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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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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

Condyloincisive length (CIL): Distance from the posteriormost margins of the occipital condyles to the anteriormost point on the upper incisors

Condylocanine 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 NanoDropTM1000 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 ≥ 200), and the potential scale reduction factor was also verified (PSRF = 1). Posterior probability values ≥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 (°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 toothrow 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 toothrow length (MANDL), canine breadth (C-C), and zygomatic breadth (ZB).

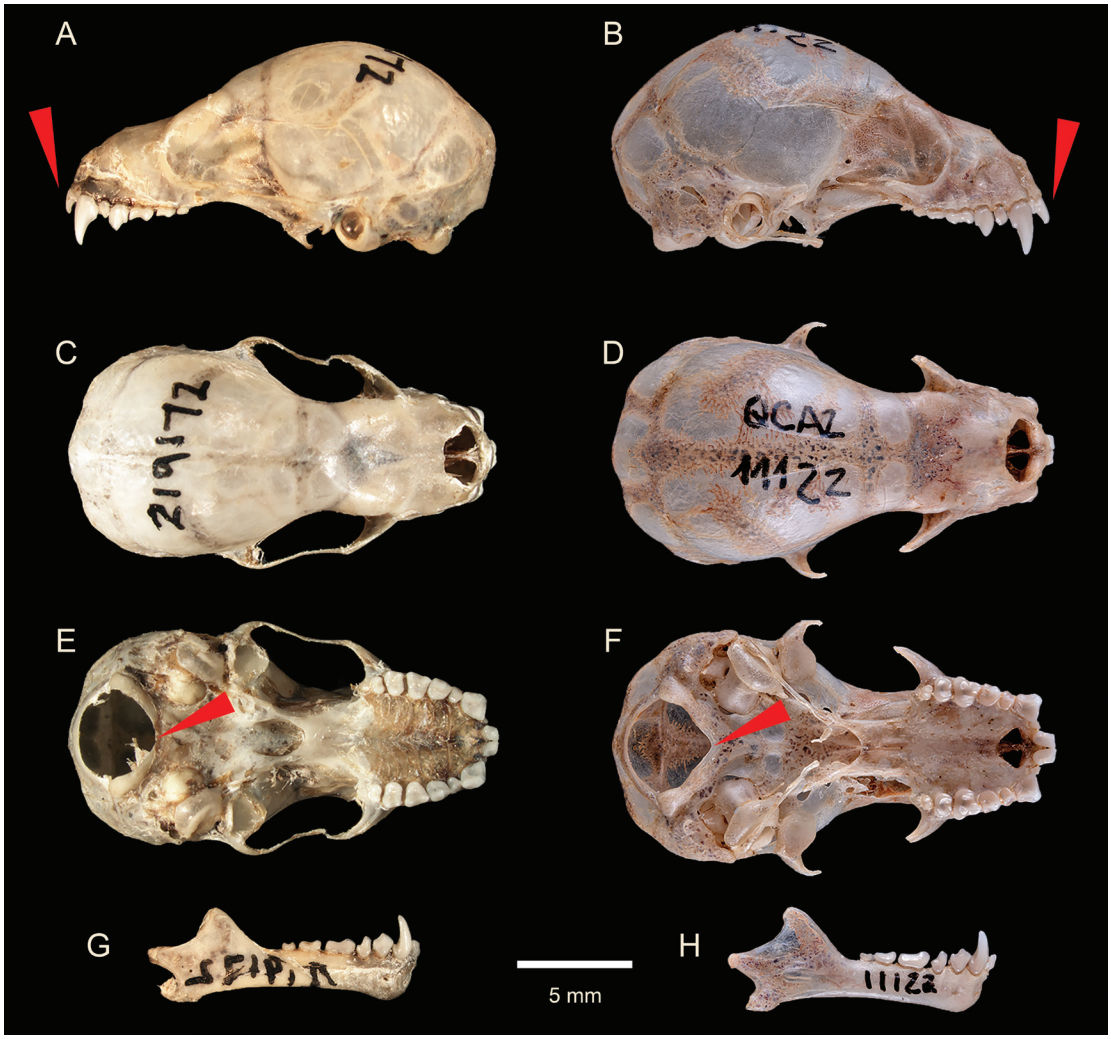

FIGURE 1. **A, B.** Lateral, **C, D.** dorsal, and **E, F.** ventral views of the skulls and **G, H.** lateral view of the mandibles of *Sturnira nana* (AMNH 219172, left column) and *Sturnira* EC (QCAZ 11122, right column). Red arrows show the differences between the two skulls.

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 toothrow 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.

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

[a] 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).

	Sturnira bidens	*Sturnira nana*	*Sturnira* EC
Sturnira bidens		0.95	0.77
Sturnira nana	7.87		0.87
Sturnira EC	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. (%)
Sturnira bidens	6.09	0.40
Sturnira nana	0.13	0.15
Sturnira EC	0.08	0.03

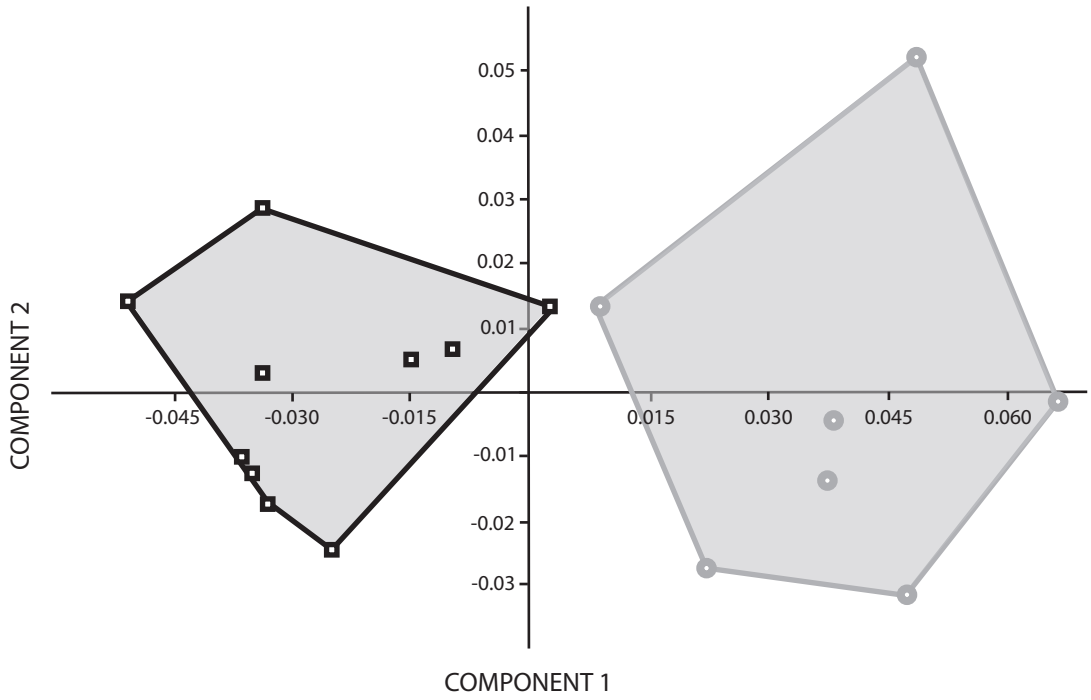

FIGURE 2. Principal component analysis of 12 craniomandibular measurements in *Sturnira nana* (N = 10, squares) and *Sturnira* EC (N = 8, circles).

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.

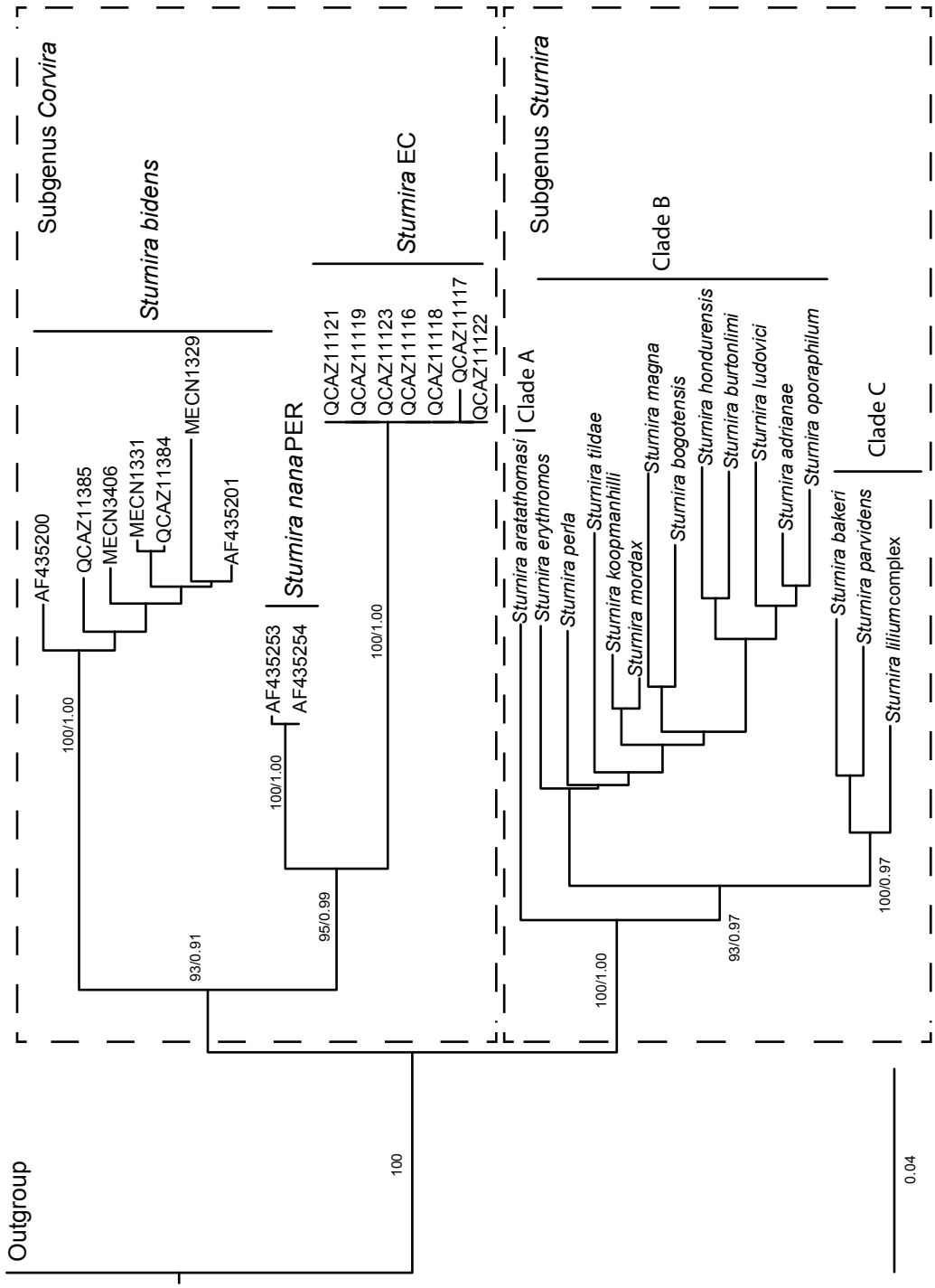

FIGURE 3. Phylogeny of *Sturnira* showing interspecific nodes via Maximum likelihood (ML) and Bayesian analyses (BA). On the branches, numbers before the slash (/) indicate ML bootstrap support (as a percentage); numbers after the slash (/) indicate Bayesian posterior probabilities.

TAXONOMIC ACCOUNTS

Family Phyllostomidae Gray, 1825

Subfamily Stenodermatinae Gervais, 1856

Genus *Sturnira* Gray, 1842

Subgenus *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 Nangaritza 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 Nangaritza 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

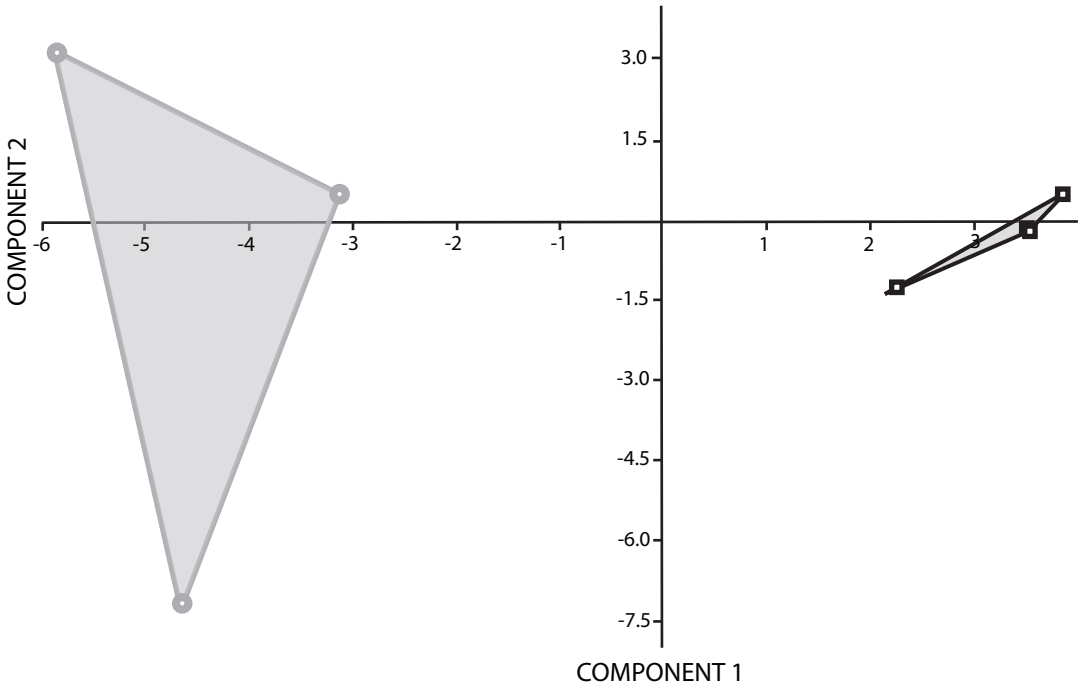

FIGURE 4. Climatic PCA based on the climatic variables from the collection localities of *Sturnira nana* (squares) and *Sturnira* EC (circles).

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.

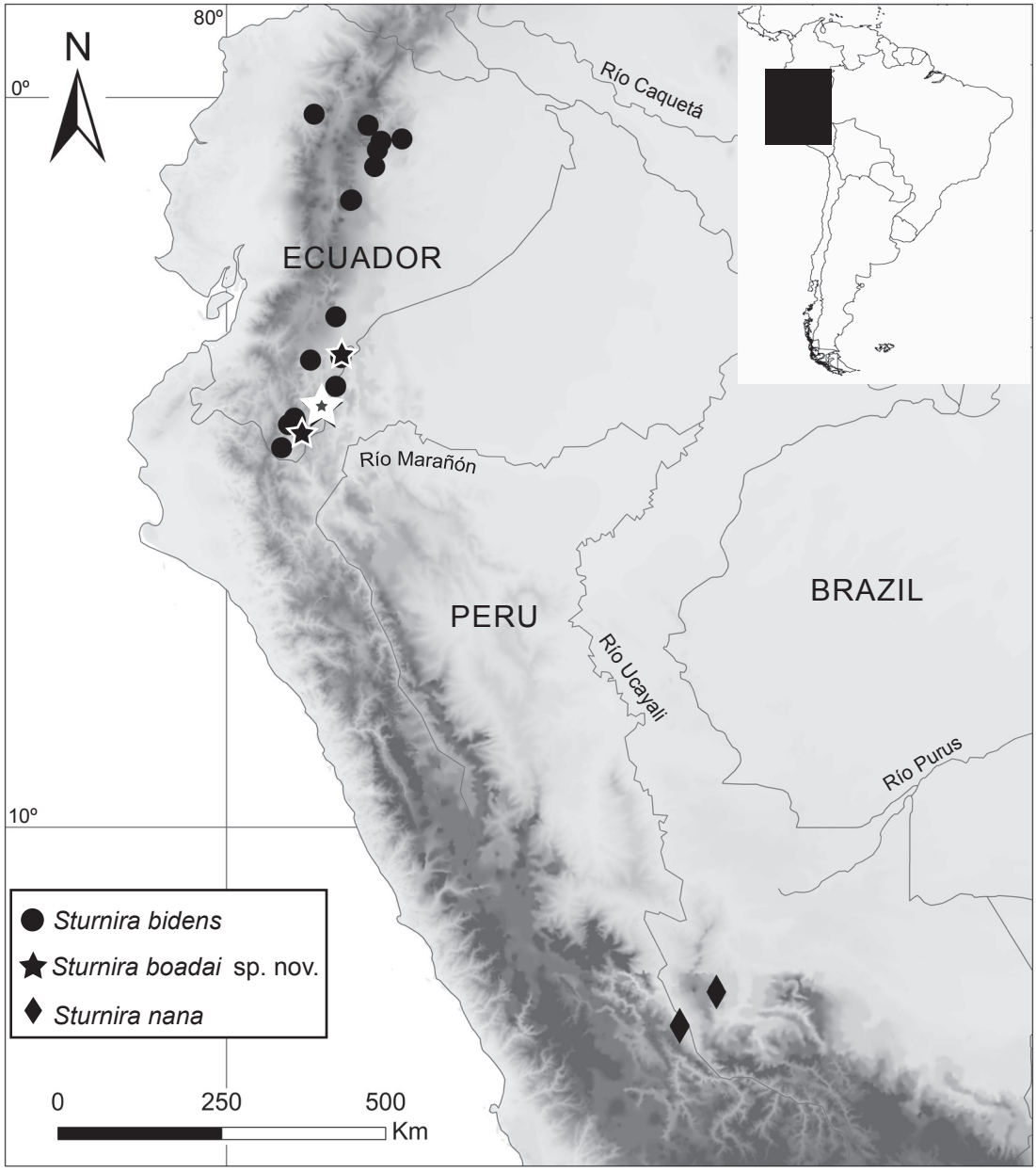

FIGURE 5. Map of NW South America showing the collection localities of *Sturnira bidens* (circles), *S. nana* (diamonds), and *Sturnira boadai*, sp. nov. (stars), analyzed in this study. The collection points of *Sturnira nana* overlap, so only two diamonds are observed.

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).

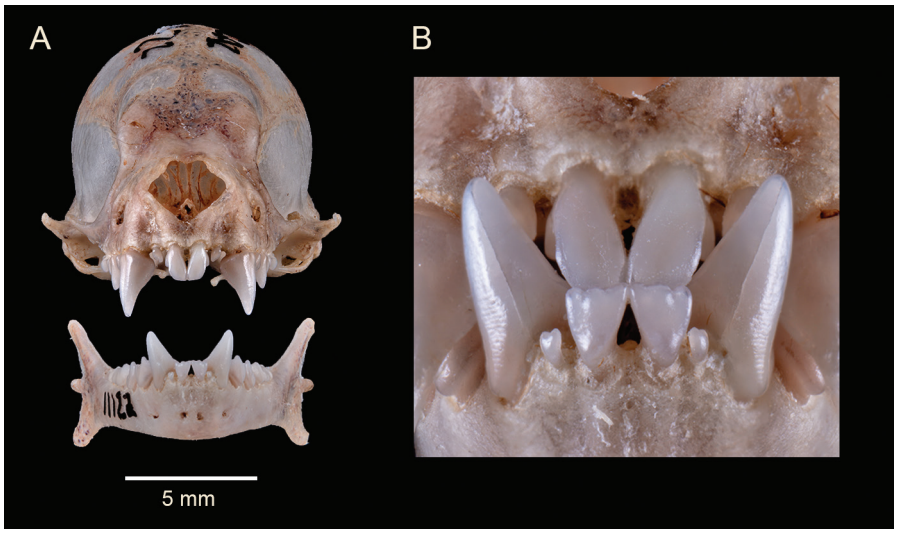

FIGURE 6. **A.** Upper and lower incisors of the holotype of *Sturnira boadai*, sp. nov. (QCAZ 11122). **B.** Detail of incisors. Photographs by Rubén D. Jarrín.

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[a]	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

[a] 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 *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 *Corvina* 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, Hypericaceare, 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 albujai* 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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REFERENCES

Boada, C. 2011. Mamíferos de los tepuyes de la cuenca alta del río Nangaritza, cordillera del Cóndor. *In* J.A. Guayasamín and E. Bonaccorso (editors), Evaluación ecológica rápida de la biodiversidad de los tepuyes de la Cuenca Alta del Río Nangaritza, Cordillera del Cóndor, Ecuador: 76–86. Quito: Conservación Internacional.

Boada, C., M.R. Marchán, and D. Tirira. 2011. Murciélago de hombros amarillos del Cóndor (*Sturnira*, sp. nov. A). *In* D. Tirira (editor), Libro rojo de los mamíferos del Ecuador, 2nd ed. Quito: Fundación Mamíferos y Conservación, Pontificia Universidad Católica del Ecuador y Ministerio del Ambiente del Ecuador.

Brito, J., et al. 2017. New species of arboreal rat of the genus *Rhipidomys* (Cricetidae, Sigmodontinae) from Sangay National Park, Ecuador. Neotropical Biodiversity 3: 65–79.

Brito, J., S. Vaca-Puente, C. Koch, and N. Tinoco. 2021a. Discovery of the first Amazonian *Thomasomys* (Rodentia, Cricetidae, Sigmodontinae): a new species from the remote Cordilleras del Cóndor and Kutukú in Ecuador. Journal of Mammalogy 102: 615–635.

Brito, J., et al. 2021b. A new species of spiny mouse, genus *Neacomys* (Cricetidae: Sigmodontinae) from Cordillera del Cóndor, Ecuador. Mastozoología Neotropical 28: 507–529.

Gardner, A.L. (editor). 2008 ("2007"). Mammals of South America. Vol. 1: marsupials, xenarthrans, shrews, and bats. Chicago: University of Chicago Press.

Gardner, A.L., and J.P. O'Neill. 1971. A new species of *Sturnira* (Chiroptera: Phyllostomidae) from Peru. Occasional Papers of the Museum of Zoology 42: 1–7.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology: A Journal of the Royal Meteorological Society 25: 1965–1978.

Iudica, C.A. 2000. Systematic revision of the Neotropical fruit bats of the genus Sturnira: A molecular and morphological approach. Ph.D. dissertation, Department of Zoology, University of Florida, Gainesville.

Kearse, M., et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649.

Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549.

Lanfear, R., P.B. Frandsen, A.M. Wright, T. Senfeld, and B. Calcott. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34: 772–773.

Marchán-Rivadeneira, M.R., P.A. Larsen, C.J. Phillips, R.E. Strauss, and R.J. Baker. 2012. On the association between environmental gradients and skull size variation in the great fruit-eating bat, *Artibeus lituratus* (Chiroptera: Phyllostomidae). Biological Journal of the Linnean Society 105: 623–634.

Marchán-Rivadeneira, M.R., V. Yánez-Fernández, S.F. Burneo, and D. Tirira. 2021. Murciélago de hombros amarillos menor (*Sturnira nana*). *In* D. Tirira (editor) Libro Rojo de los mamíferos del Ecuador. 3rd ed. Asociación Ecuatoriana de Mastozoología, Fundación Mamíferos y Conservación, Pontificia Universidad Católica del Ecuador and Ministerio del Ambiente, Agua y Transición Ecológica del Ecuador. Online resource (https://bit.ly/3GMJIGY), accessed November 20, 2022.

Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. 2010 Gateway Computing Environments Workshop (GCE) 1–8. Online resource (doi:10.1109/gce.2010.5676129)

Molinari, J., et al. 2017. A new polytypic species of yellow-shouldered bats, genus *Sturnira* (Mammalia: Chiroptera: Phyllostomidae), from the Andean and coastal mountain systems of Venezuela and Colombia. Zootaxa 4243: 75–96.

Moreno-Cárdenas, P.A., N. Tinoco, L. Albuja, and B.D. Patterson. 2021. A new species of *Rhagomys* (Rodentia, Sigmodontinae) from southeastern Ecuador. Journal of Mammalogy 102: 123–138.

Narváez-Romero, C., E. Ochoa-Luna, F. Gordillo, and D. Tirira. 2020. Nuevo registro de *Sturnira nana* (Chiroptera: Phyllostomidae) para el Ecuador. Mammalia aequatorialis 2020: 81–84.

Regalado, J., and L. Albuja. 2012. Ampliación de la distribución de *Sturnira nana* y *Lophostoma brasiliense* en el Ecuador. Revista Politécnica 2012 30: 160–165.

Roy, B.A., et al. 2018. New mining concessions could severely decrease biodiversity and ecosystem services in Ecuador. Tropical Conservation Science 11: 1–20.

Scullion, J. J., J. Fahrenholz, V. Huaytalla, E.M. Rengifo, and E. Lang. 2021. Mammal conservation in Amazonia's protected areas: a case study of Peru's Ichigkat Muja-Cordillera del Cóndor National Park. Global Ecology and Conservation 26: e01451.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. New York: Freeman.

Solari, S. 2019. Lesser yellow-shouldered bat, *Sturnira nana*. *In* D.E. Wilson and R.A. Mittermeier (editors), Handbook of the mammals of the world. Vol. 9: bats: 543. Barcelona: Lynx Edicions.

Solari, S., and C. Boada. 2016. *Sturnira nana*. The IUCN Red list of threatened species 2016: e. T20958A22050195. Internet resource (https://bit.ly/3AKcAMd), accessed November 24, 2022.

Solari, S., R.A. Medellín, B. Rodríguez-Herrera, E.R. Dumont, and S.F. Burneo. 2019. Family Phyllostomidae (New World leaf-nosed bats). *In* D.E. Wilson and R.A. Mittermeier (editors), Handbook of the mammals of the world. Vol. 9, Bats: 444–583. Barcelona: Lynx Edicions.

Thomas, O. 1915. A new genus of phyllostome bats and a new *Rhipidomys* from Ecuador. Annals and Magazine of Natural History 16: 310–312.

Tirira, D. 2012. Murciélagos del Ecuador: Una referencia geográfica, taxonómica y bibliográfica. *In* D. Tirira and S.F. Burneo (editors), Investigación y conservación sobre murciélagos en el Ecuador: 235–326. Quito: Pontificia Universidad Católica del Ecuador, Fundación Mamíferos y Conservación y Asociación Ecuatoriana de Mastozoología.

Tirira, D., J. Brito, S.F. Burneo, J.P. Carrera-Estupiñán, and Comisión de Diversidad de la AEM. 2022. Mammals of Ecuador: official updated species checklist. Version 2022.1. Quito: Asociación Ecuatoriana de Mastozoología. Internet resource (http://aem.mamiferosdelecuador.com), accessed June, 3 2022.

Trifinopoulos, J., L.T. Nguyen, A. von Haeseler, and B.Q. Minh. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44: 232–235.

Velazco, P.M., and A.L. Gardner. 2012. A new species of *Lophostoma* d'Orbigny, 1836 (Chiroptera: Phyllostomidae) from Panama. Journal of Mammalogy 93: 605–614.

Velazco, P.M., and B.D. Patterson. 2013. Diversification of the yellow-shouldered bats, genus *Sturnira* (Chiroptera, Phyllostomidae) in the New World tropics. Molecular Phylogenetics and Evolution 68: 683–698.

Velazco, P.M., and B.D. Patterson. 2014. Two new species of yellow-shouldered bats, genus *Sturnira* Gray, 1842 (Chiroptera, Phyllostomidae) from Costa Rica, Panama, and western Ecuador. ZooKeys 402: 43–66.

Velazco, P.M., and B.D. Patterson. 2019. Small mammals of the Mayo River Basin in northern Peru, with the description of a new species of *Sturnira* (Chiroptera: Phyllostomidae). Bulletin of the American Museum of Natural History 429: 1–67.

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
Artibeus obscurus	TK 104310	GU356393
Platyrrhinus helleri	USNM AVE12	GQ184736
Sturnira adrianae adrianae	CVULA I-8550	KY366231
Sturnira adrianae adrianae	CVULA I-8584	KY366232
Sturnira adrianae adrianae	CVULA I-8585	KY366233
Sturnira adrianae adrianae	CVULA I-8602	KY366234
Sturnira adrianae adrianae	CVULA I-8603	KY366235
Sturnira adrianae caripana	CVULA I-8590	KY366229
Sturnira adrianae caripana	CVULA I-8593	KY366230
Sturnira angeli	CM112363 / CAI 174	AF435158
Sturnira angeli	TTU19906 / CAI 229	AF435249
Sturnira angeli	UNSM 20062 / CAI 233	AF435251

APPENDIX 1 *continued*

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

APPENDIX 1 *continued*

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

APPENDIX 1 *continued*

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

APPENDIX 1 *continued*

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

APPENDIX 1 *continued*

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

APPENDIX 1 *continued*

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

APPENDIX 2

General Information on the Analyzed Specimens

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

[a] Geographic location included in climatic assessment analysis.
[b] Specimens not included in the morphometric analyses.

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