

A new species of *Sturnira* (Chiroptera: Phyllostomidae) from the Choco forest of Ecuador

PABLO JARRÍN-V^{1,2,3} & THOMAS H. KUNZ²

¹Estación Científica Yasuní, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076 y Roca, Quito, Pichincha, Ecuador

²Center for Ecology and Conservation Biology, Department of Biology, Boston University, #5 Cummington St. 02215 MA, Boston, USA

³Corresponding author. E-mail: psjarrin@puce.edu.ec

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Abstract

Sturnira perla, the new species described herein, is diagnosed as an independent phylogenetic lineage in hypotheses derived from mitochondrial sequences, and shows acceptable distances in terms of genetic divergence. This description also relies on the statistical interpretation of morphological dissimilarity and overlap, and avoids qualitative judgments of character variation. Overall, this new species is characterized by a spherical skull, noticeable round and robust, with pronouncedly curved zygomatic arches. Statistical evidence that supports the discrimination of other species in *Sturnira*, based on external characters such as pelage coloration or number of hairs, is absent in the literature. In this sense, the geometry of the skull for this newly described species shows the sharpest morphological boundaries, relative to other closely related and sympatric taxa. This new species is likely endemic to the Choco forest, specially at its southern limits. This is an area known for its high levels of endemism. The magnitude of environmental disruption in the Choco and the potential rarity of this new species may be negatively affecting its probability of survival.

Key words: Choco, endemism, geometric morphometrics, new species, species boundaries, *Sturnira*

Introduction

Most previous species descriptions for the genus *Sturnira* coincide, implicitly or explicitly, with the evolutionary lineage concept (Mayden 1997). Hence, species have been considered as independent historical entities, often represented as terminal branches in phylogenetic trees. It is along the topology of one of these trees that Pacheco and Patterson (1991) recognized a previously undescribed taxon in phylogenetic hypotheses and named it as *Sturnira* sp. A (i.e. “EPN E-6722”). This last specimen was “made available” by Luis Albuja, who also mentions it as an undescribed species (Albuja, 1999). Along in the same chapter on *Sturnira*, Albuja (1999) mentioned *S.* sp. B, as a second undescribed species (nowhere, in his book, does Albuja make reference to catalog numbers, except when

illustrations are included for some species in several genera). Later, Iudica (2000) proposed new phylogenetic hypotheses for *Sturnira*, based on a partial sequence of the cytochrome-*b* gene and a matrix of qualitative morphological characters. He included in his phylogenetic analyses two undescribed species, *S. sp. A.* and *S. sp. B.*, that were made available to him “through the courtesy of Timothy J. McCarthy and Luis Albuja”. By and large, the molecular evidence lead Iudica (2000) to suggest that *Sturnira sp. A.* (i.e. CMNH 112804–112821, now named *S. koopmanhilli*) and *S. sp. B.* (i.e. “CMNH, 112823” and “CMNH, 112822”, which belong to the species being described herein) are independent lineages, endemic to Ecuador, and thus far have not been found in any other region in the Neotropics. Subsequently, McCarthy *et al.* (2006) described species *S. sp. A.* as *S. koopmanhilli*. These last authors made explicit reference to EPN 6722, “which was reported as an undescribed species (*Sturnira sp. A.*)” in the work of Pacheco and Patterson (1991). These authors also included the specimens used by Iudica (CMNH 112804–112821) as paratypes in their work. The variation and boundaries of *S. sp. B.* have remained undiagnosed until now.

It is unfortunate that Gardner (2008) referred to Albuja’s *Sturnira sp. B.* as “*Sturnira species A.*”. He does not refer to any specimen in particular, but the first line in his account for this species states: “Albuja (1999:127) identified an undescribed species as “*Sturnira Sp. B.*” from northwestern Ecuador”. Hence, Gardner’s reference must not be confused with previous references to *S. sp. A.* (Albuja 1999; Iudica 2000) which is now *S. koopmanhilli*. Except for Gardner (2008), we can be certain that the use of *S. sp. B.* has been maintained in the literature due to the consistent historical references that were previously mentioned.

For some regions in the Neotropics (e.g. the Northern Neotropics), species assigned to *Sturnira* can be divided into highland (e.g. *S. ludovici* Anthony and *S. erythromos* Tschudi) and lowland groups (e.g. *S. luisi* Davis and *S. lilium* Geoffroy). This division appears to correspond not only to two or three monophyletic groups and sister taxa (Pacheco & Patterson 1991; Iudica 2000; Villalobos & Valerio 2002), but also to an apparently discrete morphological trait related to the presence or absence of certain cusps in the lower molars. de la Torre (1961) was the first to publish a dichotomous key for the genus, and the first to note the difference between lowland species having a defined entoconid and metaconid (“lingual ridge of lower molars divided into metaconid and entoconid”), versus those on highlands characterized by the absence or reduction in both cusps (“lingual ridge of lower molars with no vertical division”). According to Albuja (1999) and Tirira (1999) lowland species of *Sturnira* include *S. lilium*, *S. luisi* and *S. tildae* de la Torre.

It is among the group of lowland species that Albuja (1999) briefly referred to *Sturnira sp. B.* as occurring in the Choco lowlands of Ecuador, and having a robust skull with highly curved zygomatic arches that project outwards. Herein, we diagnose and name *S. sp. B.* as a new species that has been previously identified as an independent lineage, as part of phylogenetic hypotheses based on molecular evidence (Iudica 2000). As with any diagnosis of a new species, we explore differences and distances that would suggest the presence of an independent evolutionary lineage. We assess the morphometric space of *S. sp. B.*, measure its variability against other species and interpret its morphological boundaries based on statistical estimates. We also estimate genetic distances and suggest possible phylogenetic relationships.

A justification is made necessary by certain perspectives of taxonomy and systematics that run contrary to the philosophical approach of this study. This study is conceived on quantitative and statistical grounds. It departs, on purpose, from the form used by other descriptions that heavily invested on qualitative, and therefore inherently subjective criteria (sensu Jarrín-V. & Kunz 2008), and appreciations of variation. Instead, we use mathematics and probability statements of uncertainty. The description of complex morphological variation cannot be made with words, it requires quantitative perspectives. The use of qualitative descriptions is often based on arbitrary and subjective decisions that often contradict each other (Gift & Stevens 1997). Since quantitatively coded variation is often expressed by explicit statistical methods (Poe & Wiens 2000); then, its interpretation may be less affected by the vagueness of language that besets the qualitative description of variation (Tye 1994; Jarrín-V. *et al.* 2010). Systematics and taxonomy must be disciplines solidly founded within the full framework of science. Moreover, since science is not based on arguments from authority; then, to provide personal appreciations of color and shape in a description does not provide evidence. On the contrary, to measure and quantify variability within the context of hypothesis testing (i.e. statistics) is to provide evidence of its validity within the framework of modern scientific thought and falsificationism (Popper 1934). In this sense, we do not believe that verbally describing character states, in characters such as facial structure (i.e. vibrissae, noseleaf, warts, etc.), length of hair, number of bands on dorsal and ventral hairs, etc., help to understand variation and boundaries among species (sensu Jarrín-V. & Kunz

2008). Many of these characters can and must be interpreted quantitatively and under the sieve of statistical inference (sensu Thiele 1993). Very few will dissent with one of the fathers of the modern synthesis who suggested that: "All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms" (Mayr 1959, p. 2). Thus, we do not follow the verbal description of characters states for which we do not have evidence they can be qualitatively described or even represent real differences among species.

Methods

Morphological data analysis. A total of 279 individuals were available for the morphological analyses (Appendix 1) and are housed as follows: Departamento de Ciencias Biológicas, Escuela Politécnica Nacional, Quito (EPN); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); and Museo Ecuatoriano de Ciencias Naturales, Quito (MECN). These specimens were collected from the lowlands of Ecuador, on both sides of the Andes, below 1000 m, and correspond to at least four putative species or taxa: *Sturnira lilium*, *S. luisi*, *S. tildae* and *S. sp. B*. Our analysis was based on 27 characters (linear measurements) of the body and skull (Fig. 1; Appendix 2). These interlandmark characters were transformed to natural logarithms to improve properties of normality. The skull characters were those used mostly by Iudica (2000), with the addition of the height of the skull (HS), distance between the auditory bulla and incisors (AUL) and angle of curvature of the zygomatic arch (ACM). Characters influenced by articulate structures, such as body length, were not considered for analysis because of their dependency to the fixed position of the specimens (Hayek *et al.* 2001). All measurements were recorded to the nearest 0.01 mm using a Fowler Sylvac Ultra-cal IV digital caliper. Only adults, recognized by fused hand-wing epiphyses, were considered for analysis to homogenize data matrices and reduce the effect of non-linear allometric associations between variables (Pimentel 1992). The dorsal aspect of the skull was digitized to a resolution of 1600 x 1200 DPI and described by a set of 20 landmarks (Fig. 1). Skulls were placed directly over the glass plate of the scanner and along its middle line to avoid optical distortions. We assume that any change in the position of the skull with reference to the horizontal plane, due to different lengths of canines, are minimal and will be properly reflected in the signal of shape variables.

The material examined included a random array of missing characters. A number of dried skins included severed forearms, or missing wing or foot bones, and various skulls had broken parts or missing teeth. In general, 25% of the data was missing for any variable in any dataset or matrix. A simple maximum likelihood imputation method (an expectation-maximization or EM algorithm) was used to replace missing values (Graham & Hofer 2000; Little & Rubin 2002). However, missing values for ACM were excluded from the imputation method, because this character was considered at a later stage of the process of data acquisition. No missing characters were present for the geometric morphometric analysis of the skull. Thus, sample number may vary depending on the analysis, but this is noted when appropriate.

We combined information provided by both linear measurements and landmark-shape data. By using landmark data instead of linear measurements or ratios, resultant shape variables are mathematically free of isometric effects. With landmark data, the spatial relationships among landmarks are expressed as geometric configurations that can be depicted as deformation grids (in the spirit of Thompson, 1917). The decomposition of shape and size can be studied by principal components (i.e. relative warps) that represent directions of maximum variation (Rohlf & Marcus 1993; Rohlf *et al.* 1996; Rohlf 1999). Geometric samples were projected onto the tangent space by an orthogonal projection. The affine components were included by keeping the α parameter null (Rohlf 1993) and estimated by the complement method (Rohlf & Bookstein 2003). Aligned specimens were scaled to unit centroid size (CS) (Dryden & Mardia 1998). The distribution of samples along morphometric space was estimated by plots among PCs, RWs and the ACM. The geometric morphometric analysis was made with the TPSdig and TPSrelw modules developed by James Rohlf (Department of Ecology and Evolution, State University of New York, Stony Brook, freely distributed online at <http://life.bio.sunysb.edu/morph/>). We used a Kolmogorov-Smirnov test (K-S), corrected for bias in sample size by a Lilliefors Significance Correction, to assess the goodness of fit to normality of frequency distributions for forearm (FA) and greatest length of the skull (GLS).

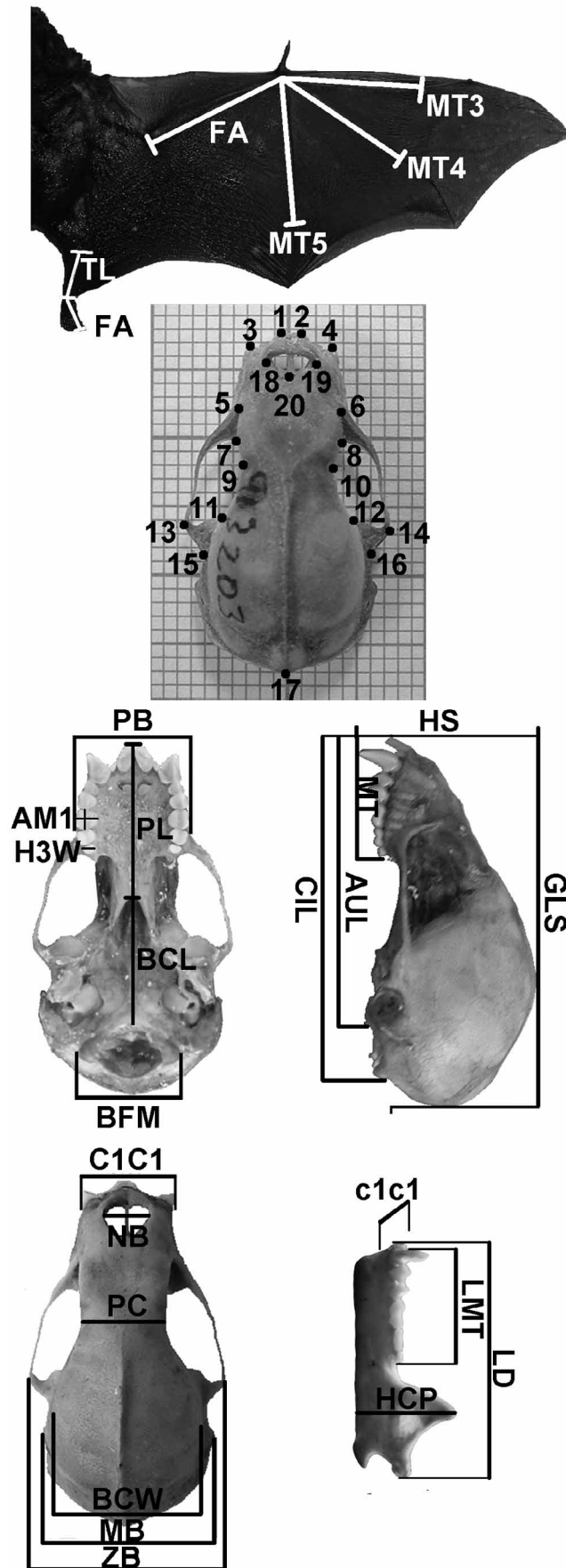


FIGURE 1. Measurement scheme and shape landmarks for the analysis of shape variation in *Sturnira*.

A principal component analysis (PCA), based on the variance-covariance matrix, was used to extract major components of variation from the 27 linear characters (ACM excluded). Although rotations of components are expected to improve the interpretation of variation; in this particular case, we found that the unrotated solution was best to differentiate the new species from other samples. The first five PCs, with eigenvalues above unity, and the ACM were compared among groups (i.e. species and sex) by a multivariate analysis of variance (MANOVA). The MANOVA included the main effect and interaction between species and sex. This interaction term was included to determine whether sex differences remained constant among species. We used Pillai's trace statistic (PT) as an estimate of probability against the null hypotheses (i.e. no differences in group means). This is a relatively robust and conservative statistic compared to others of similar kind (Olson 1974). Complementary to probability values, we also included estimates of effect size as partial-eta squared values (η^2), and tests of model robustness (homogeneity of error variances and variance-covariance matrices). The evaluation of multivariate parameters, statistical tests, and graphs were made using SPSS v. 17.0.0 (SPSS 2008).

The species membership of each of the 279 sampled individuals was determined a priori by criteria for classification found in the dichotomous key from Gardner (2008). However, it is important to note that most criteria used in this kind of dichotomous keys are based mostly on an historical process by which assumed diagnostic characters are often transferred from author to author, and where their reliability is often unknown (Jarrín-V. & Kunz 2008; Jarrín-V. *et al.* 2010). Thus, we focused primarily on the distance and boundaries of the sample representing the new species, relative to the rest of the samples. In this sense, the putative membership of samples in *Sturnira lilium*, *S. luisi* and *S. tildae* is of secondary importance to our goal of presenting evidence for the existence of a distinct lineage and describing its morphological variation and boundaries.

Molecular data analysis. Partial sequences of the cytochrome *b* gene were used to estimate the phylogenetic relationships and distances among species in *Sturnira*. The set of sequences for the analyses belong to the database of multiple sequence alignments (PopSet), and was submitted by Carlos Iudica (CAI) and collaborators to GenBank. The set used, with GeneInfo number (GI) 33314759, was reduced to match the same samples that were used by Iudica (2000), with exception of *Sturnira nana* CAI240, which was replaced in this case for the available *S. nana* CAI243. Also, the original sequences reported for both *S. sp. A.* (CAI180 = CMNH 112812) (now *S. koopmanhilli*) and *S. sp. B.* (CAI226 = CMNH 112822) were obtained from Iudica (2000) and included in the main sequence matrix. Since PopSet GI 33314759 is an aligned matrix, this facilitated the alignment by hand of both CAI180 and CAI226. This last specimen, CMNH 112822, was made available to Iudica by L. Albuja and T. McCarthy, and is part of the *S. sp. "B"*, that was mentioned by Albuja (1999) as a distinct undescribed species. The protocol for the extraction, purification and amplification of molecular sequences is explained in Iudica (2000). The list of individuals included in the matrix of molecular data is detailed in Appendix 3.

The appropriate model of nucleotide substitution, as estimated through jModelTest v. 0.1.1 (Guindon & Gascuel 2003; Posada 2008), and selected by the Akaike Information Criterion (AIC), was the GTR+I+ Γ . However, genetic distances among species were also calculated accordingly to the Kimura 2-parameter model (K80) (Kimura 1980) with no gamma parameter "for purposes of continuity and comparison across several taxonomic ranks" (Bradley & Baker 2001). K80 distances were estimated with Phylip v.3.6 (Felsenstein 2005).

A phylogenetic hypothesis was estimated by Bayesian inference (BI) using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). This hypothesis was based on a GTR model with a proportion of invariable sites combined with gamma-distributed rate variation across sites (GTR+I+ Γ). Although the general structure of the model was constrained in this Bayesian analysis, we assumed no prior knowledge about the probability density functions on its parameters (e.g. substitution rates and nucleotide frequencies) and left these as the default priors in MrBayes (e.g. the probability density as a flat Dirichlet and the gamma parameter as a uniform distribution). This allows the Markov chain Monte Carlo method (MCMC) to generate posterior probabilities for estimating these parameters, assuming no prior knowledge. The analysis was made with partitioned (site specific) codon positions, unlinked estimation of parameters within each partition, and variable rates of substitution per partition (with flat Dirichlet priors). The analysis included 21 million generations, two independent runs, and four chains per run. Hypotheses were sampled each 100 generations and the first 35% of these samples were discarded according to the behavior of the average standard deviation of split frequencies; which at 35% of the total generations reached a value of 0.003. The remaining 65% of the trees and parameters were respectively summarized in a 50% majority rule consensus tree. The parameters for the nucleotide substitution model had values of potential scale reduction factor (PSRF) that approached 1.00 after reaching the 21 million generations.

Sturnira perla, new species

Figure 2

Holotype. QCAZ 120, adult female with skin and skull (S/S). The skull is in excellent condition, while the skin is slightly damaged. Collected on 26 June 1990, by Felipe Campos. Ecuador, Provincia Santo Domingo de los Tsachilas, Bosque Protector La Perla at 200 meters of altitude (0°08'N, 79°30'W), 2 km south of La Concordia (locality # 5 in Fig. 3).

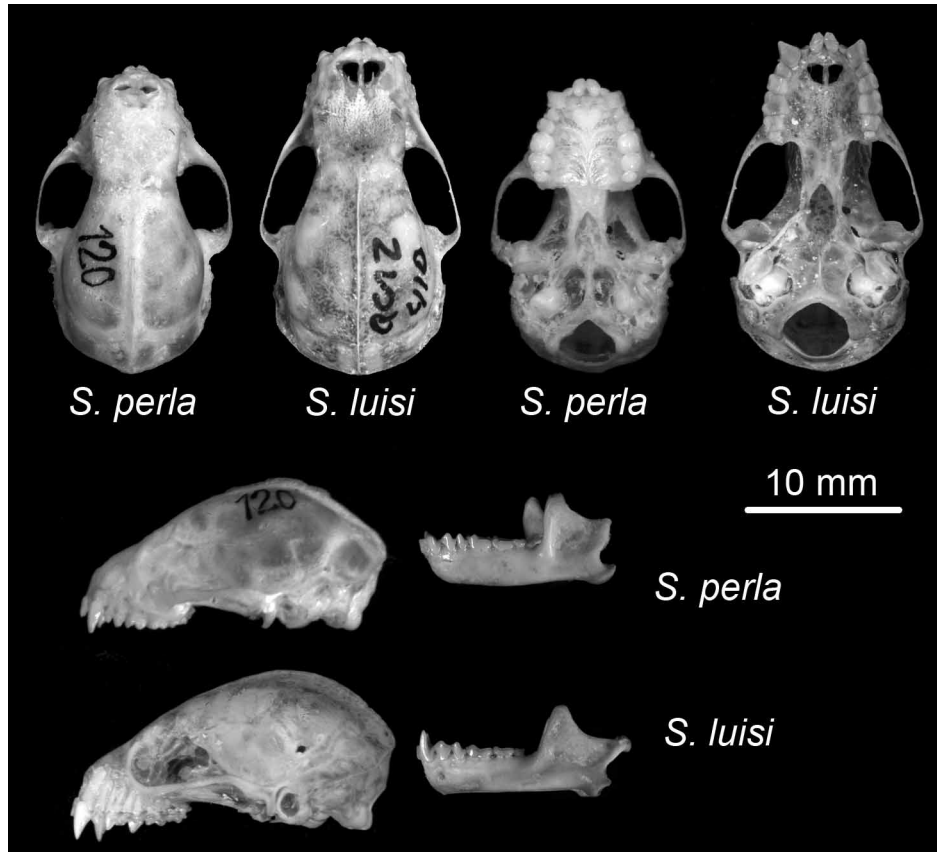


FIGURE 2. Individual aspects of the skull and mandible for *Sturnira perla* and *S. luisi* in dorsal, ventral and lateral views. The skull of the former species has an overall rounded shape relative to the latter.

Paratypes. Six additional specimens are from Bosque Protector La Perla (locality # 5 in Fig. 3), collected on 30 April 1992 by Felipe Campos, except when mentioned: QCAZ 119, pregnant (S/S), 28 April 1990; QCAZ 437, possibly lactating, alcohol and skull (A/S), 30 April 1992; QCAZ 438, adult male (A/S); QCAZ 439, adult male (A/S); QCAZ 440, adult female (A/S); QCAZ 542 (QLP-061), possibly lactating, 28 June 1990 (A/S). Three specimens from Ecuador, Provincia Esmeraldas, Borbón, Río Santiago, Estero María, comuna Selva Alegre at 50 meters of altitude (1°06'N 78°59'W), collected on 24 October 1996 by Nestor Acosta and Lincoln Nolivos: QCAZ 1909, adult female (A/S); QCAZ 1912, adult female (A/S); QCAZ 1920 adult male with scrotal testes (A/S) (locality # 1 in Fig. 3). One specimen from Provincia Esmeraldas, Borbón, Río Cayapas Angostura at 35 m (0°53'14"N, 78°50'38"W), collected on 24 October 1996 by unknown collector: QCAZ 2076, adult female (A/S) (locality # 2 in Fig. 3). One specimen from Ecuador, Provincia Esmeraldas, Reserva La Mayronga, Sector ATP, en el bosque al borde del estero at 80 m (80 m), collected on 26 October 1998 by Igor Castro and Lincoln Nolivos: MECN 1665, adult male with scrotal testes (S/S) (locality # 4 in Fig. 3).

Other specimens. Additionally, Iudica (2000) mentions two specimens that were “made available” to him “through the courtesy of Timothy J. McCarthy and Luis Albuja V.”, one of which is included in this study as part of the molecular analysis (CAI226). These two specimens are from Ecuador, Provincia Esmeraldas, “Near Nueva Vida, 1.9 km N, 10.4 km E Codesa-Sade compound at Río Esmeraldas, Manzano at 450-460 m (0°32'N, 79°17'W)”: CMNH 112823 (CAI 181), pregnant, 11 December 1991 (A/S); CMNH 112822 (CAI 226), male, 8 December 1991 (S/S) (locality # 3 in Fig. 3).

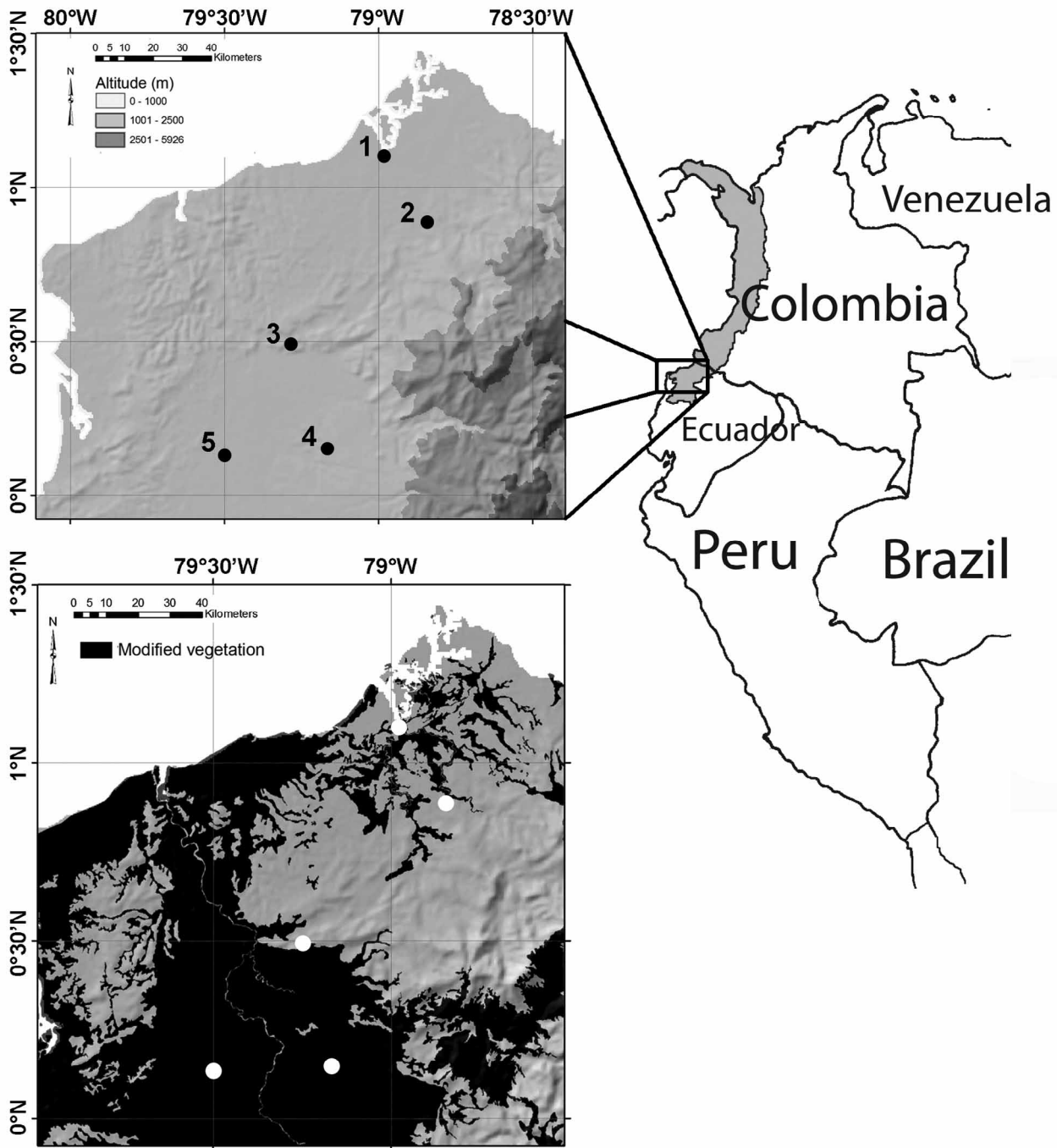


FIGURE 3. The five localities from where *Sturnira perla* is currently known, represented as dark or white spots correspondingly to each map. A considerable expanse of the original Chocoan forest has been replaced by agriculture. The depicted estimate of remaining vegetation dates to 1996, in which the amount of altered vegetation must have increased considerably since then. Numbers related to each location in the map are included in parenthesis next to the corresponding locality for *S. perla* in Appendix 1.

Etymology. *Perla* is a word with deep Latin roots having the same meaning as pearl in modern English (Segura 2006). Here the term *perla* is used as a noun in apposition. Figuratively, *perla* means something very precious. It is also a metaphor to the globular shape of the skull of this species and honors the Bosque Protector La Perla, the locality where the majority of samples were found.

Distribution. Known only from the tropical rainforest lowlands of the Choco forests in Ecuador (Fig. 3, Appendix 1). Its presence may extend to the Colombian Choco. *Sturnira perla* has been found near the coastal plain (35 m) and up to 220 m. This is the lowest elevational range registered for any other species of *Sturnira* in Ecuador, with sympatric species reaching higher altitudes up to 1618 m for *S. lilium*, 1600 m for *S. luisi* and 1450 m for *S. tildae*.

TABLE 1. Descriptive statistics for interlandmark characters and ACM. Total sample size is n=279 except for the ACM with n=207. Data is presented as: mean [95% confidence interval around the mean] (minimum-maximum) standard deviation. Two characters present no overlap in their means between *Sturnira perla* and the other species, and are highlighted by an ending asterisk. All characters are in millimeters except for ACM which is an angle in degrees. Sample size is *Sturnira lilium*=103, *S. luisi*=76, *S. perla*=12 and *S. tildae*=15.

	<i>Sturnira perla</i>	<i>S. lilium</i>	<i>S. luisi</i>	<i>S. tildae</i>
Angle of curvature of the zygomatic arch*	146.5 [144.31–148.69] (140–151) 3.45	158.95 [157.79–160.11] (149–173) 5.92	158.34 [157.07–159.61] (149–174) 5.6	158.6 [156.07–161.13] (152–166) 4.56
Forearm length	43.1 [42.71–43.5] (42.13–44.38) 0.62	42.63 [42.41–42.86] (38.43–44.99) 1.39	42.82 [42.51–43.12] (37.26–47.44) 1.58	46.57 [46.05–47.09] (45.01–48.42) 1.05
Third metacarpal length	43.5 [42.78–44.22] (41.98–46.35) 1.14	42.15 [41.88–42.41] (37.12–46.88) 1.59	42.47 [42.15–42.79] (38.53–48.16) 1.66	45.92 [44.97–46.87] (42.22–49.1) 1.91
Fourth metacarpal length	42.53 [42.17–42.89] (41.31–43.42) 0.57	41.68 [41.43–41.93] (36.98–46.22) 1.51	41.89 [41.58–42.2] (38.26–47.64) 1.62	45.51 [44.55–46.46] (41.37–48.23) 1.92
Fifth metacarpal length	43.64 [43.15–44.12] (41.98–44.76) 0.77	42.96 [42.71–43.22] (38.6–47.9) 1.55	43.07 [42.73–43.41] (39.37–49.0) 1.76	46.85 [45.82–47.87] (42.52–50.24) 2.06
Tibia length	17.63 [16.92–18.34] (15.1–18.56) 1.12	17.17 [16.94–17.41] (12.47–19.94) 1.43	17.24 [16.99–17.49] (12.58–20.07) 1.3	19.35 [18.81–19.88] (17.41–21.19) 1.08
Hind foot length	13.32 [12.81–13.82] (11.84–14.58) 0.8	13.36 [13.19–13.53] (11.1–16.48) 1.04	12.92 [12.68–13.15] (10.54–16.5) 1.21	13.62 [13.12–14.12] (11.76–15.38) 1.0
Height of the skull	11.17 [10.98–11.36] (10.72–11.62) 0.29	11.16 [11.08–11.25] (9.15–13.04) 0.51	11.25 [11.16–11.34] (10.1–12.34) 0.48	11.37 [11.19–11.54] (10.94–12.17) 0.35
Greatest length of the skull	22.71 [22.5–22.92] (22.1–23.12) 0.11	23.15 [23.04–23.26] (21.35–24.65) 0.67	23.28 [23.13–23.43] (21.37–25.05) 0.79	23.97 [23.64–24.3] (22.99–25.54) 0.67
Occipital condyles – incisors length	20.39 [20.22–20.56] (19.77–20.78) 0.27	20.89 [20.78–21.0] (19.1–23.27) 0.69	20.97 [20.83–21.12] (19.09–22.96) 0.76	21.82 [21.49–22.15] (20.5–23.3) 0.66
Auditory bula–incisors length	17.79 [17.64–17.94] (17.37–18.04) 0.23	18.26 [18.16–18.36] (16.68–20.92) 0.62	18.32 [18.2–18.45] (16.61–20.06) 0.64	18.99 [18.69–19.29] (17.73–20.25) 0.61
Mastoid breadth	11.82 [11.69–11.94] (11.34–12.15) 0.2	12.03 [11.98–12.09] (10.92–12.99) 0.35	12.16 [12.08–12.24] (11.21–13.24) 0.4	12.64 [12.4–12.88] (11.7–13.52) 0.48
Zigomatic breadth	14.51 [14.31–14.71] (13.79–14.85) 0.31	13.72 [13.66–13.78] (12.49–14.82) 0.38	13.79 [13.69–13.89] (11.95–14.95) 0.51	14.17 [13.93–14.42] (13.35–15.24) 0.49
Postorbital constriction	5.78 [5.71–5.85] (5.62–5.94) 0.11	5.83 [5.8–5.87] (5.22–6.32) 0.22	5.9 [5.85–5.94] (5.38–6.58) 0.24	6.12 [5.92–6.31] (5.47–7.25) 0.39
Braincase length	7.67 [7.5–7.84] (7.07–8.09) 0.27	8.31 [8.24–8.37] (7.42–9.46) 0.39	8.4 [8.32–8.47] (7.33–9.57) 0.38	8.79 [8.6–8.98] (8.29–9.69) 0.38
Braincase width	10.34 [10.23–10.45] (10.07–10.63) 0.17	10.52 [10.47–10.57] (9.8–11.73) 0.31	10.53 [10.47–10.6] (9.68–11.27) 0.34	10.75 [10.57–10.92] (9.92–11.34) 0.36
Breadth across foramen magnum	6.43 [6.31–6.55] (6.12–6.63) 0.19	6.36 [6.32–6.41] (5.66–6.93) 0.26	6.4 [6.35–6.45] (5.49–7.04) 0.27	6.77 [6.62–6.92] (6.09–7.26) 0.3
Nasal breadth	3.26 [3.19–3.33] (3.08–3.41) 0.11	3.21 [3.19–3.23] (2.85–3.58) 0.15	3.22 [3.19–3.25] (2.73–3.61) 0.16	3.43 [3.36–3.51] (3.19–3.7) 0.15
Palatal length	10.11 [9.97–10.25] (9.84–10.59) 0.22	10.15 [10.08–10.22] (8.58–11.18) 0.44	10.18 [10.09–10.26] (8.79–11.15) 0.45	10.55 [10.34–10.76] (9.9–11.53) 0.42
Palatal breadth	8.23 [8.14–8.32] (7.91–8.46) 0.14	8.2 [8.16–8.24] (7.43–8.91) 0.25	8.2 [8.14–8.26] (7.42–8.84) 0.3	8.27 [8.15–8.38] (7.84–8.67) 0.23

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TABLE 1. (continued)

	<i>Sturnira perla</i>	<i>S. lilium</i>	<i>S. luisi</i>	<i>S. tildae</i>
Breadth across upper canines	5.85 [5.76–5.94] (5.53–6.07) 0.14	6.35 [6.31–6.39] (5.68–7.07) 0.25	6.38 [6.33–6.44] (5.63–7.24) 0.3	6.53 [6.41–6.64] (6.19–6.92) 0.23
Length of maxillary tooththrow	6.88 [6.81–6.94] (6.66–6.99) 0.1	6.73 [6.69–6.77] (5.93–8.29) 0.26	6.73 [6.69–6.78] (6.13–7.24) 0.23	6.85 [6.76–6.94] (6.43–7.14) 0.18
Dentary length	13.72 [13.56–13.88] (13.26–14.04) 0.25	13.84 [13.76–13.92] (12.6–14.76) 0.46	13.88 [13.78–13.99] (12.46–15.18) 0.54	14.37 [14.13–14.61] (13.26–15.34) 0.48
Area of molar Molar 1	2.78 [2.69–2.87] (2.47–3) 0.14	2.85 [2.81–2.88] (2.34–3.5) 0.24	2.79 [2.74–2.84] (2.15–3.6) 0.27	2.78 [2.69–2.87] (2.33–3.03) 0.18
Molar 3 width*	1.13 [1.1–1.16] (1.05–1.2) 0.05	0.82 [0.81–0.83] (0.69–1.06) 0.06	0.83 [0.81–0.84] (0.55–1.07) 0.08	0.86 [0.84–0.88] (0.79–0.93) 0.04
Length of mandibular tooththrow	7.52 [7.36–7.68] (7.12–7.94) 0.25	7.52 [7.49–7.56] (6.98–8.12) 0.21	7.54 [7.49–7.59] (6.78–8.15) 0.24	7.71 [7.62–7.8] (7.23–8.02) 0.18
Height of coronoid process	6.61 [6.34–6.88] (5.39–6.97) 0.42	5.51 [5.47–5.55] (4.84–6.05) 0.22	5.54 [5.49–5.6] (4.68–6.18) 0.27	5.82 [5.68–5.96] (5.36–6.25) 0.28
Dentary width at canines	3.38 [3.31–3.45] (3.13–3.58) 0.12	3.63 [3.59–3.66] (3.15–4.09) 0.2	3.65 [3.6–3.69] (2.57–4.31) 0.24	3.85 [3.75–3.95] (3.48–4.2) 0.2

Diagnosis. *Sturnira perla* was previously recognized as an independent phylogenetic lineage by Iudica (2000). The globular shape of the skull is remarkably distinct, not only in terms of Euclidean distances in morphospace as is explained below, but also to the point of being distinguished by simple visual inspection (Fig. 2). The spherical skull is, in part, the consequence of an extremely blunt rostrum, robust and curved zygomatic arches and globular braincase. Also, the M3W is remarkably larger in this species against every other individual comparison.

Comparisons. Except for the overall architecture of the skull (Fig. 2), *Sturnira perla* is externally cryptic, relative to the sympatric species *S. lilium*, *S. luisi* and *S. tildae*. Together, with other lowland species, *S. perla* shares the “lingual ridge of lower molars with no vertical division” (de la Torre 1961), and therefore is distinguished by this discrete trait from other species in the highlands, such as *S. oporophilum*, *S. bogotensis*, *S. erythromos*, *S. ludovici*, and *S. koopmanhilli*. In this same sense, the presence of four lower incisors distinguishes *S. perla* from *S. bidens* and *S. nana*, both with two lower incisors. Also, and relative to other similar species, the third upper molar (M3) is remarkably large (Table 1). Thus, *S. perla* can only be recognized by an inspection of the skinned skull and the quantification of its overall geometric structure. No other morphological characters, as are currently explained in the available literature, show convincing evidence of this species being distinct from other similar and closely related congeners. As it was explained earlier, the verbal and qualitative description of character states inherently relies on typological essences, with no information on distributional properties among species (sensu Mayr 1959; Jarrín-V. & Kunz 2008). Thus, the qualitative description of characters related to the facial structure (i.e. vibrissae, noseleaf, warts, etc.), length of hair, number of bands on dorsal and ventral hairs, etc., are all irrelevant or dubious characters for the diagnosis of species in this particular case. Perhaps, subsequent studies that consider the statistical distribution of these characters within a quantitative perspective may validate their usefulness for diagnosing species.

TABLE 2. Component loadings of a principal component analysis based on the covariance matrix of the log_e-transformed linear characters for adult specimens of the *Sturnira lilium-luisi-tildae* complex in Ecuador (*n* = 279). A total of five components were extracted based on the average item variance for an eigenvalue > 1. The table includes the rescaled factor loadings for each variable, and the eigenvalues and proportion of variance explained by each component at the end of each column. Variables are ordered based on their highest loadings for PC I. Sample size is *Sturnira lilium*=103, *S. luisi*=76, *S. perla*=12 and *S. tildae*=15.

	PC I	PC II	PC III	PC IV	PC V
Greatest length-skull	0.881	0.257	0.106	0.043	0.188
Condylolincisors	0.879	0.276	0.103	-0.009	0.147

continued next page

TABLE 2. (continued)

	PC I	PC II	PC III	PC IV	PC V
Bullaincisors	0.854	0.305	0.067	-0.014	0.130
Dentary length	0.847	0.191	0.115	0.065	0.179
Dentary width at canines	0.771	0.355	0.054	0.116	0.313
Palatal length	0.770	0.196	0.054	0.131	0.137
Mastoid breadth	0.767	0.172	0.139	-0.033	0.260
Zigomatic breadth	0.762	-0.199	0.155	0.139	0.187
Mandibular toothrow	0.748	0.115	-0.037	0.236	0.116
Metacarpal 5	0.740	-0.148	-0.060	-0.411	-0.142
Metacarpal 3	0.738	-0.184	-0.128	-0.426	-0.116
Foramen magnum	0.720	0.037	0.009	-0.188	0.085
Metacarpal 4	0.715	-0.167	-0.114	-0.429	-0.131
Nasal breadth	0.711	0.061	0.020	-0.081	0.011
Forearm	0.697	-0.073	0.000	-0.412	-0.165
Upper canines	0.690	0.399	0.040	0.216	0.338
Maxillary toothrow	0.667	-0.011	-0.011	0.392	0.062
Palatal breadth	0.664	0.159	-0.007	0.530	0.145
Tibia	0.659	0.000	-0.430	-0.451	-0.277
Braincase length	0.656	0.338	0.135	-0.182	0.059
Braincase width	0.625	0.268	0.258	0.033	0.108
Postorbital constriction	0.623	0.044	0.183	-0.088	0.216
Height-skull	0.608	0.154	0.236	0.166	0.235
Coronoid process height	0.532	-0.487	0.166	0.101	-0.021
Molar M3 width	0.330	-0.911	-0.002	0.176	0.046
Hindfoot	0.317	0.104	0.812	0.138	-0.446
Area of molar M1	0.374	0.238	-0.525	0.653	-0.299
Eigenvalue	13	2.14	1.45	2.10	1.05
% of variation	48.27	7.94	5.36	7.78	3.881

Dental formula. (i 2/2, c 1/1, p 2/2; m 3/3) x 2 = total 32. This is the same as most species in *Sturnira*, except for *S. bidens* and *S. nana*.

Statistical assessment of morphological variation. Overall size appears as an indistinct trait among lowland species, as can be observed from the frequency distributions for FA and GLS (Fig. 4). The observed distribution for both traits approaches a normal curve (GLS: K-S = 0.03, $df = 278$, $P > 0.2$; FA: K-S = 0.05, $df = 278$, $P = 0.09$). This suggests a single statistically normal population; or otherwise, largely overlapping size variation among populations or species (i.e. *Sturnira lilium*, *S. luisi*, and *S. tildae*). A simple inspection on the central tendency and dispersion estimates among species, further suggests that sharp boundaries occur exclusively for the character states of ACM and M3W in *S. perla*, especially if we consider the confidence interval around the mean (Table 1). In a similar sense, there are no discernable or separate groups in the first two PCs, except for a noticeable boundary with consistently low values for PC II (Fig. 5A–B). High values in PC II represent mostly low values in M3W, as shown for loading indexes (Table 2). It is important to highlight that there is total overlap along PC I and PC III for *S. perla* in relation to its congeners. Thus, the differentiation based on this particular approach is one-dimensional. The other components above the unity eigenvalue completely overlap and are of minor comparative interest.

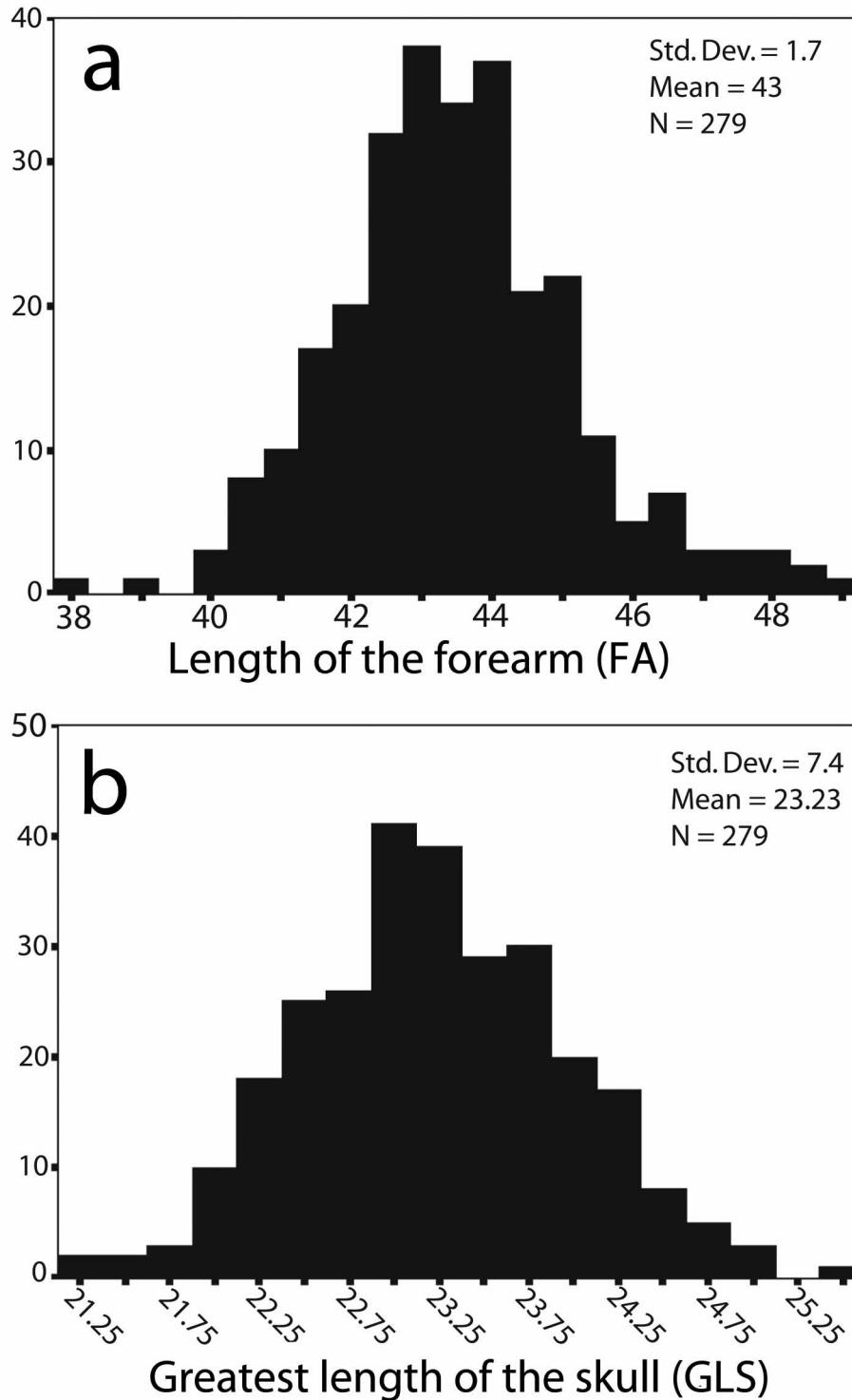


FIGURE 4. Frequency distribution for the characters FA and GLS. The delimitation of distinct groups is not possible along both distributions. Species included in both histograms are *Sturnira perla*, *S. luisi*, *S. lilium* and *S. tildae*.

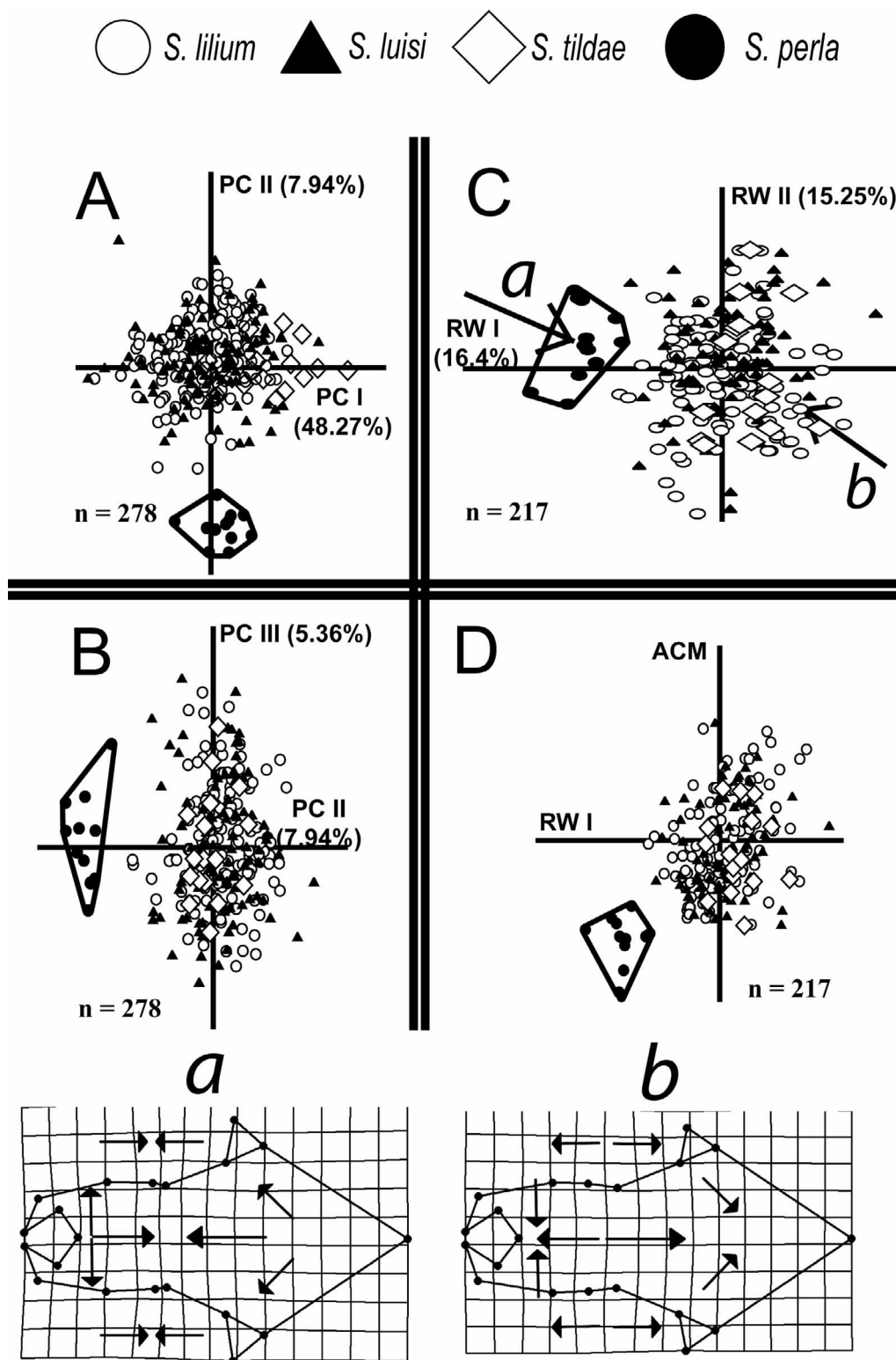


FIGURE 5. Aspects of the morphometric space for *Sturnira*. A) Plot of the first two principal components, based on the covariance of 27 interlandmark characters. B) Plot of the second and third principal components extracted from the covariation of interlandmark characters. C) Plot of the first two relative warps of geometric variation of the skull. D) Plot of the ACM and RW I. The percentage of explained variation by each PC or RW is in parenthesis. Despite the large overlap in other groups, *Sturnira perla*, highlighted by a convex hull, appears as a remarkably distinctive group. The arrows indicate the position of the estimated shape configurations depicted as *a* and *b*. The morphometric space around *S. perla* is for skulls with expanded braincases, wide and blunt rostrums and a contracted shape around the zygomatic area (*a*). An opposite pattern of shape variation is shown for the area around the selected sample that represents *S. lilium* (*b*).

TABLE 3. Results of a MANOVA for linear characters among species and sex. The MANOVA includes ACM and PC I – PC V as response variables. The results of the Bonferroni tests between marginal means for the factor species are shown only for those with $p < 0.05$ along ACM, PC I and PC II. Differences are concentrated around *Sturnira perla* along PC II and ACM, and around *S. tildae* along PC I. Sample size is *Sturnira lilium*=103, *S. luisi*=76, *S. perla*=12 and *S. tildae*=15.

MANOVA FOR PC I–PC V and ACM		<i>p</i> -value	Effect size (λ^2)
Equality of covariance	Box's M=208.11, F=1.26, df=126/3067.66	0.03	
Equality of error variances	ACM - Levene's F=2.26, df=7/198	0.03	
	PC I - Levene's F=2.53, df=7/198	0.02	
	PC II - Levene's F=1.72, df=7/198	0.11	
	PC III - Levene's F=0.48, df=7/198	0.85	
	PC IV - Levene's F=0.84, df=7/198	0.55	
	PC V - Levene's F=1.15, df=7/198	0.33	
Joint centroids (MANOVA)	Species - Pillai's trace=0.96, F=15.36, df=18/585	<0.001	0.32
	Sex - Pillai's trace=0.16, F=6.19, df=6/193	<0.001	0.16
	Species X Sex - Pillai's trace=0.52, F=0.58, df=18/585	0.92	0.02
Centroids (ANOVA)	ACM on Species - F=14.93	<0.001	0.21
	PC I on Species - F=15.06	<0.001	0.17
	PC II on Species - F=73.34	<0.001	0.55
	PC III on Species - F=0.41	0.81	0.01
	PC IV on Species - F=11.2	<0.001	0.15
	PC V on Species - F=8.05	<0.001	0.11
	ACM on Sex - F=2.58	0.11	0.01
	PC I on Sex - F=9.7	<0.01	0.05
	PC II on Sex - F=3.86	0.18	0.01
	PC III on Sex - F=2.92	0.07	0.02
	PC IV on Sex - F=0.33	0.47	<0.01
	PC V on Sex - F=6.25	<0.01	0.03
Marginal means (Bonferroni) for ACM	<i>S. perla</i> vs <i>S. lilium</i>	<0.001	
	<i>S. perla</i> vs <i>S. luisi</i>	<0.001	
	<i>S. perla</i> vs <i>S. tildae</i>	<0.001	
Marginal means (Bonferroni) for PC II	<i>S. perla</i> vs <i>S. lilium</i>	<0.001	
	<i>S. perla</i> vs <i>S. luisi</i>	<0.001	
	<i>S. perla</i> vs <i>S. tildae</i>	<0.001	
Marginal means (Bonferroni) for PC I	<i>S. tildae</i> vs <i>S. perla</i>	<0.001	
	<i>S. tildae</i> vs <i>S. lilium</i>	<0.001	
	<i>S. tildae</i> vs <i>S. luisi</i>	<0.01	

On the whole, the MANOVA points towards PC II as the factor responsible for the largest differences among species, with about half of the observed differences provided by this factor ($\eta^2 = 0.55$). No other factor shows a large effect in the MANOVA model (Table 3). Sexual differences are constant throughout, but with small effect size (i.e. interaction term with $P = 0.92$ and $\eta^2 < 0.02$). Based on the MANOVA, both ACM and PC II are responsi-

ble for the differences between *Sturnira perla* and the other species. In contrast to all other species, differences are also found for *S. tildae* along PC I; however, the differences along PC I are of minor impact relative to those attributable to PC II ($\eta^2 = 0.17$ vs. $\eta^2 = 0.55$, respectively) (Table 3). Overall, the MANOVA shows equal error variances for all response variables, except for PC I. The model does not comply with the requisite for equality of covariance among groups. We assume that the lack of homogeneity of variance-covariance matrices does not represent a serious violation of the assumptions of MANOVA, being this GLS a relatively robust model (Stevens 2002).

Boundaries are also present in the space spanned by the first two components of shape (i.e. RW 1 and RW 2), a demarcation that is also one-dimensional along RW 1 (Fig. 5C). Estimates of geometric deformation along the space depicted in Fig. 5C conform to the overall pattern of variation that makes *Sturnira perla* a clearly distinct shape. Along this space, skulls in the region delineated as *S. perla* tend to experience an expansion of the braincase, a shortening of the zygomatic region, and a widening of the rostrum, giving other species a comparatively more slender appearance (Fig. 5a-b). The clearest separation is, nevertheless, obtained in the space spanned by RW 1 and ACM, with a bidimensional demarcation along both characters. The lower corner of quadrant III in this plot is for skulls showing a combination of wide angles for ACM and the characteristic round skull as previously noted (Fig. 5D). Accordingly, contrast tests on the position of centroids for the space in Figs. 5C and 5D clearly indicate that it is only for *S. perla* where the observed differences are hardly due to chance. It is worth noting here that each model is robust (i.e. equal covariance matrices and error variance) and there are no differences in variation for shape between males and females for a given species (Table 4).

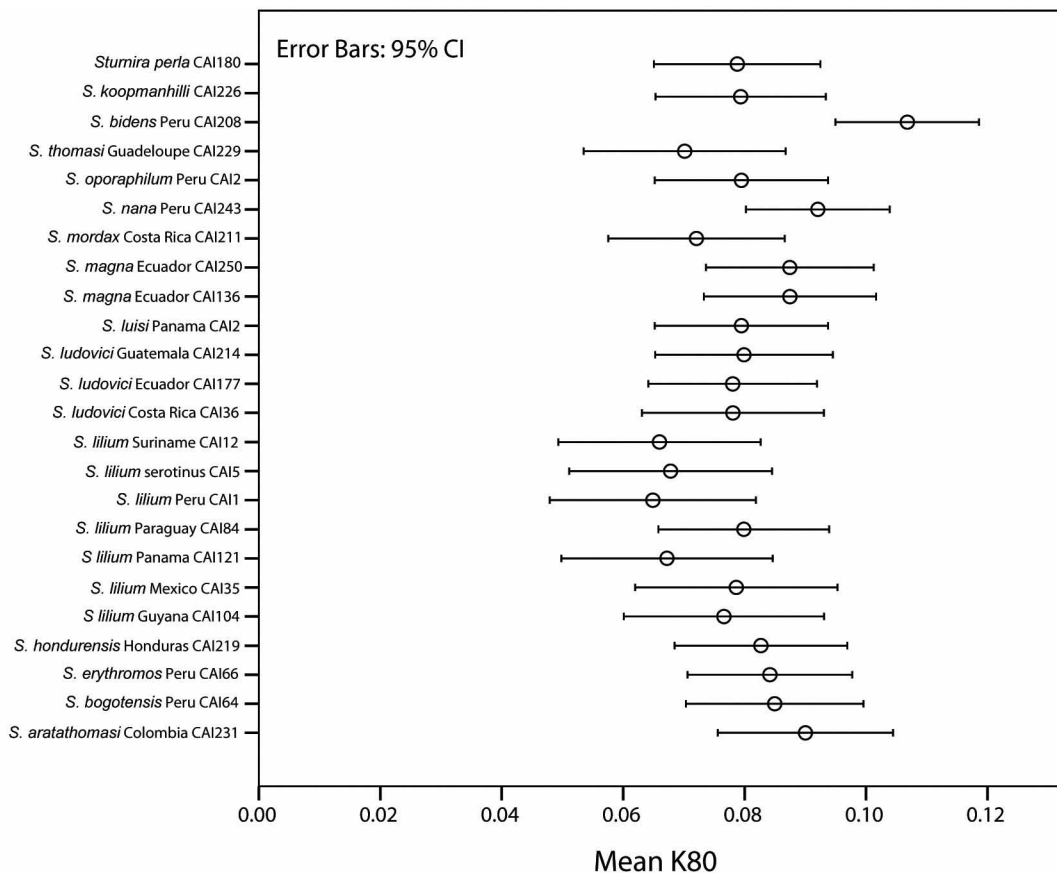


FIGURE 6. Mean distances for the Kimura 2-parameter model (K80) among species in *Sturnira*. The largest difference belongs to *S. bidens* from Peru (CAI208). *S. perla* maintains average distances to other species, but sufficiently large to support its individuality as an evolutionary lineage according to Bradley and Baker (2001).

Genetic distances and phylogenetic relationships. The matrix of distances according to the K80 model and the GTR+I+ Γ is found in Appendix 4, where the interpretation of the overall pattern is facilitated by color-coded cells. Both matrices are similar, with the same patterns of distance among taxa. For the case of K80 distances, the general pattern is for uniformity among all the ingroup species ($\bar{x}=8.0\%$, $sd=0.04$, $n=648$), except for relatively low

distances (0.05% - 2.5%) among the group of *Sturnira lilium* and *S. luisi* (CAI246, 229, 146, 121, 104, 12, 5, 1) and between the Central American *S. hondurensis* Goodwin (CAI219) and *S. ludovici* (CAI214). The largest average distance is for *S. bidens* from Peru (CAI208) (\bar{x} =11%, sd =0.03, n =27). Within the ingroup, *S. perla* maintains an average genetic distance of 7.1% (sd =0.03, n =27) relative to all other congeneric species (Fig. 6); hence, it remains clearly distinct from the lowland group of *S. lilium* and *S. luisi*.

It is remarkable that *Sturnira perla* seems to share more recent common ancestry with the highland group of species (e.g. *S. ludovici*, *S. oporaphilum*, *S. erythromos* and *S. bogotensis*)—including other typically lowland taxa as *S. tildae* and *S. magna*—rather than with emblematic and common species occurring at low elevations as are *S. lilium* and *S. luisi* (Fig. 7). The other lowland species (e.g. *S. lilium* and *S. luisi*) are related to *S. perla* through deeper nodes. The phylogenetic hypothesis presented here represents the one with the highest degree of resolution to be published so far.

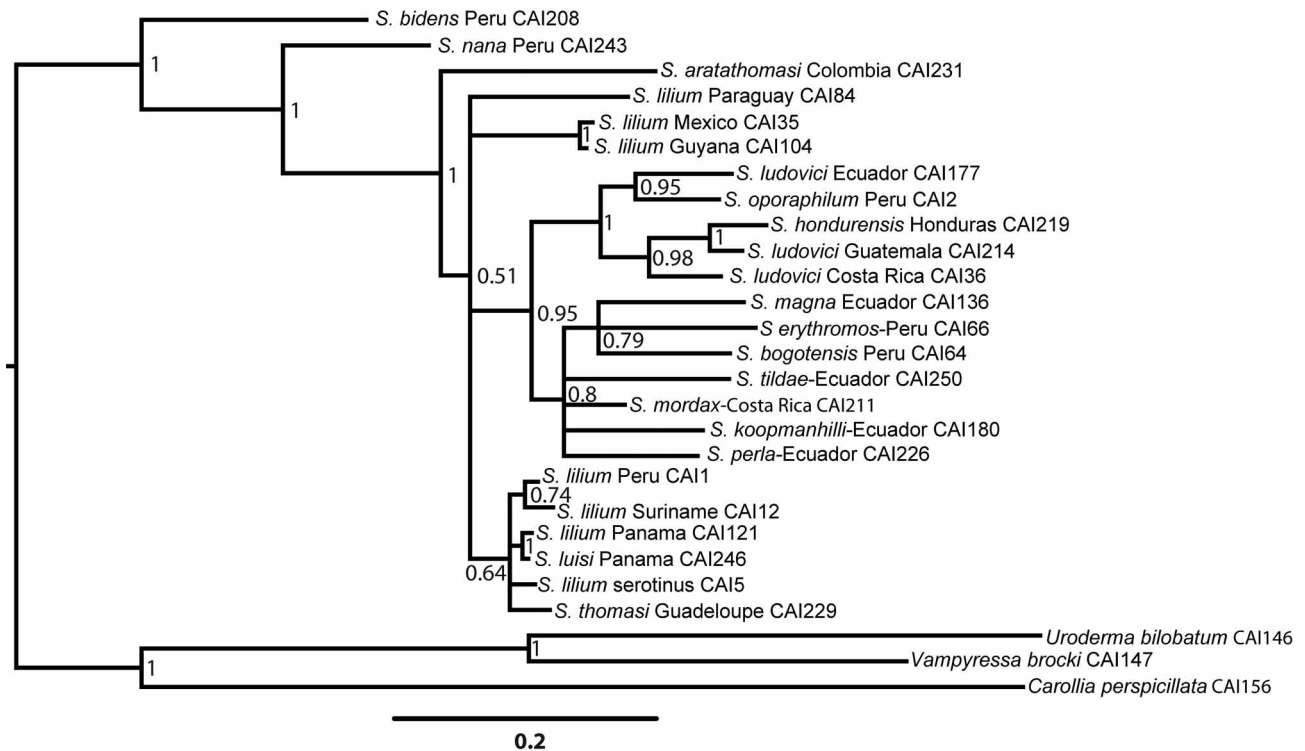


FIGURE 7. A phylogenetic hypotheses inferred from Bayesian posterior probabilities with the GTR+I+ Γ substitution model. This hypothesis is a consensus of agreement in bipartitions which are higher than 50% of all trees estimated (136500 trees). Support values at nodes are posterior probabilities. *S. perla* seems to be more related to highland taxa; a perspective that runs contrary to its general morphology (i.e. shape of cusps in lower molars) and previous phylogenetic hypotheses (Iudica, 2000).

Our contribution to understand phylogenetic relationships among *Sturnira*, although not central to the discussion of a new species, must be commented within the context of past phylogenetic propositions, which include all or most species of *Sturnira*. Owen (1987) used external body and cranial characters in an attempt to define the phenetic and phylogenetic relationships among species in the subfamily Stenodermatinae; his consensus tree did not resolve the relationships among most of the species in *Sturnira* (Fig 8A). The analysis by Pacheco and Patterson (1991) was the first phylogenetic assessment made exclusively for *Sturnira* (Fig. 8B). Their approach recognized both *S. oporaphilum* and *S. bogotensis* as different taxa and sister to *S. ludovici* and *S. erythromos* respectively. The other definable lineage was a polytomy formed by *S. lilium*, *S. luisi* and *S. thomasi*. A close relationship between *S. lilium* and *S. luisi*, on both morphological and genetic grounds was recognized, also reporting the presence of an undescribed species endemic to Ecuador, named as *S. sp. A* and currently known as *S. koopmanhilli* (McCarthy *et al.* 2006). More recently, Iudica (2000), in his unpublished thesis, defined 17 species based on a partial sequence of the cytochrome *b* gene (Fig. 8C). Iudica's work redefines *S. parvidens* and *S. hondurensis* as valid species. This phylogenetic analysis reinforced the hypotheses suggested previously by Pacheco and Patterson (1991), that *S. ludovici* and *S. erythromos* form sister pairs with *S. oporaphilum* and *S. bogotensis* respectively. Two new taxa are

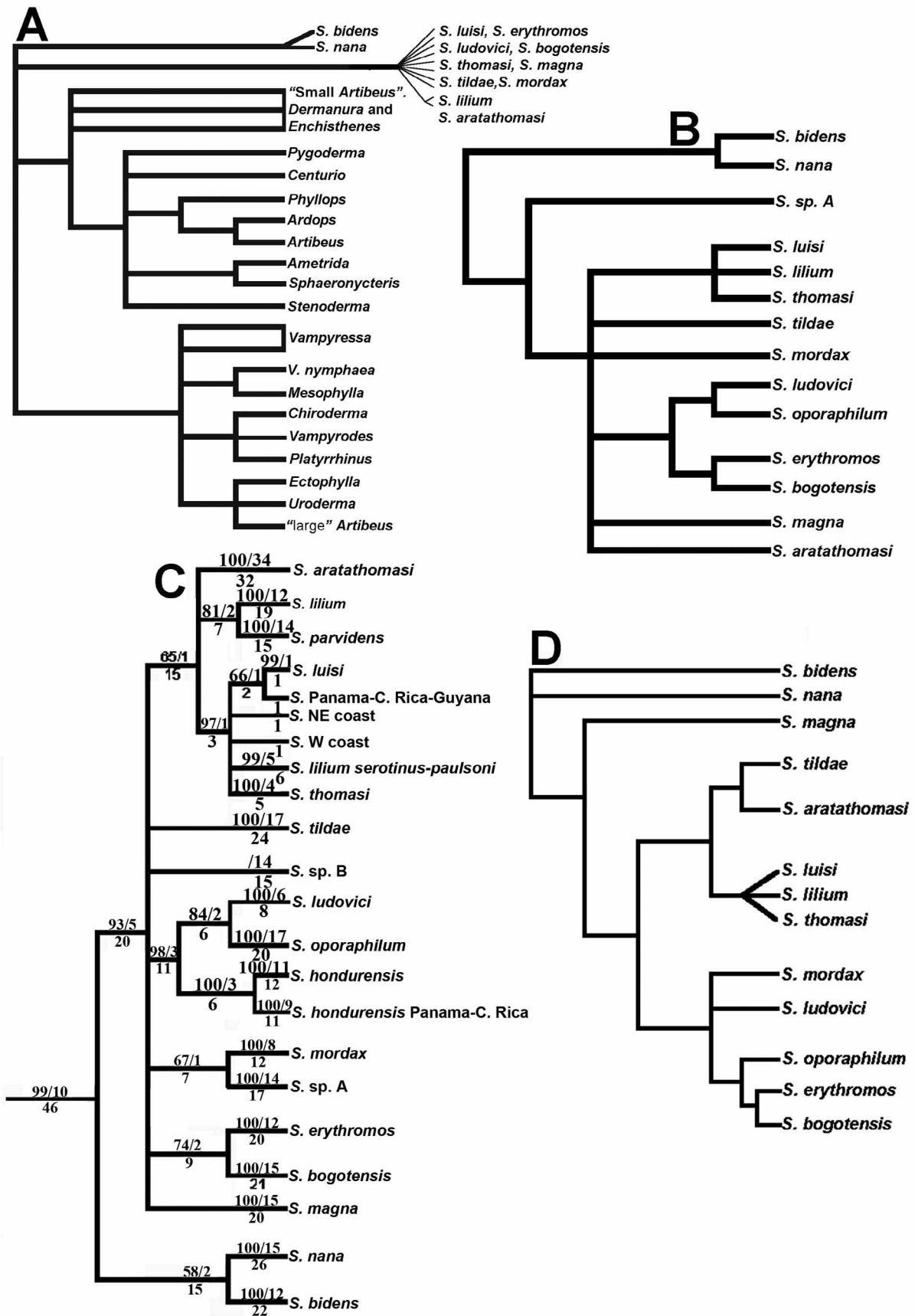


FIGURE 8. Past phylogenetic hypotheses for *Sturnira*: A) Owen (1987), B) Pacheco and Patterson (1991), C) Iudica (2000) and D) Villalobos and Valerio (2002). The four hypotheses depicted here are exact representations of the final consensus cladograms in the original publications. A, B and D lack support indexes for branch topology.

TABLE 4. Results of a MANOVA for the first two relative warps (RW I-RW II) and a MANOVA for ACM and RW I among species and sex. The results of the Bonferroni tests between marginal means for the factor species are shown only for those with $p < 0.05$ along ACM, RW I and RW II. The sole responsible for the observed differences is *Sturnira perla* on the three response variables. Sample size is *Sturnira lilium*=103, *S. luisi*=76, *S. perla*=12 and *S. tildae*=16.

MANOVA FOR RW I AND RW II		<i>p</i> -value	Effect size (λ^2)
Equality of covariance	Box's M=27.26, F=1.17, df=21/2551.49	0.27	
Equality of error variances	RW I - Levene's F=2.1, df=7/208	0.05	
	RW II - Levene's F=1.67, df=7/208	0.12	
Joint centroids (MANOVA)	Species - Pillai's trace=0.43, F=18.91, df=6/416	<0.001	0.21
	Sex - Pillai's trace=0.02, F=1.53, df=2/207	0.22	0.02
	Species X Sex - Pillai's trace=0.04, F=1.22, df=6/416	0.29	0.02
Centroids (ANOVA)	RW I on Species - F=14.93	<0.001	0.37
	RW II on Species - F=15.06	0.003	0.06
	RW I on Sex - F=2.58	0.41	<0.01
	RW II on Sex - F=9.7	<0.11	0.01
Marginal means (Bonferroni) for RW I	<i>S. perla</i> vs <i>S. lilium</i>	<0.001	
	<i>S. perla</i> vs. <i>S. luisi</i>	<0.001	
	<i>S. perla</i> vs. <i>S. tildae</i>	<0.001	
Marginal means (Bonferroni) for RW II	<i>S. perla</i> vs <i>S. lilium</i>	0.08	
	<i>S. perla</i> vs. <i>S. luisi</i>	1	
	<i>S. perla</i> vs. <i>S. tildae</i>	1	
MANOVA FOR RW I AND ACM		<i>p</i> -value	Effect size (λ^2)
Equality of covariance	Box's M=31.72, F=1.36, df=21/2568.61	0.13	
Equality of error variances	RW I - Levene's F=2.09, df=7/199	0.05	
	ACM - Levene's F=2.03, df=7/199	0.05	
Joint centroids (MANOVA)	Species - Pillai's trace=0.42, F=17.71, df=6/398	<0.001	0.21
	Sex - Pillai's trace=0.01, F=0.94, df=2/198	0.39	0.01
	Species X Sex - Pillai's trace=0.03, F=1.09, df=6/398	0.37	0.02
Centroids (ANOVA)	RW I on Species - F=39.61	<0.001	0.37
	ACM on Species - F=16.28	<0.001	0.2
	RW I on Sex - F=0.64	0.43	<0.01
	ACM on Sex - F=1.71	<0.19	<0.01
Marginal means (Bonferroni) for RW I	<i>S. perla</i> vs <i>S. lilium</i>	<0.001	
	<i>S. perla</i> vs. <i>S. luisi</i>	<0.001	
	<i>S. perla</i> vs. <i>S. tildae</i>	<0.001	
Marginal means (Bonferroni) for ACM	<i>S. perla</i> vs <i>S. lilium</i>	<0.001	
	<i>S. perla</i> vs. <i>S. luisi</i>	<0.001	
	<i>S. perla</i> vs. <i>S. tildae</i>	<0.001	

also mentioned in Iudica's hypothesis, corresponding to the *S. sp. A* and *S. sp. B* of Albuja (1999). Finally, Villalobos and Valerio (2002) combined the morphological data previously published by Owen (1987) and Pacheco and Patterson (1991) (Fig. 8D). They presented a consensus tree that, for the first time, characterized a monophyletic

group formed by *Sturnira lilium*, *S. luisi*, *S. tildae*, *S. aratathomasi*, and *S. thomasi*. They also resolved the relationships for the other species, with *S. magna* at the base of the *Sturnira* subgenus, and a ladder-like phylogenetic relationship among the remaining species, with *S. mordax* and *S. ludovici* at the base of this subgroup. In spite of being the first study to propose a fully resolved evolutionary hypothesis for the basal groups of the genus, Villalobos and Valerio (2002) did not include the rest of the taxa recognized as valid by Iudica (2000). Unfortunately, the only phylogenetic hypothesis to receive indexes of topological support was Iudica's (Fig. 8C).

Within this context, our hypothesis maintains the position of both *Sturnira bidens* and *S. nana* as basal. Yet, we suggest that *S. nana* shares a more common recent ancestor with all other species except for *S. bidens*, being this last species at the deepest node. There is considerable substructure in the taxa named as *S. lilium*, with at least two major branches, both of Central and South American origin. Also, *S. ludovici* shows large substructure, with one branch closer to *S. oporaphilum* from Peru and other closer to *S. hondurensis* from Honduras. *S. magna*, *S. erythromos* and *S. bogotensis* seem to share common ancestry. These three last taxa form a sister branch with *S. tildae*, *S. mordax*, *S. koopmanhilli* and *S. perla*, all four in a polytomy. Overall there is strong support for most nodes, except for relatively large uncertainty at two basal nodes holding most of the highland (e.g. *S. erythromos* and *S. ludovici*) and lowland species (e.g. *S. lilium* and *S. luisi*), with posterior probabilities of 0.51 and 0.64 respectively.

A detailed assessment of these hypotheses is beyond the scope of this study. For now, it may be safe to note that *S. perla* maintains relatively sound genetic distances to other species; having, in consequence a large branch in our proposed phylogeny. *S. perla* may have closer affinities to highland species (e.g. *S. ludovici* and *S. erythromos*) rather than to lowland taxa (e.g. *S. luisi* and *S. lilium*). In this case, Iudica (2000) was unable to find support for any sound relationship of *S. perla* (*S. sp. B*) to other taxa.

Conservation status. All 14 specimens known for this species come from a highly devastated area, suffering from an accelerated rate of deforestation (Brooks *et al.* 2002; Rival 2003; Fig. 3), amidst a human population affected from increasingly levels of social unrest and poverty (Sierra & Stallings 1998). The most recent collection records for *Sturnira perla* are from over a decade ago. The remaining Choco forest in the Neotropics represents 24% of the original landcover and only 18% in Ecuador (Sierra *et al.* 2002). Rates of deforestation in western Ecuador are comparatively high, ranging from 2% to 4% per year (Brooks *et al.* 2002; Sierra & Stallings 1998), one of the highest rates of loss in Latin America (Rudel 2000). Seven of the fourteen specimens known for *S. perla* were collected from an isolated patch consisting of 226 ha of primary forest, known as "Bosque Protector la Perla" (Botero 2004), and surrounded by vast expanses of monocultures consisting mostly of grazing lands, oil palms and banana trees. The Choco is well known for its biological richness (Gentry 1993), and high levels of vertebrate endemism (Mittermeier *et al.* 1999; Myers *et al.* 2000). According to Chapman (1917:106), the fauna living in the Choco is highly unique relative to other regions in South America. Some suggest that the Choco contains the highest number of plant species ever to have been reported for 0.1 ha, being perhaps the region with the highest richness of plant species on Earth (Galeano *et al.* 1998). However, this noteworthy but unknown species of mammal may be experiencing a tragedy. The same kind of tragedy that for Susy Sheppard, the late protector and owner of "La Perla", was "to see that wonderful forest, that covered hills and valleys, converted into grasslands" (Botero 2004).

Ecology. Considering that skull shape is a well known indicator of feeding behavior in bats (e.g. Freeman, 1981; Muchhala & Jarrín-V. 2002; Dumont and Herrel, 2003), the distinct shape of the skull in *Sturnira perla*, relative to the highly overlapped distribution that other lowland species have in morphometric space, suggests that this species may also be remarkably divergent in its ecological habits, especially those immediately related to feeding behavior. The ecological distinctiveness of *S. perla*, in direct relationship to its remarkable skull shape, remains as a hypothesis. Further studies are necessary in this sense, especially given the accelerated rate of deforestation in Northwestern Ecuador (i.e. the Southernmost Choco).

Discussion

This lowland new species could be hardly identified as highland taxa (e.g. *S. ludovici* and *S. erythromos* or *S. bidens* Thomas and *S. nana* Gardner and O'Neill), which remain distinct lineages, each with remarkably dissimilar morphologies (i.e. dental cusps or number of teeth). Also, previous phylogenetic hypotheses (Iudica 2000) suggested this new species is most closely associated with other lowland taxa. These are the reasons why we emphasized on measurements and contrasts within this particular region of morphometric space. Therefore, we compared

the new species with its closest sympatric relatives (i.e. *S. lilium*, *S. luisi* and *S. tildae*), since this is the space where the relevant details for the delimitation of the new species are found.

No one has previously analyzed the quantitative space of morphological variation for *Sturnira* from a geometric morphometric perspective, nor have its quantitative differences been assessed from an statistical point of view. It is along this line of evidence that a remarkable and previously unknown level of morphological overlap is possible to discern for *S. lilium*, *S. luisi* and *S. tildae* (as well as comparatively small genetic distances). The morphological overlap in these three species is a cautionary remark, suggesting to us the need to assess their presence and current distribution with a healthy dose of skepticism (c.f. Jarrín-V. & Kunz, 2008). In this sense, some may argue there is evidence suggesting that pelage coloration, shape of chin warts, hair density of the uropatagium, or particular dental cusps are valid boundaries for diagnosing or delimiting these three species. Yet, we have not found consistency among these character states (sensu Thiele 1993), at least not from a qualitative point of view, and much less from a quantitative and statistical perspective. So far, we do not argue against the existence of *S. lilium*, *S. luisi* and *S. tildae* as species, but suggest that their morphological boundaries should be appropriately interpreted and measured, and not only verbally mentioned as personal judgments of variation. It is not enough to say that a particular character state is evidence for morphological boundaries among species; instead, it is necessary to show proof of it.

The position of *Sturnira perla* in the phylogenetic hypothesis in this study contrasts largely with previous phylogenetic hypotheses that suggested this species is sister to lowland groups like *S. tildae*, *S. lilium* and *S. luisi* (i.e. Iudica 2000). Instead, the molecular evidence suggests that *S. perla* maintains large genetic distances to lowland groups, which in turn show relatively small distances among them (Appendix 4). Hence, not only does *S. perla* differentiate itself in terms of an extreme geometry of the skull, but also in relatively large genetic distances according to nucleotide substitution models (sensu Bradley & Baker 2001).

In conclusion, *S. perla* is a lowland species, having the “lingual ridge of lower molars divided into metaconid and entoconid” (de la Torre 1961); hence, distinguishing itself from all highland species (e.g. *S. ludovici* and *S. erythromos*), but also maintaining relatively large morphological and genetic distances with other lowland taxa having high cusps on the lower molars. Both molecular and morphological evidence suggests *S. perla* is an independent evolutionary lineage.

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APPENDIX 1

List of the 279 specimens used for the morphological diagnosis of *Sturnira perla*. The complete description of the museum acronyms is included in the main text. Samples are in alphabetical order by species and then by catalog number. Catalog numbers with an asterisk are those included in the geometric morphometric analysis. Numbers in parenthesis next to the localities for *S. perla* correspond to locations in Figure 3.

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
EPN	I66510	<i>S.lilium</i>	UNKNOWN	1300	Pichincha	Gualea	00°08'S 78°45'W	M
EPN	RM0045	<i>S.lilium</i>	15-aug-88	900	Napo	Huamani	00°43'06"S 78°36'42"W	M
EPN	RM0225	<i>S.lilium</i>	08-sep-88	900	Napo	Parroquia Cotundo, Huamani	00°43'06"S 78°36'42"W	M
EPN	RM0425	<i>S.lilium</i>	19-oct-88	900	Napo	Parroquia Cotundo, Huamani	00°43'06"S 78°36'42"W	F
EPN	RM0436	<i>S.lilium</i>	20-oct-88	900	Napo	Parroquia Cotundo, Huamani	00°43'06"S 78°36'42"W	M
EPN	RM0575	<i>S.lilium</i>	18-dec-88	900	Napo	Parroquia Cotundo, Centro Comunal Challuyacu	00°43'06"S 78°36'42"W	M
EPN	RM0601	<i>S.lilium</i>	09-jan-89	900	Napo	Parroquia Cotundo, Centro Comunal Challuyacu	00°43'06"S 78°36'42"W	M
QCAZ	campo-6571	<i>S.lilium</i>	29-sep-01	937	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	M
QCAZ	RMFN-104	<i>S.lilium</i>	01-dec-00	323	Sucumbíos	Shushufindi	0°11'S 76°39'W	F
QCAZ	93	<i>S.lilium</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	389	<i>S.lilium</i>	19-aug-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	390	<i>S.lilium</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	M F
QCAZ	391	<i>S.lilium</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	393	<i>S.lilium</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	425	<i>S.lilium</i>	16-aug-79	250	Los Ríos	Centro Científico Río Palenque	0°33'S 79°22'W	F
QCAZ	431	<i>S.lilium</i>	19-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	433	<i>S.lilium</i>	19-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	434	<i>S.lilium</i>	19-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	435	<i>S.lilium</i>	19-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	M
QCAZ	436	<i>S.lilium</i>	19-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	M
QCAZ	515	<i>S.lilium</i>	28-dec-91	230	Sucumbíos	Limoncocha, Reserva Biológica, "El Tablado"	0°24'S 76°38'W	M
MECN	613	<i>S.lilium</i>	13-jan-95	200	Napo	P. N. Yasuní, 24 Km S Pompeya Sur	0°38'S 76°34'W	F
MECN	675	<i>S.lilium</i>	18-may-95	200	Napo	P. N. Yasuní, 59 Km S Pompeya Sur	0°53'S 76°21'W	F
MECN	677	<i>S.lilium</i>	19-may-95	200	Napo	P. N. Yasuní, el Saladero, 76 Km S Pompeya Sur	0°25'S 76°37'W	M
MECN	773	<i>S.lilium</i>	13-oct-95	200	Napo	P. N. Yasuní, El Saladero, 76 Km S de Pompeya Sur	0°48'S 76°24'W	F
MECN	861	<i>S.lilium</i>	UNKNOWN	200	Napo	P. N. Yasuní, 73 Kms Pompeya Sur	0°48'S 76°24'W	F
MECN	880	<i>S.lilium</i>	21-feb-96	200	Napo	P. N. Yasuní, 66 Km S Pompeya Sur	0°48'S 76°24'W	F
QCAZ	911	<i>S.lilium</i>	15-jul-92	220	Sucumbíos	Cuyabeno, R.P.F., Laguna Grande	0°15'S 75°52'W	M
MECN	971	<i>S.lilium</i>	08-jun-96	200	Napo	P. N. Yasuní, 66 Km S Pompeya Sur	0°25'S 76°37'W	F
MECN	972	<i>S.lilium</i>	08-jun-96	200	Napo	P. N. Yasuní, 66 Km S Pompeya Sur	0°25'S 76°37'W	F
MECN	1066	<i>S.lilium</i>	06-oct-96	200	Napo	P. N. Yasuní, Pozo Ginta	UNKNOWN	F
QCAZ	1092	<i>S.lilium</i>	15-feb-93	540	Sucumbíos	Sinangüe, Río Aguarico alto; R.E.Cayambe-Coca	1°07'12"N 77°25'12"W	M
MECN	1125	<i>S.lilium</i>	22-aug-97	518	Napo	Tena, Parque Amazónico	0°58'29"S 77°48'W	M
QCAZ	1147	<i>S.lilium</i>	11-apr-95	250	Orellana	Yasuní, P.N. Pompeya Sur, Pozo Concordia (coordena- das de Pompeya)	0°25'12"S 76°37'12"W	M
QCAZ	1163	<i>S.lilium</i>	11-jun-93	240	Napo	Indillana, comuna, bocana del Río Indillana y Río Napo; P.N.Yasuní	0°25'S 76°38'W	F

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	1164	<i>S.lilium</i>	29-aug-95	1400	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	M
QCAZ	1168	<i>S.lilium</i>	29-aug-95	1401	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	F
QCAZ	1170	<i>S.lilium</i>	29-aug-95	1403	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	F
QCAZ	1175	<i>S.lilium</i>	29-aug-95	1404	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	F
QCAZ	1179	<i>S.lilium</i>	29-aug-95	1405	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	F
QCAZ	1184	<i>S.lilium</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	F
QCAZ	1190	<i>S.lilium</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	M
QCAZ	1200	<i>S.lilium</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	M
QCAZ	1202	<i>S.lilium</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	F
QCAZ	1238	<i>S.lilium</i>	01-sep-95	1100	Loja	Catacocha, recinto Playas, km 15 vía Macará	04°2'S 79°46'W	F
QCAZ	1245	<i>S.lilium</i>	14-nov-92	220	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F
QCAZ	1250	<i>S.lilium</i>	16-nov-92	221	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F
QCAZ	1252	<i>S.lilium</i>	18-nov-92	250	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F
QCAZ	1253	<i>S.lilium</i>	20-nov-92	250	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	M
QCAZ	1254	<i>S.lilium</i>	14-nov-92	250	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F
MECN	1390	<i>S.lilium</i>	24-apr-98	1166	Morona Santiago	P. N. Sangay, Cordillera de Huamboya, unión de los ríos Sangay y Huamboya	1°52'29.4"S 78°8'29.1"W	F
MECN	1393	<i>S.lilium</i>	24-apr-98	1400	UNKNOWN	Parque Nacional Sangay, Cordillera de Huamboya, entre los ríos Sangay y Huamboya	1°52'29.4"S 78°8'29.1"W	M
MECN	1394	<i>S.lilium</i>	24-apr-98	1166	Morona Santiago	P. N. Sangay, Cordillera de Huamboya, unión de los ríos Sangay y Huamboya	1°52'29.4"S 78°8'29.1"W	F
QCAZ	1399	<i>S.lilium</i>	05-mar-96	220	Orellana	El Edén, Río Napo bajo, cerca a la bocana del Río Yuturi	00°34'S 76°10'W	M
QCAZ	1400	<i>S.lilium</i>	06-mar-96	221	Orellana	El Edén, Río Napo bajo, cerca a la bocana del Río Yuturi	00°34'S 76°10'W	M
QCAZ	1438	<i>S.lilium</i>	06-mar-96	220	Orellana	El Edén, Río Napo bajo, cerca a la bocana del Río Yuturi	00°34'S 76°10'W	F
QCAZ	1464	<i>S.lilium</i>	26-apr-96	250	Esmeraldas	Pichiyacu, Río Cayapas; aguas arriba de Borbón (coordenadas de Borbón)	1°06'N 78°59'W	M

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	1465	<i>S.lilium</i>	26-apr-96	250	Esmeraldas	Pichiyacu, Río Cayapas; aguas arriba de Borbón (coordenadas de Borbón)	1°06'N 78°59'W	F
QCAZ	1611	<i>S.lilium</i>	17-feb-96	1350	Napo	Guagua Sumaco	0°28'S 77°36'W	F
QCAZ	1612	<i>S.lilium</i>	17-feb-96	1350	Napo	Guagua Sumaco	0°28'S 77°36'W	F
QCAZ	1614	<i>S.lilium</i>	18-feb-96	1351	Napo	Guagua Sumaco	0°28'S 77°36'W	F
QCAZ	1615	<i>S.lilium</i>	19-feb-96	1352	Napo	Guagua Sumaco	0°28'S 77°36'W	F
QCAZ	1616	<i>S.lilium</i>	21-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	M
QCAZ	1617	<i>S.lilium</i>	21-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1618	<i>S.lilium</i>	21-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1619	<i>S.lilium</i>	21-jun-96	620	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1652	<i>S.lilium</i>	05-jun-96	1450	Pichincha	Nanegal, comunidad de Chacapata	0°7'N 78°40'W	F
QCAZ	1712	<i>S.lilium</i>	22-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1713	<i>S.lilium</i>	22-jun-96	630	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1714	<i>S.lilium</i>	22-jun-96	615	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1715	<i>S.lilium</i>	22-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1716	<i>S.lilium</i>	22-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	M
QCAZ	1750	<i>S.lilium</i>	22-jun-96	650	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1751	<i>S.lilium</i>	22-jun-96	615	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1753	<i>S.lilium</i>	22-jun-96	615	Pichincha	Tinalandia	0°17'24"S 79°02'60"W	F
QCAZ	1922	<i>S.lilium</i>	24-oct-96	50	Manabí	Cabo Pasado, 17Km N vía San Vicente-Pedernales	0°22'48"S 80°29'24"W	F
QCAZ	1923	<i>S.lilium</i>	24-oct-96	50	Manabí	Cabo Pasado, 17Km N vía San Vicente-Pedernales	0°22'48"S 80°29'24"W	F
QCAZ	2031	<i>S.lilium</i>	09-jul-96	400	Pastaza	Villano	1°30'S 77°29'W	F
QCAZ	2032	<i>S.lilium</i>	09-jul-96	400	Pastaza	Villano	1°30'S 77°29'W	F
MECN	2065	<i>S.lilium</i>	01-oct-00	200	Sucumbíos	Tarapoa, Finca Cielito Lindo (coordenadas de Tarapoa)	00°08'S 76°25'W	M
QCAZ	2162	<i>S.lilium</i>	19-nov-96	35	Esmeraldas	Borbón, Río Cayapas, Río Chimbocal, comuna Corriente Grande	0°18'58.7"S 78°56'57.1"W	M
QCAZ	2172	<i>S.lilium</i>	19-nov-96	35	Esmeraldas	Borbón, Río Cayapas, comuna Viruela	01°13'N 79°03'W	M
QCAZ	2244	<i>S.lilium</i>	UNKNOWN	1480	Loja	San Pedro de Vilcabamba. Orillas del río Uchima	04°13'42"S 79°13'01"W	F
EPN	2277	<i>S.lilium</i>	15-sep-83	299	Napo	Lago Agrio	00°05'30"S 76°52'00"W	F

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Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	2515	<i>S.lilium</i>	30-apr-97	10	Esmeraldas	Terminal terrestre de Esmeraldas	0°57'N 79°39'W	F
EPN	2530	<i>S.lilium</i>	UNKNOWN		UNKNOWN	UNKNOWN	UNKNOWN	F
QCAZ	2602	<i>S.lilium</i>	15-jan-98	100	Guayas	El Triunfo, El Piedrero	0°15'S 79°10'W	F
QCAZ	2603	<i>S.lilium</i>	15-jan-98	100	Guayas	El Triunfo, El Piedrero	0°15'S 79°10'W	M
QCAZ	2604	<i>S.lilium</i>	15-jan-98	100	Guayas	El Triunfo, El Piedrero	0°15'S 79°10'W	M
QCAZ	2605	<i>S.lilium</i>	15-jan-98	100	Guayas	El Triunfo, El Piedrero	0°15'S 79°10'W	M
QCAZ	2606	<i>S.lilium</i>	15-jan-98	100	Guayas	El Triunfo, El Piedrero	0°15'S 79°10'W	F
EPN	2841	<i>S.lilium</i>	30-oct-83	200	Sucumbíos	Zancudo	0°35'S 75°29'W	F
EPN	3081	<i>S.lilium</i>	13-nov-83	300	Napo	San José de Payamino	00°30'S 077°19'W	F
QCAZ	3258	<i>S.lilium</i>	09-jun-99	600	Napo	Archidona	0°54'S 77°48'W	F
QCAZ	4471	<i>S.lilium</i>	06-apr-01	400	Loja	Mangurquillo, Bosque de la quebrada Achotes	4°2'60"S 80°15'36"W	F
QCAZ	4472	<i>S.lilium</i>	20-apr-01	180	Orellana	Comunidad de Garzacocha, Parque Nacional Yasuní	1°01'12"S 75°45'00"W	F
QCAZ	4522	<i>S.lilium</i>	05-mar-01	220	Orellana	Parque Nacional Yasuní, Estación Científica Yasuní, Km 9 vía NPF, pozo Tivacuno	00°38'S 76°30'W	F
QCAZ	4534	<i>S.lilium</i>	05-mar-01	220	Orellana	Parque Nacional Yasuní, Estación Científica Yasuní, Km 9 vía NPF, pozo Tivacuno	00°38'S 76°30'W	M
QCAZ	4585	<i>S.lilium</i>	04-sep-01	1276	Pastaza	Campamento Álvares-Miño. Antes del control policial de Mera	1°25'48"S 78°7'12"W	F
QCAZ	4704	<i>S.lilium</i>	10-nov-01	900	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	M
QCAZ	4704	<i>S.lilium</i>	10-nov-01	900	Pichincha	Unión del Río Toachi, Otongachi	0°19'48"S 78°56'24" W	M
QCAZ	4722	<i>S.lilium</i>	07-dec-01	900	Pichincha	Unión del Río Toachi, Otongachi	0°19'48"S 78°56'24" W	F
QCAZ	4723	<i>S.lilium</i>	07-dec-01	900	Pichincha	Unión del Río Toachi, Otongachi	0°19'48"S 78°56'24" W	M
QCAZ	4727	<i>S.lilium</i>	08-dec-01	900	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	F
QCAZ	4728	<i>S.lilium</i>	01-dec-01	900	Pichincha	Unión del Río Toachi, Otongachi	0°19'48"S 78°56'24" W	F
QCAZ	4729	<i>S.lilium</i>	UNKNOWN	900	Pichincha	Unión del Río Toachi, Otongachi	0°19'48"S 78°56'24" W	F
QCAZ	5066	<i>S.lilium</i>	UNKNOWN	323	Sucumbíos	Shushufindi	0°11'S 76°39'W	M
QCAZ	5638	<i>S.lilium</i>	07-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	F
QCAZ	5639	<i>S.lilium</i>	07-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	M
QCAZ	5640	<i>S.lilium</i>	10-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	M
QCAZ	5641	<i>S.lilium</i>	10-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	M

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Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	5643	<i>S.lilium</i>	10-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	M
QCAZ	5644	<i>S.lilium</i>	10-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	F
QCAZ	5645	<i>S.lilium</i>	10-aug-02	1050	Pastaza	Fuerte Militar Amazonas	1°30.389'S 78°03.642'W	F
QCAZ	5883	<i>S.lilium</i>	06-jan-02	900	Pichincha	Unión del Río Toachi, Oton- gachi	0°19'48"S 78°56'24" W	F
QCAZ	5884	<i>S.lilium</i>	06-jan-02	900	Pichincha	Unión del Río Toachi, Oton- gachi	0°19'48"S 78°56'24" W	F
QCAZ	5888	<i>S.lilium</i>	12-mar-02	1035	Azuay	Río Jubones	3°19'12"S 79°17'43,3"W	F
QCAZ	5947	<i>S.lilium</i>	10-mar-02	1618	Azuay	Santa Isabel, Tricay	03°16'S 79°19'W	F
EPN	6912	<i>S.lilium</i>	19-dec-69	200	Sucumbíos	Pañacocha	00°26'S 76°06'W	F
EPN	8217	<i>S.lilium</i>	18-nov-82	1160	Pastaza	Mera, Estación de Sanidad Ambiental	01°28'S 078°07'W	M
EPN	8257	<i>S.lilium</i>	18-nov-82	1160	Pastaza	Mera, Estación de Sanidad Ambiental	01°28'S 078°07'W	F
EPN	78913	<i>S.lilium</i>	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	F
EPN	79848	<i>S.lilium</i>	18-aug-79	300	Napo	Limoncocha	00°24'S 76°38'W	F
EPN	84106	<i>S.lilium</i>	11-aug-84	740	Imbabura	La Carolina (Gualupe), junto al río Mira (Peñas Negras)	00°45'24"N 78°17'18"W	F
EPN	84546	<i>S.lilium</i>	01-oct-84	50	Esmeraldas	2 Km al sur de Luis Vargas Torres	00°51'N 78°48'W	M
EPN	851439	<i>S.lilium</i>	24-aug-85	18	Esmeraldas	Parroquia Chontaduro, Mar- gen Izquierdo del Río Verde	00°56'N 79°23'16"W	M
EPN	871836	<i>S.lilium</i>	11-sep-87	971	Carchi	Parroquia Tobar Donoso, El Pailón	01°00'07"N 78°14'11"W	F
EPN	882103	<i>S.lilium</i>	02-apr-88	213	Napo	Cantón Aguarico, P. N. Yasuní	UNKNOWN	F
EPN	882349	<i>S.lilium</i>	02-dec-88	279	Orellana	Campamento Sunka	00°41'40"S 76°40'15"W	M
EPN	902851	<i>S.lilium</i>	17-sep-90	200	Napo	Codo Bajo	UNKNOWN	F
EPN	902875	<i>S.lilium</i>	19-sep-90	200	Sucumbíos	Codo Bajo	UNKNOWN	M
EPN	913218	<i>S.lilium</i>	10-oct-91	190	Napo	Nuevo Rocafuerte, Iripari	00°55'S 75°24'W	F
EPN	913219	<i>S.lilium</i>	10-oct-91	200	Sucumbíos	Reserva Cuyabeno, Secoya, Río Aguarico	00°02'36"N 77°06'24"W	F
EPN	913240	<i>S.lilium</i>	13-oct-91	180	Sucumbíos	Reserva Cuyabeno, Zábalo, Estero Sebuaya, Secoya, Río Aguarico	00°22'42"N 75°40'30"W	F
EPN	954195	<i>S.lilium</i>	30-apr-95	340	Sucumbíos	Cantón Cascales, Comuna Cofanes del Duvuno	00°02'S 77°07'W	F
EPN	954200	<i>S.lilium</i>	01-may-95	340	Sucumbíos	Cantón Cascales, Comuna Cofanes del Duvuno	00°02'S 77°07'W	M
EPN	954430B	<i>S.lilium</i>	23-jun-95	980	Napo	Archidona, Cooperativa Rucullacta, Tutacamo	00°53'S 77°34'W	M
EPN	954434	<i>S.lilium</i>	02-feb-96	360	Sucumbíos	Cantón Cascales, Pozo Dia- mante 3 (B1) (coordenadas de Cascales)	00°04'N 77°13'W	M
EPN	964613	<i>S.lilium</i>	08-sep-96	600	Napo	Cantón Loreto, Río Catapino	00°41'S 77°16'W	F

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Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
EPN	964799	<i>S.lilium</i>	24-nov-96	600	Manabí	Parque Nacional Machalilla, Los Tillales	01°36'51"S 80°41'50"W	M
EPN	974918	<i>S.lilium</i>	15-aug-97	570	Napo	Cantón Loreto, Santa Rosa de Arapino	00°49'54"S 77°28'39"W	F
EPN	974958	<i>S.lilium</i>	UNKNOWN	420	Pastaza	Cantón Arajuno, Parroquia Curaray, al norte del río Liquino	01°14'29"S 77°41'36"W	F
EPN	985124	<i>S.lilium</i>	14-jan-98	515	Pastaza	Cantón Pastaza, Parroquia Curaray, Río Ácaro	01°23'25"S 77°24'55"W	M
EPN	RM0367	<i>S.luisi</i>	12-oct-88	900	Napo	Huamaní	00°43'S 77°36'W	F
EPN	RM0618	<i>S.luisi</i>	12-jan-89	1000	Napo	Parroquia Cotundo, Centro Comunal Challuyacu	00°43'06"S 78°36'42"W	M
EPN	RR200	<i>S.luisi</i>	08-jan-83	1160	Pastaza	Mera	01°26'S 78°06'W	M
QCAZ	campo-6244	<i>S.luisi</i>	UNKNOWN	1400	Pichincha	Santo Domingo	0°07'N 78°48'W	F
QCAZ	JSTV-196	<i>S.luisi</i>	oct-02	662	Morona Santiago	Puente del Pastaza	UNKNOWN	F
EPN	26	<i>S.luisi</i>	27-jan-89	512	Pichincha	Lita	00°48'N 78°23'W	F
QCAZ	85	<i>S.luisi</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	88	<i>S.luisi</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	121	<i>S.luisi</i>	17-jul-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	394	<i>S.luisi</i>	15-sep-90	1100	Pichincha	Río Pachijal, 30 km NO de Nanegalito, cerca a Tulipe	00°05'00"N 78°47'01"W	M
QCAZ	396	<i>S.luisi</i>	23-mar-91	300	Esmeraldas	Playa del Muerto; 20 km O de La Unión	0°48'53"N 80°02'46"W	F
QCAZ	410	<i>S.luisi</i>	20-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	441	<i>S.luisi</i>	30-apr-94	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia	0°08'N 79°30'W	F
QCAZ	683	<i>S.luisi</i>	25-may-91	500	Napo	Jatun Sacha, Reserva; 10 km E de Misahuallí	1°03'36"S 77°35'60"W	F
QCAZ	945	<i>S.luisi</i>	11-jun-93	240	Orellana	Indillana, comuna, bocana del Río Indillana y Río Napo; P.N. Yasuní	0°25'S 76°38'W	M
QCAZ	947	<i>S.luisi</i>	11-Jun-1993	240	Napo	Indillana, comuna, bocana del Río Indillana y Río Napo; P.N. Yasuní	0°25'S 76°38'W	M
QCAZ	1097	<i>S.luisi</i>	15-may-93	540	Sucumbíos	Sinangüe, Río Aguatico alto; R.E. Cayambe-Coca	1°07'12"N 77°25'12"W	M
QCAZ	1119	<i>S.luisi</i>	30-dec-94	830	Napo	San Francisco de Borja	0°25'12"S 77°50'24"W	F
QCAZ	1120	<i>S.luisi</i>	30-dec-94	830	Napo	San Francisco de Borja	0°25'12"S 77°50'24"W	F
QCAZ	1122	<i>S.luisi</i>	30-dec-94	830	Napo	San Francisco de Borja	0°25'12"S 77°50'24"W	F
QCAZ	1244	<i>S.luisi</i>	14-nov-92	250	Sucumbíos	Reserva Biológica Limoncocha	0°24'S 76°38'W	M
QCAZ	1251	<i>S.luisi</i>	11-apr-98	1400	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F

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Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	1300	<i>S.luisi</i>	18-jul-95	200	Orellana	Parque Nacional Yasuní, Río Tiputini, Estación Científica PUCE	0°37'37"S 76°22'25"W	F
QCAZ	1644	<i>S.luisi</i>	05-jun-96	1450	Pichincha	Nanegal, comunidad de Chacapata	0°7'N 78°40'W	F
MECN	1644	<i>S.luisi</i>	08-oct-98	80	Esmeraldas	Reserva La Mayronga, Sector ENSOA, en el bosque	1.00N 79.22W	F
MECN	2044	<i>S.luisi</i>	12-may-00	40	Esmeraldas	Muisne, San Francisco, Recinto San Antonio, Río Chipa, Estero Pipón	00°36'N 80°01'W	M
MECN	2058	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Finca Cielito Lindo (coordenadas de Tarapoa)	00°08'S 76°25'W	M
MECN	2060	<i>S.luisi</i>	01-oct-00	200	Sucumbíos	Tarapoa, Finca Cielito Lindo (coordenadas de Tarapoa)	00°08'S 76°25'W	M
MECN	2061	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Finca Cielito Lindo (coordenadas de Tarapoa)	00°08'S 76°25'W	F
MECN	2063	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Finca Cielito Lindo (coordenadas de Tarapoa)	00°08'S 76°25'W	M
MECN	2069	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Comunidad Nueva Juventud (coordenadas de Tarapoa)	00°08'S 76°25'W	F
MECN	2070	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Comunidad Nueva Juventud (coordenadas de Tarapoa)	00°08'S 76°25'W	M
MECN	2072	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Comunidad Nueva Juventud (coordenadas de Tarapoa)	00°08'S 76°25'W	F
MECN	2074	<i>S.luisi</i>	oct-00	200	Sucumbíos	Tarapoa, Comunidad Nueva Juventud (coordenadas de Tarapoa)	00°08'S 76°25'W	F
MECN	2076	<i>S.luisi</i>	24-oct-96	200	Sucumbíos	Tarapoa, Comunidad Nueva Juventud (coordenadas de Tarapoa)	00°08'S 76°25'W	F
QCAZ	2451	<i>S.luisi</i>	15-apr-1997	1000	Zamora Chinchipe	Río Nangaritzza, Shaime	4°18'S 78°28'W	F
QCAZ	2580	<i>S.luisi</i>	22-aug-98	500	Pichincha	Occidente de Nanegal, Orillas del Río Guayllabamba, La Conquista, Hacienda de Jose Ivanovich	0°7'N 78°40'W	M
QCAZ	2641	<i>S.luisi</i>	16-jan-99	700	Napo	Archidona	0°54'S 77°48'W	F
QCAZ	2643	<i>S.luisi</i>	16-jan-99	700	Napo	Archidona	0°54'S 77°48'W	F
QCAZ	2710	<i>S.luisi</i>	UNKNOWN	200	Manabí	Portoviejo, Playa Prieta, San José	0°03'S 80°27'W	M
QCAZ	3132	<i>S.luisi</i>	UNKNOWN	700	Napo	Archidona	0°54'S 77°48'W	?
QCAZ	3261	<i>S.luisi</i>	09-jun-99	700	Napo	Archidona	0°54'S 77°48'W	F
QCAZ	3300	<i>S.luisi</i>	01-aug-90	250	Orellana	Parque Nacional Yasuní, Estación Científica Yasuní	0°08'N 79°30'W	M
QCAZ	3364	<i>S.luisi</i>	24-jul-98	389	Manabí	Playa Prieta, San José	0°03'S 80°27'W	—
QCAZ	4242	<i>S.luisi</i>	21-oct-00	1260	Pichincha	Santa Rosa, Río Toachi, cerca de Otongachi	0°21'00"S 78°55'12"W	M
QCAZ	4282	<i>S.luisi</i>	17-sep-01	900	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	F

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	4392	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	M
QCAZ	4393	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4394	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4395	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4396	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4397	<i>S.luisi</i>	16-jan-01	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4398	<i>S.luisi</i>	17-jan-01	304	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	M
QCAZ	4399	<i>S.luisi</i>	17-jan-01	304	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	F
QCAZ	4400	<i>S.luisi</i>	12-mar-01	345	Orellana	Laguna de San José de Chamanal, Bloque 18	0°9'31.9"S 76°58'32.0"W	F
QCAZ	4401	<i>S.luisi</i>	12-mar-01	345	Orellana	Laguna de San José de Chamanal, Bloque 19	0°9'31.9"S 76°58'32.0"W	F
QCAZ	4557	<i>S.luisi</i>	05-mar-01	220	Orellana	Parque Nacional Yasuní, Estación Científica Yasuní, Km 9 vía NPF, pozo Tivacuno	0°08'N 79°30'W	M
QCAZ	4631	<i>S.luisi</i>	12-oct-01	1072	Pastaza	Fuerte Militar Amazonas, Poblado de Shell	1°30'00"S 78°04'12"W	F
QCAZ	4659	<i>S.luisi</i>	10-dec-00	1100	Napo	Río Hollín	0°57'00"S 77°45'00"W	F
QCAZ	4712	<i>S.luisi</i>	01-dec-01	937	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	M
QCAZ	4723	<i>S.luisi</i>	07-dec-01	950	Pichincha	Unión del Río Toachi	0°18'58.7"S 78°56'57.1"W	M
QCAZ	5286	<i>S.luisi</i>	21-apr-00	10	Manabí	Pedernales, Vía a Santo Domingo	0°4'48"S 80°2'24"W	M
QCAZ	5596	<i>S.luisi</i>	20-jul-02	1330	Cotopaxi	Santa Rosa	0°20'55.6"S 78°55'4"W	F
QCAZ	5619	<i>S.luisi</i>	28-jul-02	1072	Morona Santiago	Shell, Fuerte Militar Amazonas, Base Militar, Campamento Iwía	1°30'00"S 78°04'12"W	M
QCAZ	5621	<i>S.luisi</i>	28-jul-02	1072	Morona Santiago	Shell, Fuerte Militar Amazonas, Base Militar, Campamento Iwía	1°30'00"S 78°04'12"W	M
QCAZ	5683	<i>S.luisi</i>	23-oct-02	1050	Morona Santiago	Platanera en Macas	2°18'18"S 78°07'04"W	F
QCAZ	5684	<i>S.luisi</i>	23-oct-02	1050	Morona Santiago	Platanera en Macas	2°18'18"S 78°07'04"W	F
QCAZ	5687	<i>S.luisi</i>	23-oct-02	1050	Morona Santiago	Platanera en Macas	2°18'18"S 78°07'04"W	F
QCAZ	5688	<i>S.luisi</i>	23-oct-02	1050	Morona Santiago	Platanera en Macas	2°18'18"S 78°07'04"W	F
QCAZ	5697	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	5698	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M
QCAZ	5707	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	5889	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	5890	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	5893	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M
QCAZ	5895	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M
QCAZ	5896	<i>S.luisi</i>	UNKNOWN	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	6124	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M
QCAZ	6125	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	M
QCAZ	6126	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	6127	<i>S.luisi</i>	24-oct-02	858	Morona Santiago	Platanera en Sucúa	2°27'34"S 78°10'31"W	F
QCAZ	6171	<i>S.luisi</i>	26-oct-02	662	Morona Santiago	Punte del Pastaza	UNKNOWN	F
EPN	66820	<i>S.luisi</i>	24-aug-66	360	Napo	Nororiente, Río Cotapino	00°42'S 77°26'W	M
EPN	78429	<i>S.luisi</i>	30-apr-78	50	Esmeraldas	Viche, Km 43 vía a Esmeraldas	UNKNOWN	M
EPN	78431	<i>S.luisi</i>	UNKNOWN	42	Esmeraldas	Viche, Km 43 vía a Esmeraldas	00°38'N 79°32'W	F
EPN	78439	<i>S.luisi</i>	UNKNOWN	42	Esmeraldas	Viche, Km 43 Río Esmeraldas	00°38'N 79°32'W	M
EPN	80237	<i>S.luisi</i>	15-feb-80	150	Esmeraldas	Urbina	00°58'N 78°40'W	?
EPN	80601	<i>S.luisi</i>	UNKNOWN	300	Pichincha	Monterey, a 31 Km vía Quininde, Esmeraldas	00°02'S 79°29'W	F
EPN	81334	<i>S.luisi</i>	27-mar-81	500	Pichincha	Centro Científico Río Palenque	00°33'S 79°22'W	M
EPN	81335	<i>S.luisi</i>	27-mar-81	500	Pichincha	Centro Científico Río Palenque	00°33'S 79°22'W	F
EPN	81336	<i>S.luisi</i>	27-mar-81	500	Pichincha	Centro Científico Río Palenque	00°33'S 79°22'W	F
EPN	84338	<i>S.luisi</i>	23-oct-84	125	Esmeraldas	3 Km al sur de San Miguel	00°43'N 78°55'W	M
EPN	84351	<i>S.luisi</i>	23-sep-84	125	Esmeraldas	3 Km al sur de San Miguel	00°43'N 78°55'W	F
EPN	851120	<i>S.luisi</i>	18-mar-85	40	Esmeraldas	Parroquia Tabiazo, Loma de Taquiama	00°58'N 79°42'W	F
EPN	851132	<i>S.luisi</i>	18-mar-85	40	Esmeraldas	Parroquia Tabiazo, Loma de Taquiama	00°58'N 79°42'W	F
EPN	851133	<i>S.luisi</i>	19-mar-85	40	Esmeraldas	Parroquia Tabiazo	00°58'N 79°42'W	F
EPN	851168	<i>S.luisi</i>	21-mar-85	40	Esmeraldas	Parroquia Tabiazo, Estero Tayuiama	00°58'N 79°42'W	F
EPN	851196	<i>S.luisi</i>	21-mar-85	40	Esmeraldas	Parroquia Tabiazo	00°58'N 79°42'W	F
EPN	913136	<i>S.luisi</i>		50	Esmeraldas	Mataje, Estero Molina	01°22'N 78°45'W	F

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
EPN	913216	<i>S.luisi</i>	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	F
EPN	954346	<i>S.luisi</i>	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	F
EPN	964726	<i>S.luisi</i>	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	UNKNOWN	M
EPN	964817	<i>S.luisi</i>	28-nov-96	160	Manabí	Parque Nacional Machalilla, Comunidad Vueltas Largas	01°33'S 80°42'W	F
EPN	964835	<i>S.luisi</i>	22-dec-96	500	Manabí	Espuela Perdida. E. Mocora alta. Parque Nacional Machalilla	01°36'S 80°41'W	M
EPN	975085	<i>S.luisi</i>	04-oct-97	1600	Napo	Archidona, Parroquia Cotundo, Río Sarayacu	01°44'S 79°29'W	F
QCAZ	119	<i>S.perla</i>	28-apr-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	F
QCAZ	120	<i>S.perla</i>	26-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	F
QCAZ	437	<i>S.perla</i>	30-apr-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	F
QCAZ	438	<i>S.perla</i>	30-apr-91	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	M
QCAZ	439	<i>S.perla</i>	30-apr-92	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	M
QCAZ	440	<i>S.perla</i>	30-apr-93	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	F
QCAZ	542	<i>S.perla</i>	28-jun-90	220	Pichincha	La Perla, Bosque Protector; 2 km S de La Concordia (5)	0°08'N 79°30'W	F
MECN	1665	<i>S.perla</i>	26-oct-98	80	Esmeraldas	Reserva La Mayronga, Sector ATP, en el bosque al borde del estero (3)	0°53'N, 79°10'W	M
QCAZ	1909	<i>S.perla</i>	24-oct-96	50	Esmeraldas	Borbón, Río Santiago, Estero María, comuna Selva Alegre (1)	1°06'N 78°59'W	F
QCAZ	1912	<i>S.perla</i>	24-oct-96	50	Esmeraldas	Borbón, Río Santiago, Estero María, comuna Selva Alegre (1)	1°06'N 78°59'W	F
QCAZ	1920	<i>S.perla</i>	24-oct-96	50	Esmeraldas	Borbón, Río Santiago, Estero María, comuna Selva Alegre (1)	1°06'N 78°59'W	M
QCAZ	2076	<i>S.perla</i>	01-oct-00	35	Esmeraldas	Borbón, Río Cayapas Angostura (2)	0°53'14"N 78°50'38"W	F
QCAZ	381	<i>S.tildae</i>	23-mar-91	300	Esmeraldas	Playa del Muerto; 20 km O de La Unión	0°48'53"N 80°02'46"W	M
QCAZ	946	<i>S.tildae</i>	11-jun-93	240	Orellana	Indillana, comuna, bocana del Río Indillana y Río Napo; P.N. Yasuní	0°25'S 76°38'W	F
QCAZ	948	<i>S.tildae</i>	11-jun-93	240	Orellana	Indillana, comuna, bocana del Río Indillana y Río Napo; P.N. Yasuní	0°25'S 76°38'W	F
QCAZ	1169	<i>S.tildae</i>	29-aug-95	1402	Loja	San Pedro de Vilcabamba; 3 km N de Vilcabamba	04°13'42"S 79°13'01"W	F
QCAZ	1191	<i>S.tildae</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	M
QCAZ	1209	<i>S.tildae</i>	30-aug-95	1340	Loja	Mazanamarca; 12 Km al sur de Vilcabamba	4°15'S 79°10'W	F

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APPENDIX 1. (continued)

Museum	Catalog #	Sp.	Date	Altitude	Province	Locality	Coordinates	Sex
QCAZ	1246	<i>S.tildae</i>	14-nov-92	250	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	M
QCAZ	1247	<i>S.tildae</i>	11-apr-98	1400	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	M
QCAZ	1248	<i>S.tildae</i>	11-apr-98	1400	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	M
QCAZ	1249	<i>S.tildae</i>	11-apr-98	1400	Sucumbíos	Limoncocha, Reserva Biológica	0°24'S 76°38'W	F
QCAZ	1659	<i>S.tildae</i>	05-jun-96	1450	Pichincha	Nanegal, comunidad de Chacapata	0°7'N 78°40'W	F
QCAZ	2128	<i>S.tildae</i>	25-oct-96	60	Guayas	Naranjal, La Unión	01°29'N 79°53'W	F
QCAZ	3874	<i>S.tildae</i>	24-oct-00	300	Orellana	Yasunín, Estación Científica Yasuní	0°37'37"S 76°22'25"W	M
QCAZ	5464	<i>S.tildae</i>	23-jun-02	886	Pichincha	Reserva Otongachi	0°19'32.4"S 78°56'34.4"W	F
EPN	84772	<i>S.tildae</i>	13-dec-84	1433	Pichincha	El Paraíso, Sitio La Villaflora	00°11'N 78°46'W	M
EPN	892512	<i>S.tildae</i>	11-jun-89	200	Pastaza	Pozo Danta	01°48'9"S 76°47'04"W	M
EPN	913203	<i>S.tildae</i>	08-oct-91	190	Sucumbíos	Iripari, Zancudo Cocha (coordenadas de Zancudo)	00°33'S 75°27'W	F
EPN	913204	<i>S.tildae</i>	08-oct-91	190	Napo	Nuevo Rocafuerte, Iripari (coordenadas de Nuevo Rocafuerte)	00°55'S 75°24'W	F

APPENDIX 2

Linear-measurement characters of the body and skull. Abbreviations are in parenthesis. Most characters are based on those used by Iudica (2000) and other authors (de la Torre, 1961 and Pacheco and Patterson, 1991).

Body characters

Forearm length (FA): from the olecranon process to the base of thumb and carpal bones

Third metacarpal length (MT3): from the distal end of the forearm (including carpals) to the distal end of the respective metacarpal

Fourth metacarpal length (MT4): from the distal end of the forearm (including carpals) to the distal end of the respective metacarpal

Fifth metacarpal length (MT5): from the distal end of the forearm (including carpals) to the distal end of the respective metacarpal

Tibia length (TL): from the articulation with the femur to the articulation with the foot

Hind foot length (HF): from the articulation to the tibia (tarsals) to the most distal tip of the claws

Skull characters

Height of the skull (HS): from the base of the skull to the highest point on the top of the braincase, this is measured by letting the skull rest on top of a glass surface and then subtracting the difference in the width of this surface.

Greatest length of the skull (GLS): from the anterior most part of the rostrum (including incisors), to the posterior most part of the occipital

Condylolincisors length (CIL): from the anterior most edge of the upper incisors, to the posterior most projection of the occipital condyles

Auditory bulla-incisors length (AUL): from anterior most edge of the upper incisors, to posterior most projection of the auditory bulla

Mastoid breadth (MB): least width of the skull at mastoid processes

Zygomatic breadth (ZB): greatest width across the zygomatic arches

Postorbital constriction (PC): least width of the skull at the postorbital constriction

Braincase length (BCL): from the posterior edge of the palate to the anterior most edge of the foramen magnum

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Braincase width (BCW): greatest length across parietals

Breadth across foramen magnum (BFM): greatest width between external surfaces of the occipital condyles

Nasal breadth

(NB): greatest width between internal borders of the nasal foramen

Palatal length (PL): shortest distance from the anterior border of the incisors to the posterior edge of the palate

Palatal breadth (PB): greatest width of palate across M1 (measured laterally)

Breadth across upper canines (C1C1): greatest width at cingulum from lateral edges between bases of the upper canines

Maxillary toothrow (MT): minimum length from anterior most edge of first upper canine to posterior most edge of the last upper molar

Area of Molar 1 (AM1): the product of the greatest width and greatest length of M1 at crown

Molar 3 width (M3W): greatest width of M3 at crown

Length of dentary (LD): from the anterior most point on incisors to the posterior most tip of the mandibular condyle

Length of mandibular toothrow (LMT): from anterior border of canine to the posterior border of the last molar

Height of coronoid process (HCP): perpendicular height from the ventral mandibular border (constriction) to the tip of the coronoid process

Dentary width at canines (c1c1): greatest width between the base of the lower canines

APPENDIX 3

The final matrix for molecular analysis included the following individuals: *Vampyressa brocki* Peterson (CAI147), *Uroderma bilobatum* Peters (CAI146) *Carollia perspicillata* Linnaeus (CAI156) as the outgroup. In the ingroup: *S. nana* from Peru (CAI243), *S. bidens* from Peru (CAI208), *S. thomasi* de la Torre & Schwartz from Guadeloupe (CAI229), *S. aratathomasi* Peterson & Tamsitt from Colombia (CAI231), *S. mordax* Goodwin from Costa Rica (CAI211), *S. ludovici* from Costa Rica (CAI36), *S. tildae* from Ecuador (CAI250), *S. liliium* from Paraguay (CAI84), *S. liliium* from Peru (CAI1), *S. liliium* from Suriname (CAI12) *S. liliium* from Panama (CAI121), *S. luisi* from Panama (CAI246) *S. liliium serotinus* (CAI5), *S. liliium* from Mexico (CAI35), *S. liliium* from Guyana (CAI104), *S. ludovici* from Ecuador (CAI177), *S. oporaphilum* Tschudi from Peru (CAI2), *S. hondurensis* Goodwin from Honduras (CAI219), *S. ludovici* from Guatemala (CAI214), *S. ludovici* from Costa Rica (CAI36), *S. erythromos* from Peru (CAI66), *S. bogotensis* Shamel from Peru (CAI64), *S. koopmanhilli* (CAI180), *Stumira* sp. B (CAI226).

APPENDIX 4

Distances based on K80 and GTR+I+ Γ models. The relative magnitude of distances is color-coded along a gamut of values. Blue corresponds to small distances and red to large distances. The outgroup (*Vampyressa brocki*, *Uroderma bilobatum* and *Carollia perspicillata*) maintains the largest distances relative to the ingroup (*Stumira* spp.). The smallest distances occur within the group of *Stumira liliium* and *S. luisi* (CAI246, 229, 146, 121, 104, 12, 5, 1). The largest distances within the ingroup correspond to *S. bidens* from Peru (CAI208). *S. perla* maintains average distances to the rest of congeneric species.

	CA147	CA1146	CA1156	CA1243	CA1208	CA1229	CA1231	CA1211	CA1136	CA1250	CA1184	CA11	CA112	CA1121	CA1246	CA15	CA135	CA1104	CA1177	CA12	CA1219	CA1214	CA136	CA166	CA164	CA180	CA1236
K80 Distance																											
<i>Vampyressa proscki</i> CA1147	0.142																										
<i>Urodelma bilobatum</i> CA1146	0.196	0.184																									
<i>Carallia perspicillata</i> CA1156	0.151	0.154	0.157																								
<i>S. nana</i> Peru CA1243	0.166	0.161	0.151	0.086																							
<i>S. blairi</i> CA1208	0.168	0.158	0.170	0.076	0.092																						
<i>S. thomasi</i> Guadeloupe CA1229	0.179	0.162	0.175	0.102	0.117	0.064																					
<i>S. aradziomasi</i> Colombia CA1231	0.170	0.159	0.158	0.085	0.102	0.063	0.080																				
<i>S. mordax</i> Costa Rica CA1211	0.171	0.166	0.165	0.111	0.130	0.081	0.099	0.058																			
<i>S. ludovici</i> Costa Rica CA136	0.172	0.166	0.172	0.095	0.116	0.080	0.085	0.060	0.083																		
<i>S. magna</i> Ecuador CA1250	0.173	0.160	0.161	0.090	0.106	0.066	0.089	0.068	0.083	0.079																	
<i>S. lillium</i> Paraguay CA184	0.166	0.157	0.167	0.074	0.094	0.018	0.060	0.058	0.076	0.071	0.059																
<i>S. lillium</i> Peru CA11	0.168	0.155	0.165	0.079	0.094	0.025	0.065	0.058	0.076	0.076	0.057	0.012															
<i>S. lillium</i> Suriname CA112	0.169	0.160	0.169	0.070	0.095	0.020	0.063	0.053	0.074	0.078	0.057	0.014	0.018														
<i>S. lillium</i> Panama CA1121	0.169	0.160	0.167	0.069	0.094	0.018	0.065	0.062	0.074	0.078	0.057	0.013	0.017	0.018													
<i>S. luisi</i> Panama CA1246	0.169	0.163	0.159	0.074	0.092	0.024	0.065	0.060	0.076	0.077	0.059	0.018	0.022	0.014	0.004												
<i>S. lillium</i> serotinus CA15	0.186	0.163	0.176	0.090	0.106	0.053	0.073	0.073	0.096	0.081	0.059	0.046	0.048	0.051	0.013	0.052											
<i>S. lillium</i> Mexico CA135	0.183	0.163	0.169	0.087	0.106	0.051	0.076	0.070	0.093	0.081	0.056	0.044	0.045	0.048	0.048	0.048	0.005										
<i>S. lillium</i> Guyana CA1104	0.166	0.154	0.161	0.083	0.113	0.073	0.092	0.052	0.073	0.077	0.079	0.064	0.066	0.071	0.067	0.070	0.078	0.076									
<i>S. ludovici</i> Ecuador CA177	0.171	0.157	0.162	0.092	0.113	0.068	0.093	0.058	0.078	0.081	0.074	0.071	0.070	0.080	0.067	0.078	0.078	0.078	0.044								
<i>S. ludovici</i> Peru CA12	0.160	0.165	0.160	0.106	0.106	0.082	0.098	0.067	0.080	0.091	0.074	0.071	0.070	0.080	0.068	0.068	0.078	0.078	0.062	0.057							
<i>S. hondurensis</i> Honduras CA1219	0.160	0.168	0.167	0.093	0.100	0.075	0.090	0.066	0.078	0.090	0.074	0.067	0.066	0.071	0.070	0.070	0.080	0.081	0.055	0.052	0.026	0.041					
<i>S. aparaphilum</i> CA1214	0.172	0.166	0.164	0.089	0.106	0.077	0.093	0.045	0.071	0.077	0.076	0.074	0.067	0.066	0.071	0.070	0.071	0.080	0.055	0.048	0.045	0.041					
<i>S. ludovici</i> Guatemala CA1214	0.161	0.160	0.175	0.090	0.114	0.074	0.086	0.061	0.071	0.077	0.074	0.074	0.074	0.062	0.078	0.080	0.078	0.076	0.074	0.081	0.081	0.085	0.070				
<i>S. ludovici</i> Costa Rica CA136	0.180	0.157	0.178	0.106	0.113	0.074	0.099	0.061	0.062	0.071	0.078	0.062	0.069	0.069	0.069	0.071	0.082	0.081	0.062	0.081	0.085	0.084	0.079	0.069			
<i>S. erythronos</i> Peru CA166	0.171	0.164	0.162	0.089	0.105	0.070	0.081	0.045	0.070	0.069	0.071	0.065	0.063	0.068	0.068	0.066	0.073	0.073	0.073	0.072	0.080	0.082	0.066	0.066	0.068		
<i>S. koparitis</i> Peru CA164	0.163	0.160	0.169	0.085	0.097	0.074	0.082	0.051	0.067	0.070	0.076	0.088	0.057	0.064	0.064	0.071	0.073	0.078	0.069	0.074	0.069	0.067	0.062	0.063	0.063	0.068	
<i>Sturimia</i> sp. A CA1180 (S. <i>roopmanhillii</i>)																											
<i>Sturimia</i> <i>perla</i> CA1226																											0.063

	CAI147	CAI146	CAI156	CAI243	CAI208	CAI229	CAI231	CAI121	CAI136	CAI250	CAI84	CAI1	CAI12	CAI121	CAI246	CAI5	CAI35	CAI104	CAI177	CAI2	CAI219	CAI214	CAI36	CAI64	CAI180	CAI226	
<i>Vampyressa brocki</i> _CAI147	0.569	1.145																									
<i>Uroderma bilobatum</i> _CAI146	0.834344	0.920	0.913																								
<i>Caecilia perspicillata</i> _CAI156	0.794157	0.880	0.873	0.327																							
<i>S._nana</i> _Peru_CA1208	0.910	0.996	0.989	0.263	0.403																						
<i>S._thomasi</i> _Guadeloupe_CA1229	0.977	1.062	1.055	0.329	0.470	0.204																					
<i>S._arakathomasii</i> _Colombia_CA1231	0.986	1.072	1.065	0.339	0.475	0.176	0.280																				
<i>S._mordax</i> _Costa_Rica_CA136	1.046	1.132	1.125	0.359	0.540	0.237	0.340	0.177																			
<i>S._magna</i> _Ecuador_CA1250	1.051	1.137	1.130	0.404	0.544	0.242	0.345	0.142	0.216																		
<i>S._lilium</i> _Paraguay_CA184	0.989	1.074	1.068	0.342	0.482	0.179	0.283	0.196	0.270	0.261																	
<i>S._lilium</i> _Peru_CA1	0.902811	0.988	0.981	0.255	0.396	0.044	0.197	0.169	0.243	0.234	0.172																
<i>S._lilium</i> _Suriname_CA112	0.912	0.997	0.990	0.264	0.405	0.053	0.206	0.178	0.252	0.243	0.181	0.028															
<i>S._lilium</i> _Panama_CA1121	0.899	0.984	0.978	0.252	0.392	0.041	0.193	0.165	0.240	0.230	0.168	0.033	0.042														
<i>S._luisi</i> _Panama_CA1246	0.897	0.982	0.975	0.249	0.390	0.038	0.191	0.163	0.237	0.228	0.166	0.031	0.040	0.012													
<i>S._lilium</i> _serotinus_CA15	0.901	0.986	0.979	0.253	0.394	0.042	0.195	0.167	0.241	0.232	0.170	0.035	0.044	0.031	0.029												
<i>S._lilium</i> _Mexico_CA185	0.938	1.024	1.017	0.291	0.431	0.128	0.232	0.204	0.279	0.270	0.207	0.121	0.130	0.117	0.115	0.119	0.116	0.114	0.112	0.111	0.110	0.104					
<i>S._lilium</i> _Guyana_CA1104	0.935	1.020	1.013	0.287	0.428	0.125	0.228	0.201	0.275	0.266	0.204	0.118	0.126	0.114	0.112	0.116	0.114	0.112	0.111	0.110	0.109	0.104					
<i>S._ludovici</i> _Ecuador_CA1177	1.053	1.139	1.132	0.406	0.546	0.243	0.347	0.184	0.258	0.249	0.263	0.236	0.245	0.232	0.230	0.234	0.234	0.268	0.260	0.260	0.263	0.260	0.263	0.263	0.263	0.263	0.263
<i>S._eporaphillum</i> _Peru_CA12	1.045	1.130	1.124	0.398	0.538	0.235	0.339	0.176	0.250	0.241	0.255	0.228	0.237	0.224	0.222	0.226	0.232	0.260	0.260	0.263	0.263	0.260	0.263	0.263	0.263	0.263	0.263
<i>S._hondurensis</i> _Honduras_CA1219	1.073	1.159	1.152	0.426	0.567	0.264	0.367	0.204	0.279	0.270	0.270	0.283	0.256	0.265	0.253	0.254	0.292	0.288	0.288	0.288	0.288	0.288	0.288	0.288	0.288	0.288	0.288
<i>S._ludovici</i> _Guatemala_CA1214	1.059	1.144	1.137	0.412	0.552	0.249	0.353	0.190	0.264	0.255	0.268	0.242	0.251	0.238	0.236	0.240	0.277	0.274	0.274	0.274	0.271	0.271	0.259	0.259	0.259	0.259	0.259
<i>S._evythromus</i> _Peru_CA166	1.068	1.153	1.146	0.420	0.561	0.258	0.362	0.158	0.190	0.224	0.277	0.251	0.244	0.231	0.229	0.249	0.286	0.282	0.282	0.282	0.271	0.256	0.243	0.243	0.243	0.243	0.243
<i>S._evythromus</i> _Peru_CA164	1.052	1.138	1.131	0.405	0.545	0.242	0.346	0.143	0.175	0.208	0.262	0.235	0.244	0.231	0.229	0.233	0.270	0.267	0.267	0.267	0.254	0.239	0.226	0.226	0.226	0.226	0.226
<i>Sturria</i> _sp._A_ from_Ecuador_CA1180	1.035	1.121	1.114	0.388	0.528	0.225	0.329	0.126	0.160	0.191	0.245	0.218	0.227	0.214	0.212	0.216	0.253	0.250	0.250	0.250	0.254	0.239	0.226	0.226	0.226	0.226	0.226
<i>Sturria</i> _sp._B_ from_Ecuador_CA1226	1.031	1.117	1.110	0.384	0.524	0.221	0.325	0.122	0.156	0.187	0.241	0.214	0.223	0.210	0.208	0.212	0.249	0.246	0.246	0.249	0.231	0.222	0.203	0.203	0.203	0.203	0.203