TTCTTCCTTTGTCATTGCTGAG
SLC38	SLC38-R3	5′-AGTTGAAGATAAAGTACCGGGG
OGT	OGT-F1	5′-AAATCATTTCATCGACCTTTCTCAG
OGT	OGT-R1	5′-GCTGCTTTTCCATTACAGGGAAT
Anon128	Anon128F	5′-CTTACACCAGGCACCAACTCTGAGACA
Anon128	Anon128R	5′-CTCTAAACTGCCATCCCAGGGTCACTC

APPENDIX 3

Percent Uncorrected Pairwise Sequence Divergence among Putative Species of *Philander*[a]

	quica	canus	pebas	melanurus	pallidus	andersoni	mcilhennyi	opossum
quica	**0.9**							
canus	11.2	**0.8**						
pebas	9.9	1.8	**1.3**					
melanurus	10.5	4.5	4.6	**0.8**				
pallidus	11.9	5.4	5.0	3.9	**0.3**			
andersoni	11.8	5.9	5.2	6.0	6.9	**0.4**		
mcilhennyi	10.8	4.1	3.2	5.2	5.4	6.1	**1.2**	
opossum	11.2	3.5	3.0	4.5	5.1	5.6	3.0	**0.8**

[a] At the cytochrome-*b* locus; diagonal elements (in boldface) are mean uncorrected within-group distances.

APPENDIX 4

Analyzed Craniodental Samples of Adult Male *Philander* with Generalized (Mahalanobis) Distances

	N[a]	Generalized distance (D)							
		quica	canus	pebas	melanurus	pallidus	andersoni	mcilhennyi	opossum
quica	19	0.00							
canus	21	3.89	0.00						
pebas	22	6.48	5.99	0.00					
melanurus	21	5.91	5.71	3.12	0.00				
pallidus	21	5.00	4.60	3.69	2.20	0.00			
andersoni	23	5.29	5.86	3.86	1.91	2.59	0.00		
mcilhennyi	10	7.31	7.58	4.22	3.45	4.25	3.07	0.00	
opossum	25	4.61	5.13	3.47	2.08	1.75	1.74	3.43	0.00

[a] Sample size.

APPENDIX 5

ON THE TYPE LOCALITY OF *DIDELPHYS FRENATA* OLFERS, 1818

Robert S. Voss and Renate Angermann[13]

Although the gray four-eyed opossum of southeastern Brazil is now commonly known as *Philander frenatus* following Patton and da Silva (1997), this usage is not consistent with available information about where the holotype was collected. The epithet was first made available by Olfers (1818: 204), but Olfers attributed the name to Karl Illiger, first director of the newly founded zoological museum in Berlin, who had previously used *frenata* as a nomen nudum (Illiger, 1815). Olfers is known to have studied the mammal collection of the Berlin museum in 1816 or early 1817 (Voss and Angermann, 1997), where he must have seen Illiger's original material.[14] Olfers (1818) treated *frenata* as a variety of *Didelphys opossum* and stated only that it occurred in South America.

As explained elsewhere (Voss and Angermann, 1997), the nucleus of the mammal collection of the Berlin Zoological Museum (ZMB) at its inception in 1810 was a large series of Brazilian specimens donated by Johann Centurius von Hoffmannsegg, a wealthy patron of German science. As far as known, all of Hoffmannsegg's Brazilian mammals were collected either by Friedrich Wilhelm Sieber, who worked in eastern Amazonia from 1803 to 1812, or by Francisco Agostinho Gomes, who lived at Bahia (now Salvador) and sent specimens to Hoffmannsegg from 1801 to 1807. The earliest known catalog of the ZMB collection—a manuscript entitled "Catalogus mammalium et avium Musei Regii" dated 1810 and preserved in the museum's archives (Historische Bild- und Schriftgutsammlungen)—lists *Didelphys frenata* as a new species based on material donated by Hoffmannsegg, and a penciled specimen tally in the margin indicates that only a single specimen was present. Our inspection of the ZMB accessions register ("Eingangskatalog") suggests that no additional material identified as *D. frenata* was received by the museum prior to Olfer's visit.

All the mammal specimens in the early ZMB collection were mounted in lifelike poses (with the skull inside) for exhibition in the museum's public galleries, probably between 1811 and 1814, and any original collectors' labels were probably lost or discarded at that time; such data as now accompany early 19th-century specimens in the ZMB were copied from the exhibition labels when many live-mounts were remade as conventional study skins with extracted skulls in the 1900s (Voss and Angermann, 1997). The appearance of the specimen currently cataloged as the type of *Philander frenatus*, ZMB_MAM 2325 (the skin and skull of an old adult female) is consistent with this scenario; its labeling records the locality as "Brasilien," the collector as "Sieber," and the donor as "v. Hoffmannsegg." The fur color of this specimen is now faded almost beyond recognition, but the skull and dentition are substantially intact. Although

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[14] Ignatz von Olfers (b. 1793), a young member of the Prussian legation to Brazil, arrived at Rio de Janeiro in the late spring or early summer of 1817. For additional information about his work, the Berlin collections he studied, and other relevant historical background (including manuscript documents mentioned in the following text), see Voss and Angermann (1997).

Olfers (1818: 205) stated that he had seen young examples of *Philander* in Brazil, none is known to have survived as a museum specimen, and it is not clear that any served as the basis for his description of *P. frenatus*. In the absence of evidence to the contrary, we consider ZMB_MAM 2325 to be the holotype by monotypy.

Because at least one ZMB specimen collected by Gomes is known to have been misattributed to Sieber (the holotype of *Chaetomys subspinosus*; Voss and Angermann, 1997), we examined manuscript invoices of Gomes's shipments from Bahia. These lists suggest that Gomes sent only a single marsupial specimen to Hoffmannsegg, of which only the head was preserved,[15] so Gomes' opossum cannot be the skin and skull now cataloged as ZMB_MAM 2325. Therefore, the holotype of *Philander frenatus* must have been collected by Sieber, as it is now labeled.

The only documentary evidence of where in Brazil the holotype might have been collected is the penciled annotation "Para" (the old name for Belém, the largest city in eastern Amazonia) beneath the inked entry for ZMB_MAM 2325 in the mammal department's general catalog (initiated by Wilhelm Peters sometime after 1857; Angermann, 1989). As previously noted, Sieber is known to have collected in eastern Amazonia (Urban, 1906), and measurements of the molar dentition of the holotype fall within the range of variation observed among specimens of *Philander* subsequently collected in that region; for example, we obtained a value of 13.7 mm for LM from the holotype of *frenatus*, whereas the mean value for LM in a sample of 42 specimens from eastern Amazonia is 13.8 ± 0.4 mm. By contrast, southeastern Brazilian specimens have much smaller molars (LM = 12.3 ± 0.4 mm, $N = 40$), so the morphology of ZMB_MAM 2325 is also consistent with its inferred eastern Amazonian origin. Eastern Amazonian populations of *Philander* seem to be minimally differentiated from Guianan populations in both molecular and phenotypic traits, so we treat *frenatus* as a junior synonym of *P. opossum*.

Current usage of the epithet *frenatus* for the southeastern Brazilian species that we recognize as *Philander quica* seems to be based on Hershkovitz (1959: 343), who stated that the type was collected by "Herr Kaehne" at Bahia. According to Hershkovitz, this information was provided by Wagner (1843: 44), but Wagner simply remarked that a specimen identified as *Didelphys frenata* by "Lichtenstein" (= Hinrich Lichtenstein, Illiger's successor as ZMB director) was collected by Kaehne in Bahia. Because Kaehne (= Franz Kaehne, a former apothecary from Prenzlau) collected in Brazil from 1831 to 1838 (Sick, 1960), his specimen cannot have been the one seen by Olfers (1818). Hershkovitz (1997: 51) subsequently alleged that the type was "collected before 1815 by Herr Kaehne" but provided no reference for this clearly erroneous statement.

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[15] This specimen was identified as *Didelphys cayopollin* in a document entitled "Envoy de la Caisse Nr. 7 du 24 May 1802." With few exceptions, the name *D. cayopollin* was consistently used by 19th-century authors for the species currently known as *Caluromys philander* (see Gardner, 2008: 10–11).