



**On the Taxonomic Identity of *Sturnira nana* Gardner and O'Neil, 1971 (Chiroptera: Phyllostomidae), from Ecuador, with the Description of a New Species of *Sturnira***

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On the taxonomic identity of *Sturnira nana*  
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description of a new species of *Sturnira*

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## ABSTRACT

The lesser yellow-shouldered bat, *Sturnira nana*, is a member of the most diverse genus of the New World leaf-nosed bats (Phyllostomidae). This species was considered endemic to Peru until 2009 when researchers captured a series of individuals in the Cordillera del Cóndor of southeastern Ecuador and identified them as *S. nana*. To assess the taxonomic status of this Ecuadorian population in relation to *S. nana* from Peru, we analyzed cytochrome *b* gene sequences and craniodental measurement data. In addition, we used principal component analysis to elucidate differences in climatic niches. Our analyses suggest that populations cur-

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rently identified as *S. nana* from Ecuador and Peru are genetically, morphologically, and ecologically divergent. Herein, we formally describe the population of small *Sturnira* from Ecuador as a new species.

## INTRODUCTION

*Sturnira* Gray, 1842, is the most diverse genus in the family Phyllostomidae, with 24 recognized species (Velazco and Patterson, 2013, 2014; Molinari et al., 2017; Velazco and Patterson, 2019) that collectively range from Mexico to northern Argentina (Solari et al., 2019). *Sturnira* species have traditionally been grouped into two subgenera. The subgenus *Corvira* Thomas, 1915, which included *Sturnira bidens* and *S. nana*, was characterized by two missing or reduced and probably functionless outer lower incisors (Gardner and O'Neil, 1971); by contrast, the subgenus *Sturnira* Gray, 1842, which includes all the remaining species (Gardner, 2008), was characterized by having four lower incisors. Using a multilocus phylogenetic approach, however, Velazco and Patterson (2013) challenged the recognition of two subgenera in *Sturnira*. They did not recover *bidens* and *nana* as a monophyletic group and recommended that *Corvira* be considered a synonym of *Sturnira*.

*Sturnira nana* Gardner and O'Neil, 1971, is one of the least known and the smallest species in the genus. For four decades, it was considered endemic to Peru, known only from the type locality in the montane forests of Ayacucho department. Subsequently, Boada (2011), Regalado and Albuja (2012), and Narváez-Romero et al. (2020) reported 11 specimens that morphologically resembled *S. nana* from the Cordillera del Cóndor in southern Ecuador. These Ecuadorian specimens were assigned to *S. nana*, thereby increasing the species' distributional range 1051 km to the north. However, the allopatric distribution of these populations and the presence of morphological characteristics unique to each suggest the need for a taxonomic and systematic revision of the species. Herein we evaluate the taxonomic status of both populations based on morphological, morphometric, molecular, and climatic data.

## MATERIALS AND METHODS

To assess the taxonomic status of populations of *Sturnira nana*, we used mitochondrial gene sequences and standard morphological and morphometric comparisons. The specimens examined and tissues used for this study, including the voucher material for sequences downloaded from GenBank (appendix 1) are deposited in the following museum collections: AMNH, American Museum of Natural History (New York, NY); CM, Carnegie Museum of Natural History (Pittsburgh, PA); CVULA, Colección de Vertebrados de la Universidad de Los Andes (Mérida, Venezuela); FMNH, Field Museum of Natural History (Chicago, IL); LSUMZ, Museum of Natural Science, Louisiana State University (Baton Rouge, LA); MECN, Museo Ecuatoriano de Ciencias Naturales, Instituto Nacional de Biodiversidad (Quito, Ecuador); MEPN, Museo de la Escuela Politécnica Nacional "Gustavo Orcés V." (Quito, Ecuador); MPEG, Museu Paraense Emilio Goeldi (Belém, Brazil); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque, NM); MUSM, Universidad Nacional Mayor de San Mar-

cos (Lima, Peru); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley, CA); MZFC-M, Colección de Mamíferos del Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (Mexico City, Mexico); QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador (Quito, Ecuador); ROM, Royal Ontario Museum (Toronto, Canada); TTU, Museum of Texas Tech University (Lubbock, TX); USNM, National Museum of Natural History, Smithsonian Institution (Washington, D.C.). Four uncataloged specimens were also used, with the field acronyms TJM (T.J. McCarthy), BDP (B.D. Patterson), CAI (C.A. Iudica). Lastly, the information on the genetic sequences of six specimens with field or collector acronyms FURB-SLA, IP, MN, SP, MN, and MNCRM have not been published, and the names of collectors or the museum in which they are deposited could not be verified (appendix 1).

**MORPHOLOGICAL AND MORPHOMETRIC ANALYSES:** We examined 10 specimens of *Sturnira nana* from Peru and eight specimens previously identified as *S. nana* from Ecuador (hereafter *Sturnira* EC). One Ecuadorian specimen identified as *Sturnira nana* by Narváez-Romero et al. (2020) is not included in these analyses because it could not be located. Likewise, two of the nine specimens reported by Boada (2011) were excluded from the analysis because the skulls were poorly preserved (appendix 2).

We evaluated 12 craniodental measurements following Velazco and Gardner (2012) and Velazco and Patterson (2014). In addition, we included forearm length. Other external measurements were omitted from our analyses due to the variable preservation methods of the specimens. All measurements were taken using digital calipers with 0.01 millimeters (mm) of accuracy, and each one was taken three times and averaged to keep experimental error within acceptable limits. The selected craniomandibular variables were:

- Breadth across canines (C-C): Distance across the outermost extremities of the cingula of the upper canines
- Breadth across molars (M2-M2): Greatest width across labial margins of the alveoli of the second upper molars
- Breadth of braincase (BB): Greatest breadth of the globular part of the braincase, excluding the mastoid and paraoccipital processes
- Condylolincisive length (CIL): Distance from the posteriormost margins of the occipital condyles to the anteriormost point on the upper incisors
- Condyllocanine length (CCL): Distance from the occipital condyles to the anterior border of the upper canines
- Dentary length (DENL): Distance from the midpoint of the mandibular condyle to the anteriormost point of the dentary
- Greatest length of skull (GLS): Distance from the posteriormost point on the occiput to the anteriormost point on the premaxilla, including the incisors
- Post-orbital constriction breadth (PB): Least breadth at the postorbital constriction
- Mandibular toothrow length (MANDL): Distance from the anteriormost surface of the lower canine to the posteriormost surface of m3

Maxillary toothrow length (MTRL): Distance from the anteriormost surface of the upper canine to the posteriormost surface of the crown of M3

Palatal length (PL): Distance from the posterior palatal notch to the anteriormost border of the incisive alveoli

Zygomatic breadth (ZB): Greatest breadth across the zygomatic arches

Descriptive univariate statistics (mean, standard deviation, and minimum and maximum values) were computed for each population sample.

To evaluate morphometric variation and divergence between *Sturnira nana* and *Sturnira* EC, we assessed the equality of means for both populations. Prior to selecting an appropriate statistical test for comparing morphological traits, we verified the normal distribution within each population using the Shapiro-Wilk test (Sokal and Rohlf, 1995).

We employed the independent-samples t-test to identify mean differences between the populations. Our null hypothesis (H0) suggested no significant difference in the means of the chosen morphological traits between the two populations, while the alternative hypothesis (H1) proposed the existence of a notable disparity in population means.

Additionally, a principal component analysis (PCA) was conducted on the 12 craniodental measurements. Principal components were derived from the variance-covariance matrix of log-transformed data. Statistical analyses were performed using SPSS statistics for Macintosh, v.25 (2017; IBM Corporation, Armonk, NY).

**MOLECULAR ANALYSES:** We extracted genomic DNA from seven *Sturnira* EC and five *Sturnira bidens* specimens (appendix 1). Total genomic DNA was extracted from 5 mg of tissue preserved in 95% ethanol using the Dneasy Tissue kit (Qiagen, Inc.) following the manufacturer's protocol for all samples of *Sturnira* EC. For the samples of *S. bidens*, the protocol of Bilton and Jaarola (1996) was used. DNA concentration and quality were measured using the NanoDrop™1000 v. 3.7. Cytochrome *b* gene sequences were amplified using the forward glo7L and reverse glo6H primers for polymerase chain reactions following Hoffman and Baker (2001). We used a matrix of 212 sequences that ranged in length from 700 to 1100 base pairs (bp), including 200 sequences obtained from GenBank (appendix 1) for representatives of most species of the genus *Sturnira* and selected outgroups (*Artibeus*, *Platyrrhinus*, *Uroderma*, *Vampyriscus*).

Sequences were edited and aligned using the ClustalOmega tool in Geneious Prime 2021.2 (Kearse et al., 2012). To choose the best-fit substitution models, we used the PartitionFinder2 (Lanfear et al., 2016) tool using the Bayesian information criterion (BIC) on the CIPRES Science Gateway platform (Miller et al., 2010) as a model-selection method. For the Bayesian inference (BI) analysis, the best substitution models for cytochrome *b* were: first codon position K80 + I + G, second codon position HKY + I + G, and third codon position GTR + I + G, while for Maximum Likelihood (ML) analysis, the substitution model was the General Time-Reversible (GTR + I + G) model.

The Bayesian inference analysis was conducted using MrBayes v3.2.2 on the CIPRES Science Gateway platform (Miller et al., 2010). The analysis was performed using the fol-

lowing settings: 4 Markov Chain Monte Carlo, 10 million generations, tree sampling every 1000 generations with the first 25% of all trees discarded as burn-in; the remaining trees were used to compute a 50% majority rule consensus tree. Convergence was evaluated by the effective sample size ( $ESS \geq 200$ ), and the potential scale reduction factor was also verified ( $PSRF = 1$ ). Posterior probability values  $\geq 95\%$  were considered strong support. Maximum likelihood analysis was conducted using the IQ-TREE (Trifinopoulos et al., 2016) tool in the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at>). The selected tree was determined by a bootstrap of 1000. Nodal support was evaluated using the nonparametric bootstrap (BS), where values  $< 70\%$  were considered low support. We calculated uncorrected pairwise (p) distances within and among samples of *Sturnira nana*, *S. EC*, and *S. bidens* using MEGA X (Kumar et al., 2018).

**CLIMATIC ASSESSMENT:** A total of 22 records (appendix 2) of three unique localities reported for *Sturnira EC* and four unique localities for *Sturnira nana* from Peru were used to perform a climatic principal component analysis, including nineteen climatic variables to assess variation in the climatic niches occupied by these geographically distant populations. Following Marchán-Rivadeneira et al. (2012), environmental data were extracted at each collection locality using the package “princomp” in R from 19 bioclimatic layers (Hijmans et al., 2005). Along with measures of isothermality, these layers included the following temperatures ( $^{\circ}\text{C}$ ): seasonality, annual mean, mean diurnal range, maximum of warmest month, minimum of coldest month, annual range, mean of wettest quarter, mean of driest quarter, mean of warmest quarter, and mean of coldest quarter; and the following data of precipitation (mm): annual, wettest month, driest month, seasonality, wettest quarter, driest quarter, warmest quarter, and coldest quarter. The environmental data matrix was standardized, and a principal component analysis was carried out to assess the variation in the climatic breadth throughout the geographic range that each proposed species occupy.

## RESULTS

**MORPHOLOGICAL ANALYSIS:** Three qualitative characteristics proved to be effective in differentiating *Sturnira nana* from *Sturnira EC*: (1) the braincase is more globular in *Sturnira EC* by comparison with *Sturnira nana* (fig. 1A, B); (2) the inner upper incisors in *Sturnira nana* are projected inward (fig. 1A: arrow) whereas these teeth in *Sturnira EC* are notably procumbent (fig. 1B: arrow); and (3) the anteroventral margin of the foramen magnum is more rounded in *Sturnira nana* (fig. 1E: arrow) whereas it is acutely angular in *Sturnira EC* (fig. 1F: arrow).

**MORPHOMETRIC ANALYSES:** Descriptive statistics are shown in table 1. The observed ranges for most measurements of these taxa overlap with the exception of breadth across canines (C-C), breadth of braincase (BB), and mandibular tooththrow length (MANDL), all of which are substantially smaller in *Sturnira nana*. Measurements of both taxa are normally distributed (Shapiro-Wilk significance values  $> 0.05$ ; not shown), and two-tailed t-test revealed statistically significant sample differences in four measurements: braincase breadth (BB), mandibular tooththrow length (MANDL), canine breadth (C-C), and zygomatic breadth (ZB).



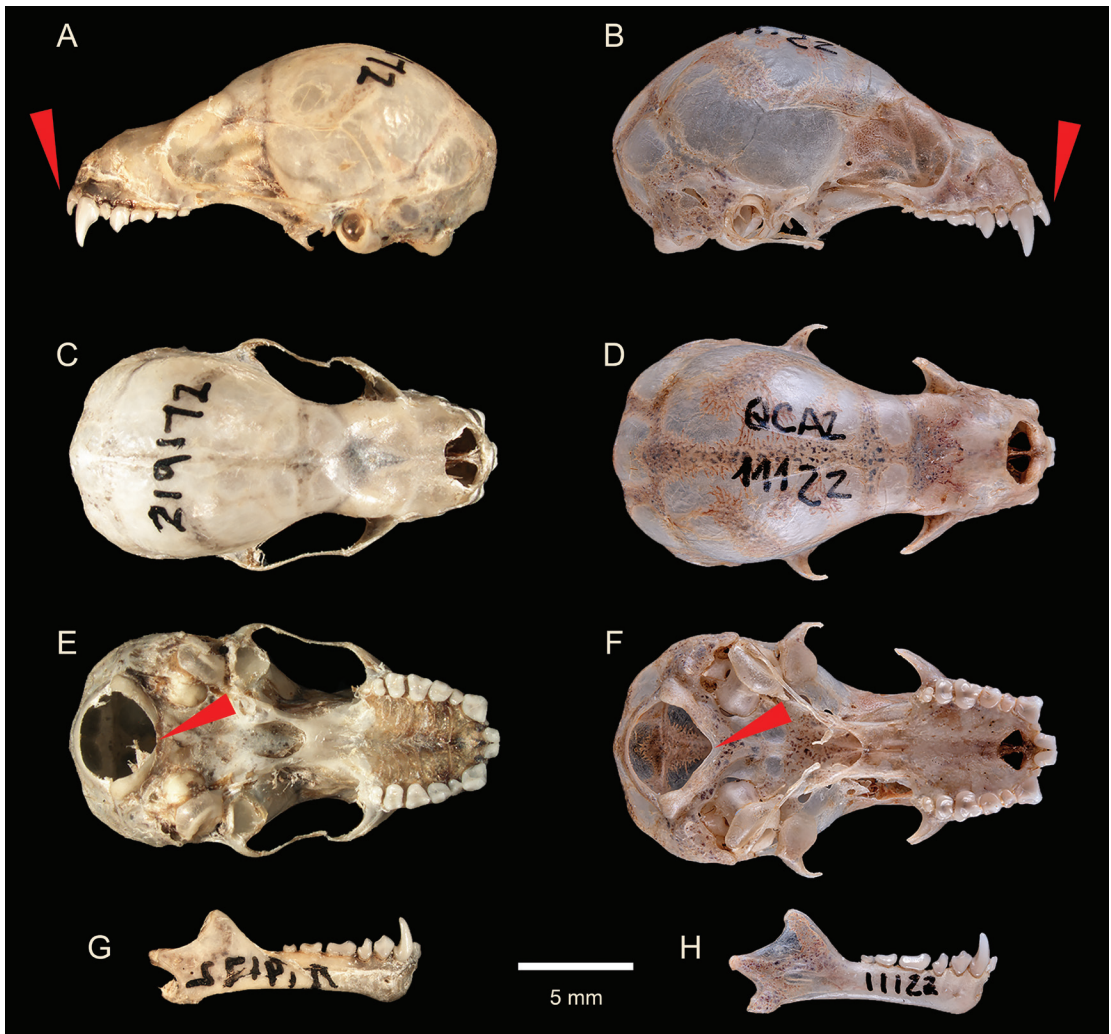


FIGURE 1. A, B. Lateral, C, D. dorsal, and E, F. ventral views of the skulls and G, H. lateral view of the mandibles of *Sturnira nana* (AMNH 219172, left column) and *Sturnira EC* (QCAZ 11122, right column). Red arrows show the differences between the two skulls.

The first three principal components explained 82.35% of the total variance in the log-transformed data (table 2). The first principal component (with coefficients varying in sign and magnitude) is a shape factor that largely accounts for variation in canine breadth (C-C), breadth of braincase (BB), mandibular tooththrow length (MANDL), and zygomatic breadth (ZB), whereas PC2 (with uniformly positive elements) appears to reflect general size variation, with notably large coefficients for condyloincisive length (CIL), greatest length of skull (GLS), and palatal length (PL). Consistent with the univariate test results, species separation in the plane of the first two axes (fig. 2) is completely accounted for by PC1, whereas PC2 accounts for intraspecific variation.

**PHYLOGENETIC ANALYSES:** Our maximum-likelihood and Bayesian analyses recovered the monophyly of the genus *Sturnira* with strong support. Additionally, both the ML and BI trees

TABLE 1. Measurements (in mm) of *Sturnira nana* and *Sturnira* EC. Tabulated sample statistics include the observed range and the mean plus or minus one standard deviation. N = sample size.

|       | <i>S. nana</i><br>(N = 10)  | <i>Sturnira</i> EC<br>(N = 8) | Difference <sup>a</sup> |
|-------|-----------------------------|-------------------------------|-------------------------|
| C-C   | 4.05–4.38<br>4.18 ± 0.11    | 4.42–4.76<br>4.52 ± 0.13      | 0.000**                 |
| M2-M2 | 5.51–5.93<br>5.72 ± 0.12    | 5.63–6.09<br>5.86 ± 0.19      | 0.100                   |
| BB    | 8.20–8.70<br>8.47 ± 0.17    | 8.71–9.14<br>8.89 ± 0.14      | 0.000**                 |
| CCL   | 15.98–16.57<br>16.27 ± 0.19 | 15.71–16.32<br>16.01 ± 0.22   | 0.018*                  |
| CIL   | 16.13–17.00<br>16.58 ± 0.28 | 16.10–17.06<br>16.71 ± 0.32   | 0.574                   |
| DENL  | 11.42–12.00<br>11.67 ± 0.23 | 11.33–11.70<br>11.55 ± 0.13   | 0.231                   |
| GLS   | 18.49–19.43<br>18.89 ± 0.31 | 18.28–19.20<br>18.33 ± 0.30   | 0.437                   |
| PB    | 4.60–5.00<br>4.76 ± 0.13    | 4.73–5.00<br>4.85 ± 0.09      | 0.127                   |
| MANDL | 4.98–5.73<br>5.52 ± 0.22    | 5.79–6.26<br>6.06 ± 0.20      | 0.000**                 |
| MTRL  | 4.78–5.17<br>4.99 ± 0.14    | 4.73–5.00<br>4.92 ± 0.10      | 0.198                   |
| PL    | 7.49–8.40<br>7.85 ± 0.25    | 7.13–8.50<br>7.75 ± 0.54      | 0.226                   |
| ZB    | 9.66–10.25<br>10.01 ± 0.21  | 10.07–10.94<br>10.57 ± 0.33   | 0.001**                 |

<sup>a</sup> Results of two-tailed t-tests for equality of sample means (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ ). Levene's tests for equality of sample variances were not significant for any variable.

showed similar ingroup topologies with the subgenus *Corvira* (as traditionally recognized) encompassing three lineages (*Sturnira bidens*, *S. nana*, and *S. EC*) and the subgenus *Sturnira* containing all the other analyzed congeneric species in three clades (A, B, and C; fig. 3). Within the subgenus *Corvina*, sequences of *S. bidens* formed a well-supported clade, and *Sturnira nana* from Peru (AF435253, AF435254) was recovered in a well-supported clade sister to an equally well-supported *Sturnira EC* (QCAZ 11116–11119, 11121–11123).

The mean pairwise uncorrected sequence distance between *Sturnira nana* and *Sturnira EC* is 7.45%, whereas the distance between *Sturnira EC* and *Sturnira bidens* is 9.87% (table 3). Computed intraspecific divergence values varied across these species, ranging from an average of 0.08% within *Sturnira EC* to 6.09% within *Sturnira bidens* (table 4).

CLIMATIC ANALYSIS: Our climatic PCA showed that populations of *Sturnira nana* and *Sturnira EC* occupy different climatic niche spaces (fig. 4). The first two PCs accounted cumulatively for 87.55% of the climatic variation (table 5). Factor loadings on PC1, which effectively



TABLE 2. Principal components coefficients based on a covariance matrix of the 12 linear measurements for adult specimens of *Sturnira nana* and *Sturnira* EC.

|                        | Components |        |        |
|------------------------|------------|--------|--------|
|                        | PC 1       | PC 2   | PC 3   |
| C-C                    | 0.298      | 0.151  | 0.007  |
| M2-M2                  | 0.157      | 0.069  | 0.205  |
| BB                     | 0.381      | 0.101  | 0.073  |
| CCL                    | -0.176     | 0.339  | 0.337  |
| CIL                    | 0.117      | 0.455  | -0.316 |
| DENL                   | -0.131     | 0.268  | -0.064 |
| GLS                    | 0.005      | 0.457  | 0.586  |
| PB                     | 0.081      | 0.012  | 0.225  |
| MANDL                  | 0.496      | 0.054  | -0.177 |
| MTRL                   | -0.023     | 0.128  | 0.292  |
| PL                     | -0.260     | 0.572  | -0.472 |
| ZB                     | 0.599      | 0.116  | -0.040 |
| Proportion of variance | 52.61%     | 17.96% | 11.78% |

TABLE 3. Uncorrected average pairwise (p) sequence divergence (scaled as percentages, below the diagonal) and their standard errors (above the diagonal) at the cytochrome *b* locus among species of the subgenus *Corvira*. Sample sizes: *S. bidens* ( $N = 7$ ), *S. nana* ( $N = 2$ ), and *S. EC* ( $N = 7$ ).

|                        | <i>Sturnira bidens</i> | <i>Sturnira nana</i> | <i>Sturnira EC</i> |
|------------------------|------------------------|----------------------|--------------------|
| <i>Sturnira bidens</i> |                        | 0.95                 | 0.77               |
| <i>Sturnira nana</i>   | 7.87                   |                      | 0.87               |
| <i>Sturnira EC</i>     | 9.87                   | 7.45                 |                    |

TABLE 4. Uncorrected average pairwise (p) sequence differences and their standard errors (S.E.) within species of the subgenus *Corvira*.

|                        | Distance (%) | S.E. (%) |
|------------------------|--------------|----------|
| <i>Sturnira bidens</i> | 6.09         | 0.40     |
| <i>Sturnira nana</i>   | 0.13         | 0.15     |
| <i>Sturnira EC</i>     | 0.08         | 0.03     |

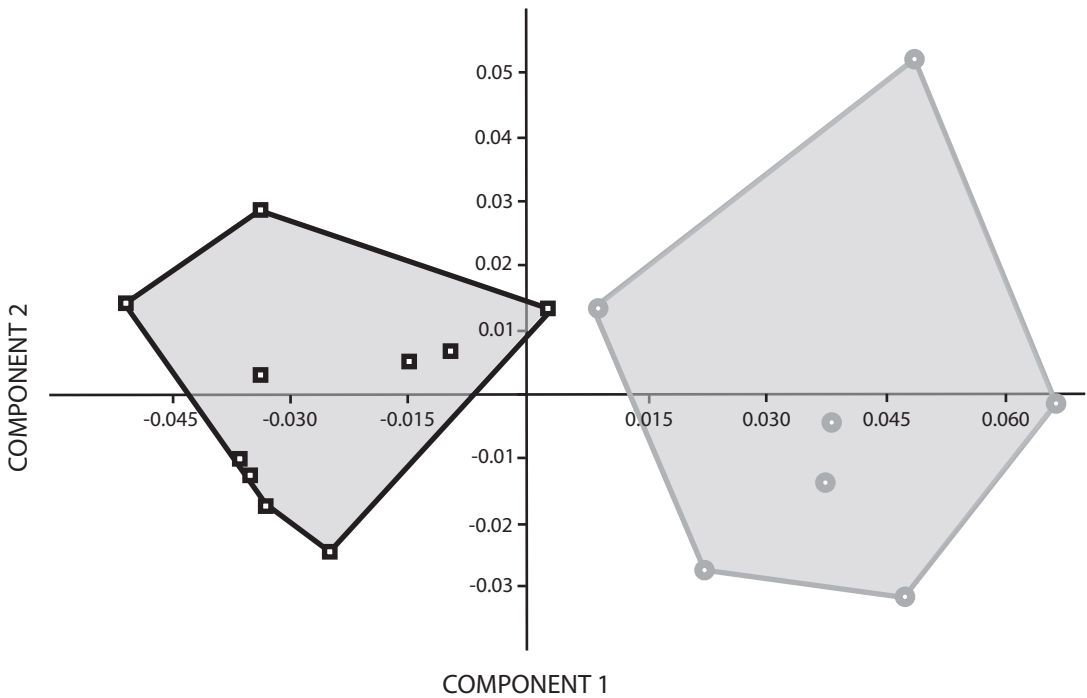


FIGURE 2. Principal component analysis of 12 craniomandibular measurements in *Sturnira nana* (N = 10, squares) and *Sturnira EC* (N = 8, circles).

accounts for all the climatic divergence between these populations, suggest differences in temperature and precipitation variables.

Climatic variation in the areas where *Sturnira nana* has been reported shows an average temperature of 22.2° C annually compared to the annual average of 19.7° C for *Sturnira EC*. Even more significant variation can be seen in precipitation, accumulating 1512 mm annually for *S. nana* and 2243 mm for *S. EC*, and seasonality (standard deviation of the monthly temperature multiplied by 100), where *S. nana* shows a value of 78.8 and *S. EC* of 50.0. So, even though both species inhabit areas with moderate temperatures (warmer for *S. nana*), *S. EC* occupies substantially wetter and more thermally stable climates throughout the year.

**TAXONOMIC REMARKS:** Our study confirms the distinctness of *Sturnira nana* and *S. EC* previously inferred by Boada et al. (2011) based on different lines of evidence. Morphological differences between the two species are evident in three distinct qualitative characters and several craniodental variables (e.g., C-C, BB, ZB, MANDL) that display significant size differences. Moreover, differences in morphometric space, as indicated by the principal component analysis, revealed variations in size variables. In addition, the molecular analysis showed that sequences from *Sturnira EC* formed a well-supported clade, distinct from the clade formed by sequences of *Sturnira nana*, with a substantial genetic distance between the two. Finally, both populations differ in their climatic niche spaces. Based on the aforementioned information, we conclude that *S. EC* represents an unnamed species of *Sturnira* that we describe below.

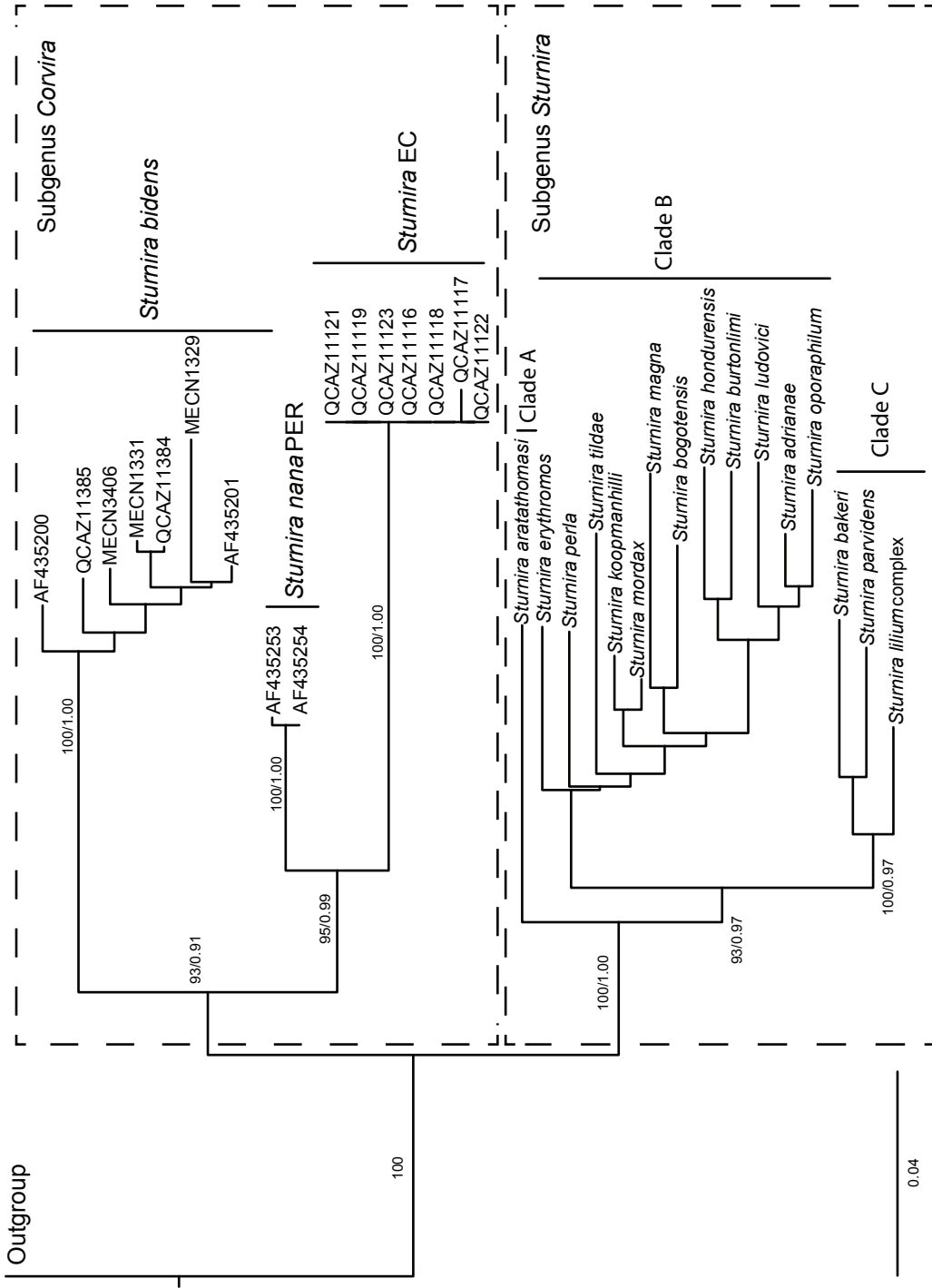


FIGURE 3. Phylogeny of *Sturnira* showing interspecific nodes via Maximum likelihood (ML) and Bayesian analyses (BA). On the branches, numbers before the slash (/) indicate ML bootstrap support (as a percentage); numbers after the slash (/) indicate Bayesian posterior probabilities.

## TAXONOMIC ACCOUNTS

Family Phyllostomidae Gray, 1825

Subfamily Stenodermatinae Gervais, 1856

Genus *Sturnira* Gray, 1842Subgenus *Corvira* Thomas, 1915***Sturnira boadai***, sp. nov.

Boada's Yellow-shouldered Bat

Murciélago de hombros amarillos de Boada

*Sturnira nana*: Boada, 2011: 76.*Sturnira nana*: Regalado and Albuja, 2012: 160.*Sturnira* sp. A: Tirira, 2012: 268.*Sturnira nana*: Solari et al., 2019: 543 (pt.)*Sturnira nana*: Narváez-Romero et al., 2020: 81.*Sturnira nana*: Tirira et al., 2022: 33.

**HOLOTYPE:** An adult female (QCAZ 11122) collected on March 12, 2009, by Carlos Boada. The body is preserved in 75% ethanol, with the skull removed and cleaned. Muscle and liver tissues preserved in 95% ethanol are also deposited at QCAZ.

**TYPE LOCALITY:** Las Orquideas, Miazi Alto near Nangaritzza River basin, Zamora Chinchipe province, Ecuador, 04°15.48'S, 78°40.59'W, between 1250–1430 m (fig. 5).

**PARATYPES:** One female (QCAZ11120) and four males (QCAZ11116, QCAZ11119, QCAZ11121, QCAZ11123) were also collected at the type locality on March 12, 2009 by Carlos Boada. All specimens are preserved in 75% ethanol, with the skulls removed and cleaned.

**DISTRIBUTION:** Known from two confirmed localities in Zamora Chinchipe Province: Las Orquideas, Miazi Alto near Nangaritzza River basin (04°15'29.30" S; 78°40'53.40" W) and Military Detachment Cóndor Mirador, El Pangui (03°38'08" S; 78°23'22" W) near the border of Ecuador and Peru (fig. 5). We expect that *S. boadai* also occurs in adjacent, climatically similar habitats of northeastern Peru.

**DIAGNOSIS:** *Sturnira boadai* is a small species (FA = 32.5–33.8 mm, GLS = 18.3–19.2 mm; tables 1, 6) that is externally distinguished from other congeners by lacking shoulder glands (epaulettes), and by its sparsely haired hind feet, interfemoral membrane, and forearm. The braincase is globular, and the zygomatic arches are incomplete. The foramen magnum has an acutely angled anteroventral margin. The inner upper incisors protrude notably from the skull profile, and in rostral view, the distal third of their medial surfaces are in contact. Two to four lower incisors are present, of which the inner incisors are trilobed and subtriangular. The outer lower incisors (when present) are small, bilobed, with blunt edges, and inclined towards the inner incisors. In the series of specimens collected in Miazi Alto (N = 9), some intraspecific variation is observed in relation to the number and presence of the outer lower incisors: most

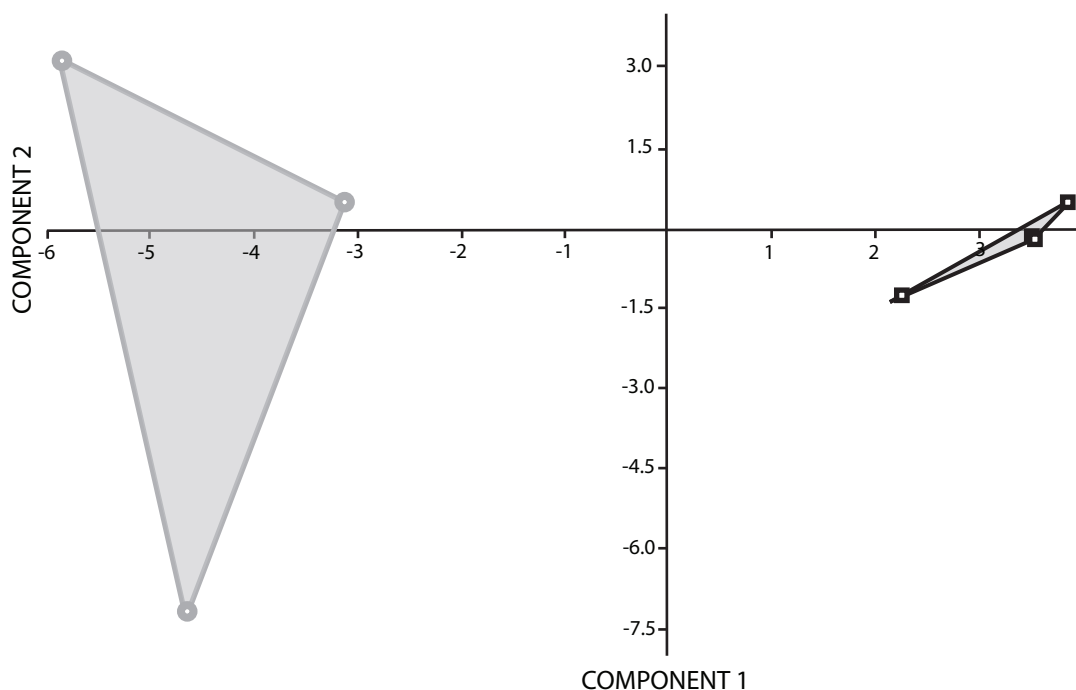


FIGURE 4. Climatic PCA based on the climatic variables from the collection localities of *Sturnira nana* (squares) and *Sturnira* EC (circles).

specimens exhibit four lower incisors (e.g., QCAZ11122) and, in specimens where the outer lower incisors are absent (e.g., QCAZ11121), superficial alveoli or diastemata are observed. One specimen (QCAZ11119) has no outer lower incisors, alveoli, or spaces between  $i1$  and the canine. Lastly, two specimens (QCAZ11120 and QCAZ11123) exhibit only one outer incisor. In one of the latter cases (QCAZ 11123), the external incisor is minuscule and difficult to observe with the naked eye.

**DESCRIPTION:** *Sturnira boadai* is one of the two smallest species of yellow-shouldered bats, with most measurements overlapping those of *S. nana*. The dorsal fur is dense and dark brown, with long (6–7 mm) hairs. Dorsal hairs are tetracolored with a narrow white basal band of around 10% of the hair length, an epibasal brown band of about 40% of the hair length, a subterminal light-brown band of about 30% of the hair length, and a dark-brown apical band that covers 20% of the hair length. The ventral fur and underparts are lighter than the dorsal fur. Ventral hairs are tricolored due to lacking the terminal dark brown tip of the dorsal hairs. The fur is sparsely distributed at the dorsal surface of the femur, tibia, hind feet, interfemoral membrane, and upper forearm. The wing membranes are grayish to blackish brown. Shoulder glands are absent. The nose leaf is dark brown, long, and narrow.

The skull of *Sturnira boadai* has a globular braincase with a flattened rostrum by comparison with other members of the subgenus *Corvira*. A sagittal crest is not developed. The zygomatic arches are always incomplete. The basisphenoid pits and septum are shallow. The anteroventral margin of the foramen magnum is angular.

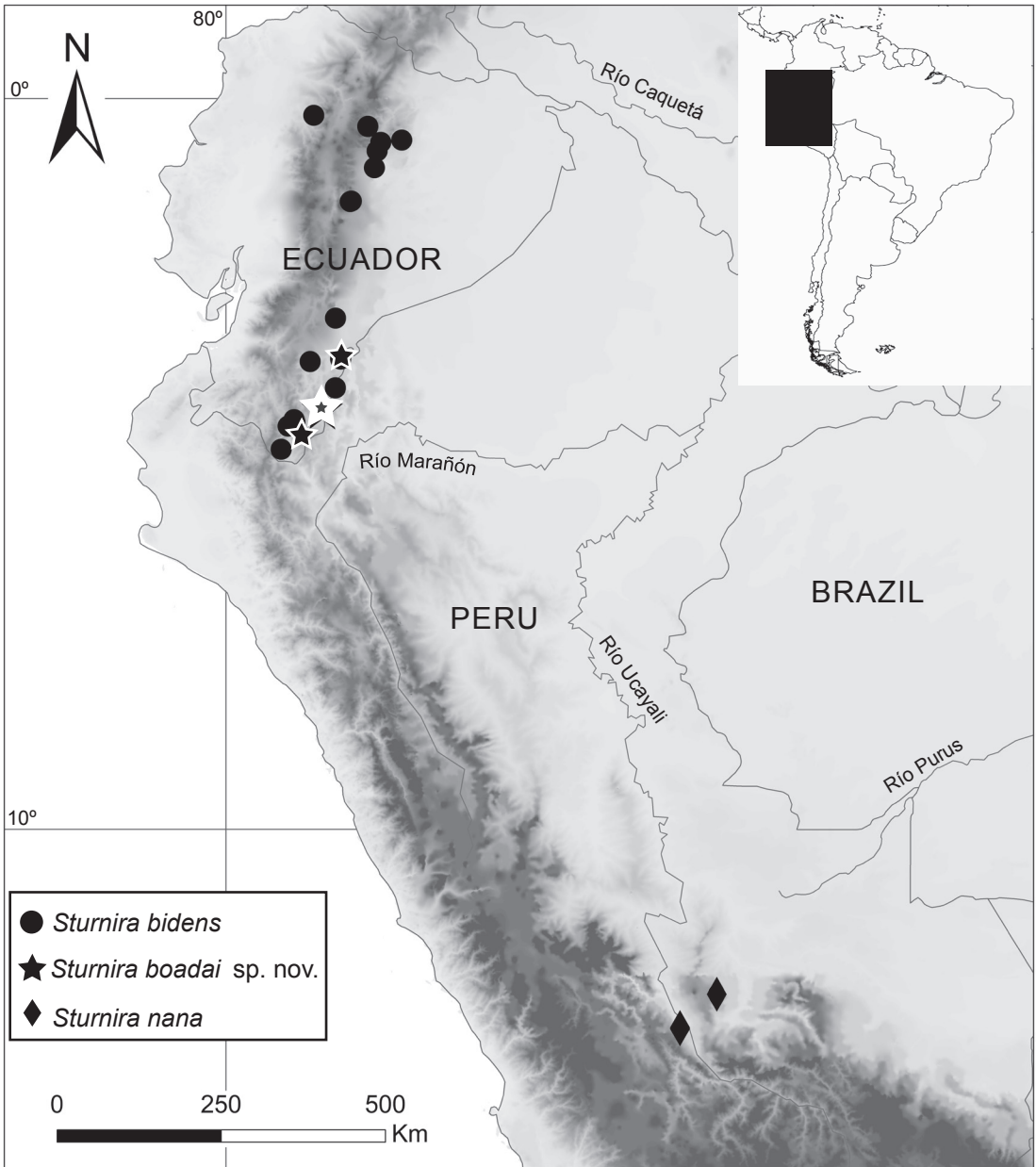


FIGURE 5. Map of NW South America showing the collection localities of *Sturnira bidens* (circles), *S. nana* (diamonds), and *Sturnira boadai*, sp. nov. (stars), analyzed in this study. The collection points of *Sturnira nana* overlap, so only two diamonds are observed.



TABLE 5. Component loadings of the principal components analysis based on a correlation matrix of the 19 bioclimatic variables collection localities of *Sturnira nana*, and *S. EC* (N = 7). The table includes the first two principal components and the proportion of variance explained by each component.

|   | Components |           |
|---|------------|-----------|
|   | PC 1       | PC 2      |
| Annual mean temperature -BIO1               | 0.94767    | 0.24599   |
| Mean diurnal range - BIO2                   | 0.93301    | 0.28858   |
| Isothermality - BIO3                        | 0.93906    | 0.24825   |
| Temperature seasonality - BIO4              | -0.87055   | 0.45631   |
| Maximum temperature of warmest month – BIO5 | -0.20329   | 0.78056   |
| Minimum temperature of coldest month – BIO6 | -0.96516   | 0.17681   |
| Temperature annual range – BIO7             | 0.94094    | -0.11996  |
| Mean temperature of wettest quarter – BIO8  | -0.13235   | 0.78517   |
| Mean temperature of driest quarter – BIO9   | -0.96462   | 0.19795   |
| Mean temperature of warmest quarter – BIO10 | -0.21603   | 0.80937   |
| Mean temperature of coldest quarter – BIO11 | -0.965     | 0.23675   |
| Annual precipitation – BIO12                | 0.97492    | -0.1052   |
| Precipitation of wettest month – BIO13      | -0.93227   | -0.25005  |
| Precipitation of driest month – BIO14       | 0.97346    | 0.19309   |
| Precipitation seasonality – BIO15           | 0.97448    | 0.18217   |
| Precipitation of wettest quarter – BIO16    | -0.4039    | 0.54498   |
| Precipitation of driest quarter – BIO17     | 0.97769    | -0.049589 |
| Precipitation of warmest quarter – BIO18    | 0.94914    | 0.1972    |
| Precipitation of coldest quarter – BIO19    | 0.6817     | 0.56847   |
| Proportion of variance                      | 70.49%     | 17.06%    |

The dental formula is I2/1–2, C1/1, P2/2, M3/3 x 2 = 30–32. The inner upper incisor (I1) is proodont, with a straight occlusal edge and a well-developed posterolateral cusp. The outer upper incisors (I2) are small and opisthodont. I2 is close to but not in contact with the posterolateral cusp of the I1 (fig. 6A). I1 is more than three times the height of I2. The upper canine (C1) is long and robust. The first upper premolar (P3) is small, narrow, and half the height of the second upper premolar (P4). P4 is broad, with a blunt distal cusp that is more noticeable in some specimens than in others, but it is always present. Diastemata are present between P3 and C1, and between P3 and P4. M1 and M2 are broad. The anteroposterior length of the first upper molar (M1) is greater than that of M2 (fig. 1B). In occlusal view, the paracone of M1 is shorter than the metacone. The second upper molar (M2) is ovoid and has a broad crown. The third upper molar (M3) is small, with a crown area approximately one-half that of M2 (fig. 1F).

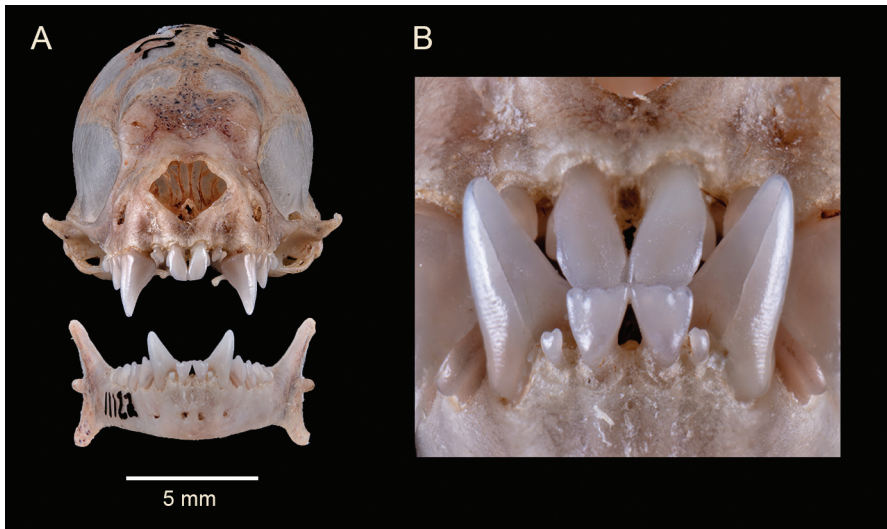


FIGURE 6. **A.** Upper and lower incisors of the holotype of *Sturnira boadai*, sp. nov. (QCAZ 11122). **B.** Detail of incisors. Photographs by Rubén D. Jarrín.

Two to four lower incisors are present. The inner lower incisor (i1) is trilobed. When present, the outer lower incisor (i2s) is minute, bilobed, and approximately one-third the size of i1. The anterior surface of the lower canine (c1) is in contact with the entire posterior surface of the i2 (fig. 6B), but when i2 is missing, the c1 is in contact with i1. The lower canines are long, narrow, robust, and laterally divergent, with their shafts slanted outward. The anteroposterior length of the first lower premolar (p2) is greater than that of the second lower premolar (p4). In lateral view, p2 exhibits an irregular, tricuspid border that is wider (anteroposterior dimension) than the crown of the tooth is tall. By contrast, p4 is taller than it is wide, and it has a well-developed main cusp. Both lower premolars are separated by a diastema (fig. 1H). The first lower molar (m1) is broad. The anteroposterior length of m1 is larger than that of the second lower molar (m2). The third lower molar (m3) is small, with two well-defined lobes separated by a notch between the metaconid and entoconid. The metaconid and entoconid of m1 and m2 are moderately defined. Adjacent upper and lower teeth are separated by narrow diastemata (fig. 1H).

**COMPARISONS:** Among other species traditionally referred to the subgenus *Corvina*, *Sturnira boadai* differs from *S. bidens* in size, being notably smaller. Morphologically, *S. boadai* has sparsely haired hind feet and uropatagium, whereas both structures are densely haired in *S. bidens*. Additionally, *S. boadai* possesses one or two pairs of lower incisors, whereas *S. bidens* always has a single pair of lower incisors. The anterior margin of the foramen magnum in *S. boadai* is angular, whereas it is rounded in most *S. bidens* specimens. Lastly, the zygomatic arches are incomplete in *S. boadai*, whereas they can be complete or incomplete in *S. bidens*.

Externally, *Sturnira boadai* and *S. nana* are similar. Epaulettes (patches of stained shoulder hairs) are not evident in either species. The dorsal fur is long and tetracolored in both species, and the forearm, legs, feet, proximal segments of the wings, and uropatagium

TABLE 6. Forearm and craniodental measurements (mm) analyzed for the type series of *Sturnira boadai*.

| Measurements | QCAZ11122 <sup>a</sup> | QCAZ11120 | QCAZ11116 | QCAZ11119 | QCAZ11121 | QCAZ11123 |
|--------------|------------------------|-----------|-----------|-----------|-----------|-----------|
| FA           | 33.67                  | 33.79     | 33.36     | 33.80     | 32.52     | 33.35     |
| C-C          | 4.64                   | 4.47      | 4.46      | 4.45      | 4.76      | 4.43      |
| M2-M2        | 6.03                   | 6.09      | 5.89      | 6.04      | 5.72      | 5.97      |
| BB           | 9.03                   | 8.85      | 8.94      | 9.09      | 8.78      | 8.84      |
| CIL          | 16.97                  | 16.61     | 16.10     | 16.69     | 17.06     | 16.83     |
| CCL          | 16.14                  | 15.85     | 15.73     | 16.00     | 16.32     | 16.30     |
| DENL         | 11.62                  | 11.33     | 11.51     | 11.68     | 11.70     | 11.75     |
| GLS          | 19.17                  | 18.72     | 18.54     | 18.81     | 19.04     | 18.85     |
| PB           | 4.92                   | 5.00      | 4.72      | 5.03      | 4.85      | 4.69      |
| MANDL        | 5.73                   | 6.11      | 5.74      | 5.63      | 6.24      | 5.62      |
| MTRL         | 5.00                   | 5.00      | 5.20      | 4.73      | 5.00      | 4.96      |
| PL           | 7.45                   | 7.13      | 7.46      | 7.37      | 8.50      | 7.40      |
| ZB           | 10.93                  | 10.46     | 10.55     | 11.04     | 10.78     | 10.38     |

<sup>a</sup> Holotype.

are sparsely covered with long hairs. However, both species can be distinguished by several craniodental characteristics. The skull has a globular braincase and a less elongated rostrum in *S. boadai*, whereas the braincase is relatively long with a narrow, sloping rostrum in *S. nana*. The anterior margin of the foramen magnum is angular in *S. boadai*, whereas it is rounded in *S. nana*. The zygomatic arches are always incomplete in *S. boadai*, whereas they can be complete or incomplete in *S. nana*. P3 is small, narrow, sharp crowned, and not in contact with either C1 or P4 in *S. boadai*, whereas P3 is broader and in contact with both C1 and P4 in *S. nana*. Lastly, M3 is less wide in lateral view, whereas M3 is broader in *S. nana*.

**ETYMOLOGY:** The epithet *boadai* is dedicated to the memory of the Ecuadorian mammalogist Carlos Boada (1973–2015). Carlos was passionate about studying small mammals, especially bats and rodents. His academic contributions to the knowledge of Ecuadorian mammals were remarkable and primarily included taxonomic assessments and biological inventories. Carlos trained an extensive group of young mammalogists in the country, and herein we commemorate his early departure by naming this new species in his honor.

## DISCUSSION

Our study provides compelling evidence for recognizing *Sturnira boadai* as a distinct species based on morphological, morphometric, molecular, and climatic data analyses. This discovery raises the number of recognized *Sturnira* species to 25, of which 15 occur in Ecuador. Our examination reveals significant differences in cranial and mandibular features and size when compared to closely related congeners, including *S. nana* and *S. bidens*.

Although our phylogenetic analysis recovered a highly supported clade corresponding to the traditionally recognized subgenus *Corvira*, this result was obtained from a single molecular marker, and it is inconsistent with the results obtained by Velazco and Patterson (2013), who analyzed sequence data from multiple loci. Whether a multigene analysis might also recover *Corvira* by including *S. boadai* (and additional, previously unsequenced congeners) is unknown. Future research based on denser taxonomic sampling is needed to test the validity of subgeneric taxa in *Sturnira*.

Velazco and Patterson (2013) suggested that the split between *S. bidens* and *S. nana* occurred in the Late Miocene, around 7.5 Ma, perhaps coinciding with the simultaneous uplift of the Eastern Cordillera and the Cordillera del Cóndor. Based on the results presented here, we speculate that the split between *S. nana* and *S. boadai* might also have occurred by allopatric speciation when an ancestral population was subdivided by the orogeny of the Cordillera del Cóndor and the formation of the Marañón valley. However, this hypothesis should be tested with model-based divergence time estimates and other demographic parameters.

Despite the comprehensive analyses conducted on *Sturnira boadai* specimens, significant gaps still exist in our understanding of the natural history of this species. The limited availability of information on this taxon underscores the need for further research and investigation to discover additional aspects of its ecology and behavior. As was speculated with *S. nana* (Solari, 2019), *S. boadai* might be a highland specialist with a diet similar to that of other species of small montane forest *Sturnira*, including fruits from species of Solanaceae, Hypericaceae, Piperaceae, or Araceae.

In the latest Red List of the mammals of Ecuador (Marchán-Rivadeneira et al., 2021), *Sturnira boadai* (“*Sturnira nana*”) was categorized as Endangered due to its restricted distribution in the southeastern forests of Zamora Chinchipe province. The Cordillera del Cóndor provides unique geophysical conditions that influence the distribution and diversity of wildlife (Scullion et al., 2021). Recent expeditions to these mountains have resulted in the description of new species of endemic mammals, including *Rhipidomys albuja* Brito et al., 2017; *Thomasomys pardignasi* Brito et al., 2021a; *Neacomys auriventer* Brito et al., 2021b; and *Rhagomys septentrionalis* Moreno-Cárdenas et al., 2021. Unfortunately, this unique fauna is threatened by severe habitat conversion, including small subsistence farms and logging (Roy et al., 2018; Solari and Boada, 2016; Scullion et al., 2021). Therefore, the conservation status of *Sturnira boadai*, currently known only from this area, should be maintained as endangered given the current environmental situation.

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## APPENDIX 1

## LIST OF SPECIMENS USED FOR PHYLOGENETIC ANALYSIS

Species, voucher numbers, and GenBank accession codes given for *Sturnira* species and the outgroup. Asterisks (\*) identify sequences obtained in this study. Collection acronyms: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; CVULA, Colección de Vertebrados de la Universidad de Los Andes; FMNH, Field Museum of Natural History; LSUMZ, Museum of Natural Science, Louisiana State University; MECN, Museo Ecuatoriano de Ciencias Naturales; MEPN, Museo de la Escuela Politécnica Nacional “Gustavo Orcés V.”; MPEG, Museu Paraense Emilio Goeldi; MSB/NK, Museum of Southwestern Biology, University of New Mexico; MUSM, Universidad Nacional Mayor de San Marcos; MVZ, Museum of Vertebrate Zoology, University of California; MZFC-M, Museo de Zoología, Universidad Nacional Autónoma de México; QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador; ROM, Royal Ontario Museum; TTU/TK, Museum of Texas Tech University; USNM, National Museum of Natural History, Smithsonian Institution.

| Species                           | Museum voucher / Collector number | GenBank Accession number |
|-----------------------------------|-----------------------------------|--------------------------|
| <i>Artibeus obscurus</i>          | TK 104310                         | GU356393                 |
| <i>Platyrrhinus helleri</i>       | USNM AVE12                        | GQ184736                 |
| <i>Sturnira adrianae adrianae</i> | CVULA I-8550                      | KY366231                 |
| <i>Sturnira adrianae adrianae</i> | CVULA I-8584                      | KY366232                 |
| <i>Sturnira adrianae adrianae</i> | CVULA I-8585                      | KY366233                 |
| <i>Sturnira adrianae adrianae</i> | CVULA I-8602                      | KY366234                 |
| <i>Sturnira adrianae adrianae</i> | CVULA I-8603                      | KY366235                 |
| <i>Sturnira adrianae caripana</i> | CVULA I-8590                      | KY366229                 |
| <i>Sturnira adrianae caripana</i> | CVULA I-8593                      | KY366230                 |
| <i>Sturnira angeli</i>            | CM112363 / CAI 174                | AF435158                 |
| <i>Sturnira angeli</i>            | TTU19906 / CAI 229                | AF435249                 |
| <i>Sturnira angeli</i>            | UNSM 20062 / CAI 233              | AF435251                 |

APPENDIX 1 *continued*

| Species                     | Museum voucher / Collector number | GenBank Accession number |
|-----------------------------|-----------------------------------|--------------------------|
| <i>Sturnira aratahomasi</i> | ROM 70874                         | AF435252                 |
| <i>Sturnira bakeri</i>      | TK 135051                         | KC753830                 |
| <i>Sturnira bakeri</i>      | TTU 85395                         | MF441772                 |
| <i>Sturnira bakeri</i>      | TTU 85434                         | MF441773                 |
| <i>Sturnira bakeri</i>      | TK 135049                         | KC753829                 |
| <i>Sturnira bakeri</i>      | TK 135127                         | KC753828                 |
| <i>Sturnira bidens</i>      | CM112824 / CAI 175                | AF435200                 |
| <i>Sturnira bidens</i>      | LSUMZ 26924 / CAI 208             | AF435201                 |
| <i>Sturnira bidens</i> *    | MECN 1329                         | OQ994956                 |
| <i>Sturnira bidens</i> *    | MECN 1331                         | OQ994957                 |
| <i>Sturnira bidens</i> *    | MECN 3406                         | OQ994958                 |
| <i>Sturnira bidens</i> *    | QCAZ 11384                        | OQ994966                 |
| <i>Sturnira bidens</i> *    | QCAZ 11385                        | OQ994967                 |
| <i>Sturnira boadai</i> *    | QCAZ 11116                        | OQ994959                 |
| <i>Sturnira boadai</i> *    | QCAZ 11117                        | OQ994960                 |
| <i>Sturnira boadai</i> *    | QCAZ 11118                        | OQ994961                 |
| <i>Sturnira boadai</i> *    | QCAZ 11119                        | OQ994962                 |
| <i>Sturnira boadai</i> *    | QCAZ 11121                        | OQ994963                 |
| <i>Sturnira boadai</i> *    | QCAZ 11122                        | OQ994964                 |
| <i>Sturnira boadai</i> *    | QCAZ 11123                        | OQ994965                 |
| <i>Sturnira bogotensis</i>  | FMNH 128787                       | KC753783                 |
| <i>Sturnira bogotensis</i>  | FMNH 128788                       | AF435248                 |
| <i>Sturnira bogotensis</i>  | FMNH 128788                       | KC753784                 |
| <i>Sturnira bogotensis</i>  | FMNH 128789                       | AF435246                 |
| <i>Sturnira bogotensis</i>  | FMNH 128789                       | KC753785                 |
| <i>Sturnira bogotensis</i>  | FMNH 128790                       | KC753786                 |
| <i>Sturnira bogotensis</i>  | MUSM24778 / VPT 3504              | KC753787                 |
| <i>Sturnira burtonlimi</i>  | MVZ 174432                        | KC753825                 |
| <i>Sturnira burtonlimi</i>  | ROM 104294                        | KC753826                 |
| <i>Sturnira burtonlimi</i>  | ROM 104295                        | KC753827                 |
| <i>Sturnira erythromos</i>  | FMNH 162521                       | KC753790                 |
| <i>Sturnira erythromos</i>  | FMNH162522                        | KC753791                 |
| <i>Sturnira erythromos</i>  | SP 14                             | KP134548                 |

APPENDIX 1 *continued*

| Species                     | Museum voucher / Collector number | GenBank Accession number |
|-----------------------------|-----------------------------------|--------------------------|
| <i>Sturnira erythromos</i>  | FMNH 128811                       | KC753789                 |
| <i>Sturnira erythromos</i>  | FMNH 162522                       | KC753788                 |
| <i>Sturnira erythromos</i>  | FMNH 174800                       | KC753792                 |
| <i>Sturnira erythromos</i>  | FMNH 174809                       | FJ154179                 |
| <i>Sturnira erythromos</i>  | IP4430_1                          | JX444094                 |
| <i>Sturnira erythromos</i>  | TK 22784                          | DQ312399                 |
| <i>Sturnira giannae</i>     | AMNH 268545                       | KC753831                 |
| <i>Sturnira giannae</i>     | FMNH 128825                       | KC753833                 |
| <i>Sturnira giannae</i>     | FMNH 128845                       | KC753834                 |
| <i>Sturnira giannae</i>     | FMNH 203587                       | KC753843                 |
| <i>Sturnira giannae</i>     | ROM 103552                        | KC753842                 |
| <i>Sturnira giannae</i>     | ROM 107936                        | KC753844                 |
| <i>Sturnira giannae</i>     | ROM 117642                        | KC753845                 |
| <i>Sturnira giannae</i>     | TK 19138                          | KC753832                 |
| <i>Sturnira giannae</i>     | TK 22781                          | KC753849                 |
| <i>Sturnira giannae</i>     | TK 25035                          | KC753848                 |
| <i>Sturnira giannae</i>     | TK 25100                          | KC753847                 |
| <i>Sturnira giannae</i>     | TK 25163                          | KC753846                 |
| <i>Sturnira giannae</i>     | TTU 46263                         | MF441755                 |
| <i>Sturnira giannae</i>     | TTU 46264                         | MF441752                 |
| <i>Sturnira giannae</i>     | TTU 46265                         | MF441758                 |
| <i>Sturnira giannae</i>     | TTU 46266                         | MF441760                 |
| <i>Sturnira giannae</i>     | TTU 46267                         | MF441753                 |
| <i>Sturnira giannae</i>     | TTU 46268                         | MF441754                 |
| <i>Sturnira giannae</i>     | TTU 46269                         | MF441756                 |
| <i>Sturnira giannae</i>     | TTU 46271                         | MF441757                 |
| <i>Sturnira giannae</i>     | TTU 46272                         | MF441759                 |
| <i>Sturnira giannae</i>     | TTU 84983                         | MF441748                 |
| <i>Sturnira giannae</i>     | TTU 85109                         | MF441749                 |
| <i>Sturnira giannae</i>     | TTU 85110                         | MF441750                 |
| <i>Sturnira giannae</i>     | TTU 85121                         | MF441751                 |
| <i>Sturnira hondurensis</i> | MVZ 223172                        | KC753793                 |
| <i>Sturnira hondurensis</i> | MVZ 223178                        | KC753794                 |
| <i>Sturnira hondurensis</i> | MVZ 223393                        | KC753795                 |

APPENDIX 1 *continued*

| Species                      | Museum voucher / Collector number | GenBank Accession number |
|------------------------------|-----------------------------------|--------------------------|
| <i>Sturnira hondurensis</i>  | ROM 101366                        | KC753796                 |
| <i>Sturnira hondurensis</i>  | ROM 101474                        | KC753797                 |
| <i>Sturnira hondurensis</i>  | TK 101014                         | KC753799                 |
| <i>Sturnira hondurensis</i>  | TK 150033                         | KC753798                 |
| <i>Sturnira koopmanhilli</i> | CM 112804 / CAI-2003A             | AF435203                 |
| <i>Sturnira koopmanhilli</i> | CM112812 / CAI 180                | AF435202                 |
| <i>Sturnira lilium</i>       | MN 36314                          | DQ903815                 |
| <i>Sturnira lilium</i>       | MN 36638                          | DQ903814                 |
| <i>Sturnira lilium</i>       | TK22810                           | DQ312398                 |
| <i>Sturnira lilium</i>       | BDP 3174                          | KC753805                 |
| <i>Sturnira lilium</i>       | FMNH 128816                       | AF435268                 |
| <i>Sturnira lilium</i>       | FMNH 162524                       | KC753800                 |
| <i>Sturnira lilium</i>       | FMNH 162542                       | KC753801                 |
| <i>Sturnira lilium</i>       | MVZ 154711                        | KC753802                 |
| <i>Sturnira lilium</i>       | ROM 104204                        | EF536949                 |
| <i>Sturnira lilium</i>       | ROM 104395                        | EF536951                 |
| <i>Sturnira lilium</i>       | ROM 104416                        | EF536952                 |
| <i>Sturnira lilium</i>       | ROM 105269                        | EF536953                 |
| <i>Sturnira lilium</i>       | ROM 105694                        | EF536954                 |
| <i>Sturnira lilium</i>       | ROM 105706                        | EF536955                 |
| <i>Sturnira lilium</i>       | ROM 111064                        | EF536957                 |
| <i>Sturnira lilium</i>       | ROM 114178                        | EF536962                 |
| <i>Sturnira lilium</i>       | ROM 114179                        | EF536963                 |
| <i>Sturnira lilium</i>       | ROM 114180                        | EF536964                 |
| <i>Sturnira lilium</i>       | ROM 114181                        | EF536965                 |
| <i>Sturnira lilium</i>       | ROM 115545                        | EF536966                 |
| <i>Sturnira lilium</i>       | TK 61777                          | KC753804                 |
| <i>Sturnira lilium</i>       | TK 63779                          | KC753803                 |
| <i>Sturnira lilium</i>       | TTU 106051                        | MF441768                 |
| <i>Sturnira lilium</i>       | TTU 94024                         | MF441771                 |
| <i>Sturnira lilium</i>       | TTU 94259                         | MF441769                 |
| <i>Sturnira lilium</i>       | TTU 96816                         | MF441770                 |
| <i>Sturnira ludovici</i>     | TK 135783                         | KC753806                 |
| <i>Sturnira ludovici</i>     | TK 135787                         | KC753807                 |

APPENDIX 1 *continued*

| <b>Species</b>           | <b>Museum voucher / Collector number</b> | <b>GenBank Accession number</b> |
|--------------------------|--|---------------------------------|
| <i>Sturnira ludovici</i> | TK 22506 / CAI 21                        | AF435160                        |
| <i>Sturnira luisi</i>    | LSUMZ 25178                              | MF441762                        |
| <i>Sturnira luisi</i>    | LSUMZ 25478                              | MF441763                        |
| <i>Sturnira luisi</i>    | ROM 104349                               | MF441765                        |
| <i>Sturnira luisi</i>    | ROM 104359                               | MF441766                        |
| <i>Sturnira luisi</i>    | USNM 578239 / CAI 247                    | AF435164                        |
| <i>Sturnira luisi</i>    | USNM 579052                              | KC753815                        |
| <i>Sturnira luisi</i>    | LSUMZ 25177                              | MF441761                        |
| <i>Sturnira luisi</i>    | ROM 104204                               | KC753809                        |
| <i>Sturnira luisi</i>    | ROM 104348                               | MF441764                        |
| <i>Sturnira luisi</i>    | ROM 104359                               | EF536950                        |
| <i>Sturnira luisi</i>    | ROM 105807                               | KC753810                        |
| <i>Sturnira luisi</i>    | TK 135818                                | KC753811                        |
| <i>Sturnira luisi</i>    | TK 22506                                 | KC753812                        |
| <i>Sturnira luisi</i>    | TTU 19907 / CAI 230                      | AF435250                        |
| <i>Sturnira luisi</i>    | TTU 85440                                | MF441767                        |
| <i>Sturnira luisi</i>    | USNM 449721                              | KC753813                        |
| <i>Sturnira luisi</i>    | USNM 578239                              | KC753814                        |
| <i>Sturnira luisi</i>    | USNM 579051 / CAI 248                    | AF435255                        |
| <i>Sturnira magna</i>    | AMNH 272787                              | KC753816                        |
| <i>Sturnira magna</i>    | FMNH 174829                              | KC753817                        |
| <i>Sturnira magna</i>    | FMNH 174830                              | KC753818                        |
| <i>Sturnira magna</i>    | ROM 104000                               | KC753819                        |
| <i>Sturnira magna</i>    | ROM 104000                               | KC753819                        |
| <i>Sturnira magna</i>    | TK 22722                                 | AF435180                        |
| <i>Sturnira magna</i>    | USNM 574555                              | KC753820                        |
| <i>Sturnira mordax</i>   | CAI 253                                  | AF435214                        |
| <i>Sturnira mordax</i>   | CAI 255                                  | AF435216                        |
| <i>Sturnira mordax</i>   | CM92487 / AK 7069                        | KC753823                        |
| <i>Sturnira mordax</i>   | CM92488 / AK 7070                        | KC753824                        |
| <i>Sturnira mordax</i>   | MVZ 174439                               | KC753821                        |
| <i>Sturnira mordax</i>   | TJM6741 / AK 7023                        | KC753822                        |
| <i>Sturnira nana</i>     | LSUMZ 16522                              | AF435253                        |
| <i>Sturnira nana</i>     | LSUMZ 16523                              | AF435254                        |

APPENDIX 1 *continued*

| Species                     | Museum voucher / Collector number | GenBank Accession number |
|-----------------------------|-----------------------------------|--------------------------|
| <i>Sturnira oporaphilum</i> | FMNH 128925                       | KC753850                 |
| <i>Sturnira oporaphilum</i> | FMNH 128926                       | KC753851                 |
| <i>Sturnira oporaphilum</i> | FMNH 174843                       | KC753852                 |
| <i>Sturnira oporaphilum</i> | FMNH 174844                       | KC753853                 |
| <i>Sturnira oporaphilum</i> | FMNH 203589                       | KC753854                 |
| <i>Sturnira oporaphilum</i> | MUSM39428 / RCO 1132              | KC753855                 |
| <i>Sturnira oporaphilum</i> | NK 12703                          | AF435211                 |
| <i>Sturnira oporaphilum</i> | NK 25441                          | AF435209                 |
| <i>Sturnira oporaphilum</i> | TK 104198                         | KC753856                 |
| <i>Sturnira parvidens</i>   | LSUMZ 25192                       | MF441779                 |
| <i>Sturnira parvidens</i>   | LSUMZ 28341                       | KC753857                 |
| <i>Sturnira parvidens</i>   | LSUMZ 28341                       | MF441778                 |
| <i>Sturnira parvidens</i>   | LSUMZ 29528                       | MF441774                 |
| <i>Sturnira parvidens</i>   | LSUMZ 29529                       | MF441775                 |
| <i>Sturnira parvidens</i>   | LSUMZ 29530                       | MF441776                 |
| <i>Sturnira parvidens</i>   | MNCRM 1264                        | MF441777                 |
| <i>Sturnira parvidens</i>   | MSB 53756                         | KC753858                 |
| <i>Sturnira parvidens</i>   | MSB 53758                         | KC753859                 |
| <i>Sturnira parvidens</i>   | MSB 53759                         | KC753860                 |
| <i>Sturnira parvidens</i>   | MSB 53760                         | KC753861                 |
| <i>Sturnira parvidens</i>   | MSB 82218                         | KC753863                 |
| <i>Sturnira parvidens</i>   | MSB 822216                        | KC753862                 |
| <i>Sturnira parvidens</i>   | MZFC-M 16148                      | MF441922                 |
| <i>Sturnira parvidens</i>   | MZFC-M 16149                      | MF441923                 |
| <i>Sturnira parvidens</i>   | MZFC-M 16151                      | MF441925                 |
| <i>Sturnira parvidens</i>   | MZFC-M 16152                      | MF441926                 |
| <i>Sturnira parvidens</i>   | MZFC-M 16150                      | MF441924                 |
| <i>Sturnira parvidens</i>   | ROM 112201                        | MF441927                 |
| <i>Sturnira parvidens</i>   | ROM 96276                         | KC753864                 |
| <i>Sturnira parvidens</i>   | ROM 97412                         | KC753865                 |
| <i>Sturnira parvidens</i>   | ROM 99284                         | KC753866                 |
| <i>Sturnira parvidens</i>   | TK 101765                         | KC753874                 |
| <i>Sturnira parvidens</i>   | TK 101951                         | KC753875                 |
| <i>Sturnira parvidens</i>   | TK 136014                         | KC753867                 |



APPENDIX 1 *continued*

| Species                      | Museum voucher / Collector number | GenBank Accession number |
|------------------------------|-----------------------------------|--------------------------|
| <i>Sturnira parvidens</i>    | TK 150047                         | KC753869                 |
| <i>Sturnira parvidens</i>    | TK 150240                         | KC753868                 |
| <i>Sturnira parvidens</i>    | TK 27085                          | KC753870                 |
| <i>Sturnira parvidens</i>    | TK 34623                          | KC753872                 |
| <i>Sturnira parvidens</i>    | TK 34761                          | KC753873                 |
| <i>Sturnira parvidens</i>    | TK 97414                          | KC753871                 |
| <i>Sturnira paulsoni</i>     | TK 128280                         | KC753882                 |
| <i>Sturnira paulsoni</i>     | TK 144594                         | KC753883                 |
| <i>Sturnira paulsoni</i>     | TK 144620                         | KC753884                 |
| <i>Sturnira paulsoni</i>     | TK 161231                         | KC753885                 |
| <i>Sturnira paulsoni</i>     | TK 161519                         | KC753881                 |
| <i>Sturnira paulsoni</i>     | TK 18602                          | KC753876                 |
| <i>Sturnira paulsoni</i>     | USNM 580674                       | KC753886                 |
| <i>Sturnira perla</i>        | CM 112822                         | AF435205                 |
| <i>Sturnira perla</i>        | CM 112823                         | AF435204                 |
| <i>Sturnira tildae</i>       | AMNH 268556                       | KC753887                 |
| <i>Sturnira tildae</i>       | FMNH 174860                       | KC753889                 |
| <i>Sturnira tildae</i>       | FMNH 174862                       | KC753890                 |
| <i>Sturnira tildae</i>       | FMNH 174865                       | KC753891                 |
| <i>Sturnira tildae</i>       | FMNH 174871                       | KC753892                 |
| <i>Sturnira tildae</i>       | FURB-SLA 1120                     | DQ903816                 |
| <i>Sturnira tildae</i>       | MPEG20844 / BDP 2128              | KC753893                 |
| <i>Sturnira tildae</i>       | TK 10462                          | AF435199                 |
| <i>Sturnira tildae</i>       | TK 145286                         | KC753894                 |
| <i>Sturnira tildae</i>       | TK 17702                          | KC753888                 |
| <i>Sturnira tildae</i>       | TK 25139                          | KC753895                 |
| <i>Sturnira tildae</i>       | USNM 560796                       | KC753896                 |
| <i>Sturnira tildae</i>       | USNM 560796                       | KC753896                 |
| <i>Sturnira tildae</i>       | USNM 574556                       | KC753897                 |
| <i>Uroderma magnirostrum</i> | FMNH 174907                       | FJ154180                 |
| <i>Vampyriscus bidens</i>    | MPEG20840 / ALG 14898             | FJ154181                 |

## APPENDIX 2

## GENERAL INFORMATION ON THE ANALYZED SPECIMENS

| Species                | Catalog number                                 | Country | Province/<br>Departament | Specific Locality   | Coordinates              |
|------------------------|--|---------|--------------------------|---|--------------------------|
| <i>Sturnira nana</i>   | LSUMZ 15683<br>Holotype <sup>a</sup>           | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | LSUMZ 16519 <sup>a</sup>                       | Peru    | Ayacucho                 | Río Santa Rosa, San José  | -12.733, -73.767         |
| <i>Sturnira nana</i>   | LSUMZ 16520 <sup>a,b</sup>                     | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | LSUMZ 16521 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | LSUMZ 16522 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | LSUMZ 16523 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | LSUMZ 16524 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.733, -73.783         |
| <i>Sturnira nana</i>   | AMNH 219138 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.26, -73.28           |
| <i>Sturnira nana</i>   | AMNH 219171 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.716, -73.783         |
| <i>Sturnira nana</i>   | AMNH 219272 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.716, -73.783         |
| <i>Sturnira nana</i>   | AMNH 219173 <sup>a</sup>                       | Peru    | Ayacucho                 | Huanhuachayo  | -12.716, -73.783         |
| <i>Sturnira boadai</i> | QCAZ 11115 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11116 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11117 <sup>a,b</sup>                      | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11118 <sup>a,b</sup>                      | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11119 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11120 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11121 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11122 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | QCAZ 11123 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Miazi Alto  | -4.25814, -78.6815       |
| <i>Sturnira boadai</i> | MECN 11133 <sup>a</sup>                        | Ecuador | Zamora<br>Chinchipe      | Military Detachment<br>Cónдор Mirador, El<br>Pangui             | -3.635833,<br>-78.38968  |
| <i>Sturnira boadai</i> | Narváez-Romero<br>et al. (2020) <sup>a,b</sup> | Ecuador | Zamora<br>Chinchipe      | Near Reserva Biológica<br>Cerro Plateado, Zona<br>alta, Palanda | -4.620028,<br>-78.899222 |

<sup>a</sup> Geographic location included in climatic assessment analysis.<sup>b</sup> Specimens not included in the morphometric analyses.

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