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A new polytypic species of yellow-shouldered bats, genus *Sturnira* (Mammalia: Chiroptera: Phyllostomidae), from the Andean and coastal mountain systems of Venezuela and Colombia

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Abstract

Sturnira is the most speciose genus of New World leaf-nosed bats (Phyllostomidae). We name *Sturnira adrianae*, new species. This taxon is born polytypic, divided into a larger subspecies (*S. a. adrianae*) widespread in the mountains of northern and western Venezuela, and northern Colombia, and a smaller subspecies (*S. a. caripana*) endemic to the mountains of northeastern Venezuela. The new species inhabits evergreen, deciduous, and cloud forests at mainly medium (1000–2000 m) elevations. It has long been confused with *S. ludovici*, but it is more closely related to *S. oporaphilum*. It can be distinguished from other species of *Sturnira* by genetic data, and based on discrete and continuously varying characters. Within the genus, the new species belongs to a clade that also includes *S. oporaphilum*, *S. ludovici*, *S. hondurensis*, and *S. burtonlimi*. The larger new subspecies is the largest member of this clade. The two new subspecies are the most sexually dimorphic members of this clade. The smaller new subspecies is restricted to small mountain systems undergoing severe deforestation processes, therefore can be assigned to the Vulnerable (VU) conservation category of the International Union for Conservation of Nature (IUCN).

Keywords: Andes, evolutionary species concept, geographic variation, morphometrics, sexual dimorphism

Introduction

With 22 currently recognized species, four of them described in the last decade (McCarthy *et al.* 2006; Jarrín-V. & Kunz 2011; Velazco & Patterson 2014), *Sturnira* is the most speciose genus of New World leaf-nosed bats (Phyllostomidae). Members of *Sturnira*, known as yellow-shouldered bats, are primarily frugivorous (Parolin *et al.* 2016), and are found in forests from Sonora and Tamaulipas (Mexico) and the Lesser Antilles in the north, to northern Argentina and Uruguay in the south (Simmons 2005). The application of a molecular perspective to *Sturnira*, pioneered by Iudica (2000), and more recently elaborated by Velazco & Patterson (2013), has greatly enhanced our understanding of the pattern of diversification, biogeography, and taxonomy of the genus: *Sturnira* is hypothesized to have diverged as a separate genus between 12.6 and 15.9 Ma, in the central and northern Andes (Velazco & Patterson 2013); a robust phylogenetic tree for *Sturnira* allocates 18 of 21 species to two clades, Clade A including 11 morphologically heterogeneous and predominantly montane species from South and Central America, and Mexico, and Clade B including seven morphologically homogeneous and predominantly lowland species from the full geographic range of the genus (Velazco & Patterson 2013, 2014).

The species described herein belongs to one of the two subclades of Clade A, up to now including four species: *S. oporaphilum* (Tschudi), occurring in Ecuador, Peru, Bolivia, and Argentina; *S. ludovici* Anthony, occurring in Ecuador and Colombia, and postulated to also occur in Venezuela; *S. hondurensis* Goodwin, occurring from Mexico south to Nicaragua; and *S. burtonlimi* Velazco & Patterson, occurring in Costa Rica and Panamá (Pacheco & Patterson 1992; Bárquez *et al.* 1999; Velazco & Patterson 2013, 2014). We will refer to these four species, and to the species described herein, as the *S. oporaphilum* clade.

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The taxonomic history of the members of the *S. oporaphilum* clade has been plagued by confusion. Hershkovitz (1949), Cabrera (1958), and Hall (1981) listed *S. hondurensis* and *S. bogotensis* Shamel as synonyms of *S. ludovici*. Cabrera (1958) listed *S. oporophilum* (= *oporaphilum*) as a synonym of *S. lilium* (E. Geoffroy). De la Torre (1961) recognized *S. oporaphilum* as distinct from *S. ludovici*: however, he listed *S. hondurensis* as a junior synonym of the former. Jones & Carter (1976) suggested *S. oporaphilum* and *S. bogotensis* to be valid species or subspecies related to *S. ludovici*. Anderson *et al*. (1982), Koopman (1994), and McCarthy et al. (2006) regarded *S. bogotensis* as a junior synonym of *S. oporaphilum*. Pacheco & Patterson (1992) recognized *S. oporaphilum*, *S. ludovici*, and *S. bogotensis* as different species: however, they suggested that *S. ludovici* might simply represent a large geographic variant of *S. oporaphilum*, with Venezuelan populations referred to *S. ludovici* representing yet another variant. Sánchez-Hernández *et al*. (2005) listed Venezuelan specimens that we deem to represent a single new species (Appendix), identifying some of them as *S. ludovici* and others as *S. hondurensis*. Gardner (2008) applied the names *S. oporaphilum oporaphilum* for bats from Peru, Bolivia, and Argentina, and *S. o. ludovici* for bats from Ecuador, Colombia, and Venezuela. Jarrín-V. & Clare (2013) found *S. oporaphilum* and *S. ludovici* from Ecuador to be genetically quite distinct and reciprocally monophyletic: however, they could not distinguish them morphologically and therefore listed both as *S. ludovici*. Finally, using both molecular and morphological information, Velazco & Patterson (2013, 2014) settled these controversies by showing that *S. oporaphilum*, *S. ludovici*, *S. hondurensis*, and *S. burtonlimi* represent different species in a clade that does not include *S. bogotensis*.

During a genetic assessment of the genus *Sturnira* in Venezuela, we found that the *S*. "*ludovici*" from the country does not bear a sister-group relationship with Ecuadorian *S. ludovici*, but instead with what is currently known as *S. oporaphilum*. In the light of the equivocal taxonomic history of *S*. "*ludovici*" north of Ecuador, this finding led us to investigate taxonomically the members of the *S. oporaphilum* clade occurring in Venezuela. We conclude that Venezuelan yellow-shouldered bats until now referred to as *S*. "*ludovici*" represent an undescribed taxon, which we name as a new species and two new subspecies.

Materials and methods

Species concept and taxonomic criteria. We stand by the evolutionary species concept, according to which 'a species is a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies' (Simpson 1951). As it can happen in descriptions involving allopatric distributions, we lack direct evidence indicating that the new species would not merge with its sister species if their populations would come together. The converse is also true, we are describing two allopatric subspecies for which we lack direct evidence indicating that their populations would merge if the geographic barrier separating them could disappear. The history of taxonomy is rich in examples of how this limitation can be overcome by relying on the congruence of several distinct lines of evidence generally useful to distinguish species. This study is based on this practical principle: in addition to being genetically distinctive, the new species is differentiated by discrete and continuously varying morphological characters at a taxonomically relevant level.

Material included. Museum acronyms for specimens examined are: AMNH, American Museum of Natural History, New York, USA; CML, Colección de Mamíferos Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Tucumán, Argentina; CMNH, Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CVULA, Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela; EBRG, Museo de la Estación Biológica de Rancho Grande, Maracay, Venezuela; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

Museum/collector acronyms that appear only in Table 1 are: BDP, B.D. Patterson field acronym; LSUMZ, Louisiana State University, Museum of Natural Science, Baton Rouge, Louisiana, USA; MPEG, Museu Paraense Emilio Goeldi, Belém, Brazil; MSB, Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; TJM, T.J. McCarthy field acronym; TTU, Museum of Texas Tech University, Lubbock, Texas, USA; USNM, United States National Museum of Natural History, Washington, D.C., USA.

TABLE 1. GenBank accession numbers for the Cyt-*b* sequences (*Sturnira* and outgroup species) included in the Maximum Likelihood tree (Fig. 2). For the locality data of *S. adrianae*, see Appendix. For the locality data of other species, see Velazco and Patterson (2013, 2014). For the description of acronyms, see Materials and methods.

Species: collection/collector acronym and number (GenBank accession number)

Sturnira adrianae adrianae: CVULA 8550 (KY366231), 8584 (KY366232), 8585 (KY366233), 8602 (KY366234), 8603 (KY366235)

Sturnira adrianae caripana: CVULA 8590 (KY366229), 8593 (KY366230)

Sturnira bakeri: TTU 102351 (KC753828), 102661 (KC753829), 102663 (KC753830)

Sturnira bogotensis: FMNH 128787 (KC753783), 128788 (KC753784), 128789 (KC753785), 128790 (KC753786); MUSM 24778 (KC753787)

Sturnira burtonlimi: MVZ 174432 (KC753825); ROM 104294 (KC753826), 104295 (KC753827)

Sturnira erythromos: FMNH 128809 (KC753788), 128811 (KC753789), 162521 (KC753790), 162522 (KC753791), 174800 (KC753792), 174809 (FJ154179)

Sturnira hondurensis: MVZ 223172 (KC753793), 223178 (KC753794), 223393 (KC753795); ROM 101366 (KC753796), 101474 (KC753797); TTU 83675 (KC753799), 104945 (KC753798)

Sturnira lilium: BDP 3174 (KC753805); FMNH 162524 (KC753800), 162542 (KC753801); MVZ 154711 (KC753802); TTU 99168 (KC753803), 99277 (KC753804)

Sturnira ludovici: TTU 102457 (KC753806), 102461 (KC753807)

Sturnira luisi: LSUMZ 25478 (KC753808); ROM 104204 (KC753809), 105807 (KC753810); TTU 103217 (KC753811); USNM 449721 (KC753813), 578239 (KC753814), 579052 (KC753815)

Sturnira magna: AMNH 272787 (KC753816); FMNH 174829 (KC753817), 174830 (KC753818); ROM 104000 (KC753819); USNM 574555 (KC753820)

Sturnira mordax: CMNH 92487 (KC753823), 92488 (KC753824); MVZ 174439 (KC753821); TJM 6741 (KC753822)

Sturnira new species 3: AMNH 268545 (KC753831); CMNH 78567 (KC753832); FMNH 128825 (KC753833), 128845 (KC753834), 172153 (KC753835), 203416 (KC753837), 203420 (KC753838), 203582 (KC753839), 203587 (KC753840), 203590 (KC753841); ROM 103552 (KC753842), 105875 (KC753843), 107936 (KC753844), 117642 (KC753845); TTU 44085 (KC753846), 44090 (KC753847), 44092 (KC753848), 46270 (KC753849)

Sturnira oporaphilum: FMNH 128925 (KC753850), 128926 (KC753851), 174843 (KC753852), 174844 (KC753853), 203589 (KC753854); MUSM 39428 (KC753855); TTU 84970 (KC753856)

Sturnira parvidens: LSUMZ 28341 (KC753857); MSB 53756 (KC753858), 53758 (KC753859), 53759 (KC753860), 53760 (KC753861), 82216 (KC753862), 82218 (KC753863); ROM 96276 (KC753864), 97412 (KC753865), 99284 (KC753866); TTU 44789 (KC753870), 61103 (KC753871), 62410 (KC753872), 62411 (KC753873), 84422 (KC753874), 84608 (KC753875), 104285 (KC753867), 104631 (KC753868), 105076 (KC753869)

Sturnira paulsoni: CMNH 63413 (KC753876); TTU 105466 (KC753882), 105654 (KC753883), 105679 (KC753884), 109255 (KC753880), 109256 (KC753881), 109257 (KC753878), 109258 (KC753879), 109259 (KC753877), 109260 (KC753885); USNM 580674 (KC753886)

Sturnira tildae: AMNH 268556 (KC753887); CMNH 77643 (KC753888); FMNH 174860 (KC753889), 174862 (KC753890), 174865 (KC753891), 174871 (KC753892); MPEG 20844 (KC753893); TTU 44094 (KC753895), 106027 (KC753894); USNM 560796 (KC753896), 574556 (KC753897)

Carollia manu: FMNH 172078 (KC753898)

Lionycteris spurrelli: MVZ 166632 (AF423096)

Rhinophylla pumilio: AMNH 267158 (AF187029)

Vampyriscus bidens: MPEG 20840 (FJ154181)

Geographic scope. For morphological analysis, we included 247 specimens belonging to the *S. oporaphilum* clade, including 218 of the new species (Appendix) from all the mountain systems of Venezuela to the north of the Orinoco River (Fig. 1). The physical characteristics and mammalian biogeography of these systems has been considered in detail in recent studies (Molinari 2007; Anderson & Gutiérrez 2009; Anderson *et al.* 2012; Quiroga-Carmona & Molinari 2012; Gutiérrez *et al.* 2015). A succinct description of these mountain systems, and the Venezuelan political divisions (within parentheses) from which we examined specimens, are: 1) Cordillera Oriental [de Colombia], on its Venezuelan side (Táchira, SW of the Táchira Depression; Apure); 2) Sierra de Perijá (or

Serranía de Perijá), a northwest continuation of the Cordillera Oriental shared in its northern half by Venezuela (Zulia) and Colombia; 3) Cordillera de Mérida, a northeast continuation of the Cordillera Oriental, separated from it by the Táchira Depression, lying entirely in Venezuela (Táchira, NE of the Táchira Depression; Mérida, Barinas, Trujillo, Portuguesa, Lara); 4) Sierra de San Luis (Falcón), a small mountain range part of a larger mountain system known as Sistema Coriano; 5) Sierra de Aroa, and Sierra de Bobare (Yaracuy), two small mountain ranges separated from the Cordillera de Mérida by the dry Lara Depression, and from the Cordillera de la Costa by the moist Yaracuy Depression; 6) Cordillera de la Costa (Carabobo, Aragua, Vargas, Guárico, Miranda, Distrito Capital), often considered to also comprise other coastal mountain ranges of Venezuela (Sistema Coriano, Sierra de Aroa, Turimiquire Massiff, mountains of the Araya and Paria Peninsulas), separated from the Turimiquire Massiff by the ample and dry Unare Depression; 7) Turimiquire Massiff and neighboring mountains in the Paria Peninsula (Anzoátegui, Sucre, Monagas).

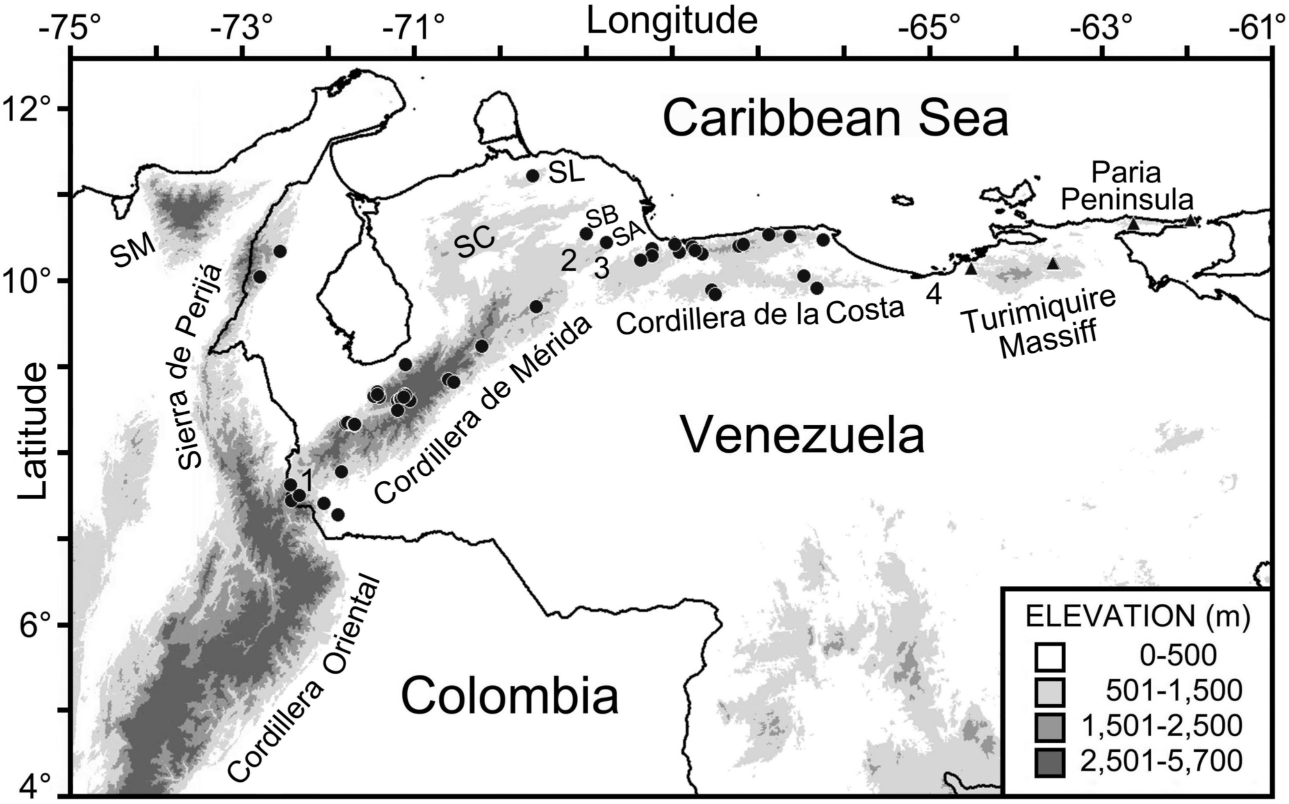

FIGURE 1. Map of Venezuela and neighboring Colombia showing the collection localities of specimens of *Sturnira adrianae*, new species. Solid circles correspond to *S. a. adrianae*. Solid triangles correspond to *S. a. caripana*. Abbreviations are: SA, Sierra de Aroa; SB, Sierra de Bobare; SC, Sistema Coriano; SL, Sierra de San Luis (part of SC); SM, Sierra Nevada de Santa Marta; 1, Táchira Depression; 2, Lara Depression; 3, Yaracuy Depression; 4, Unare Depression. For locality data, see Appendix.

Molecular analysis. We obtained Cyt-*b* sequences from DNA isolated and amplified from 10–100 mg muscle samples of seven museum specimens of the new species (Table 1). We digested muscle samples using the proteinase K-based method (Sambrook & Russell 2001). We subjected each digested sample to three successive chloroform extractions, after which the final aqueous phase was precipitated using two volumes of 99% ethanol. After visualizing the concentration and quality of DNA by agarose gel electrophoresis, we amplified the Cyt-*b* gene by PCR using primers specifically designed for this study: SatYR, 5´-ATGACCACCATTCG-3 and SatYF, 5´, GATGCTGTTTGGCC-3´. The experimental PCR conditions included an initial denaturation step at 94ºC for 2 min, followed by 35 cycles of denaturation at 92ºC for 1 min, annealing at 39ºC for 1 min, extension at 72ºC for 5 min: an additional extension step at 72ºC for 5 min was also included. DNA from all amplicons in single, clear bands was salt- and ethanol-precipitated, and sent for sequencing to Macrogen, Inc. (Seoul, Korea). Both bands per amplicon per sample were sequenced and the individual contigs obtained using the CAP application of BioEdit (Hall 1999). We uploaded to the GenBank the seven resulting Cyt-*b* sequences, each 792 bp long (Table 1).

We retrieved from the GenBank the Cyt-*b* sequences listed and used by Velazco & Patterson (2013), including those used as outgroups (Table 1). Then we aligned these sequences and our sequences using Clustal X (Larkin *et al*. 2007). Most of the sequences used by Velazco & Patterson (2013) were longer at both extremes than ours. We trimmed these sequences (1140 bp long) to the same length as our sequences (792 bp long) and included them in our final analysis. Some of the sequences used by Velazco and Patterson (2013) were shorter at one extreme than ours; therefore, we excluded them from this analysis. The excluded sequences are: *S. angeli* (AF435158, AF435159, AF435249, AF435251); *S. aratathomasi* (AF435252); *S. bidens* (AF435200, AF435201); *S. koopmanhilli* (AF435202, AF435203); *S. nana* (AF435253, AF435254); and *S. perla* (AF435204, AF435205). In addition, we excluded another sequence (*S. luisi*, KC753812) that did not cluster exclusively with conspecific sequences in a preliminary Maximum Likelihood analysis. In all, we included in our final analyses 125 sequences: seven for the new species, 114 for other species of *Sturnira*, and four for outgroup taxa.

For phylogenetic analyses, we used MEGA7 (Kumar *et al*. 2016). Based on the Bayesian (BIC = 13992.93) and the Akaike (AIC = 11568.97) information criteria, we selected a Hasegawa-Kishino-Yano (HKY+G+I) nucleotide substitution model (Hasegawa *et al*. 1985) for Maximum Likelihood (ML) analysis. A discrete Gamma distribution (+G, 5 categories, parameter = 1.21) was used to model evolutionary rate differences among sites. The rate variation model allowed for some sites to be evolutionarily invariable (+I, 57.39% of sites). The ML tree was bootstrapped using 1000 repetitions. For the calculation of genetic distances, expressed as uncorrected pairwise sequence divergences (%), we also used MEGA7.

Genetic identification of Ecuadorian specimens. By comparing Cyt-*b* sequences, both our own and those that we trust were assigned to correctly identified species by Velazco & Patterson (2013), we found Venezuelan "*S. ludovici*" to be more similar to Ecuadorian and Peruvian *S. oporaphilum* than to Ecuadorian *S. ludovici*. By comparing COI sequences, both our own (same specimens with Cyt-*b* sequences) and those referred to "*S. ludovici* A" and "*S. ludovici* B" by Jarrín-V. & Clare (2013), we concluded that the latter was—and that the former was not—likely to be *S. oporaphilum*. The examination of skulls and study skins indicated that "*S. ludovici* A" is *S. ludovici*, and that "*S. ludovici* B" is *S. oporaphilum*. Thereafter, we centered our attention on specimens of both species with COI sequences. As a result, the morphological identification to species level of all QCAZ specimens used for taxonomic comparisons (Appendix) in this study is backed by genetic data. These specimens and their accession numbers are: *S. oporaphilum*, QCAZ 1386 (JN659693), 2300 (JN659704), 3708 (JN659706), 4632 (JN659738), 4635 (JN659696), 4890 (JN659731); *S. ludovici*, 1644 (JN659694), 2103 (JN659720), 2553 (JN659750), 2701 (JN659712), 2742 (JN659716), 2757 (JN659717), 2769 (JN659722), 2776 (JN659725), 2783 (JN659768), 3273 (JN659711).

Morphometric characters. Discretely varying characters of descriptive and diagnostic value are considered in the taxonomy section. Continuously varying characters consist of 11 cranial and four wing measurements of adult specimens, obtained using digital calipers with a 0.01 mm resolution. We also present descriptive statistics for external measurements taken from specimen labels, namely total length, hind-foot length, and ear length (in mm), and body masses (in g) of males, and of non-pregnant females. Cranial measurements are those described by Velazco & Patterson (2014). In addition to forearm length, we obtained three wing measurements: third, fourth, and fifth metacarpal lengths, defined as the distance between the proximal and distal ends of each bone.

Morphometric analysis. We used SPSS for Windows, version 17, to carry out all statistical procedures. For one-way ANOVAs and *t*-tests, we used skull length as a surrogate of cranial size, and forearm length as a surrogate of wing size.

To merge samples from neighboring mountain systems based on morphometric similarity, we defined six preliminary geographic groups. The first for *S. oporaphilum* from (1) Ecuador, Perú, and Bolivia. The remaining five (Fig. 1) for its putatively sister species, *S. adrianae* new species (= Venezuelan *S.* "*ludovici*") from (2) the Cordillera Oriental (including the Sierra de Perijá), (3) the Cordillera de Mérida, (4) the Sierra de San Luis, (5) the Cordillera de la Costa (including the Sierra de Aroa, and the Sierra de Bobare), and (6) the Turimiquire Massiff and Paria mountains. We created four separate data sets of values assigned to these groups: male cranial lengths, male forearm lengths, female cranial lengths, female forearm lengths. We carried out a one-way ANOVA for each data set. Based on the results of post-hoc test (Tukey's HSD), we merged the Venezuelan groups lacking statistically significant differences among them in skull and forearm lengths. This procedure resulted in the recognition of three final geographic groups differing significantly in cranial and wing dimensions, namely *S. oporaphilum* from (1) Ecuador, Perú, and Bolivia, *S. adrianae adrianae* from (2–5) western and north-central Venezuela, and *S. a. caripana* from (6) northeastern Venezuela.

To establish whether sexual dimorphism in cranial or wing size is present in any of the three final geographic/taxonomic groups, we carried out six *t*-tests, each involving a different combination of the two measurements (skull length, forearm length) with the three groups. To avoid the increased probability of finding false positives (Type I errors) as a consequence of carrying out multiple tests, without increasing the probability of finding false negatives (Type II errors), we adjusted the *p*-values using a sequential correction method (Benjamini & Hochberg 1995).

We used Multiple Discriminant Analysis (MDA) to compare morphometrically *S. oporaphilum*, *S. a. adrianae*, and *S. a. caripana*. In this analysis, we considered simultaneously all wing and cranial measurements. Because our objective was to compare different taxa, not males and females, we did not divide the specimens according to sex. However, after the analysis was completed, for graphical representation, we separated males and females according to their MDA scores. In an attempt to automatically select the "best" subset of measurements to be included in the MDA, we tried the six stepwise variable selection methods available in SPSS. These methods identified six measurements (condyloincisive, dentary, and fifth metacarpal lengths; braincase, M2-M2, and postorbital breadths) as the "best" subset. However, including only this "best" subset in the MDA produced exactly the same graphical result as including all measurements. Therefore, we included all measurements in the final MDA. With two exceptions, both involving *S. a. caripana* ($n = 9$), we excluded from the MDA all specimens with any missing cranial or wing measurement. The exceptions were a specimen with broken zygomatic arches (MHNLS 2092), and a specimen lacking the mandible (EBRG 20597). To include both specimens in MDAs, we used linear regression analysis to estimate their missing measurements from the other cranial measurements of all nine specimens of the taxon.

For the display of interspecific and intersexual differences in skull length, forearm length, and MDA scores, we use box-and-whisker plots (Tukey 1977). This graphical method allows the direct and easy visualization of several major statistical attributes, namely central tendency, spread, symmetry, and potential outliers.

Results

Molecular analysis. Maximum Likelihood analysis of Cyt-*b* sequences revealed five strongly supported clades within the *S. oporaphilum* clade (Fig. 2), four of them corresponding to previously recognized species (*S. ludovici*, *S. oporaphilum*, *S. burtonlimi*, *S. hondurensis*), and another one corresponding to the new species (*S. adrianae*). Most importantly, the analysis negates the implicitly assumed reciprocal monophyletic relationship between *S. adrianae* (= Venezuelan *S.* "*ludovici*") and Ecuadorian *S. ludovici*, thus supporting the recognition of *S. adrianae* as a separate species. In spite of being represented by samples from distant localities from throughout their ample ranges (Fig. 2), three of the species, namely *S. oporaphilum* (specimens from Ecuador, northern Peru, and southern Peru), *S. hondurensis* (specimens from Central America and Central Mexico), and *S. adrianae* (specimens from four Venezuelan mountain systems) show little or no geographic substructure. Both specimens of *S. a. caripana* appear together in a well-supported clade, with respect to which the five specimens of *S. a. adrianae* form a paraphyletic assemblage. However, not only sample sizes are small, but intraspecific branch lengths are short. Genetic distances (Table 2) are consistent with the recognition of five species within the *S. oporaphilum* clade: conspecific specimens differ genetically less from each other than from specimens of the remaining species.

TABLE 2. Genetic *p*-distances (mean ± SD) within and among species of the *Sturnira oporaphilum* clade. Values represent pairwise sequence divergences (%) between 792 bp fragments of the Cyt-*b* gene. Sample sizes are: $n = 2$ (*S. ludovici*); $n = 3$ (*S. burtonlimi*); $n = 7$ (*S. adrianae*, *S. oporaphilum*, *S. hondurensis*).

	S. ludovici	*S. adrianae*	*S. oporaphilum*	*S. burtonlimi*	*S. hondurensis*
S. ludovici	0.38				
S. adrianae	4.32 ± 0.15	1.05 ± 0.46			
S. oporaphilum	4.93 ± 0.18	3.82 ± 0.28	1.32 ± 0.67		
S. burtonlimi	5.37 ± 0.21	3.93 ± 0.25	4.69 ± 0.19	0.00 ± 0.00	
S. hondurensis	5.74 ± 0.46	4.54 ± 0.33	5.69 ± 0.43	4.26 ± 0.29	1.67 ± 1.07

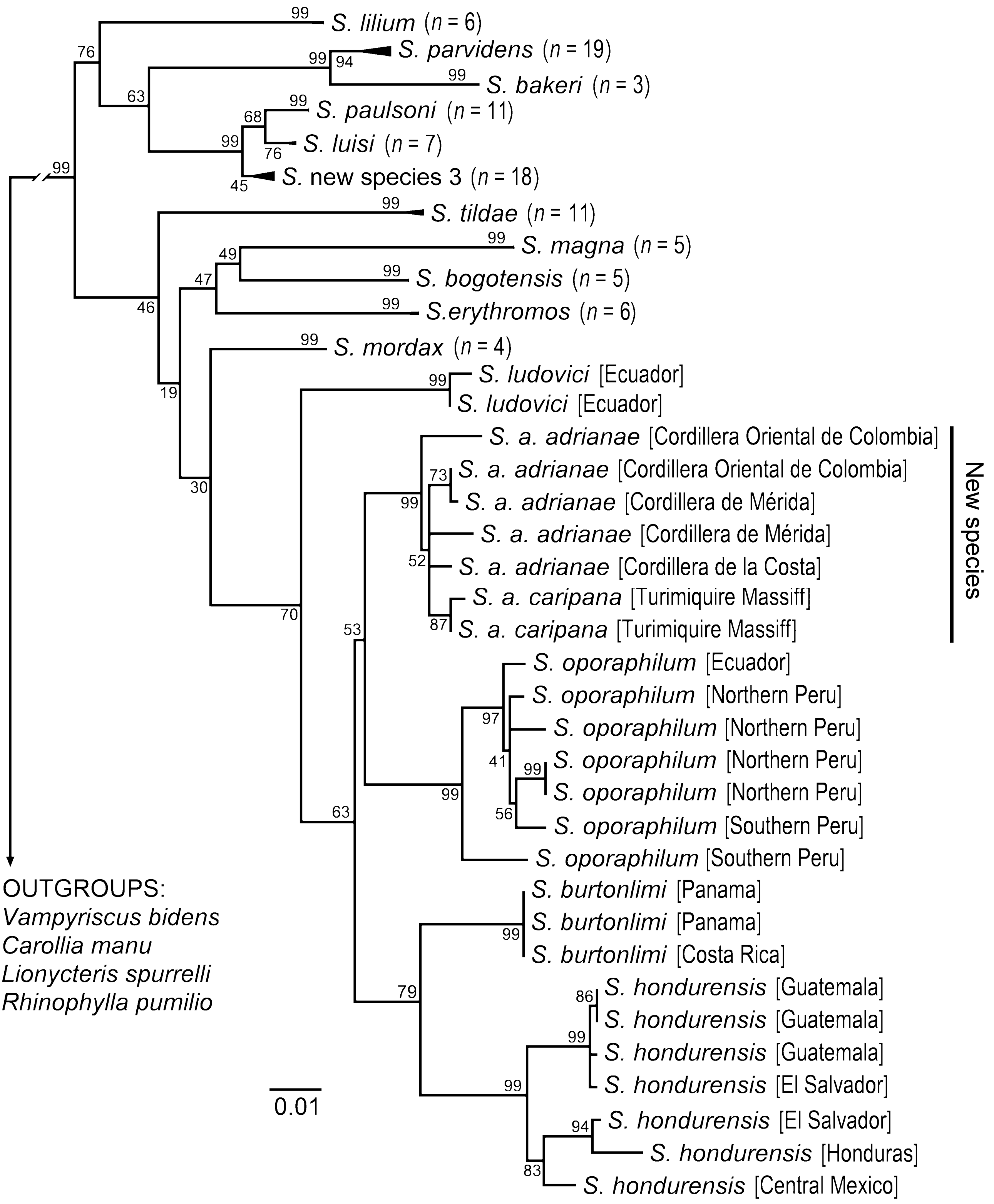

FIGURE 2. Maximum-likelihood (ML) tree based on Cyt-*b* sequence data used to assess the phylogenetic position of *Sturnira adrianae* in relation to other species of *Sturnira*. The tree shown is the one with the highest log likelihood (-5445.3367). Bootstrap support values (% of trees in which the associated taxa clustered together after 1000 repetitions) for nodes are indicated next to interior branches. The name '*S.* new species 3' is used following Velazco and Patterson (2013). Individual specimens are particularized only in branches of the *S. oporaphilum* clade. From top to bottom, GenBank accession numbers for these specimens are: KC753807, KC753806 (*S. ludovici*); KY366235, KY366234, KY366232, KY366233, KY366231, KY366230, KY366229 (*S. adrianae*); KC753856, KC753850, KC753854, KC753851, KC753855, KC753853, KC753852 (*S. oporaphilum*); KC753826, KC753827, KC753825 (*S. burtonlimi*); and KC753794, KC753793, KC753795, KC753796, KC753797, KC753799, KC753798 (*S. hondurensis*).

TABLE 3. Measurements (mm) and body masses (g) of *Sturnira oporaphilum*, *S. adrianae adrianae*, and *S. a. caripana*. Descriptive statistics are: mean (minimum–maximum) standard deviation [sample size].

	Sturnira oporaphilum[1] (Ecuador to NW Argentina)	*Sturnira adrianae adrianae* (W and N Venezuela)		*Sturnira adrianae caripana* (NE Venezuela)	
	Males/females	Males	Females	Males	Females
Skull length	23.1 (22.0–24.1) [21]	24.6 (23.2–26.1) 0.5 [92]	24.2 (23.0–25.1) 0.5 [101]	23.5 (23.1–23.9) 0.3 [7]	22.8 (22.8–22.8) 0.0 [2]
Condyloincisive length	21.4 (20.4–22.0) [18]	23.2 (21.8–24.5) 0.5 [91]	22.7 (21.2–23.5) 0.4 [100]	22.1 (21.8–22.3) 0.2 [7]	21.2 (21.1–21.3) 0.1 [2]
Condylocanine length	20.6 (19.6–21.4) [18]	22.0 (20.8–23.0) 0.4 [91]	21.6 (20.2–22.3) 2.5 [102]	20.9 (20.6–21.3) 0.2 [7]	20.2 (20.2–20.2) 0.0 [2]
Postorbital breadth	6.1 (5.8–6.5) [21]	6.4 (5.8–7.0) 0.2 [92]	6.2 (5.7–6.6) 0.2 [102]	6.0 (5.9–6.4) 0.2 [7]	5.8 (5.7–5.8) 0.0 [2]
Braincase breadth	10.5 (10.1–10.8) [21]	10.9 (10.3–11.5) 0.2 [92]	10.7 (10.2–11.4) 0.2 [102]	10.7 (10.4–11.2) 0.3 [7]	10.5 (10.5–10.5) 0.0 [2]
Mastoid breadth	12.2 (11.7–12.7) [21]	12.8 (12.0–13.7) 0.3 [92]	12.6 (11.8–14.4) 0.3 [102]	12.2 (12.0–12.5) 0.2 [7]	11.9 (11.8–12.0) 0.1 [2]
Zygomatic breadth	13.8 (12.8–14.7) [21]	14.6 (13.1–15.4) 0.4 [88]	14.3 (13.4–15.4) 0.4 [100]	13.6 (13.1–13.9) 0.3 [6]	13.4 (13.3–13.6) 0.2 [2]
Maxillary toothrow length	6.8 (6.4–7.2) [21]	7.1 (6.7–7.7) 0.2 [92]	7.0 (6.4–7.5) 0.2 [101]	6.8 (6.7–7.1) 0.1 [7]	6.6 (6.6–6.6) 0.0 [2]
M2-M2 breadth	8.1 (7.6–8.6) [21]	8.4 (7.5–9.1) 0.3 [92]	8.3 (7.6–9.0) 0.3 [102]	8.1 (7.8–8.3) 0.2 [7]	7.8 (7.7–7.9) 0.1 [2]
Dentary length	14.9 (14.1–15.5) [21]	16.3 (15.4–17.2) 0.3 [91]	15.9 (15.2–16.7) 0.3 [101]	15.4 (15.0–15.8) 0.3 [6]	14.8 (14.7–14.9) 0.1 [2]
Mandibular toothrow length	7.6 (7.1–8.5) [21]	8.0 (7.6–8.5) 0.2 [92]	7.9 (7.2–8.4) 0.2 [100]	7.6 (7.4–7.8) 0.1 [6]	7.3 (7.3–7.4) 0.1 [2]
Forearm length	45.7 (43.0–48.0) [20]	47.7 (45.0–52.1) 1.2 [90]	47.2 (43.9–50.0) 1.2 [98]	44.8 (44.3–45.6) 0.5 [7]	43.8 (43.5–44.2) 0.4 [2]
Third metacarpal length	42.6 (40.2–45.7) [11]	44.3 (41.4–47.9) 1.2 [90]	43.8 (39.3–48.6) 1.5 [99]	41.8 (40.5–42.5) 0.8 [7]	41.1 (40.0–42.2) 1.6 [2]
Fourth metacarpal length	42.6 (40.5–45.4) [11]	44.3 (41.5–48.2) 1.3 [90]	43.7 (39.2–46.2) 1.4 [99]	41.4 (40.2–42.7) 0.9 [7]	40.7 (40.1–41.3) 0.8 [2]
Fifth metacarpal length	44.3 (42.0–47.0) [11]	46.0 (42.4–49.8) 1.3 [90]	45.5 (40.9–48.6) 1.4 [99]	42.6 (41.1–44.0) 1.2 [7]	42.7 (41.6–43.7) 1.5 [2]
Total length	65.5 (57.0–83.0) [5]	74.6 (65.0–85.0) 5.5 [76]	72.6 (55.0–84.0) 4.8 [82]	70.3 (67.0–75.0) 2.4 [7]	68.5 (67.0–70.0) 2.1 [2]
Hind-foot length	10.5 (9.0–11.7) [9]	14.7 (11.0–17.0) 1.6 [76]	14.5 (11.0–17.0) 1.5 [77]	14.1 (13.0–15.0) 0.7 [7]	13.5 (12.0–15.0) 2.1 [2]
Ear length	15.3 (13.0–18.5) [9]	17.9 (12.0–21.0) 2.1 [77]	17.8 (14.0–21.0) 1.8 [82]	17.4 (16.0–18.0) 0.7 [7]	17.5 (17.0–18.0) 0.7 [2]
Body mass	21.6 (20.0–24.0) [3]	27.6 (19.0–35.0) 3.1 [67]	25.0 (20.0–33.4) 2.6 [60]	24.0 (22.5–26.3) 1.3 [6]	20.0 (20.0–20.0) [1]

[1] Morphometric information for *S. oporaphilum* is scarce. For the sake of representativeness, means, minima, and maxima for this species were compiled from all available sources: Barquez et al. (1999), Velazco and Patterson (2014), this study (*n* = 3, *n* = 7, and *n* = 11, respectively). The resulting grand sample includes 6 Ecuadorian, 7 Peruvian, 5 Bolivian, and 3 Argentinian specimens.

Morphometric analysis. In spite of the Táchira, Lara, and Yaracuy Depressions (Fig. 1) being potential barriers to gene flow, *S. a. adrianae* from different mountain systems are similar in skull and forearm length: the means of the two best samples ($n > 30$ for each sex), namely those of the Cordillera de Mérida and the Cordillera de la Costa, converged to equal or nearly equal values.

Based on the analysis of unpublished measurements, Pacheco & Patterson (1992) cautiously asserted 'it seems that *S. oporaphilum* tends to be a sexually dimorphic species'. However, we could not detect ($p > 0.88$) sexual dimorphism in our small sample (males, $n = 5$; females, $n = 6$) of the species (Appendix): mean skull length was 23.0 mm in males, and 23.1 mm in females; mean forearm length was 45.2 mm in males, and 45.3 mm in females. Should males be markedly larger than females in the species, it would likely be evident even in our small sample. Published measurements of *S. oporaphilum* (Barquez *et al.* 1999; Velazco & Patterson 2014) do not distinguish between males and females, thus do settle the question. Given the negligible size differences between males and females in our sample of *S. oporaphilum*, we did not subdivide the data for the species according to sex.

For *S. adrianae* (Table 3), the males-females comparisons yielded significant results. In the combined sample (*S. a. adrianae*) from western and northern Venezuela (Fig. 1), $p < 0.01$ for skull lengths, and $p < 0.03$ for forearm lengths. In the small sample (*S. a. caripana*) from northeastern Venezuela (Turimiquire Massiff, Paria mountains; Fig. 1), $p < 0.03$ for skull lengths, and $p < 0.08$ for forearm lengths. Therefore, for taxonomic comparisons, we assume that a clear sexual dimorphism in both cranial and wing size distinguishes *S. adrianae* from *S. oporaphilum*.

Based on measurements reported in two studies (McCarthy *et al.* 2006; Velazco & Patterson 2014), we calculated the pooled means of a sample of Ecuadorian *S. ludovici*. For skull lengths, the means were different (males, 24.2 mm, $n = 18$; females, 23.8 mm, $n = 15$). While analyzing Venezuelan samples, we found 0.4 mm differences in skull length to be significant. For forearm lengths, the means were similar (males, 46.5 mm, $n = 12$; females, 46.6 mm, $n = 11$). While analyzing Venezuelan samples, we found 0.1 mm differences in forearm length to be not significant. Therefore, for taxonomic comparisons, we assume that a clear sexual dimorphism in wing size distinguishes *S. adrianae* from *S. ludovici*.

Sturnira adrianae and *S. oporaphilum* overlap in skull length. In particular, the smaller *S. a. caripana* overlaps broadly with *S. oporaphilum* in this measurement (Fig. 3A). The four plots (Fig. 3) show both *S. a. adrianae* and *S. a. caripana* to be sexually dimorphic in cranial and wing size. The first plot (Fig. 3A) implies that *S. a. adrianae* will seldom overlap in skull length with *S. oporaphilum*, particularly if the comparison involves males of the former. Males and females of *S. a. adrianae* overlap broadly in skull length, but males of this subspecies will seldom overlap in this measurement with females of *S. a. caripana*. With regard to forearm lengths (Fig. 3B), the pattern is similar but less marked in the comparison between *S. a. adrianae* and *S. oporaphilum*, and similar but more marked in the comparison between *S. a. adrianae* and *S. a. caripana*.

MDA made yet more evident the morphometric differences among the three forms. Because it ranks taxa and sexes in the same order as the skull and forearm plots (Fig. 3A, B), no doubt the first axis plot (Fig. 3C) emphasizes size differences. It particularly separates well *S. oporaphilum* from *S. a. adrianae*, with no overlap between the males/females of the former and males of the latter. This is not true for the second axis plot (Fig. 3D): in spite of their similar skull and wing dimensions (Fig. 3A, B; Table 3), the two smaller-sized taxa (*S. oporaphilum*, *S. a. caripana*) are ranked as opposites (this is particularly evident in the comparison between males/females of the former and females of the latter), with the largest-sized taxon (*S. a. adrianae*) in-between. Therefore, the second axis of MDA (Fig. 3D) also emphasizes shape differences.

Taxonomy

Sturnira adrianae **new species**

Sturnira adrianae adrianae **new subspecies**

Adriana's Yellow-shouldered Bat
Murciélago de Charreteras de Adriana

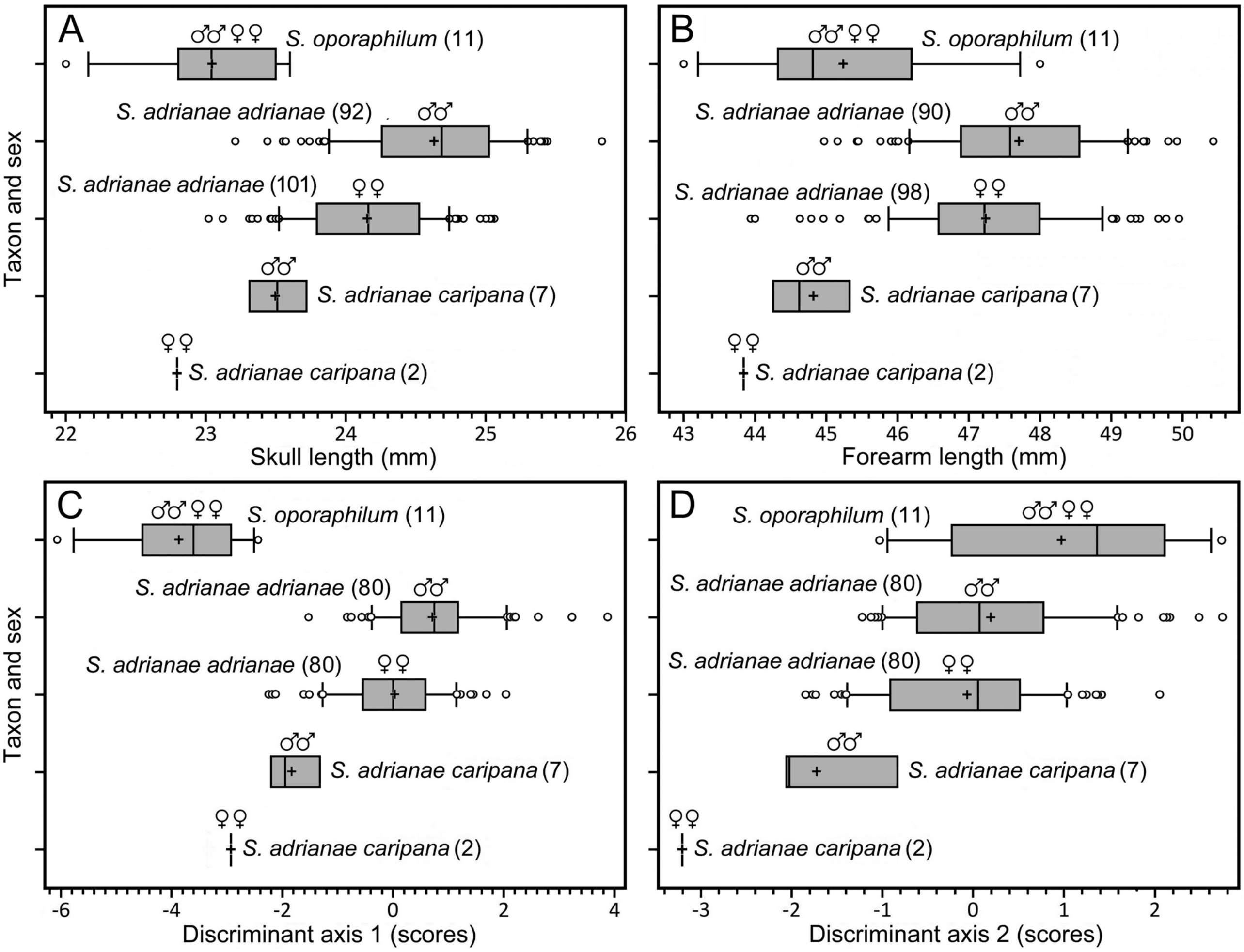

FIGURE 3. Box-and-whisker plots summarizing the cranial and wing dimensions of *Sturnira oporaphilum*, *S. adrianae adrianae*, and *S. a. caripana*. Plots A and B consider the single measurements most representative of cranial and wing dimensions. Plots C and D consider all measurements by displaying specimen scores in the two axes of a Multiple Discriminant Analysis (MDA). In this MDA, the first axis accounts for 82.3% and the second axis for 17.7% of the variance. Crosses and vertical lines within gray boxes represent, respectively, means and medians. Gray box widths span the interval between the 25th and 75th percentiles, containing the middle 50% of the data points. Horizontal lines, or "whiskers", extend this interval to the 10th and 90th percentiles, containing 80% of the data points. At least nine data points are required to compute the 10th and 90th percentiles, hence no whiskers are plotted for *S. a. caripana*. Open circles represent potential outliers. Sample sizes indicated after taxon names.

Holotype (Fig. 4)**.** An adult male (CVULA 8570), consisting of cranium, mandibles, partial postcranial skeleton, and study skin.

Type locality. Venezuela, Estado Barinas, Carretera Santo Domingo–Barinitas, 1 km frontera Mérida–Barinas: latitude, 8.865°; longitude, -70.593°; elevation, 1560 m.

Paratypes. We designate as paratypes one female (CVULA 8770) from the type locality, and one male (CVULA 8586) and one female (CVULA 8585) from Venezuela, Estado Mérida, Sector Cucuchica, 5.8 km ENE Tovar, 8.337°, -71.701°, 930 m. Prepared as the holotype. For all the specimens referred to the species, see Appendix.

Measurements of the type material. The linear measurements (mm) and body masses (g) of the types, males first (CVULA 8570, 8586, 8585, 8770), are: skull length, 24.7, 24.7, 23.7, 23.5; condyloincisive length, 23.1, 23.3, 22.3, 22.4; condylocanine length, 21.8, 22.1, 21.0, 21.4; postorbital breadth, 6.6, 6.5, 6.5, 6.5; braincase breadth, 11.1, 11.2, 10.8, 11.0; mastoid breadth, 12.9, 13.3, 12.8, 12.5; zygomatic breadth, 15.1, 14.8, 14.4, 14.3; maxillary toothrow length, 7.3, 7.4, 7.0, 6.9; M2-M2 breadth, 9.1, 8.8, 8.6, 8.2; dentary length, 16.7, 16.4, 15.4, 15.5; mandibular toothrow length, 8.2, 8.1, 7.9, 7.8; forearm length, 47.1, 47.0, 48.1, 44.8; third metacarpal length, 43.9, 43.2, 42.9, 40.6; fourth metacarpal length, 44.4, 43.8, 42.9, 41.0; fifth metacarpal length, 45.2, 45.2, 44.8, 40.9;

total length, 76.0, 77.0, 73.0, 71.0; hind-foot length, 13.0, 16.0, 14.5, 12.0; ear length, 18.0, 18.0, 18.0, 18.0; body mass, 25.0, 29.0, 23.5, 20.5.

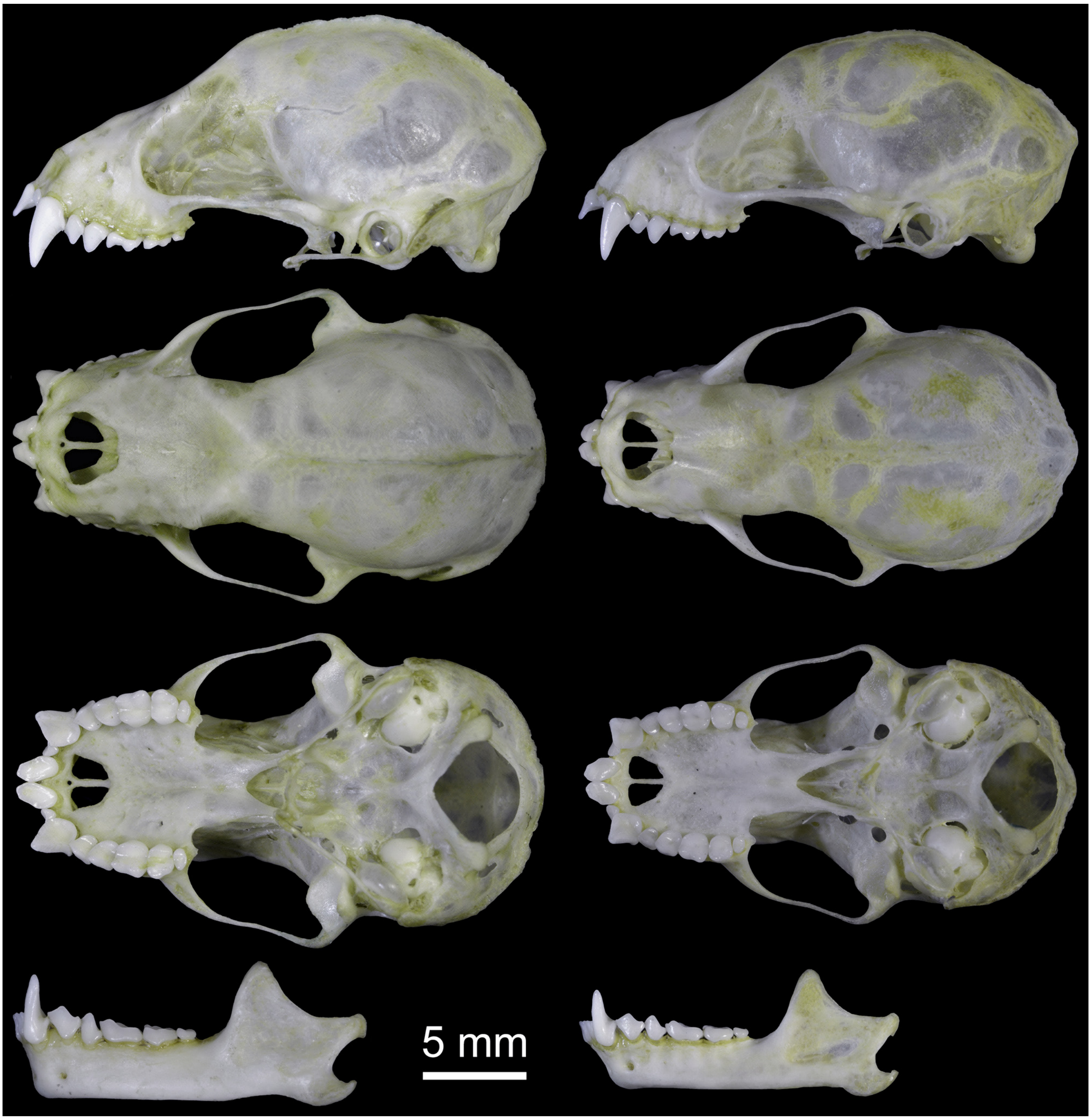

FIGURE 4. Lateral, dorsal, and ventral views of the crania, and lateral views of the mandibles of the holotypes. Left: *Sturnira adrianae adrianae* (male, CVULA 8570). Right: *S. a. caripana* (male, CVULA 8593).

Diagnosis. Epaulettes (yellow shoulders) present. Lower molars with continuous lingual cusps. All four lower incisors well developed, bilobed. Upper middle incisor long, bilobed, pointed, strikingly protrudent, tip laterally diverging. Lower canine long, narrow. Upper premolars broad and long in labial view. Molars with no gaps between them. Zygomatic arch complete, not bowed outwards. Occiput low. Preorbital frontal ridges well developed. Foramen ovale touching the caudal pterygoid process.

Description. Cranial and wing size medium-large for the genus, largest for the *S. oporaphilum* clade (Table 3). Males larger than females in cranial and wing size (Fig. 3). Pelage pale grayish-brown in overall coloration: exceptions involve tawny or ochraceous browns. Fur woolly, 5–8 mm long between shoulders, 4–5 mm long on chest. Forearm, femur, and tibia furred with short and thick hairs dorsally, with short and thin hairs ventrally. Foot sparsely furred dorsally with short and thin hairs. Interfemoral membrane sparsely furred with 4–6 mm long hairs. Wing membranes grayish- to blackish-brown. Dorsal hairs with a blackish-brown basal band one-fourth to one-third their length, a pale-grayish medial band about half their length, and a grayish-brown terminal band one-sixth to one-fourth their length. Ventral hairs with a blackish-brown basal band about five-eighths their length, and a grayish-brown to pale grayish-brown terminal band about three-eighths their length. Epaulettes present. Third and fourth metacarpals of similar length. Upper middle incisor long, strikingly protrudent frontally, with two similarly broad lobes, abruptly tapering in lateral view, tip narrow and markedly diverging outwards in frontal view. Lower incisors numbering four, all well developed and bilobed. Upper canine long and robust in both sexes, moderately protrudent frontally. In lateral view, lower canine long and narrow: the posterior longitudinal ridge hidden by the shaft except for a small portion near the base of the tooth. Lower canines laterally divergent, with shafts slanted outwards. Upper toothrow relatively straight, gently arched inwards posteriorly. Upper premolars—especially the second—broad and long in labial view: labial edges highly developed. Lower molars with continuous lingual cusps: a vertical notch separating the metaconid and entoconid is absent. Adjacent upper and lower molars not separated by gaps, thus in contact with each other. Braincase broad, and markedly domed. Rostrum elongated, broad anteriorly thus providing space to accommodate broad-at-base incisors, canines, and premolars. Sagittal crest, and preorbital frontal ridges converging to it, well developed. Zygomatic arch complete, moderately open, relatively straight, converging obliquely to the rostrum. Occiput low with respect to zygomatic arches, much closer to the zygomatic plane than to its parallel epiparietal plane: the former is defined as the plane along the right and left zygomatic arches; the latter is defined as the plane, parallel to the zygomatic plane, at the level of the highest point of the saggital crest. Occiput usually rounded in dorsal and ventral views. Sphenorbital fissure elliptical. Foramen ovale subcircular, located at the base of the vertical wall (partly under this wall) of the caudal pterygoid process. Clinoid processes moderately developed, variable in size and shape.

Comparisons (Table 3; Figs. 4–6**)**. We compare species in phylogenetic order (Velazco & Patterson 2013), from more to less related to *S. adrianae*. Within clades, we compare first with species more likely to be confused with *S. adrianae*. The characters of *S. a. adrianae* are followed by the characters (enclosed in parentheses) of the species with which it is being compared. For the *S. oporaphilum* clade, we use discretely varying characters defined and scored by Velazco & Patterson (2014).

Compared to *S. oporaphilum*: 1) largest cranial and wing size of members of the *S. oporaphilum* clade (medium); 2) males larger than females in cranial and wing dimensions (similar-sized); 3) pelage pale grayish-brown (dark grayish brown, or dark brown); 4) epaulettes present (inconspicuous or absent); 5) upper canine long and robust, moderately protrudent frontally (shorter and weaker, not protrudent); 6) upper middle incisor long, strikingly protrudent, abruptly tapering in lateral view, tip narrow and markedly diverging outwards in frontal view (shorter, less protrudent, gently tapering, tip broad and moderately diverging outwards); 7) upper premolars broad and long in labial view: labial edges highly developed (narrower and shorter: labial edges moderately developed); 8) rostrum elongated (shorter); 9) in lateral view, lower canine long and needle-like: posterior longitudinal ridge hidden by the shaft (short: posterior longitudinal ridge visible in the background); 10) occiput low with respect to zygomatic arches (high: equidistant to the zygomatic and epiparietal planes); 11) sphenorbital fissure elliptical (subcircular); 11) clinoid processes moderately developed (weakly developed).

Compared to *S. ludovici*: 1) males larger than females in wing dimensions (similar); 2) dorsal pelage pale grayish-brown (brown); 3) ventral pelage grayish-brown or pale grayish-brown (dark brown); 4) upper middle incisor long, strikingly protrudent, abruptly tapering in lateral view, tip narrow and markedly diverging outwards in frontal view (shorter, less protrudent, gently tapering, tip broad and moderately diverging outwards); 5) upper canine protrudent frontally (not protrudent); 6) braincase broad, and markedly domed (narrower, moderately domed); 7) sphenorbital fissure elliptical (subcircular).

Compared to *S. burtonlimi*: 1) largest cranial and wing size of members of the *S. oporaphilum* clade (smallest); 2) ventral pelage grayish-brown or pale grayish-brown (dark gray); 3) third and fourth metacarpals of similar length (fourth shorter); 4) upper middle incisor bilobed, tip markedly diverging (unilobed, tip moderately diverging); 5) sphenorbital fissure elliptical (subcircular).

Compared to *S. hondurensis*: 1) largest cranial and wing size of members of the *S. oporaphilum* clade (small); 2) ventral fur with two color bands (one); 3) third and fourth metacarpals of similar length (fourth shorter); 4) upper middle incisor long, strikingly protrudent, bilobed, abruptly tapering in lateral view (shorter, not protrudent, unilobed, gently tapering); 5) upper canine long (shorter); 6) rostrum and palate broad (narrower); 7) in lateral view, lower canine long and needle-like: posterior longitudinal ridge hidden by the shaft (shorter: posterior longitudinal ridge visible in the background); 8) braincase broad (narrower); 9) sphenorbital fissure elliptical (subcircular); 10) clinoid processes present (absent).

Compared to *S. mordax* (Goodwin), and *S. koopmanhilli* McCarthy *et al.*: 1) upper middle incisor bilobed, both lobes nearly equal in breadth, pointed, with a markedly diverging tip (weakly bilobed, inner lobe broader than outer, square- or round-tipped, moderately diverging tip); 2) upper premolars broad and long (narrower and shorter in *S. koopmanhilli*); 3) adjacent upper and lower molars not separated by gaps (separated in *S. koopmanhilli*); 4) rostrum and palate broad (narrower); 5) braincase broad and domed (narrower, moderately domed).

Compared to *S. erythromos* (Tschudi), *S. bogotensis*, and *S. sorianoi* Sánchez-Hernández *et al.*: 1) cranial and wing size medium-large for the genus (medium to small. Mean body mass of Venezuelan specimens: *S. erythromos*, 15.4 g; *S. bogotensis*, 18.8 g); 2) upper middle incisor long, strikingly protrudent, bilobed, tip narrow in frontal view (short, not protrudent, unilobed or indistinctly bilobed, tip broad); 3) upper toothrow relatively straight (upper dentition horseshoe-shaped in occlusal view); 4) rostrum and palate elongated (much shorter); 5) zygomatic arch moderately open (wide open). The last four differences are also evident when comparing the often confused pair *S. oporaphilum* and *S. bogotensis*.

Compared to *S. tildae* de la Torre: 1) upper middle incisor long, strikingly protrudent, bilobed, tip narrow and markedly diverging outwards in frontal view (short, not protrudent, weakly bilobed, tip broad and barely diverging); 2) lower incisors bilobed (faintly trilobed); 3) lower molars with continuous lingual cusps (metaconid and entoconid separated by a moderately developed vertical notch).

Compared to *S. magna* de la Torre: 1) cranial and wing size medium-large for the genus (large: mean body mass, 43.1 g; Tamsitt & Häuser 1985); 2) upper middle incisor narrow-tipped (broad-tipped).

Compared to *S. perla* Jarrín-V. & Kunz: 1) cranial and wing size medium-large for the genus (medium); 2) zygomatic arch moderately open, relatively straight, converging obliquely to the rostrum (wide open, markedly bowed outwards, not converging to the rostrum).

Compared to *S. lilium*, *S. parvidens* Goldman, *S. angeli* de la Torre, *S. paulsoni* de la Torre & Schwartz, *S. luisi* Davis, *S. mistratensis* Contreras Vega & Cadena, *S. bakeri* Velazco & Patterson, and *S.* new species 3 (Velazco & Patterson 2013): 1) cranial and wing size medium-large for the genus (medium); 2) lower incisors bilobed (trilobed); 3) lower molars with continuous lingual cusps (metaconid and entoconid separated by a deep vertical notch).

Compared to *S. aratathomasi* Peterson & Tamsitt: 1) cranial and wing size medium-large for the genus (largest: mean body mass, 50.4 g; Soriano & Molinari 1987); 2) lower molars with continuous lingual cusps (metaconid and entoconid separated by a deep vertical notch).

Compared to *S. nana* Gardner & O'Neill, and *S. bidens* (Thomas): 1) cranial and wing size medium-large for the genus (medium to small; mean body mass of *S. bidens*, 17.6 g, Molinari & Soriano 1987; *S. nana* much smaller); 2) epaulettes present (absent); 3) All four lower incisors well developed (outer lower incisors absent or vestigial); 4) adjacent upper and lower molars not separated by gaps (separated); 5) zygomatic arch complete (often incomplete).

Distribution (Fig. 1)**.** Known from all the Andean and coastal mountain systems of Venezuela, except those east of the Unare Depression. Presumably, also distributed throughout the Cordillera Oriental in Colombia: 1) our samples from the Venezuelan side of the Cordillera Oriental are from localities near or almost exactly on the border of both nations; 2) populations from the Venezuelan slope of the Sierra de Perijá and Cordillera Oriental are necessarily connected by populations occurring in mountains lying entirely in Colombian territory; 3) *S.* "*ludovici*" has been reported from the Colombian slope of the Sierra de Perijá (Muñoz-Saba 2009), and eastern foothills of the Sierra Nevada de Santa Marta (Hershkovitz 1949).

Etymology. The epithet *adrianae*, a feminine noun in the genitive case, is dedicated to the memory of the Colombian-Venezuelan bat biologist, Adriana Ruiz, 1971–2012. Adriana was a charismatic, imaginative, and dedicated colleague. She published 14 papers and book chapters. Owing to her untimely departure, much of her most valuable research was left unpublished. Adriana had a particularly keen interest in species of *Sturnira*. We are privileged to name after her a member of the genus wandering in the environments in which she so joyfully conducted much of her field work.

FIGURE 5. Lateral, dorsal, and ventral views of the crania, and lateral views of the mandibles of the two South American relatives of *Sturnira adrianae*. Left: *S. ludovici* (male, AMNH 67328, holotype). Right: *S. oporaphilum* (female, AMNH 246551).

Sturnira adrianae caripana new subspecies

Caripe Yellow-shouldered Bat
Murciélago de Charreteras de Caripe

Holotype (Fig. 4)**.** An adult male (CVULA 8593), consisting of cranium, mandibles, partial postcranial skeleton, and study skin.

Type locality. Venezuela, Estado Monagas, 1.5 ESE Sabana de Piedra: latitude, 10.213°; longitude, -63.564°; elevation, 1350 m.

Paratypes. We designate as paratypes two males (CVULA 8590, 8771) from the type locality, and one male (EBRG 14454) from Venezuela, Monagas, San Agustín, 5 km N Caripe, 10.203°, -63.546°, 1180 m. CVULA 8590 and 8771 prepared as the holotype. EBRG 14454 prepared as a study skin with skull. For all the specimens referred to the species, see Appendix.

Measurements of the type material. The linear measurements (mm) and body masses (g) of the types (CVULA 8593, 8590, 8771; EBRG 14454) are: skull length, 23.5, 23.4, 23.3, 23.7; condyloincisive length, 22.1, 22.1, 22.3, 22.2; condylocanine length, 20.9, 20.8, 20.8, 21.0; postorbital breadth, 5.9, 5.9, 5.9, 6.2; braincase breadth, 10.8, 10.9, 10.4, 10.4; mastoid breadth, 12.0, 12.2, 12.1, 12.1; zygomatic breadth, 13.6, 13.8, 13.8, 13.1; maxillary toothrow length, 6.7, 6.8, 6.9, 6.8; M2-M2 breadth, 7.8, 8.0, 8.2, 8.2; dentary length, 15.0, 15.1, 15.4, 15.4; mandibular toothrow length, 7.4, 7.7, 7.7, 7.7; forearm length, 44.3, 44.6, 45.1, 44.6; third metacarpal length, 41.4, 41.3, 42.1, 42.5; fourth metacarpal length, 41.3, 40.4, 41.9, 41.2; fifth metacarpal length, 41.6, 42.0, 43.9, 41.8; total length, 71.0, 69.0, 75.0, 67.0; hind-foot length, 14.0, 15.0, 15.0, 14.0; ear length, 17.5, 16.0, 18.0, 18.0; body mass, 22.5, 24.0, 23.0, 26.3.

Diagnosis. Identical to that of *S. a. adrianae*, except for: 1) upper premolars narrower and shorter in labial view; 2) preorbital frontal ridges little developed; 3) foramen ovale not touching the caudal pterygoid process.

Description. The description of *S. a. adrianae* applies to *S. a. caripana*, except for: 1) cranial and wing size medium for both *Sturnira* and the *S. oporaphilum* clade; 2) interfemoral membrane sparsely furred with 2–4 mm long hairs; 3) in dorsal view, skull more elongated: braincase and rostrum narrower, occiput more prominent; 4) sagittal crest and preorbital frontal ridges less developed; 5) palate proportionally narrower; 6) upper premolars narrower and shorter in labial view: labial edge less developed; 7) molariform teeth proportionally smaller; 8) foramen ovale not touching the vertical wall of the caudal pterygoid process, thus entirely located in the osseous plane internal to the mandibular fossa, and occlusally not covered by this process.

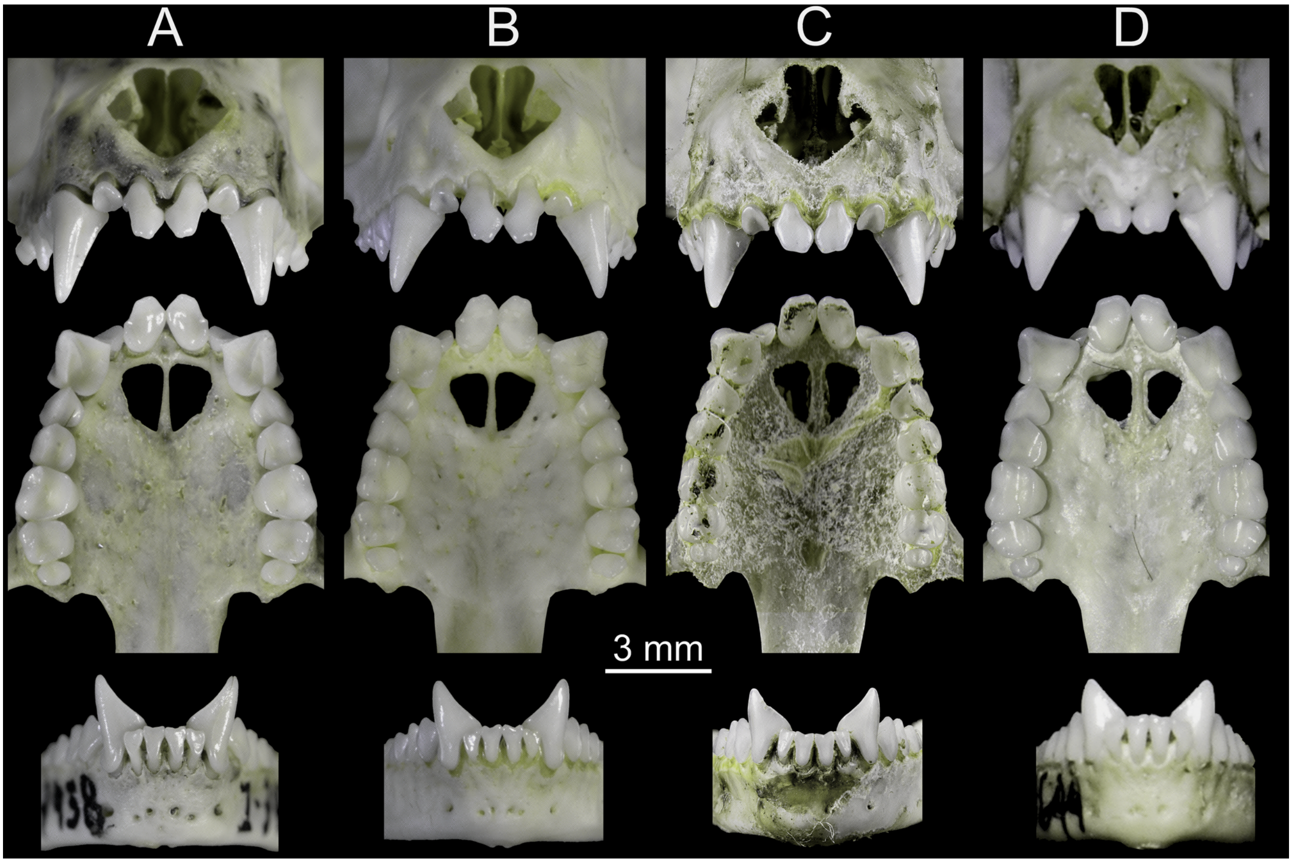

FIGURE 6. From top to bottom, frontal views of the upper incisors and canines, occlusal view of the upper dentition, and frontal view of the lower incisors and canines of: A) *Sturnira adrianae adrianae* (male, CVULA 7938); B) *S. a. caripana* (male, CVULA 8590); C) *S. oporaphilum* (male, QCAZ 2300); and D) *S. ludovici* (male, QCAZ 1644).

Comparisons (Table 3; Figs. 4–6)**.** *S. a. caripana* differs from other species of *Sturnira* in the same manner as *S. a. adrianae*, except for: 1) it is more similar to *S. oporaphilum*, and to *S. bogotensis*, in cranial and wing size; 2) it is more similar to *S. oporaphilum*, and to *S. koopmanhilli*, in the poorer development of the labial edges of upper premolars; 3) it differs more (skull more elongated; braincase, rostrum, and palate narrower) from *S. oporaphilum*, and less from *S. ludovici*, *S. hondurensis*, *S. mordax*, and *S. koopmanhilli*, in cranial shape.

Distribution (Fig. 1). Known from four localities in the Turimiquire Massiff, and from two localities in the neighboring Paria Peninsula (Appendix). Presumably, endemic to the mountain ranges of northeastern Venezuela, east of the Unare Depression.

Etymology. The epithet *caripana* [Carip(e) + -ana], a feminine adjectival toponym, is derived from Caripe, a town near the type locality made known to science in the book "Travels to the Equinoctial Regions of America, During the Years 1799–1804", of the famous German explorer and naturalist Alexander von Humboldt.

Discussion

Taxonomy. In contrast with the results of Velazco and Patterson (2013), our ML tree (Fig. 2) does not place *S. hondurensis* in the most external node of the *S. oporaphilum* clade, and does not show a node joining *S. oporaphilum* and *S. ludovici*. These differences are not strongly supported by our bootstrap values. Moreover, the dataset of Velazco and Patterson (2013) is much larger than ours: 1140 bp, as opposed to 792 bp for Cyt-*b* sequences; three mitochondrial (Cyt-*b*, ND2, D-loop) and two nuclear (RAG1, RAG2) markers, as opposed to a single mitochondrial (Cyt-*b*) marker. Therefore, our ML tree (Fig. 2) is not to be viewed as a competitive phylogeny of the genus *Sturnira*. Instead, it is to be viewed as evidence supporting the notion that *S. adrianae* is a valid species.

The combined genetic, morphological, and morphometric differences of *S. adrianae* in comparison with other species of the *S. oporaphilum* clade, particularly *S. oporaphilum* and *S. ludovici*, are equivalent to differences found between other closely related species pairs of *Sturnira*, such as *S. erythromos* and *S. bogotensis*, or *S. mordax* and *S. koopmanhilli*. In absence of genetic data (we acknowledge that mitochondrial DNA is not necessarily useful to prove conspecificity; *e.g*., Good *et al.* 2008), by applying the diagnosability version of the phylogenetic species concept, we might have recognized both *S. a. adrianae* and *S. a. caripana* as full species.

The failure up to now to recognize *S. adrianae* as different from *S. ludovici* is understandable: both species are closely related, and similar in size and skull characters. Only Pacheco & Patterson (1992) came close to recognizing the distinctness of *S. adrianae* by noting that 'Ecuadorian (including types) and Colombian *ludovici* did not differ much from the Peruvian *oporaphilum*, at least as compared to the samples from Venezuela'. These authors concluded that the resolution of the problem needed to 'await a more integral revision that includes the taxa *hondurensis* Goodwin, 1940 and *occidentalis* Jones and Phillips, 1974'. On the other hand, the long-standing confusion of *S. oporaphilum* with *S. bogotensis* is difficult to comprehend, given the sharp differences between them. No doubt this confusion originates in the fact that both species are close in body size, and possess overlapping geographic and altitudinal distributions.

Investigating the identity and affinities of bats referred to *S. ludovici* from the Cordilleras Central and Occidental de Colombia is crucial to understand the taxonomy and biogeography of the *S. oporaphilum* clade. *S. oporaphilum, S. ludovici*, and even *S. adrianae* may occur there. The ancestral populations that gave rise to Central American *S. hondurensis* and *S. burtonlimi* necessarily came from this region.

The type localities of *S. oporaphilum* and *S. erythromos* are customarily given as "Peru" (Simmons 2005). However, in his description of these species, Tschudi (1844) was environmentally and latitudinally explicit: 'Die beiden neuen Arten Ph. oporaphilum und erythromos kommen in der mittlem Waldregion zwischen 12 und 14° S' [The two new species Ph. oporaphilum and erythromos occur in the mid-slope forest region between 12 and 14° S]. Given its ample distribution, *S. oporaphilum* needs a morphometric and phylogeographic assessment. If differentiation exists, specimens from southern Peru and Bolivia (*e.g*., AMNH 246551; Fig. 5) represent the typical form.

Natural history. We georeferenced 348 specimens (Pacheco & Patterson 1992; Velazco & Patterson 2013, 2014; Appendix) of *S. oporaphilum*, Ecuadorian *S. ludovici*, and *S. adrianae*. For *S. oporaphilum* (n = 103), elevations have a mean of 1437 m and a range of 480–2750 m, with 66% of specimens from 1000–2000 m. For *S. ludovici* (n = 27), elevations have a mean of 1416 m and a range of 80–2000 m, with 81% of specimens from 1000–2000 m. For *S. adrianae* (n = 218), elevations have a mean of 1413 m and a range of 60–2400 m, with 62% of specimens from 1000–2000 m. Therefore, as earlier concluded by Tschudi (1844), South American members of the *S. oporaphilum* clade are bats of mid-elevation forests. In the case of *S. adrianae*, these include, in order of importance, evergreen, deciduous, and cloud forests (Handley 1976).

We found *S. adrianae* to be sexually dimorphic in size to a greater degree than *S. oporaphilum* and *S. ludovici*. It has been suggested that males tend to be larger than females in bat species under stronger sexual selection, or in which investing in harem defense is needed to maintain a polygynous mating system (Dechmann *et al.* 2005; Campbell 2008).

As most frugivorous phyllostomid bats, *S. a. adrianae* (referred to as *S.* "*ludovici*") possesses (Molinari & Soriano 2014) a reproductive pattern termed bimodal polyestry, consisting in the production of one offspring per female twice during the breeding season.

Our samples from cloud forests of the Cordillera de Mérida indicate that, as in other *Sturnira*, including *S. oporaphilum* (Sánchez *et al.* 2012; Parolin *et al.* 2016), fruits of the genera *Solanum* and *Piper* make the bulk of the diet of *S. a. adrianae*. Species of *Sturnira*, including *S. adrianae*, lack the striking pelage markings (pale facial and dorsal stripes) of most frugivorous phyllostomids. Presence or absence of such markings in these bats has been related to divergent roosting and foraging strategies (Molinari 1993; Soriano 2000): unlike foliage-roosting bats, cavity-roosting bats are not diurnally exposed to visually-oriented predators, thus would not benefit from pelage markings making them cryptic; their continued use of the same cavities as roosts is possible because they depend on dense and predictable food sources (e.g., *Solanum* and *Piper* fruits) found within cost-effective flight distances. Little is known about the roosting habits of bats of the genus *Sturnira*. Recent research shows that they typically roost in tree cavities situated several meters above ground (Fenton *et al.* 2000; Evelyn & Stiles 2003; Ortiz-Ramírez *et al.* 2006; Loayza & Loiselle 2008; Cortés-Delgado & Sosa 2014).

Sturnira a. adrianae is relatively common and is distributed in at least six large to small mountain systems (Fig. 1). On the other hand, *S. a. caripana* is restricted to two small mountain systems undergoing severe deforestation processes, even within national parks (Manzanilla *et al.* 2005; personal observation). In terms of technical conservation parameters (IUCN 2001), *S. a. adrianae* can be categorized as Least Concern (LC), and *S. a. caripana* as Vulnerable (VU). In the case of the latter, by application of criteria B1a,b(i–v), which imply an extent of occurrence less than 20000 km^2, a declining extent and quality of habitat, and a fragmentation and reduction of subpopulations (IUCN 2001).

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APPENDIX: SPECIMENS EXAMINED

Specimens of species belonging to the *Sturnira oporaphilum* clade used in the present study. Unless otherwise indicated that only images were used, specimens were examined physically and in most cases measured. Specimens are listed according to taxon, country, secondary political division, locality, coordinates (latitude, longitude), elevation, sex, catalog number, and observations (if needed). Holotypes are marked with one asterisk. Paratypes are marked with two asterisks. Males = m, females = f.

S. adrianae adrianae (*n* = 209).—**VENEZUELA: Apure**, 3 km NE El Nula, 7.28°, -71.88°, 220 m (m, EBRG 14493, 14494). **Aragua**, Aponte, 5.5 km S Ocumare de la Costa, 10.40°, -67.77°, 60 m (m, EBRG 1779); Cerro Geremba, 7.5 km E Colonia Tovar, 10.41°, -67.22°, 2290 m (f, CVULA 8550); Estación Biológica Rancho Grande, Parque Nacional Henri Pittier, 14 km NW Maracay, 10.35°, -67.69°, 1140 m (m, CVULA 3530, 3532; EBRG 57, 250, 1777, 1978, 2676, 4294, 14431, 28487, 28497, 28501, 28504; f, EBRG 97, 102–114, 117, 119, 1778, 2135, 2933, 28486, 28498, 28499, 28500, 28503, 28505); Estación Experimental de Fauna de El Limón, 10.32°, -67.65°, 535 m (m, EBRG 10908, 23462); Sector La Guamita, carretera Maracay–Ocumare de la Costa, Parque Nacional Henri Pittier, 10.36°, -67.73°, 650 m (m, EBRG 8076). **Barinas**, Carretera Santo Domingo–Barinitas, 1 km frontera Mérida–Barinas, 8.87°, -70.59°, 1560 m (m, CVULA 8570*; f, CVULA 8770**); Cerro Alto, 2 km NW La Soledad, 8.82°, -70.54°, 1460 m (m, CVULA 5912, 5958, 6122; f, CVULA 5952, 5961, 6115, 6129). **Carabobo**, Campamento La Justa, Río Morón, 8.5 km NE Canoabo, 10.38°, -68.23°, 350 m (m, EBRG 17111); Campamento Palmichal, 6 km E Canoabo, 10.30°, -68.23°, 780 m (m, EBRG 17133, 27734; f, EBRG 17119, 17128, 17184, 17195, 28502); Cerro La Copa, 4 km NW Montalbán, 10.25°, -68.37°, 1537 m (m, EBRG 14455, 14456, 14458, 14459; f, EBRG 14457); Fila La Josefina, 5 km NW Tronconero, 10.33°, -67.92°, 1350 m (f, EBRG 10166, 10167); Fundo Santo Domingo, Santa Rosa del Sur, Municipio Carlos Arvelo, 9.90°, -67.53°, 900 m (f, EBRG 24225); Hacienda Saint Jean, near Borburata, 10.43°, -67.97°, 120 m (m, EBRG 8071). **Distrito Capital**, Hotel Humboldt, Pico Avila, 12 km N Caracas, 10.54°, -66.88°, 2120 m (m, EBRG 14433–14435; f, EBRG 14432, 14436). **Falcón**, Sierra de San Luis, Parque Nacional Juan Crisóstomo Falcón, 11.22°, -69.62°, 1350 m (m, MHNLS 9476, 9483, 9487; f, MHNLS 9475, 9477–9482, 9484, 9486, 9489, 9492). **Guárico**, Cerro Platillón, Monumento Natural Juan Germán Roscio, 9.85°, -67.50°, 1045 m (m, EBRG 26977, 27313); Hacienda La Elvira, 10 km NE Altagracia de Orituco, 9.92°, -66.32°, 630 m (m, EBRG 14441–14444). **Lara**, El Blanquito, Parque Nacional Yacambú, 9.8 km ESE Sanare, 9.71°, -69.58°, 1580 m (m, CVULA 2686, 2713; f, CVULA 2706, 6186, 6188, 7046). **Mérida**, Asentamiento Monterrey, 9.6 km NNE Mérida, 8.68°, -71.11°, 2340 m (m, CVULA 1376,1378; f, CVULA 1370, 1371, 1375, 1396, 1440, 7073); Bosque San Eusebio, 8 km SSE La Azulita, 8.65°, -71.41°, 2370 m (m, CVULA 1359; f, CVULA 2112–2114); Cueva de los Mantequeros, Quebrada Azul, 7.5 km SSW La Azulita, 8.67°, -71.47°, 1505 m (m, CVULA 6833); Cueva del Pirata, 0.6 km SE La Azulita, 8.72°,

-71.43°, 900 m (m, CVULA 6822); El Guamal, 5 km NW Santa Apolonia, 9.03°, -71.10°, 400 m (m, CVULA 6859); El Mirabel, 3 km SSE La Azulita, 8.68°, -71.43°, 1500 m (f, CVULA 6057, 6065); El Paramito, 2 km SW Zea, 8.35°, -71.75°, 1100 m (m, CVULA 6304, 6305, 6311; f, CVULA 6306); Finca El Cumbe, 3.5 km SW Zea, 8.35°, -71.80°, 1300–1550 m (m, CVULA 3027, 3056, 3059, 3062; f, CVULA 3015, 3026, 3055, 3057, 3058, 3061, 3063); La Mucuy, 4 km ESE Tabay, 8.62°, -71.05°, 2200–2400 m (m, CVULA 2660; f, CVULA 2663, 7066); La Pedregosa Norte, 5.5 km ESE Mérida, 8.61°, -71.19°, 1775 m (f, CVULA 8772); Monte Zerpa, 4.5 km NNW Mérida, 8.63°, -71.16°, 2050 m (m, CVULA 1420, 2084, 2092, 2136, 7930, 7938; f, CVULA 1323, 1417, 1421, 2109, 2164, 7934, 7954); Prado Verde, 9.5 km NE Mérida, 8.67°, -71.11°, 2200 m (m, CVULA 2099, 2101; f, CVULA 2130); Quebrada Los Churruscos, 2 km SSE Zea, 8.36°, -71.78°, 1150 m (m, CVULA 2993, 2994, 6326, 6367, 7215); Santa Rosa, 3.7 km NNW Mérida, 8.63°, -71.15°, 1920 m (f, CVULA 384); Sector Cucuchica, 5.8–7.0 km ENE Tovar, 8.34°, -71.70°, 930–1250 m (m, CVULA 5973, 5974, 6006, 5975, 8586**; f, CVULA 8584, 8585**); Sector Los Camellones, El Valle, 7 km NE Mérida, 8.65°, -71.12°, 1945 m (m, CVULA 7084, 7085); Vía a El Morro, 6.8 km NNE El Morro, 8.50°, -71.19°, 2265 m (m, CVULA 5860, 5863; f, CVULA 5859, 5861). **Miranda**, Agua Blanca, Parque Nacional Guatopo, 10.07°, -66.47°, 400 m (m, CVULA 2759); Birongo, 10.48°, -66.24°, 60 m (m, EBRG 14492); Curupao, 5 km NNW Guarenas, 10.52°, -66.63°, 1150 m (m, EBRG 14446; f, EBRG 14445, 14447–14451). **Táchira**, Betania, 7.45°, -72.43°, 2250 m (m, MHNLS 4669; f, MHNLS 4685); Cerro El Teteo, 15 km SW El Piñal, 7.42°, -72.05°, 1000 m (f, EBRG 1782); Río Doradas, 28 km SSW Pregonero, 7.78°, -71.85°, 590 m (f, CVULA 5847); San Vicente de la Revancha, 7.51°, -72.34°, 1730 m (f, CVULA 8580); Sector Matamula, 5.7 km ENE Bramón, 7.63°, -72.44°, 2010 m (m, CVULA 8602; f, CVULA 8603). **Trujillo**, Finca La Nona, 5.5 km ESE Boconó, 9.25°, -70.22°, 2040 m (m, CVULA 3108, 3109; f, CVULA 3125). **Vargas**, Petaquire, Carretera Carayaca–El Junquito, 20 ESE El Junquito, 10.43°, -67.17°, 1750 m (f, EBRG 14437, 14453). **Yaracuy**, Finca El Jaguar, Serranía de Bobare, 16 km NO Aroa, 10.55°, -69.00°, 750 m (m, EBRG 20599; f, EBRG 20598, 20600, 20601); Sector Los Bacos, Municipio Bolívar, Sierra de Aroa, 10.45°, -68.77°, 800 m (m, EBRG 25963); **Zulia**, Cerro Las Antenas, Sierra de Perijá, 10.35°, -72.56°, 1449–1602 m (m, MHNLS 12379, 12391, 12408, 12424, 12428; f, 12356, 12357, 12377, 12378, 12380, 12382, 12383, 12399, 12403, 12407, 12410, 12413, 12415); Kunana, Sierra de Perijá, 10.05°, -72.79°, 1130 m (m, MHNLS 154).

S. adrianae caripana (*n* = 9).—**VENEZUELA: Anzoátegui**, Pekín, abajo del Río Neverí, 10.15°, -64.52°, 200 m (m, MHNLS 2092). **Monagas**, 1.5 ESE Sabana de Piedra, 10.21°, -63.56°, 1350 m (m, CVULA 8590**, 8593*, 8771**); San Agustín, 5 km N Caripe, 10.20°, -63.55°, 1180 m (m, EBRG 14454**); Toma de Agua, Sabana de Piedra, 10.22°, -63.57°, 1300 m (f, MHNLS 1526). **Sucre**, Las Melenas, Parque Nacional Península de Paria, 13 km NNW Irapa, 10.68°, -62.62°, 680 m (m, EBRG 20595; f, EBRG 20596); Uquire, Parque Nacional Península de Paria, 6 km NNW Macuro, 10.71°, -61.96°, 100 m (m, EBRG 20597).

S. burtonlimi (*n* = 2).—**COSTA RICA; Cártago**, Moravia, 9.85°, -83.43°, 1116 m (m UMMZ 111339; photographs of skull, Myers *et al.* 2016). **PANAMA: Chiriquí**, Ojo de Agua, 2 km N of Santa Clara, 8.70°, -82.75°, 1500 m (m, ROM 104294*; photographs of the skull, Velazco and Patterson 2014).

S. hondurensis (*n* = 2).—**HONDURAS: La Paz**, La Cruz Grande, a hill on the outskirts of San José, 14.25°, -87.96°, 1300 m (f, AMNH 126811*; photographs of skull and study skin accessed on 31 August 2016 at at http://www.amnh.org/our-research/vertebrate-zoology/mammalogy/database/). **MEXICO: Oaxaca**, 3.2 km E San Gabriel Mixtepec, 16.10°, -97.06°, 670 m (m, AMNH 189780; photograph of skull, not including mandible, Goodwin 1969).

S. ludovici (*n* = 12).—**ECUADOR: Cotopaxi**, Reserva Otonga, 27 km SE Santo Domingo de los Tsáchilas, -0.42°, -79.00°, 1950 m (m, QCAZ 2553, 2701). **Esmeraldas**, Los Pambiles, confluence of unnamed river with Río Las Piedras, Reserva Ecológica Cotacachi–Cayapas, 0.52°, -78.62, 1200 m (m, CMNH 112835; photographs of the skull, McCarthy *et al.* 2006). **Pichincha**, Gualea, 0.07, -78.44, about 1200 m (m, AMNH 67328*; photographs of skull and study skin accessed on 31 August 2016 at http://www.amnh.org/our-research/vertebratezoology/mammalogy/database/); Nanegal, Comunidad de Chacapata, 0.12°, -78.67°, 1450 m (m, QCAZ 1644); Río Guajalito, 32 km W Quito, -0.23°, -78.82°, 2000 m (m, QCAZ 2783; f, QCAZ 2103, 2742, 2757, 2769, 2776, 3273).

S. oporaphilum (*n* = 13).—**ARGENTINA: Jujuy**, Arroyo Sauzalito, Parque Nacional Calilegua, -23.06°, -64.57°, 550 m (f, CML 2932; photographs of the skull, Barquez *et al.* 1999). **BOLIVIA: La Paz**, Coroico River Valley, 6.6 km downstream Caranavi, -15.80°, -67.62°, 653 m (f, AMNH 246551). **ECUADOR: Napo**, Confluencia de ríos Oyacachi y Chalpi, 15 km ESE Oyacachi, -0.27°, -77.97°, 2550 m (f, QCAZ 2300); Río Hollín, vía Hollín–Loreto, -0.68°, -77.73, 1050 m (m, QCAZ 1386). **Pastaza**, Fuerte Militar Amazonas, Poblado de Shell, -1.52°, -78.07°, 1072 m (m, QCAZ 4632). **Tungurahua**, Cascadas de Machay, sector Machay, carretera Baños–Puyo, -1.40°, -78.27°, 1900 m (f, QCAZ 3708); Comuna Los Angeles, cerca del poblado de Río Negro, -1.42°, -78.20°, 1220 m (m, QCAZ 4635); Hostería El Otro Lado, Cascada El Pailón del Diablo, -1.41°, -78.30°, 1420 m (m, QCAZ 4890). **PERU: Cuzco**, 72 km by road NE Paucartambo (at km marker 152, just above San Pedro), -13.12, -71.28°, 1460 m (f, UMMZ 160658; photographs of skull, Myers *et al.* 2016); Marcapata, Amacho, -13.50°, -70.92°, 2740 m (m, FMNH 75187; f, FMNH 75186, 75188, 75189).