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Systematics and biogeography of *Anoura cultrata* (Mammalia, Chiroptera, Phyllostomidae): a morphometric, niche modeling, and genetic perspective, with a taxonomic reappraisal of the genus

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Abstract

The nectar-feeding bats of the genus *Anoura* are widely distributed in the Neotropics, but are most speciose in the Andes. *Anoura cultrata* is a rare mid-elevation bat occurring in South and Central America. It is thought to be one of the few bat species exemplifying a latitudinal cline in body size. We address three systematic and biogeographic questions: 1) is the geographic variation in *A. cultrata* continuous, as argued to justify its current monotypic status? 2) do ecogeographic barriers to dispersal affect such variation? and 3) how do the genetic divergence and biogeography of the species compare to those of other members of the genus? To answer these questions, we used morphometric analyses, ecological niche modeling, and DNA barcoding. We divided the samples of *A. cultrata* into six geographic groups, delimited by topographic depressions separating mountain systems. We did not find significant correlations between body size and the geographic coordinates within five groups. Therefore, we conclude that ecogeographic barriers to dispersal between the regions occupied by such groups influenced morphometric variation in *A. cultrata*, and that despite its general north to south reduction in body size, the species does not show continuous clinal variation. A recent phylogenetic study of the genus *Anoura* concluded that it contains seven valid species. Our DNA barcoding analysis and morphological examination indicated that at least 10 species should be recognized, including *A. peruana* distinct from *A. geoffroyi*, and *A. aequatoris* and *A. luismanueli* distinct from *A. caudifer*. Moreover, we show that Central and South American populations of *A. cultrata* differ from each other at least at the subspecific level, thus we respectively refer to them as *A. cultrata cultrata* and as *A. c. brevirostrum*. Similarly, we refer to Central American and Mexican populations of '*A. geoffroyi*' as *A. peruana lasiopyga*, and to their South American counterparts as *A. p. peruana*. The range of the latter subspecies reaches northeastern Venezuela. The Andes from southern Colombia to northern Peru appear to be the ancestral range of the genus.

Key words: body size, DNA barcoding, ecogeographic barriers, geographic variation, past distributions, subspecies, tropical mountains

Resumen

Los murciélagos nectarívoros del género *Anoura* están ampliamente distribuidos en el Neotrópico, aunque son más diversos en los Andes. *Anoura cultrata* es un murciélago raro de elevaciones intermedias distribuido en América del Sur y Central. Se cree que es una de las pocas especies de murciélago que ejemplifica una clina latitudinal en tamaño corporal. Abordamos tres preguntas sistemáticas y biogeográficas: 1) ¿es la variación geográfica en *A. cultrata* continua, tal como se ha argumentado para justificar su condición monotípica actual? 2) ¿afectan las barreras ecogeográficas para la dispersión dicha variación? y 3) ¿Cómo se compara la divergencia genética y biogeografía de la especie con las de otros miembros del género? Para responder estas preguntas, usamos análisis morfométricos, modelado de nicho ecológico y códigos de barras de ADN. Dividimos las muestras de *A. cultrata* en seis grupos geográficos, delimitados por depresiones topográficas que separan sistemas montañosos. No encontramos correlaciones significativas entre el tamaño del cuerpo y

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las coordenadas geográficas dentro de cinco de los grupos. Por ende, concluimos que las barreras ecogeográficas para la dispersión entre las regiones ocupadas por dichos grupos han influenciado la variación morfométrica de *A. cultrata*, y que a pesar de la reducción general de norte a sur de su tamaño corporal, la especie no muestra variación clinal continua. Un estudio filogenético reciente del género *Anoura* concluyó que contiene siete especies válidas. Nuestros análisis de código de barras de ADN y revisión morfológica indicaron que deben reconocerse al menos 10 especies, incluyendo *A. peruana* distinta de *A. geoffroyi*, y *A. aequatoris* y *A. luismanueli* distintas de *A. caudifer*. Más aún, demostramos que las poblaciones centro y sudamericanas de *A. cultrata* difieren entre sí al menos al nivel subespecífico, por lo cual respectivamente nos referimos a ellas como *A. cultrata cultrata* y *A. c. brevirostrum*. De manera similar, nos referimos a las poblaciones centroamericanas y mexicanas de '*A. geoffroyi*' como *A. peruana lasiopyga* y a sus contrapartes suramericanas como *A. p. peruana*. La distribución de la última subespecie alcanza el noreste de Venezuela. Los Andes desde el sur de Colombia hasta el norte de Perú parecen representar la distribución ancestral del género.

Palabras clave: barreras ecogeográficas, código de barras de ADN, distribuciones pasadas, montañas tropicales, subespecies, tamaño corporal, variación geográfica

Introduction

Physical and ecological barriers to dispersal are major and interacting causes of geographic variation and speciation (Pyron & Burbrink, 2010). They attain their maximum variety and complexity in tropical mountain systems, which therefore harbor a disproportionately large fraction of the global terrestrial biodiversity (Rahbek *et al.*, 2019*a*,*b*; Tenorio *et al.*, 2023). For tropical montane organisms, barriers to dispersal consist of unsuitable environments, such as dry or humid regions interrupting distributions (Killeen *et al.*, 2007; Särkinen *et al.*, 2012), high-elevation ridges separating sister taxa in opposite slopes of mountain ranges (Patterson *et al.*, 2012; Rahbek *et al.*, 2019*a*), and lowlands (sometimes restricted to narrow passes called depressions) isolating 'sky' islands or archipelagos inhabited by disjunct populations (Anderson *et al.*, 2012; Anthelme *et al.*, 2014; Hazzia *et al.*, 2018).

Anoura Gray, 1838 is a genus of nectar-feeding bats of the subfamily Glossophaginae in the family Phyllostomidae, or New World leaf-nosed bats. The most recent treatment of its taxonomy recognizes seven species (Calderón-Acevedo *et al.*, 2022). Of these, five [*A. cadenai* Mantilla-Meluk & Baker, 2006; *A. caudifer* (E. Geoffroy, 1818); *A. fistulata* Muchhala, Mena, & Albuja, 2005; *A. javieri* Pacheco, Sánchez-Vendizú, and Solari, 2018; and *A. latidens* Handley, 1984] are exclusively South American, one (*A. geoffroyi* Gray, 1838) is South American, Central American, and Lesser Antillean, and one (*A. cultrata* Handley, 1960) is South and Central American (Genoways *et al.*, 1998; Griffiths & Gardner, 2008; Pacheco *et al.*, 2018; Calderón-Acevedo *et al.*, 2022). All species of *Anoura* are restricted to the tropics, where they occur at elevations ranging from sea level to over 4,100 m (Handley, 1976; Graham, 1983; Dick, 2013).

Anoura cultrata Handley, 1960 is a rare bat found mainly at mid elevations (500–2,000 m) in the mountain systems of Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, and Bolivia, between 11° N and 16° S. Among other characters, it is distinguished by the possession of faceted upper canines interlocking, as scissors, with enlarged blade-like first lower premolars (Figs. 1 and S2.1). These teeth are unique among nectar-feeding bats, and may function as a flower-piercing device to allow forced access to nectar. In the only taxonomic review of the species, Nagorsen & Tamsitt (1981) subsumed *Anoura brevirostrum* Carter, 1968 and *Anoura werckleae* Starrett, 1969 as junior synonyms of *A. cultrata*. The type localities are: *A. cultrata*, 'Tacarcuna Village, 3,200 ft., Río Pucro, Darién, Panama'; *A. brevirostrum*, '31 km S Tingo Maria, 850 m, Huánuco, Perú'; and *A. werckleae*, '6.8 mi. S restaurant "La Georgina" along Interamerican Highway, 2500 m, Cerro de la Muerte massif, Province of San José, Costa Rica'.

Nagorsen & Tamsitt (1981) deemed *A. cultrata* to be monotypic, basing this judgment on a morphometric analysis through which they purported to show variation in size to be continuous throughout its geographic range, with the largest specimens occurring in Central America and northern Venezuela, and the smallest in central and southern Peru. Ever since, this concept has remained unchanged: thus, *A. cultrata* is thought to be one of the few bat species exemplifying a latitudinal cline in body size (Owen *et al.*, 1984; Bogdanowicz, 1990; Ashton *et al.*, 2000; Meiri & Dayan, 2003; Hedrick, 2021).

The study of Nagorsen & Tamsitt (1981) was the first to apply univariate and multivariate analyses to describe a presumed cline in a tropical bat species and to explore the potential ecological causes of such a pattern. During the more than four decades that have elapsed since their study, many more museum specimens of *A. cultrata* and other

species of *Anoura*, and new analytical methods, have become available. We take advantage of these circumstances to update and expand the systematic and biogeographic knowledge of *A. cultrata*, and to carry out comparisons with other species of the genus. Scientific progress is built on incremental knowledge, thus we express our recognition to their important pioneering effort, which served as inspiration for the present contribution.

We address three systematic and biogeographic questions: 1) is the geographic variation in *A. cultrata* continuous, as argued to justify its current monotypic status? 2) can ecogeographic barriers to dispersal, past and present, be used to explain this variation? and 3) how does the genetic divergence and biogeography of the species compare to those of its congeners? To answer these questions, we carry out morphometric analyses, perform ecological niche modeling for *A. cultrata*, and use DNA barcoding to clarify the species limits in the genus.

Materials and methods

Institutions, specimens, and measurements. For morphometric analyses, we examined 236 specimens of *Anoura cultrata* (Appendix 1), and specimens of other species of the genus, housed in the following collections: AMNH, American Museum of Natural History, New York, USA; CTUA, Colección Teriológica de la Universidad de Antioquia, Medellín, Colombia; CVULA, Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela; EBRG, Museo de la Estación Biológica Rancho Grande, Maracay, Venezuela; IAvH, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; FMNH, Field Museum of Natural History, Chicago, USA; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas, Venezuela; MCNG, Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; MEPN, Museo de la Escuela Politécnica Nacional, Quito, Ecuador; MNHN, Muséum national d'Histoire naturelle, Paris; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; ROM, Royal Ontario Museum, Toronto, Canada; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University, College Station, USA; and USNM, National Museum of Natural History, Washington, USA.

In addition, we included locality data, and measurements, if available, from 27 specimens listed in the literature whose identification we assume to be correct (Carter *et al.*, 1966; Starrett, 1969; Gardner *et al.*, 1970; Nagorsen & Tamsitt, 1981; Pacheco *et al.*, 1993; Rivas-Pava *et al.*, 2007; Griffiths & Gardner, 2008; Torres *et al.*, 2014). When possible, we used museum databases to verify information on these specimens, which are housed in the following collections: CUS-M, Colección de Mamíferos de la Universidad de Santa Rosa de Cabal, Santa Rosa de Cabal, Colombia; FMNH, USA; KU, Museum of Natural History, University of Kansas, Lawrence, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, USA; LSUMZ, Louisiana State University Museum of Zoology, Baton Rouge, USA; MHNUC, Museo de Historia Natural de la Universidad del Cauca, Popayán, Colombia; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; and TTU, The Museum, Texas Tech University, Lubbock, USA.

We included 27 linear measurements (mm) that were used in a previous study (Molinari, 1994). Summary statistics are provided in Appendix 3. Six external measurements (head and body length, with tail; tail length; hind foot length, with claws; ear length; tibia length; and calcar length) and the body mass (g) are presented for descriptive purposes. The remaining measurements, of which 7 are external (wing) and 14 are cranial, were used in morphometric analyses. External measurements are: forearm length, distance from the elbow to the wrist, including the carpals; third digit, metacarpal length; third digit, first phalanx length; fourth digit, metacarpal length; fourth digit, first phalanx length; fifth digit, metacarpal length; and fifth digit, first phalanx length. Cranial measurements (Fig. 1) are: greatest length of skull (GLS), henceforth referred to as skull length, distance from the anterior edge of the premaxillae to the most posterior point of the cranium; condylobasal length (CBL), distance from the anterior edge of the premaxillae to the occipital condyles; palatal length (PL), distance from the anterior edge of the premaxillae to the posterior edge of the palate lateral to the posteromedial projection; C–M3 length, maximum distance between the labial edge of the alveoli of the upper canine and the third upper molar; rostrum breadth (RB), minimum distance across the maxillae; postorbital constriction (PC), minimum interorbital distance across the frontals; zygomatic breadth (ZB), maximum distance across the outer margins of the zygomatic arches; breadth of braincase (BB), maximum distance across the parietals; mastoid breadth (MB), maximum distance across the mastoid processes;

braincase height (BH), minimum distance from the highest point of the braincase to the line between the posterior central border of the palatine bone and the anterior central border of the foramen magnum; C–C breadth, maximum distance between the labial edges of the alveoli of the upper canines; M3–M3 breadth, maximum distance between the labial edges of the alveoli of the third upper molars; length of mandible (LM), distance from the mandibular condyle to the anterior extreme of the ramus; and c–m3 length, maximum distance between the lower canine and the third lower molar at the level of the alveoli.

Sexual dimorphism in size. To determine whether there are significant differences between the sexes in *A. cultrata* with respect to forearm and skull lengths, we used a separate *t*-test for each of the six geographic groups described in the next section. To avoid Type I errors (without incurring Type II errors) as a consequence of carrying out multiple tests, we adjusted the *p*-values obtained by applying an improved Bonferroni correction (Benjamini & Hochberg, 1995).

Morphometric analyses. Similarly to Nagorsen & Tamsitt (1981), we divided our sample into six geographic groups, but used potential lowland barriers to dispersal (Fig. 2) instead of geopolitical units to demarcate them. Our groups are: 1) COPA, Costa Rica and W Panama, delimited by the Nicaragua Depression (DN) to the northwest, and the Central Panamanian Lowlands (CPL) to the southeast; 2) EPA, E Panama, delimited by the Central Panamanian Lowlands to the northwest, and the Atrato–San Juan Depression (DASJ) to the southeast; 3) NVE, N Venezuela (Venezuelan Coast Range, Sierra de Aroa, and Serranía de Bobare), delimited by the Unare Depression (DU) to the east, and the Lara Depression (DL) to the west (Molinari *et al.*, 2017); 4) WVE, W Venezuela, delimited by the Lara Depression to the northeast, and the Tachira Depression (DT) to the southwest; 5) COEC, Colombia and Ecuador, delimited by the Atrato–San Juan Depression to the northwest, the Tachira Depression to the northeast, and the Huancabamba Depression (DH) to the south; and 6) PEBO, Peru and Bolivia, delimited by the Huancabamba Depression to the north, and the Southern Andes to the south.

To search for significant differences in size between geographic groups, we used analyses of variance, followed by post hoc (THSD, Tukey's Honestly Significant Difference) tests. These included: 1) Multiple Analysis of Variance (MANOVA) to compare forearm and skull lengths; 2) Analysis of Variance (ANOVA) to compare specimen scores on the first axis (PC1) based on the PCA of 6 wing measurements (forearm length was excluded to avoid redundancy with the MANOVA); and 3) ANOVA to compare specimen scores on the first axis (PC1) of the PCA based on 13 cranial measurements (skull length was excluded to also avoid redundancy with the MANOVA). To not exclude specimens lacking a complete set of either wing or cranial measurements, we used a separate ANOVA based on each instead of a single MANOVA based on the two sets of measurements. Because all the variable loadings on PC1 were positive, we deemed specimen scores on these axes to be unidimensional summaries of the multivariate size (Gutiérrez & Molinari, 2008) defined by the variables not used in MANOVAs. Thus, the PC1 based on wing measurements is complementary to forearm length as a measure of wing size, and the PC1 based on cranial measurements is complementary to skull length as a measure of cranial size.

We used Linear Discriminant Analysis (LDA) to visualize the differences between geographic groups based on the 21 wing and cranial measurements (i.e., forearm and skull lengths not excluded). Using a single analysis allowed the determination of the relative contribution of wing and cranial variables to the differences between groups. Because the variable loadings on each LDA axis were both positive and negative, we deemed specimen scores on these axes to represent at least partially unidimensional summaries of multivariate shape. To search for significant differences among geographic groups with respect to scores in the LDA axes, we used a MANOVA followed by post hoc (THSD) tests.

To determine whether the geographic variation is clinal, we calculated the Pearson correlation coefficient (r) between one of four size variables at a time (forearm length; skull length; scores on PC1 of the two PCAs described above), and the two geographic coordinates. We adjusted the significances of the correlation coefficients using the Benjamini-Hochberg procedure.

We used PAST, version 4.07 (Hammer, 2021) to compute LDA and PCA, and to plot the results; SPSS, version 17, to compute ANOVAs and MANOVAs, and to calculate correlation coefficients; an online calculator (Radua & Albajes-Eizagirre, 2010) to obtain Benjamini-Hochberg probabilities; and OriginPro, Version 2021 (OriginLab Corporation, Northampton, MA, USA) to create box-and-whisker plots. In these procedures, we excluded specimens with missing measurements, with a single exception: in the calculation of r between GLS and the geographic coordinates, we used linear regression to estimate GLS from CBL for the single Bolivian specimen (LSUMZ 22962).

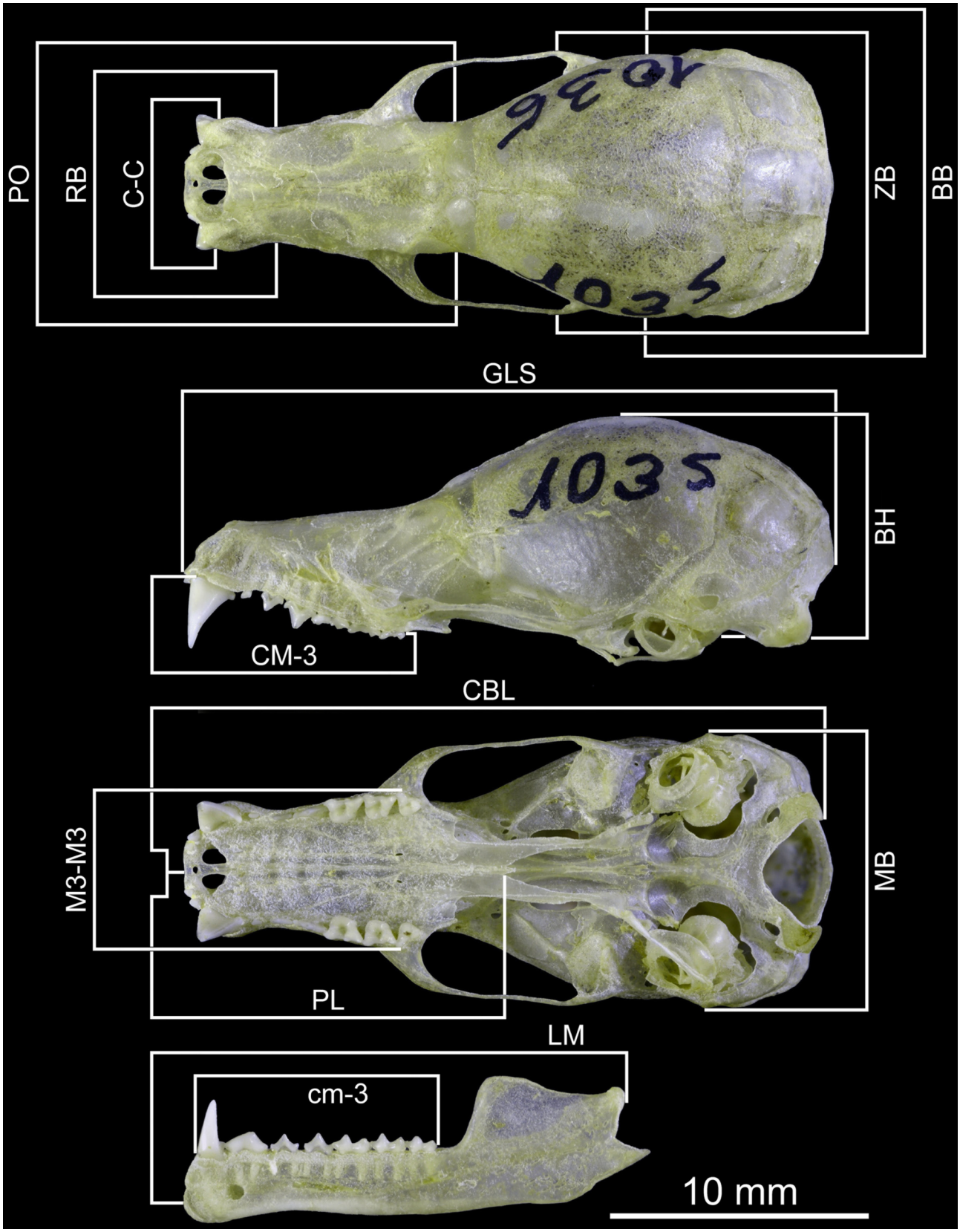

FIGURE 1. Craniodental measurements used in morphometric analyses. The dorsal, lateral, and ventral views of the cranium, and lateral view of the mandible correspond to a male specimen of *Anoura cultrata* (MCNG 1035) from Venezuela (Merida Cordillera). Abbreviations are: BB, breadth of braincase; BH, braincase height; CBL, condylobasal length; C–C breadth; C–M3 length; c–m3 length; GLS, greatest length of skull; LM, length of mandible; M3–M3 breadth; MB, mastoid breadth; PL, palatal length; PC, postorbital constriction; RB, rostrum breadth; and ZB, zygomatic breadth.

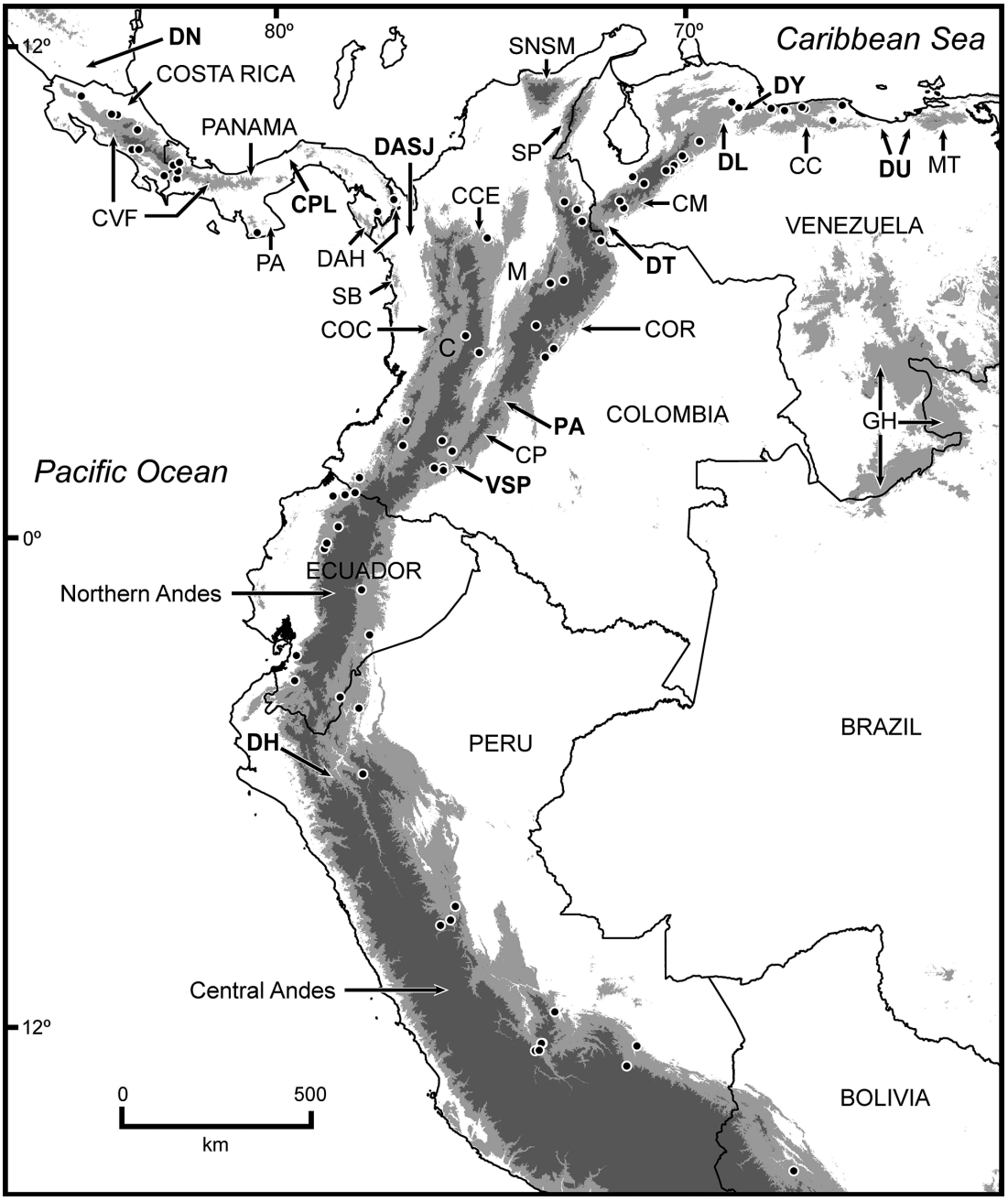

FIGURE 2. Mountain systems of SE Central America and NW South America in which *Anoura cultrata* has been recorded (filled circles). Elevations above 500 m are indicated in light grey. Elevations above 2,000 m are indicated in dark grey. Abbreviations for mountain systems are: **CC**, Venezuelan Coast Range [*Cordillera de la Costa*]; **CCE**, Colombian Central Cordillera [*Cordillera Central de Colombia*]; **CM**, Merida Cordillera [*Cordillera de Mérida*]; **COC**, Colombian Western Cordillera [*Cordillera Occidental de Colombia*]; **COR**, Colombian Eastern Cordillera [*Cordillera Oriental de Colombia*]; **CP**, Putumayo corridor [*Corredor de Putumayo*]; **CVF**, Chorotega Volcanic Front [*Frente Volcánico de Chorotega*]; **DAH**, Darien Highlands [*montañas del Darién*]; **GH**, Guiana Highlands [*Macizo* (*or Escudo*) *Guayanés*]; **MT**, Turimiquire Massif [*Macizo de Turimiquire*]; **PA**, Azuero Peninsula Highlands [montañas de la Península de Azuero]; **SB**, Baudo Mountains [*Serranía del Baudó*]; **SNSM**, Santa Marta Mountain Range [*Sierra Nevada de Santa Marta*]; **SP**, Perija Mountain Range [*Serranía* (*or Sierra*) *de Perijá*]. Abbreviations for depressions [highlighted in bold in the map] separating mountain systems are: **C**, Cauca Valley [*Valle del Cauca*]; **CPL**, Central Panamanian Lowlands [*Tierras Bajas Centrales de Panamá*]; **DASJ**, Atrato–San Juan Depression [*Depresión del Atrato–San Juan*]; **DH**, Huancabamba Depression [*Depresión de Huancabamba*]; **DL**, Lara Depression [*Depresión de Lara*]; **DN**, Nicaragua Depression [*Depresión de Nicaragua*]; **DT**, Tachira Depression [*Depresión del Táchira*]; **DU**, Unare Depression [*Depresión de Unare*]; **DY**, Yaracuy Depression [*Depresión de Yaracuy*]; **M**, Magdalena Valley [*Valle del Magdalena*]; **PA**, Andalucia pass [*Paso de Andalucía*]; **VSP**, Suaza-Pescado valleys [*Valles de Suaza-Pescado*].

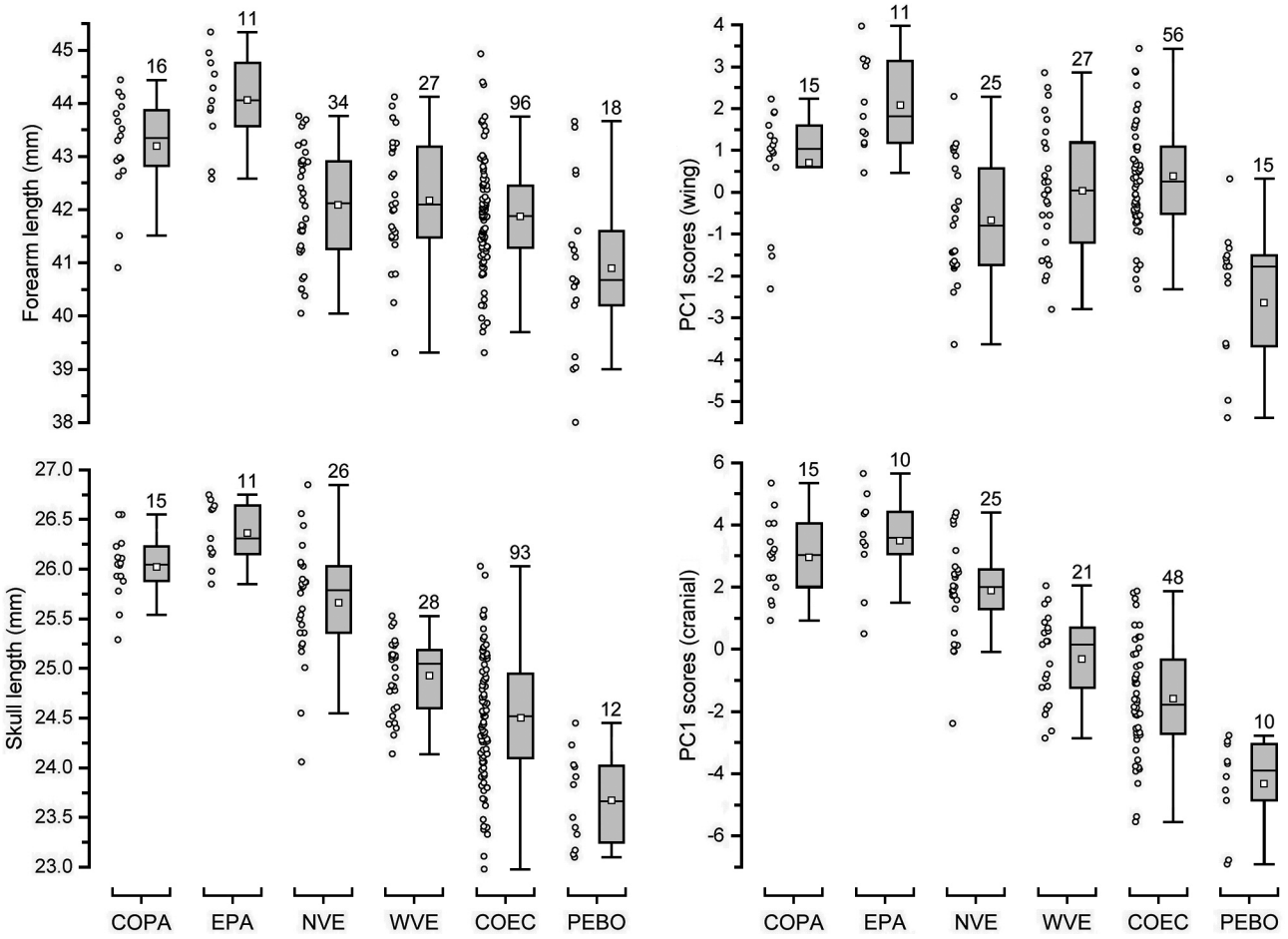

FIGURE 3. Box-and-whisker plots comparing the wing and cranial sizes of six geographic groups of *Anoura cultrata*: COPA, Costa Rica–W Panama; EPA, E Panama; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Peru–Bolivia. The height of each gray box represents the interquartile range (IQR), containing 50% of data points. Within each box, the horizontal line represents the median, and the empty square the mean. The upper and lower 'whiskers' respectively indicate the distance from the box of the largest value within Q3 + 1.5 × IQR, and the smallest value within Q1 - 1.5 × IQR. The numbers on the top of upper 'whiskers' indicate the sample sizes. The distribution of the values on which each plot is based is shown to its left. Values above the upper 'whisker' and below the lower 'whisker' are considered outliers. Scores on the first axes (PC1) of Principal Components Analyses were used as proxies of wing (6 measurements, forearm length excluded) and cranial (13 measurements, skull length excluded) sizes. The PC1 of wing measurements accounts for 57.19 %, and the PC1 of cranial measurements for 58.36 % of variance. Eigenvalues and variable loadings for the two PCAs are provided in Supplementary Information S1.

Ecological niche modeling. We estimated the present and past abiotically suitable areas for *A. cultrata* by means of ecological niche modeling (ENM) analyses using Maxent (for ENM terminology, see Peterson *et al.*, 2011). These analyses were based on high-quality presence data, climatic variables, a study region for model calibration selected by recommended criteria, and model algorithm settings tuned for optimal balance between model complexity and performance (Anderson & Raza, 2010). To obtain species presence data of adequate quality for ENM, we georeferenced all localities using Google Earth Pro version 7.3.4.8248 (https://www.google.com/earth/), and the combination of various sources of information, including zoological and botanical literature (e.g., Paynter, 1997; Anderson & Gutiérrez, 2009), museum databases, collector's field notes, official documents, and web pages. The resulting dataset contained 92 localities with unique geographic coordinates (Fig. 2; Appendix 1).

We used 19 bioclimatic variables from Worldclim (Hijmans *et al.*, 2005; http://biogeo.berkeley.edu/worldclim/worldclim.htm) that are widely used in ENM-based studies on vertebrate distributions, and which have been successfully used for Neotropical montane mammals (e.g., Gutiérrez *et al.*, 2015). All models (preliminary or final, see below) were calibrated with variables for contemporary bioclimatic conditions (1,950–2,000) at 30 arc-seconds

resolution (ca. 1 km^2 at the Equator). The final model was projected on these contemporary conditions, as well as on bioclimatic conditions estimated for the Holocene Climatic Optimum (HCO: ~6,000 YBP = years before present), for the Last Glacial Maximum (LGM: ~22,000 YBP), and for the Last Interglacial Maximum (LIG: ~125,000 YBP), derived from the Model for Interdisciplinary Research on Climate (Watanabe *et al.*, 2011). The contemporary, HCO and LIG variables were at 30 arc-seconds resolution, whereas those from the LGM were at 2.5 arc-minutes resolution.

Because study regions have important effects on the model calibration process (Peterson *et al.*, 2011; Anderson, 2012, 2013; Gutiérrez, 2016), we proceeded according to the proposed principles for their proper selection (Anderson & Raza, 2010; Barve *et al.*, 2011; Gutiérrez *et al.*, 2014). For model calibration only, we selected four subareas within the range of *A. cultrata* (Fig. 2). These subareas, termed minimum convex polygons (MCPs), were those circumscribed by polygons connecting the marginal localities of each of the major clusters of localities distinguished visually. We added a 0.5° wide buffer zone around each of the MCPs, which were: 1) Costa Rica and Panama, west of the Atrato–San Juan Depression; 2) western and northern Venezuela, and central Colombia; 3) southwestern Colombia, Ecuador, and northern Peru, north of the Huancabamba Depression; and 4) central and southern Peru, and Bolivia, south of the Huancabamba Depression. This operational strategy aimed to exclude any extensive regions separating major MCPs which, in spite of possessing suitable climatic conditions, are not occupied by *A. cultrata*, either because of the presence of barriers to dispersal, or as a result of biotic interactions (Gutiérrez *et al.*, 2014). Prior to calibration, we masked areas outside MCPs using the 'mask' function of the R package 'raster', version 2.4-20 (Hijmans, 2017; RDCT, 2015), then carried out model calibration by sampling background data for environmental variables only from within MCPs.

To model the abiotically suitable areas, we used the maximum entropy method implemented in Maxent ver. 3.3.3h (Elith *et al.*, 2006; Phillips *et al.*, 2006; Phillips & Dudík, 2008). We tuned Maxent settings for optimal balance between model complexity and performance. For this, we used the R package ENMeval version 0.2.0 (Muscarella *et al.*, 2014) to construct and compare a series of preliminary models to identify the optimal combinations of feature classes and regularization multipliers. The regularization multiplier was varied from 0.5 to 5 in increments of 0.5, and the following four feature classes (or combinations thereof) were tested: 1) linear, quadratic, and hinge; 2) linear, quadratic, hinge, and product; 3) linear, quadratic, hinge, and threshold; and 4) linear, quadratic, hinge, product, and threshold (Supplementary Information S1).

ENMeval allows three different data-partitioning schemes, which are a variation of the methods referred to as 'masked geographically structured' data partitioning (Radosavljevic & Anderson, 2014). We employed the 'checkerboard2' scheme, generating checkerboard grids across the study region by partitioning the localities into bins. These bins are formed using two levels of spatial aggregation (i.e., fine- and coarse-grained; Muscarella *et al.*, 2014). We used default grid sizes for the 'checkerboard2' scheme. Our primary optimality criterion for selecting the best Maxent settings (i.e., the combination of feature classes and regularization multiplier) was the Akaike Information Criterion corrected for small sample sizes (AICc; Warren & Seifert, 2011; Warren *et al.*, 2014). The final model was constructed employing all localities, and the Maxent settings that yielded the lowest value of AICc. Because AICc only identifies the best from among a set of models, and does not directly assess model performance, we inspected the OR_{10} (10% omission rate) and AUC (Area Under the Curve of the Receiver Operating Characteristic plot) of the preliminary model that yielded the lowest AICc (Peterson *et al.*, 2008, 2011).

In addition, because we projected the final model onto different regions than those used for calibrating the model, we inspected the multivariate environmental similarity surfaces and clamping maps produced by Maxent. These procedures allowed us to determine whether environmental variables on other regions were outside the range of climatic conditions present in the calibration regions. We converted the projections of the final models into binary maps of 'suitable' vs. 'unsuitable' habitat using Max SSS ('SeSpmax'; Nenzén & Araújo, 2011), with the maximum training sensitivity plus specificity threshold calculated with Maxent. The Max SSS threshold has been shown to produce accurate predictions and is considered among the best performing thresholds when only presence data is available (Manel *et al.*, 2001; Liu *et al.*, 2005, 2013; Jiménez-Valverde & Lobo, 2007).

Molecular analysis. For the molecular study, 657 basepairs of the mitochondrial cytochrome c oxidase subunit 1 (CO1) gene were analyzed for 193 samples of *Anoura* and two outgroups represented by *Choeroniscus godmani* and *Glossophaga soricina* (Appendix 3). Of these samples, 162 were downloaded from Genbank and 33 were newly generated sequences with accession numbers OQ944940–OQ944972. DNA extraction of the new samples, PCR amplification, and nucleotide sequencing methods were outlined in Clare *et al.* (2007) with modifications following

Lim (2017). Sequences were visually inspected for the absence of stop codons and indels, which would indicate nuclear mitochondrial (NUMT) DNA, before aligning using Sequencher version 4.8 (Gene Codes Corp, 2007). Phylogenetic analysis was done using maximum likelihood with 1,000 bootstrap replicates and a best-fit model of DNA substitution as implemented in MEGA7 (Kumar *et al.*, 2016). In addition, average genetic divergence was calculated within and between species based on the best-fit model.

Results

Sexual dimorphism in size. For each of the six geographic groups of *A. cultrata*, we performed *t*-tests to determine whether there are significant differences in forearm and skull lengths between males and females. Initially, four tests indicated significant differences. These involved EPA, WVE, and PEBO (forearm length), and NVE (skull length). After applying the Benjamini-Hochberg correction, only the forearm comparisons remained significant. For the groups in question, the forearm and skull lengths of males and females are provided separately in the footnote of Appendix 2. Males had shorter forearms than females in two groups (EPA, WVE), and the inverse in the other (PEBO). We did not include body mass in morphometric analyses. However, males averaged 18.4 g (n = 13) and females 15.7 g (n = 16) in NVE, 15.7 g (n = 16) and 16.0 g (n = 5) in WVE, and 16.7 g (n = 29) and 15.7 g (n = 24) in COEC.

Morphometry. Because only 3 of the 12 tests used for comparisons within geographic groups of *A. cultrata* indicated significant differences between the sexes in forearm or skull length, we do not separate males and females in descriptive statistics (Appendix 2), nor in subsequent morphometric analyses. We used box plots to compare geographic groups with respect to wing and cranial sizes (Fig. 3). As size indicators, we use forearm and skull lengths, and PC1 scores of the other wing or cranial measurements. The significances of the comparisons are shown in Tables 1 and 2.

TABLE 1. Post hoc significance values resulting from the simultaneous comparison (MANOVA) of six geographic groups (Fig. 2) of *Anoura cultrata* with respect to forearm (upper triangular matrix) and skull (lower triangular matrix) lengths. The full results of the MANOVA are provided in Supplementary Data SD1. COPA, Costa Rica–W Panama; EPA, E Panama; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Peru–Bolivia.

	COPA	EPA	NVE	WVE	COEC	PEBO
COPA	—	0.343	0.010**	0.055	0.001**	0.000**
EPA	0.630	—	0.000**	0.000**	0.000**	0.000**
NVE	0.335	0.007**	—	0.977	1.000	0.007**
WVE	0.000**	0.000**	0.000**	—	0.910	0.001**
COEC	0.000**	0.000**	0.000**	0.022**	—	0.002**
PEBO	0.000**	0.000**	0.000**	0.000**	0.000**	—

**Significant ($p < 0.01$)

Regarding overall wing size (forearm length and scores on the wing PC1), the following size hierarchy is observed: [COPA ≈ EPA] > NVE ≈ WVE ≈ COEC > PEBO (Fig. 3). EPA differs significantly from the four South American groups. COPA also differs significantly from these groups, except NVE. Among South American groups, NVE does not differ significantly from its neighbor WVE, but it does from COEC and PEBO. The two North Andean groups, WVE and COEC, do not differ significantly from each other, but both do so from PEBO (Tables 1 and 2). Regarding overall cranial size (skull length and scores on the cranial PC1), the following size hierarchy is observed: [COPA ≈ EPA] > NVE > WVE > COEC > PEBO (Fig. 3). All groups differ significantly from each other, except in the comparisons between COPA and EPA, and COPA and NVE (Tables 1 and 2). Based on wing size, the groups can be assigned to three categories: large (COPA, EPA); medium (NVE, WVE, COEC); and small (PEBO). However, based on cranial size, the only two groups that can be joined in a similar size category are COPA and EPA: there is a large gap in average cranial size between these groups and their closest South American neighbor, COEC (Fig. 3).

TABLE 2. Post hoc significance values resulting from the ANOVA comparisons of six geographic groups (Fig. 2) of *Anoura cultrata* with respect to PC1 values of wing measurements, excluding forearm length (upper triangular matrix), and PC1 values of cranial measurements, excluding skull length (lower triangular matrix). One separate ANOVA was carried out for each of the two sets of PC1 values. The full results of the ANOVAs, and eigenvalues and variable loadings for the PCAs, are provided in Supplementary Data SD1. COPA, Costa Rica–W Panama; EPA, E Panama; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Peru–Bolivia.

	COPA	EPA	NVE	WVE	COEC	PEBO
COPA	—	0.201	0.064	0.749	0.980	0.000**
EPA	0.963	—	0.000**	0.003**	0.011*	0.000**
NVE	0.331	0.089	—	0.529	0.044*	0.001**
WVE	0.000**	0.000**	0.000**	—	0.920	0.000**
COEC	0.000**	0.000**	0.000**	0.030*	—	0.000**
PEBO	0.000**	0.000**	0.000**	0.000**	0.000**	—

*Significant ($p < 0.05$). **Significant ($p < 0.01$)

TABLE 3. LDA confusion matrix for 122 specimens of *Anoura cultrata* belonging to 6 geographic groups. For each geographic group, the percentage of correctly classified specimens is underlined. The analysis (Fig. 3) included 7 cranial and 14 wing measurements. COPA, Costa Rica–W Panama; EPA, E Panama; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Peru–Bolivia. Eigenvalues and variable loadings are provided in Supplementary Data SD1.

	% classified as					
	COPA	EPA	NVE	WVE	COEC	PEBO
COPA ($n = 15$)	80	13	0	7	0	0
EPA ($n = 10$)	0	100	0	0	0	0
NVE ($n = 24$)	8	0	88	4	0	0
WVE ($n = 21$)	0	0	5	76	19	0
COEC ($n = 43$)	2	0	5	16	75	2
PEBO ($n = 9$)	0	0	0	0	0	100

TABLE 4. Post hoc significance values resulting from the simultaneous comparison (MANOVA) of six geographic groups of *Anoura cultrata* (Fig. 3) with respect to their specimen scores in the first four axes of a Linear Discriminant Analysis of 7 wing and 14 cranial measurements (Fig. 4). COPA, Costa Rica–W Panama; EPA, E Panama; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Peru–Bolivia. The full results of the MANOVA, and eigenvalues and variable loadings for the LDA, are provided in Supplementary Data SD1.

	COPA	EPA	NVE	WVE	COEC	PEBO
	Axis 1 (upper triangular matrix) \ Axis 2 (lower triangular matrix)					
COPA	—	0.000**	0.000**	0.000**	0.000**	0.000**
EPA	0.000**	—	0.040*	0.000**	0.000**	0.000**
NVE	0.000**	0.000**	—	0.000**	0.000**	0.000**
WVE	0.000**	1.000	0.000**	—	0.041*	0.000**
COEC	0.000**	0.107	0.000**	0.053	—	0.000**
PEBO	0.000**	0.999	0.000**	0.999	0.525	—
	Axis 3 (upper triangular matrix) \ Axis 4 (lower triangular matrix)					
COPA	—	0.000**	0.325	0.007**	0.000**	0.050**
EPA	0.000**	—	0.006**	0.521	0.861	0.000**
NVE	1.000	0.000**	—	0.335	0.015*	0.000**
WVE	1.000	0.000**	1.000	—	0.947	0.000**
COEC	0.892	0.000**	0.874	0.882	—	0.000**
PEBO	0.017*	0.912	0.006**	0.007**	0.029*	—

*Significant ($p < 0.05$). **Significant ($p < 0.01$)

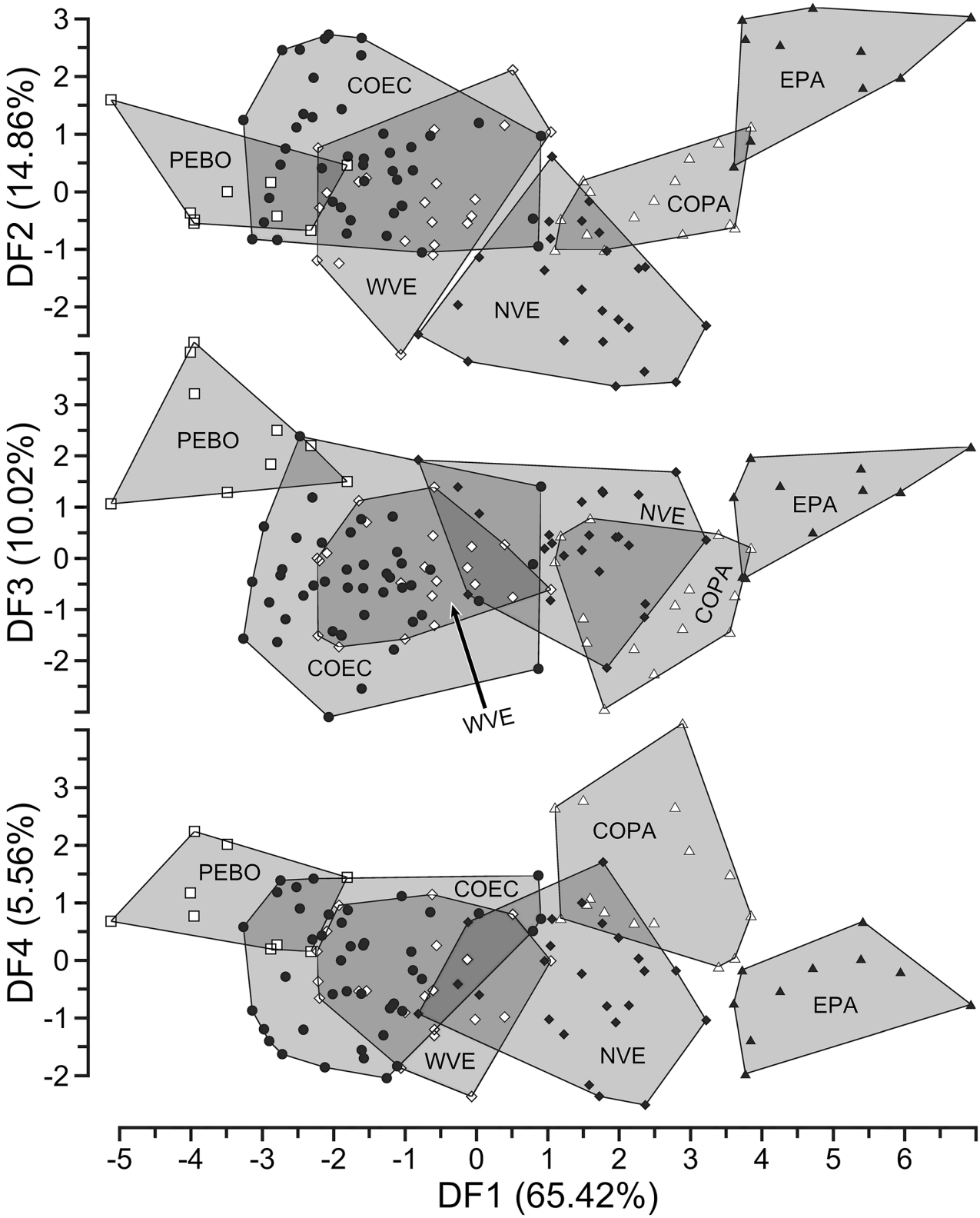

FIGURE 4. Relative position of six geographic groups and 122 specimens of *Anoura cultrata* in the space defined by a Linear Discriminant Analysis (LDA) of the 7 wing and 14 cranial measurements considered in the study. Specimen scores obtained by means of the second, third, and fourth discriminant functions (DF2, DF3, DF4) were plotted against those obtained by means of the first (DF1). The percentage of variance accounted by each of the four axes is indicated in their legends. COPA, Costa Rica–W Panama (empty triangles); EPA, E Panama (filled triangles); NVE, N Venezuela (filled diamonds); WVE, W Venezuela (empty diamonds); COEC, Colombia–Ecuador (filled circles); PEBO, Peru–Bolivia (empty squares). Eigenvalues and variable loadings are provided in Supplementary Information S1.

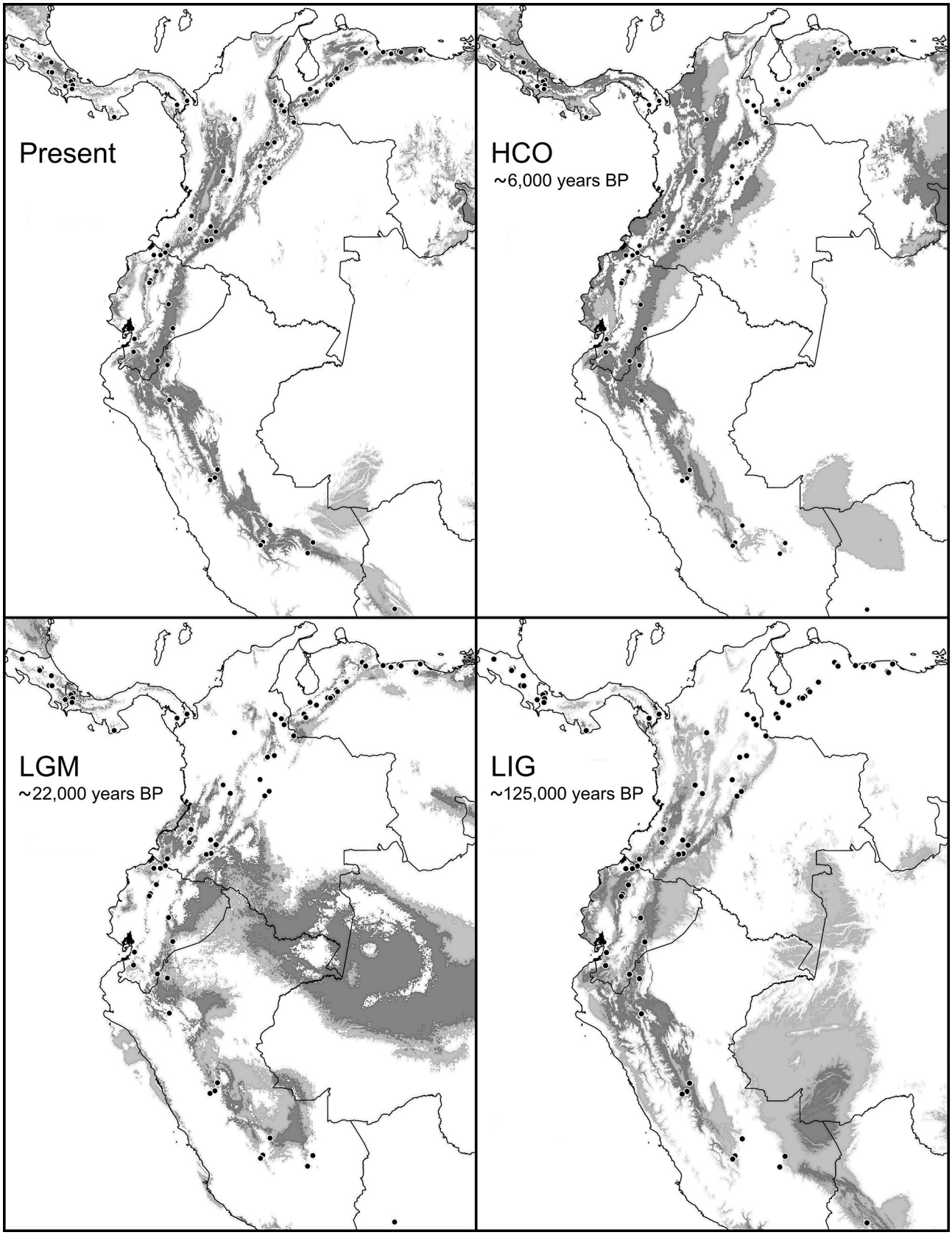

FIGURE 5. Maps of SE Central America and NW South America showing in gray present and past abiotically suitable areas for *Anoura cultrata*, as predicted by ecological niche modeling analyses. Darker shades of gray indicate stronger model support. Filled circles represent records for the species. Climatic scenarios are: top left, present climatic conditions; top right, HCO, Holocene Climatic Optimum; bottom left, LGM, Last Glacial Maximum; bottom right, LIG, Last Interglacial.

To determine the degree to which our six geographic groups are separable based on the 21 measurements combined, we carried out a LDA (Fig. 4; Table 3). Unlike specimen scores on PC1 (Fig. 3) which are all positive and thus reflect size, specimens scores on all LDA axes are both positive and negative (Supplementary Information S1), meaning that at least partly they represent shape comparisons. On the first LDA axis (Fig. 4), accounting for 65.42% of the variance, a large separation is observed between the Central American EPA and its neighboring South American group, COEC. Also, a large separation is observed between the northernmost (NVE) and southernmost (PEBO) South American groups, which are not geographic neighbors. On the second LDA axis (Fig. 4), accounting for 14.86% of the variance, the two most distinct groups are EPA and NVE, despite both being composed of relatively large specimens (Fig. 3). On the third LDA axis (Fig. 4), accounting for 10.02% of the variance, PEBO, which is composed of the smallest specimens (Fig. 3), is the most distinct group. On the fourth LDA axis (Fig. 4), accounting for 5.56% of the variance, the two most distinct groups are COPA and EPA, despite their vicinity in Central America (Fig. 2) and similarity in size (Fig. 3). The discriminant functions achieved high rates of correct specimen classification: EPA and PEBO, 100%; COPA, 80% (93% identified as Central American, i.e., COPA or EPA); NVE, WVE, and COEC, respectively 88, 76, and 75% (Table 3), despite their geographic contiguities (Fig. 2).

TABLE 5. Correlation of forearm and skull lengths with latitude and longitude within five geographic groups of *Anoura cultrata*. EPA is not included because of the reduced geographic distance between samples. Values within brackets to the right of correlation coefficients (*r*) are the *p*-values for the coefficients. COPA, Costa Rica–W Panamá; EPA, E Panamá; NVE, N Venezuela; WVE, W Venezuela; COEC, Colombia–Ecuador; and PEBO, Perú–Bolivia.

	Forearm vs. latitude	Forearm vs. longitude	Skull vs. latitude	Skull vs. longitude
COPA[1]	0.66 [0.005]*	-0.73 [0.001]*	0.07 [0.818]	-0.05 [0.868]
NVE	0.07 [0.728]	-0.21 [0.278]	-0.08 [0.687]	-0.22 [0.285]
WVE	0.31 [0.120]	0.31 [0.116]	0.11 [0.582]	0.03 [0.871]
COEC	0.06 [0.541]	0.02 [0.863]	0.14 [0.190]	-0.11 [0.313]
PEBO	-0.11 [0.685]	0.19 [0.457]	-0.45 [0.125]	0.41 [0.162]

[1]Only specimens from the Chorotega Volcanic Front are included.
*Remains significant when the Benjamini-Hochberg correction is applied.

TABLE 6. Sequence divergence based on Tamara Nei model with gamma distribution of nucleotide substitutions for the cytochrome c oxidase subunit 1 (CO1) mitochondrial DNA gene of the nectar-feeding bats of the genus *Anoura*. Within species difference on the diagonal and between species differences in the lower matrix.

	Outgroup	*A. geoffroyi*	*A. aequatoris*	*A. caudifer*	*A. cultrata*	*A. peruana*	*A. luismanueli*	*A. latidens*
Outgroup	**0.263**							
A. geoffroyi	0.266	**0.008**						
A. aequatoris	0.239	0.236	**0.006**					
A. caudifer	0.235	0.159	0.184	**0.015**				
A. cultrata	0.239	0.218	0.189	0.186	**0.031**			
A. peruana	0.254	0.069	0.203	0.173	0.200	**0.026**		
A. luismanueli	0.270	0.209	0.181	0.178	0.223	0.204	**0.028**	
A. latidens	0.268	0.142	0.201	0.224	0.211	0.143	0.201	**0.001**

The LDA axes are mostly contrasts of cranial measurements (Supplementary Information S1). Note that overall the greatest contribution is made by cranial breadth rather than cranial length measurements. To determine whether the differences among groups (Fig. 4) are significant, we performed a MANOVA, with specimen scores on the first four LDA axes being used as dependent variables (Supplementary Information S1). This resulted in 15 post hoc comparisons per axis (Table 4). Along the first LDA axis, significant differences were found by all comparisons. Along the second LDA axis, nine comparisons yielded significant differences: those that did not are EPA vs. WVE, COEC and PEBO, WVE vs. COEC and PEBO, and COEC vs. PEBO. Along the third LDA axis, 10 comparisons yielded significant differences: those that did not are NVE vs. COPA, WVE vs. EPA

and NVE, and COEC vs. EPA and WVE. Along the fourth LDA axis, eight comparisons yielded significant differences: those that did not are COPA vs. NVE, WVE and COEC, EPA vs. PEBO, NVE vs. WVE and COEC, and WVE vs. COEC. These results provide statistical support to our preceding remarks on the LDA graphical output (Fig. 4).

With the exception of EPA, the samples within each of our geographic groups span geographic distances long enough for clinal variation to potentially occur. For example, within both COEC and PEBO, these distances exceed 1,200 km along the Andes. *Anoura cultrata* has been postulated to show a continuous north to south clinal variation in cranial and wing sizes (Nagorsen & Tamsitt, 1981). Based on this reasoning, we calculated Pearson correlations coefficients (*r*) and their significances between either forearm or skull length and either latitude or longitude within our geographic groups except EPA (Table 5). This analysis provided evidence of statistically significant clinal variation only within COPA, in which forearms in the northwest were longer than in the southeast. Though sample sizes are small, this result suggests that within COPA *A. cultrata* decreases in wing size in the direction to EPA. Forearm lengths are 43.5 ± 0.6 (42.6–44.4) [12] in NW Costa Rica, and 41.8 ± 1.1 (40.9–43.0) [3] in W Panama and adjacent Costa Rica (t = 3.803; 2-tailed p = 0.002).

Within COEC, there is no evidence of north to south or east to west clinal variation (Table 5). Skull lengths average larger near Peru, than near the Merida Cordillera, but the differences are not significant: 24.7 ± 0.8 (23.4–26.0) [14] in Ecuador, and 24.2 ± 0.7 (23.3–25.2) [8] in the Colombian Eastern Cordillera (t = -1.451; 2-tailed p = 0.162). Closer to Central America, in the Colombian Central Cordillera, skull length is 24.7 ± 0.4 (23.9–25.6) [57], the same as in Ecuador. In the middle, in S Colombia, skull length is 24.5 ± 0.6 (23.0–25.6) [67]. Within PEBO, there is no evidence either of N to S or E to W clinal variation (Table 5), but we do not have measurements for the northern quarter of the range.

Our finding that within each group body size does not change in the direction of neighboring groups indicates that *A. cultrata* does not show a continuous north to south reduction in size, as concluded by Nagorsen & Tamsitt (1981). Instead, the species can be divided into relatively uniform geographic groups. Central American bats are the largest. South American bats are larger in northern Venezuela, intermediate sized in the Andes of Venezuela, Colombia and Ecuador, and smaller in southern Peru, and Bolivia.

Ecological niche modeling. The abiotically suitable areas for *A. cultrata*, as predicted by ecological niche models (ENMs), appear to have changed considerably in extent and connectivity during the last 125,000 years (Fig. 5). Over this time, the species may have occurred in large areas along the Peruvian, Ecuadorian, and Colombian Andes, and in smaller areas of Central America. In contrast, the species may have nearly vanished in Venezuela during the LIG, and in Bolivia during the LGM. During the HCO, suitable areas expanded considerably, but otherwise were similarly distributed as the present.

The Huancabamba Depression in northern Peru appears to have contained suitable areas for *A. cultrata* at all times. The opposite is true for the Atrato–San Juan Depression, which separates the South and Central American populations. During the HCO, the Central Panamanian Lowlands likely contained suitable areas for the species, thus all the Central American populations may have been connected. Likewise, the eastern half of the Nicaragua Depression may have contained suitable areas for the species, though at present it is not found to the north of Costa Rica. The Cauca Valley, which separates the Colombian Western and Central Cordilleras, contains ample suitable areas for the species at present, and to a lesser degree did during the HCO. The Magdalena Valley, which separates the Colombian Central and Eastern Cordilleras, does not contain suitable areas for the species at present, but did during the HCO.

During the LIG, the depressions of Venezuela may have been irrelevant, because suitable areas for *A. cultrata* were small and mutually isolated, or did not exist, in the country. During the LGM and the HCO, the Tachira Depression is not likely to have been a barrier for the dispersal of the species, and even at present this depression may have a limited role in isolating the populations of the Colombian Eastern Cordillera from those of the Merida Cordillera. This also may be true for the Lara Depression. At present, the Yaracuy Depression appears to fully isolate the populations of the Venezuelan Coast Range from those of the neighboring Sierra de Aroa, the Serranía de Bobare, and the Merida Cordillera. However, during the LGM and the HCO these populations apparently were connected. At all times, the Unare Depression, and the lowlands to the east of the Andes and to the south of the Venezuelan Coast Range, appears to have been barriers impeding the dispersal of *A. cultrata* to the Turimiquire Massif, and to the Guiana Highlands.

Molecular results. The best-fit DNA model of nucleotide substitution for *Anoura* CO1 sequences was Tamura-Nei with rates among sites gamma distributed with invariant sites. The maximum likelihood phylogenetic tree recovered seven reciprocally monophyletic species clades (*A. geoffroyi, A. peruana, A. latidens, A. caudifer, A. luismanueli, A. aequatoris*, and *A. cultrata*) that were well-supported with bootstraps of at least 94% (Fig. 6). However, most interspecific relationships were poorly supported except for *A. geoffroyi* and *A. peruana* as sister taxa (98%) and *A. latidens* as sister (89%) to this lineage. In turn, there was a trichotomy with this clade to *A. caudifer* and *A. luismanueli*. The remaining species (*A. cultrata* and *A. aequatoris*) formed another trichotomy with the other species. Within two species, well-supported (99% bootstraps) phylogeographic structuring was present at the subspecies-level with *A. p. peruana* from northwestern South America and *A. p. lasiopyga* from Central America. Similarly, *A. c. cultrata* was distributed in Central America and *A. c. brevirostrum* in northwestern South America.

Genetic distances supported the phylogenetic tree with high interspecific sequence divergence ranging from an average of 14.2% between *A. geoffroyi* and *A. latidens* to 23.6% between *A. geoffroyi* and *A. aequatoris* (Table 6). By contrast, intraspecific divergence was lower and ranged from an average of 0.001% in *A. latidens* to 3.1% in *A. cultrata*. For the two species with phylogeographic structuring, the average genetic distance between the subspecies of *A. cultrata* was 7.4% and 4.2% for the subspecies of *A. peruana*.

Discussion

Sexual dimorphism in size. Nagorsen & Tamsitt (1981) concluded that *A. cultrata* differs from other members of its genus in possessing significant sexual dimorphism in body size, with males being larger than females, a trait subsequently deemed to be of systematic relevance (Jarrín-V. & Kunz, 2008). This judgement was based on the comparison of 24 males and 26 females from a single locality in Colombia with respect to their scores in presumably the first axis of a LDA, which included 29 linear measurements. Of 11 external measurements, the hindfoot and forearm lengths were the most important. Of 18 cranial measurements, condylobasal (GLS was not measured) and mandible lengths were the most important. Besides its minimal geographic scope, one problem with this approach is that LDA axes may separate specimens based on shape as much as on size.

Our results do not support the notion of a marked sexual dimorphism in the main external (forearm) and cranial (GLS) linear measurements in *A. cultrata*. The forearm of males was significantly shorter within two groups (EPA, WVE), significantly longer within one group (PEBO), and similar to females within three groups (COPA, COEC, NVE). The skull lengths of both sexes did not differ significantly in length within any of our six groups. However, males did tend to possess a greater body mass than females, but not within all groups. Therefore, our data indicate that sexual dimorphism in size is not evident in *A. cultrata*, and that in this respect the species is similar to other members of the genus.

Morphometry. Nagorsen & Tamsitt (1981) concluded that *A. cultrata* shows continuous clinal variation, with body size increasing northwards from Peru to Central America, a view that has subsequently been accepted (Handley, 1984; Griffiths & Gardner, 2008; Jarrín-V. & Kunz, 2008; Calderón-Acevedo *et al.*, 2022). However, there were two major limitations. First, the study included only two Colombian localities (in Huila and Tolima) just 320 km away from each other, and no specimens from Ecuador were available. Second, the populations of N Venezuela were not in an intermediate geographical position between NW South America and Panama, as implicitly assumed in the analysis (latitude, but not longitude, was considered in the plots).

We posit that if, as proposed by Nagorsen & Tamsitt (1981), geographic variation is continuously clinal, then: 1) within groups, body size should be correlated with latitude and longitude; and 2) between neighboring groups, body size should be more similar in their adjacent regions. Based on forearm and skull lengths (Table 5), we could not detect any of both trends. However, we did not have measurements for specimens from northern Peru, where the intergradation between the larger Ecuadorian and the smaller Central Peruvian forms could occur. Thus, we cannot exclude the possibility of a continuous south to north cline in N Peru.

An alternative scenario to that of a continuous cline is a stepped cline (Salomon, 2002), which our data partially support, with geographical groups that are joined by narrow intergradation zones. At least three (COEC, WVE, NVE) of our four South American groups of *A. cultrata* may represent a stepped southwest to northeast cline in cranial size. Although distinctions in cranial size (Fig. 3; Tables 1, 2) and shape (Fig. 4; Tables 3, 4) exist among them, the three groups overlap broadly in wing size (Fig. 3; Tables 1, 2).

In the Central American range of *A. cultrata*, there is also a pattern not consistent with the notion of body size continuously increasing northwards. Within COPA, there is evidence of variation in wing size (Table 5), with forearms being shorter towards the SE, in the direction of Eastern Panama. Thus, in Central America, wing size is greater towards the extremes (near Nicaragua and near Colombia) than in the middle (E Costa Rica and W Panama). The large gap in wing and cranial size (Fig. 3; Tables 1, 2), and cranial shape (Fig. 4; Tables 3, 4) between E Panamanian and Andean-Colombian *A. cultrata* suggests that intergradation between both forms has not occurred in a recent past. Thus, Central American populations of *A. cultrata* are not likely to be part of a stepped cline with its South American neighbors.

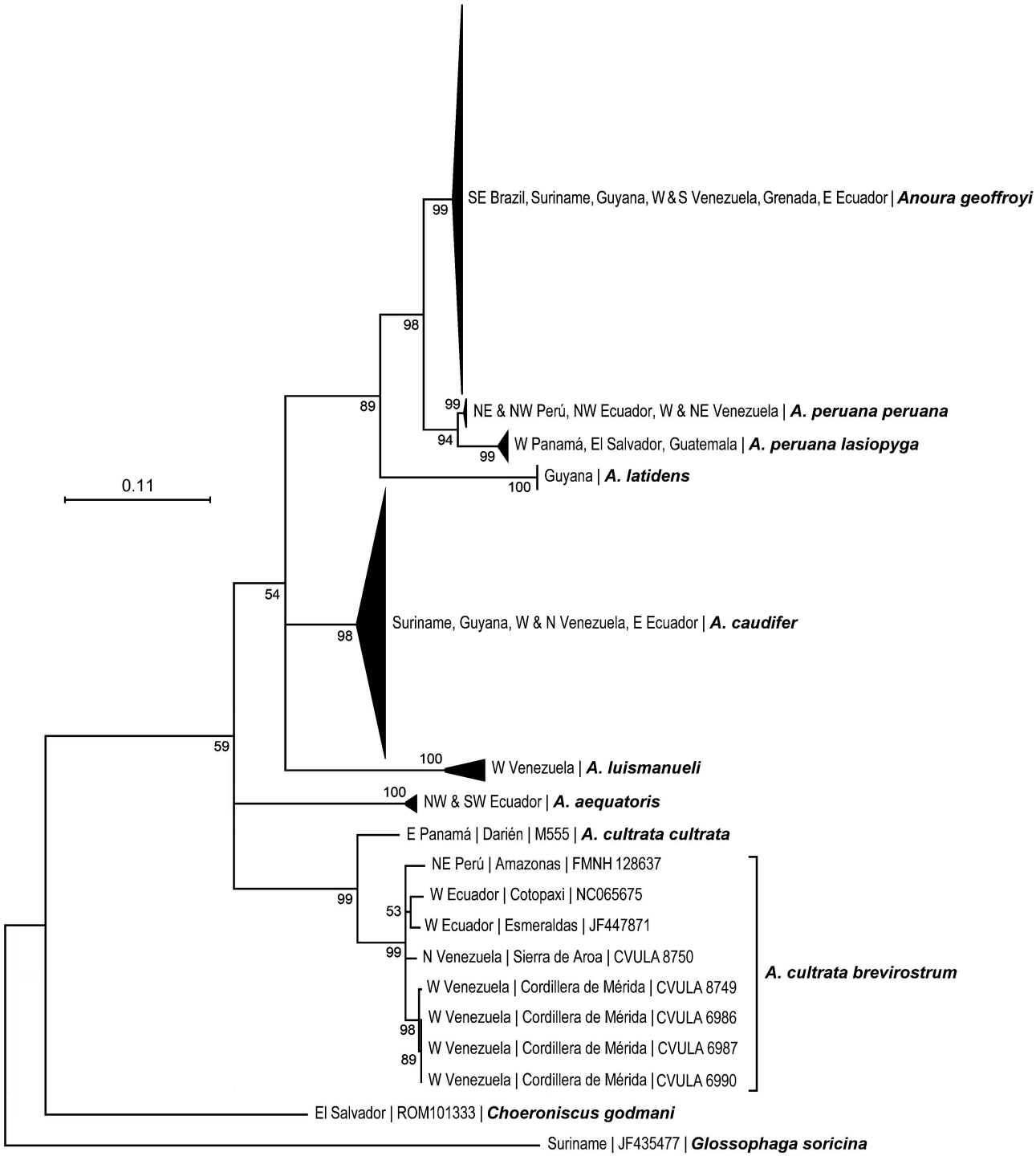

FIGURE 6. Maximum likelihood tree of cytochrome c oxidase subunit 1 DNA sequences in species of the nectar-feeding bat *Anoura*. Bootstrap support percentages from 1,000 replications are at the nodes. The geographic origins of samples included in the tree are indicated.

Molecular phylogeny. Twelve species names have been used for *Anoura*, of which seven are undisputed: *A. caudifer*, *A. geoffroyi*, *A. cultrata*, *A. latidens*, *A. fistulata*, *A. cadenai*, and *A. javieri* (Griffiths & Gardner, 2008; Pacheco *et al.*, 2018; Calderón-Acevedo *et al.*, 2022). A comprehensive molecular phylogeny of the genus, based on ultraconserved elements (UCE), supports the validity of these species, except for *A. javieri*, which was not included in the analyses (Calderón-Acevedo *et al.*, 2022).

The five species names that have been questioned are: 1) *A. peruana* (Tschudi, 1844), proposed (Wenzel, 1976: 112, 166; Mantilla-Meluk & Baker, 2010) and negated (Calderón-Acevedo *et al.*, 2022) to be distinct from *A. geoffroyi*; 2) *A. lasiopyga* (Peters, 1868), proposed (Vargas-Arboleda *et al.*, 2020) and not recognized (Calderón-Acevedo *et al.*, 2022) to be distinct from *A. geoffroyi*; 3) *A. aequatoris* (Lönnberg, 1921), proposed (Mantilla-Meluk & Baker, 2006) and negated (Jarrín-V. & Kunz, 2008; Calderón-Acevedo & Muchhala, 2018; Calderón-Acevedo *et al.*, 2022) to be distinct from *A. caudifer*; 4) *A. luismanueli* Molinari, 1994, proposed to be a synonym of *A. caudifer* (Jarrín-V. & Kunz 2008; Calderón-Acevedo *et al.*, 2022); and 5) *A. carishina* Mantilla-Meluk & Baker, 2010, shown to be a synonym of *A. latidens* (Calderón-Acevedo *et al.*, 2021, 2022). However, our DNA barcoding results (Fig. 6) show *A. peruana* to be clearly distinct and reciprocally monophyletic from *A. geoffroyi* throughout its South American range; *A. lasiopyga* to be distinct but closely related to *A. peruana*; and *A. caudifer*, *A. aequatoris*, and *A. luismanueli* to be reciprocally monophyletic to each other. Thus we conclude that *A. peruana*, *A. aequatoris*, and *A. luismanueli* deserve recognition at the species level. In the case of *A. lasiopyga*, based on its genetic similarity (Case 6 of Molinari, 2023*a*) to *A. peruana*, we deem it valid at the subspecies level, i.e., as *A. peruana lasiopyga* (Peters, 1868); see Arroyo-Cabrales and Gardner (2003) for a description of the type specimen. The South American form should be referred to as *A. peruana peruana* (Tschudi, 1844). Further studies involving other genetic markers and morphometric analyses are needed to determine whether *A. p. lasiopyga* should be elevated to species, as already proposed (Vargas-Arboleda *et al.*, 2020).

DNA barcoding is a reliable method for species identification (Clare *et al.*, 2011; Galimberti *et al.*, 2015; Lim, 2017); however, deeper interspecific relationships may not be recovered, as is the case within *Anoura* (Fig. 6). UCE-based phylogenomics has emerged as a powerful tool to infer the evolutionary history of animals at all levels of taxonomic divergence (Faircloth *et al.*, 2012; Zhang *et al.*, 2019). Our phylogeny of *Anoura* based on DNA barcoding (Fig. 5) differs from that of Calderón-Acevedo *et al.* (2022) based on UCE in having a larger number of sequences (196 vs. 40; Appendix 3), in including samples from Central America and Venezuela, and in not including samples of *A. cadenai* and *A. fistulata*. Each of the recognized species of *Anoura* is reciprocally monophyletic and highly supported in our analysis. However, there is poor support and resolution for more basal relationships in the genus (Fig. 6). This probably indicates that the deeper phylogenetic signal in the COI gene is saturated given that *Anoura* is a relatively old genus (6–7 mya; Calderon-Acevedo *et al.*, 2022), thus containing species that diverged a long time ago. Assuming that UCE-based trees are just as effective as DNA barcoding for species identification, we think that the contradictions between our results (Fig. 6) and the conclusions of Calderón-Acevedo *et al.* (2022) with respect to *A. peruana*, *A. aequatoris*, and *A. luismanueli* result from their misidentification of these species caused by a bias, based on Jarrín-V. & Kunz (2008), against the use of certain characters in the taxonomy of *Anoura* (Supplementary Information S2). In a previous contribution, Calderón-Acevedo & Muchhala (2018) presented the photograph of a fresh specimen which they identified as *A. caudifer* (their Fig. 2). However, it clearly represents *A. aequatoris* because it has short and densely furred interfemoral membrane, unlike that of *A. caudifer*, and a long rostrum, unlike that of *A. luismanueli* (Figs. S2.3, 2.5, 2.6, and 2.8–2.10). They also used as a source of measurements for *A. luismanueli* at least one specimen (ICN 21566; 4.05° N, 73.79° W; 855 m) unmistakably representing *A. caudifer* because it has a relatively broad and thinly haired interfemoral membrane, unlike that of *A. luismanueli* (Figs. S2.5, 2.6, and 2.9).

In Calderón-Acevedo *et al.* (2022), Clade 4 is composed of two subclades (Fig. 7) with one that includes both *A. geoffroyi* and *A. peruana*, and the other *A. latidens.* However, one specimen (Alat90 = ICN 4398) of the latter was grouped with *A. cultrata* in Clade 3 (not included in Fig. 7). This may be an artifact caused by a mix-up of museum specimens or tissue samples, or may represent a case of unsorted ancestral polymorphism, as they argue. Whichever is the case, this finding was not used to propose taxonomic changes. Thus, it does not affect the discussion that follows.

Calderón-Acevedo *et al.* (2021) had previously concluded that Acar115, which is one of the paratypes of '*A. carishina*', is *A. geoffroyi*, with which we agree based on the photograph of its skull (Mantilla-Meluk & Baker, 2010). As expected, in the phylogenetic tree of Calderón-Acevedo *et al.* (2022) Acar115 groups with *A. geoffroyi* (Fig. 7; Clade 4).

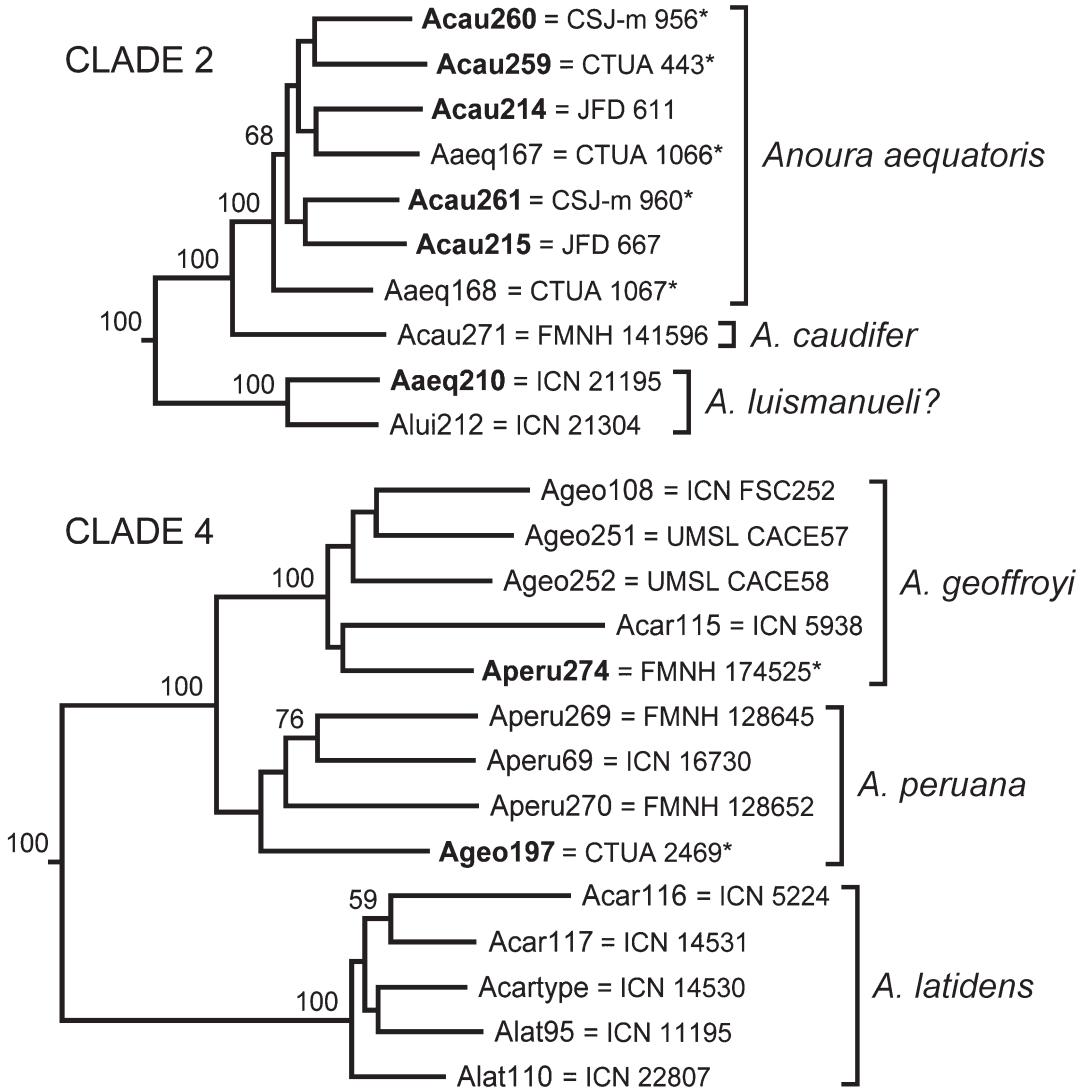

FIGURE 7. Amendments to Clades 2 and 4 of the phylogeny of Calderón-Acevedo *et al.* (2022). Alphanumeric codes to the left of the equal signs are those used by these authors to label their samples (Aaeq = *A. aequatoris*; Acar = *A. carishina*; Acau = *Anoura caudifer*; Ageo = *A. geoffroyi*; Alat = *A. latidens*; Alui = *A. luismanueli*; and Aperu = *A. peruana*). Acronyms to the right of the equal signs are those of the museums in which the specimens are housed, except for JFD which are the collector's initials. These acronyms are followed by catalog or field numbers. Bold type indicates specimens whose taxonomic identifications are being challenged. Asterisks indicate specimens examined by JM. The species names to the right of brackets indicate the taxonomic identities assumed in our study. In the original tree (Calderón-Acevedo *et al.*, 2022), all specimens in Clade 2 were deemed to be *A. caudifer*, and all specimens in the *A. geoffroyi*-*A. peruana* subclade of Clade 4 were deemed to be *A. geoffroyi*.

In the *A. geoffroyi*-*A. peruana* subclade (Fig. 7; Clade 4), one specimen of '*A. peruana*' (Aperu274) groups with three *A. geoffroyi* and with Acar115, and one specimen of '*A. geoffroyi*' (Ageo197) groups with three *A. peruana*. Based on the apparent intermingling of both species, Calderón-Acevedo *et al.* (2022) concluded that *A. peruana* is a synonym of *A. geoffroyi*. However, one of us (JM) examined the specimen Aperu274, as well as another (FMNH 174519) from the same locality (13.02° S, 71.49° W, 978 m), and three others (FMNH 203527, 203528, 203529) from a similar elevation (6.08° S, 76.98° W, 970 m; Velazco & Patterson, 2019) along the Amazonian slope of the Peruvian Andes, concluding that all of them are *A. geoffroyi*. Traditionally, *'A. geoffroyi peruana*' has been thought to be the form occurring in Peru, as well as in Ecuador and Colombia (Sanborn 1933; Tamsitt & Valdivieso 1963), and certainly *A. peruana* (e.g., FMNH 174521, 174523, 174527; 13.18° S, 71.60° W, 2,880 m; examined by JM) also occurs on the Amazonian slope of the Peruvian Andes, but usually at higher elevations. Owing to the very high elevation (3,330 m) of its locality (4.48° N, 75.50° S) in Colombia, Ageo197 is expected to be *A. peruana*.

Examination (JM) of photographs of this specimen confirms that this is the case. The re-identification of Aperu274 and Ageo197 results in *A. geoffroyi* and *A. peruana* being reciprocally monophyletic (Fig. 7), supporting the validity of both species (Fig. 6).

In their Clade 2 (Fig. 7), Calderón-Acevedo *et al.* (2022) found five *'A. caudifer*' (Acau214, 215, 259, 260, 261) intermingled with two *A. aequatoris* (Aaeq167, 168), all of them sister to an *A. caudifer* (Acau271) from São Paulo, Brazil (the type locality of *A. caudifer* is in SE Brazil, where no other small species of *Anoura* is known to occur). Four of these five *'A. caudifer*' are from two neighboring localities (6.52–6.54° N, 76.24–76.25° W) at mid elevations (1,410–1,740 m) in the Pacific slope of the Colombian Western Cordillera, and another (Acau259) is from one locality (6.19° N, 75.55° W) at a higher elevation (1,975 m) in the western slope of the Central Cordillera. The two *A. aequatoris* are from one locality (5.50° N, 75.89° W) at a yet higher elevation (2,220 m) in the Pacific slope of the Western Cordillera. These localities for *'A. caudifer*' are high in the western Andes of Colombia, where *A. aequatoris* is the common small species of *Anoura* (Mantilla-Meluk *et al.*, 2009), as it is also the case in the same range of elevations in the neighboring Andes of northwestern Ecuador, as indicated by numerous specimens examined by JM. Hence, the *'A. caudifer*' in question (Acau214, 215, 259, 260, 261) likely are *A. aequatoris* rather than *A. caudifer*. Examination (JM) of the photographs of three of these *'A. caudifer*' (Acau259, 260, 261) and the two *A. aequatoris* (Aaeq167, 168) clearly confirms (based on their very short and densely furred interfemoral membranes; as in Fig. S2.5) that all of them represent the same species, namely *A. aequatoris*.

The second subclade of Clade 2 (Fig. 7) includes one *A. luismanueli* (Alui212) from a locality (7.08° N, 73.03° W) also at high elevation (2,200 m) in the northwestern slope of the Eastern Cordillera, and one *'A. aequatoris*' (Aaeq210) from a locality (2.84° N, 75.61° W) at a high elevation (2,570 m) in the southeastern slope of the Central Cordillera. There is little genetic divergence between both specimens, thus they may represent the same species (unless unsorted polymorphism or introgression is involved). Based on its locality, close to the Merida Cordillera, Alui212 almost certainly is *A. luismanueli*, especially considering that there are records for the species in the northeastern portion of Eastern Cordillera, two of them genetically confirmed (CVULA I-9088, 9089, from 7.63° N, 72.44° W, 2,010 m, Venezuela; both included in our analysis as *A. luismanueli*; see Fig. 6). If this is the case, Aaeq210 would represent the southernmost record, and also the first record outside the Eastern Cordillera, for *A. luismanueli*. If both Alui212 and Aaeq210 are indeed *A. luismanueli* (we encourage a re-examination of both specimens, as well as others from the western slope of Central Cordillera identified as '*A. luismanueli*' by Calderón-Acevedo *et al.* 2018), the UCE-based tree of Calderón-Acevedo *et al.* (2022) would agree with our tree (Fig. 6) in showing that this species is clearly distinct from *A. caudifer* and *A. aequatoris*.

Calderón-Acevedo *et al.* (2022) found one specimen of *A. cultrata* from the southeastern slope of the Colombian Central Cordillera (Acul208 = ICN 21196; not shown in Fig. 7) to group with Ecuadorian specimens, as expected given their geographic proximity. In our tree (Fig. 6), the WVE specimens (from two mutually distant localities in the Merida Cordillera) group together with their South American conspecifics at low genetic divergence. On the other hand, the single Central American specimen is in its own separate branch (Fig. 6). This result, combined with the finding that Central American *A. cultrata* is highly diagnosable morphometrically (Fig. 4), and that it has apparently been separated from its South American relatives for a long time (Fig. 5), may indicate that two species are involved (Case 9 of Molinari, 2023*a*). Pending further study involving Panamanian and Costa Rican specimens, and more genetic markers, we conservatively assign the Central American populations to *A. cultrata cultrata* Handley, 1960, and the South American populations to *A. cultrata brevirostrum* Carter, 1968. Future studies should include more Central American specimens (genetic markers), and more South American specimens, especially from throughout Peru and Bolivia (genetic markers and morphometry) and northern Venezuela (genetic markers). Such studies should aim at clarifying whether South American *A. cultrata* represents a separate species (under the name *A. brevirostrum*), and whether it is divisible into subspecies.

Biogeography. On continents, conspecific bats separated by long distances do not generally undergo greater changes in body size than those separated by short distances (Molinari, 2023*b*). *A. cultrata* exemplifies this pattern, as indicated by the absence within most geographic groups of significant correlations between size measures and latitude or longitude. The concept of 'sky' island assumes that, similarly to the sea around real islands, lowlands around mountains hamper gene flow thus causing geographic variation and speciation (Garg & Chattopadhyay, 2021). This also appears to be the case of *A. cultrata* given that lowland barriers to dispersal have a greater influence than isolation by distance on the geographic variation in size of the species.

The Atrato–San Juan Depression (DASJ) separates the Colombian Western Cordillera (COC) from the Baudo Mountains (SB), along the northwestern coast of Colombia, and the Darien Highlands (DAH), including the Darien and Pirre Cordilleras, along the Panamanian-Colombian border (Fig. 2). This depression consists of two rivers basins: that of the 650 km long Atrato River, which flows northwards (ending in extensive marshes) to the Gulf of Urabá (Caribbean Sea); and that of the 380 km long San Juan River, which flows southwards (ending in a delta) to the central Pacific coast of Colombia. This depression is one of the rainiest regions of the world and the elevation at the divide between the Atrato and San Juan basins is less than 150 m. Detailed maps and useful accounts of the biogeographical aspects of this depression were provided by Hershkovitz (1969) and Haffer (1970). The ecological niche models imply that this depression has been abiotically unsuitable for *A. cultrata* over the past 125,00 years (Fig. 5), which may explain the marked morphometric gap between COEC and EPA groups of *A. cultrata* (Figs. 3, 4). This supports our proposal that South and Central American populations of the species are at least subspecifically distinct. On the other hand, EPA and COPA may have been well connected across the Central Panamanian Lowlands during the HCO, though they are not connected at present, nor were they during the LIG and LGM (Fig. 5).

The southwest (= Putumayo Corridor, CP) and northwest portions of the Colombian Eastern Cordillera (COR) are separated by the Andalucia Pass (PA), also known as Las Cruces Pass, a depression (Fig. 2) covered by humid forests, of elevations as low as 1,200–1,500 m (Miller, 1952; Cleef, 1981; Avendaño *et al.*, 2013). In turn, the Putumayo Corridor, which reached its present elevation ~3–5 Ma ago (Rodríguez-Muñoz *et al.*, 2022), is separated from the Central Cordillera by the Suaza-Pescado valleys (VSP) of ~2,000 m elevations (Ujueta, 1999; Cadena *et al.*, 2016). The 'filter' for the exchange of higher elevation organisms between both Cordilleras represented by both passes is unlikely to divide the distribution of *A. cultrata* and other mid-elevation bats.

The Tachira Depression (DT) separates the Colombian Eastern Cordillera (of which the Tamá Massif extends into Venezuela) from the Merida Cordillera (CM). It is a low (600 m) and partly semi-arid connection between the Maracaibo and Orinoco basins (Duellman, 1979; Gutiérrez *et al.*, 2015). The Lara Depression (DL) separates the Merida Cordillera from the Sierra de Aroa and the Serranía de Bobare. It is low (500 m) and largely semi-arid (Duellman, 1979). The Yaracuy Depression (DY) separates the Sierra de Aroa and the Venezuelan Coast Range (CC). It is low (300 m) and humid. In addition, it is narrow (15 km) and with steep mountains on both sides. The Merida Cordillera is an area of endemism for montane birds (Herzog & Kattan, 2011), and some mammals (Gutiérrez *et al.*, 2015). Despite also possessing its own biotic elements, the Sierra de Aroa shares with the Venezuelan Coast Range numerous endemic vertebrates, including mammals (Quiroga-Carmona & Molinari, 2012; García *et al.*, 2016; Molinari *et al.*, 2017). Similarly to the Huancabamba Depression (DH) in northern Peru, the Tachira Depression may have limited gene flow in *A. cultrata*, despite not interrupting its distribution (Fig. 5). Possibly, the Yaracuy Depression, acting in combination with the Lara Depression, may have limited gene flow between the Merida Cordillera and the Venezuelan Coast Range to a greater degree.

The Huancabamba Depression consists of the deep valleys of the Chamaya–Marañón River (a tributary of the Amazon), which together with the Pacific lowlands, interrupt the central and eastern cordilleras of Peru. In the region, the connection between the northern and central Andes is limited to a comparatively low (2,145 m) and narrow pass in the western cordillera, known as the Abra de Porculla (5.8397° S, 79.5052° W). On both slopes of this pass, semi-arid conditions prevail, and elevations quickly descend to less than 1,000 m (Duellman, 1979; Parker *et al.*, 1985; Cadle, 1991; Pennington & Lavin, 2017; Saldaña *et al.*, 2020). The Huancabamba Depression sets the northern or southern limit for numerous Andean vertebrates (Parker *et al.*, 1985; Cadle, 1991; Prado & Percequillo, 2018). Although the Huancabamba Depression is not likely to have bisected the distribution of *A. cultrata* at any time (Fig. 5), it may have limited gene flow in the species. Owing to the paucity of specimens from northern Peru, it cannot be established whether this would explain the morphometric differentiation to the center and south of the country (Figs. 3, 4).

To the east of the Eastern (Colombia) and the Merida Cordilleras, and to the south of the Venezuelan Coast Range and the Turimiquire Massif (MT, northeastern Venezuela), lies the Colombian-Venezuelan savanna corridor known as the Llanos. This flat and wide lowland region appears to have been unsuitable for *A. cultrata*, thus impeding its dispersal to the Guiana Highlands (Fig. 5). The Unare Depression (DU), which is about 100 km wide, is a semi-arid extension of the Llanos reaching the Caribbean Sea. It appears to have also been a barrier for the species at all times (Fig. 5), which would explain why it appears absent in the Turimiquire Massif. However, *Sturnira adrianae*, a common bat also with Andean affinities and inhabiting mid-elevations, has colonized this massif (Molinari *et al.*, 2017), as also has *A. peruana* (see below).

Our clarification of species limits allows a better interpretation of the distributional patterns of the genus *Anoura*. Members of the only two widespread montane species of the genus, *A. cultrata* and *A. peruana*, have been able to cross the Atrato–San Juan Depression, albeit in the case of the former not likely in a recent past (Fig. 5), which is reflected in their taxonomic differentiation in Central America. But note that *A. c. cultrata* and *A. p. lasiopyga* are likely to also occur in the Colombian Baudo Mountains (Fig. 2). The rarity of *A. cultrata* may be associated with a reduced colonizing capacity since this species appears to have been unable to reach suitable regions to the east of the Unare Depression in Venezuela, and to the north of the Nicaragua Depression. Dependence on suitable caves, a variable not included in niche models (Fig. 5), may be one of the factors limiting the abundance of *A. cultrata*. By contrast, though characteristic of mid to very high elevations (usually > 1,000 m; more typically 1,500–3,000 m), *A. peruana* is a common bat, which may explain why it has been able to cross the Unare Depression to reach the Turimiquire Massif in northeastern Venezuela, and the Nicaragua Depression to reach Mexico. Despite occurring in western Colombia, one common (*A. aequatoris*) and two rare (*A. latidens*, *A. fistulata*) species of *Anoura* have apparently not been able to reach Central America because the Atrato–San Juan Depression is a difficult barrier to cross for montane bats.

A. latidens can be found at elevations as high as 2,600 m, which may explain why it is both cis- and trans-Andean, and at elevations as low as 50 m, which may explain why its distribution extends to the Guianan Shield. *A. geoffroyi* is typically found below 1,500–1,000 m down to sea level, though in the Guiana Shield, where its potential competitor *A. peruana* appears to be absent, it can be found as high as > 2,500 m in Tepuy summits (Lew & Lim, 2019). Probably reflecting that it is more a lowland species than other species of the genus (except *A. caudifer*, see below), its distribution extends to the Guiana Shield, the Amazon region, SE Brazil, and the Lesser Antillean island of Grenada (Genoways *et al.*, 1998; Griffiths & Gardner, 2008; Lim & Tavares, 2012).

There are few records reported as '*A. geoffroyi*' for the Pacific lowlands (< 1,000 m) of Colombia, Ecuador, and Peru, and these have been variously identified as *A. geoffroyi*, '*A. geoffroyi lasiopyga*', and *A. peruana* (Claps *et al.*, 2005; Griffiths & Gardner, 2008; Bonifaz *et al.*, 2020). Based on one specimen (QCAZ 18218) included in our phylogeny (Fig. 6), we confirm that the *A. peruana* has been collected at a low elevation on the western slope (-0.84, -79.20; 590 m) of the Ecuadorian Andes. Griffiths & Gardner (2008) deemed '*A. g. geoffroyi*' to be cis-Andean, with which we tend to agree. The absence of *A. geoffroyi* in the Pacific slope of the Andes might explain why its potential competitor, *A. peruana*, occurs there at lower elevations. In turn, this would explain why *A. peruana* was able to cross the Atrato–San Juan Depression to reach Central America.

In Venezuela, and elsewhere in South America, *A. peruana* appears to be the only host of the ectoparasitic bat fly, *Exastinion deceptivum* Wenzel, 1976 (Streblidae) (Wenzel, 1976; Dick, 2013; Dick *et al.*, 2007). This fly species has not been recorded in Central America or Mexico, where putative '*A. geofroyi*' (what we recognize as *A. peruana lasiopyga*) is parasitized by *Exastinion clovisi* (Pessôa & Guimarães, 1937), just as *A. cultrata* in Central America, and *A. geoffroyi*, *A. latidens* and *A. caudifer* in South America (Dick, 2013; Frank *et al.*, 2014). Both fly species have never been found on the same individual bat, and as expected based on the distribution of their hosts, typically occur at different elevations: for example, in Manu (Peru), *E. deceptivum* at 1,920–4,137 m, and *E. clovisi* at 1,000–1,920 m (Dick, 2013). Therefore, either *E. deceptivum* is intolerant of low elevations, thus it could not cross the Atrato–San Juan Depression along with its host, or it evolved in *A. p. peruana* after the separation of this subspecies and *A. p. lasiopyga*. Future studies must also consider *Anastrebla modestini* Wenzel, 1966 (Streblidae): in Venezuela, individuals of this species with a reduced number of setae (1–5 instead of 12–20) on the sixth vein of the wing show a strong tendency to co-occur with *E. deceptivum* on the same bats (Wenzel, 1976).

Together with *A. geoffroyi*, *A. caudifer* is typically a mid-elevation to lowland species. It occurs in the Guiana Shield, the Amazon region, and SE Brazil. Its dispersal across the Amazonian lowlands may have been facilitated by its capacity to use varied diurnal refuges. As other species of *Anoura*, *A. caudifer* roosts in caves and tunnels, but also in culverts, tree cavities, the underside of earth banks and fallen logs, and abandoned houses (Handley, 1976; Díaz & Barquez, 2009; Mendes *et al.*, 2011; Chaves *et al.*, 2012; Voss *et al.*, 2016). It even roosts in corrugated-tin cabins (JM).

If *A. luismanueli* originated in the Colombian Eastern Cordillera or farther to the north, its distribution may have been severely fragmented during the LIG. The Andalucia Pass, combined with the narrowness and past lower elevations of the Putumayo Corridor (Fig. 2), may have had a role in the speciation and allopatric distributions of the potential competitors, *A. aequatoris* and *A. luismanueli*.

The southern Northern Andes (Colombia, Ecuador) and the northern Central Andes (Peru) have remained abiotically suitable for *A. cultrata* over the past 125,000 years (Fig. 5) and may have remained so for other species of *Anoura*, most of which still occur there. Therefore, we concur with Calderón-Acevedo *et al.* (2022) that the Andes from southern Colombia to northern Peru should be considered the ancestral range for the genus.

Problems in taxonomic delimitation. Concepts on the species limits and geographic distributions of bats of the genus *Anoura* are changing at an accelerated pace. Calderón-Acevedo *et al.* (2022) synonymized *A. aequatoris* with *A. caudifer*, and *A. peruana* with *A. geoffroyi*, and proposed *A. luismanueli* to be a synonym of *A. caudifer*. However, we are resurrecting these species (*A. peruana*, *A. aequatoris*, and *A. luismanueli*) based on re-identifications of specimens that result in three reciprocally monophyletic species, contrary to Calderón-Acevedo *et al.* (2022), thus raising the number of recognized species in the genus to 10. In addition, we are recognizing the subspecies *A. c. brevirostrum* (deemed a synonym of *A. cultrata* since Nagorsen & Tamsitt, 1981) and *A. p. lasiopyga* (by omission, Calderón-Acevedo *et al.* 2022 maintained it in the synonymy of *A. geoffroyi*).

In their review of the taxonomic history of *Anoura*, Jarrín-V. & Kunz (2008) misquoted previous authors, which has led to confusion in the taxonomy of the genus. For example, in his key to the species *Anoura*, Handley (1984) separated *A. geoffroyi* and *A. latidens* from *A. caudifer* based on the absence in the latter of a *'*medial internal cusp' (= posterior lingual cingulum; Phillips, 1971) in the third upper premolar. Molinari (1994) noted that this character is variable in *A. luismanueli*, thus not useful to diagnose this species. However, Jarrín-V. & Kunz (2008) erroneously interpreted that Molinari (1994) intended to say that this character is constant in the genus *Anoura*. Also, Jarrín-V. & Kunz (2008:259) asserted that Tamsitt & Valdivieso (1966) 'criticized the rationale used by Husson (1962) to divide the original *Anoura* specimens into a different genus *Lonchoglossa* depending on the presence or absence of a tail'. However, Husson (1962:140) stated that 'There are hardly any arguments to justify the separation of the two monotypical genera *Lonchoglossa* and *Anoura*. As pointed out by Sanborn (1933, p. 24; 1943), the two genera are only distinguished by the size, the development of the calcar, and the extent of the fur, while such characters usually are considered to be of specific value only'. Husson (1962) was merely following Sanborn (1933) in maintaining the generic distinction, whereas Tamsitt & Valdivieso agreed with Cabrera (1957) that the two species were congeneric. Jarrín-V. & Kunz (2008) attributed to Tamsitt & Nagorsen (1982) expressing that the *'*presence or absence of a tail, together with the size of the calcar and the state of ossification of the zygomatic arch' are *'*dubious characters for establishing limits among species in *Anoura*'. Tamsitt & Nagorsen (1982:1) simply stated that these characters *'*warrant study before they are accepted as diagnostic characters'. As pointed out by several authors (Sanborn, 1933; Husson, 1962; Handley, 1984; Molinari, 1994; Griffiths & Gardner, 2008; Pacheco *et al.*, 2018), such characters (Supplementary Information S2) are useful to distinguish species in the genus, thus ignoring them can lead to misidentifications.

Although Jarrín-V. & Kunz (2008) largely devoted their article to advocate the necessity of large samples in taxonomy, they questioned the validity of *A. luismanueli* despite not having seen any material of the species. Their sole 'evidence' was photographs of the interfemoral membranes of 10 specimens of '*A. caudifer*' (all of them *A. aequatoris*) from Ecuador purportedly showing them to exhibit the variation in furriness attributed to *A. caudifer* and *A. luismanueli*. However, what these photos do show is the relative uniformity of the densely haired interfemoral membrane of *A. aequatoris*, and its distinctness from the thinly haired interfemoral membrane of *A. caudifer*. Based on this 'evidence', they argued that all small *Anoura* (*A. caudifer*, *A. aequatoris*, and *A luismanueli*) represent a single species, namely *A. caudifer*. Jarrín-V. & Coello (2012) went further, inferring this supposedly single species to be highly variable morphometrically. In turn, Calderón-Acevedo & Muchhala (2018), and Calderón-Acevedo *et al.* (2022: 10), echoed this conclusion to support the view that '*Anoura caudifer* is widely recognized as the most phenotypically variable species within the genus'.

Calderón-Acevedo *et al.* (2022) did not note the ranges of forearm (29.9–45.3 mm) and skull (20.2–26.5 mm) lengths provided by Jarrín and collaborators for '*A. caudifer*' to be suspiciously large (we estimate that corresponding body masses would be 5–18 g). These samples are from a relatively small geographic range, suggesting that gross measurement errors or misidentified species led to exaggerated (several standard deviations away from the mean) extreme values. As a reference, our measurements (mean ± standard deviation (minimum–maximum) [sample size]) of Ecuadorian specimens of *A. aequatoris* are: forearm, 35.9 ± 1.0 (33.3–38.2) [64]; skull, 21.8 ± 0.4 (20.6–22.7) [67]; and body mass (from specimen labels), 9.5 ± 1.3 (7.1–13.0) [29]. To compare with *A. caudifer* and *A. luismanueli*, see Molinari (1994). Jarrín-V. & Kunz (2008) may have included a specimen with mutilated humeri (e.g., QCAZ 1587, *A. aequatoris*, sourced from Molina, 2005) to obtain their minimum for forearm length. Misidentifications were

confirmed (JM) through the examination of 42 of the '*A. caudifer*' specimens used by Jarrín-V. and collaborators (including some of those that Jarrín-V. & Coello, 2012 deemed morphometrically 'deviant' and possibly 'members of a new species'), 35 of which were found to be *A. aequatoris*. Those not representing this species were: QCAZ 2562*, 2766*, 2771*, and 3839*, *A. peruana*; QCAZ 3480*, *A. geoffroyi*; QCAZ 6232, *A. caudifer*; and QCAZ 472*, *Glossophaga soricina* (* = 'deviant'). For photographs showing differences in skull size within the genus *Anoura*, see Figs. S2.1–2.3. Note that *A. peruana* and *A. geoffroyi* are considerably larger than *A. aequatoris*. *G. soricina* is about the same size as *A. luismanueli*.

In summary, we reviewed the systematics and biogeography of *A. cultrata* and its phylogenetic relationships in the context of the genus. However, there was an inadequate taxonomic framework in earlier studies due to the neglect of morphological characters useful for species identification. Some species of *Anoura* possess striking characteristics that facilitate their identification, but others do not, thus they can be difficult to distinguish (Case 7 of Molinari, 2023*a*). We provide annotated photographs of skulls, study skins, and live bats of several species of *Anoura* in which useful characters can be visualized (Supplementary Information S2). Our study recognized three additional species, and subspecies within two species. But the taxonomic diversity of the genus is not yet fully known, which requires further research incorporating different methodologies, including morphological identification of specimens and molecular analyses in an integrative biological approach.

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Online supplementary information

Two files are available online at the figshare online data repository.

Supplementary Information S1 (https://doi.org/10.6084/m9.figshare.22794176).—MS Excel spreadsheet containing the results of the data analyses.

S1.1. Maxent settings, tune up.

S1.2. PCA, cranial measurements.

S1.3. PCA, wing measurements.

S1.4. LDA, cranial and wing measurements.

S1.5. MANOVA, GLS and FA.

S1.6. ANOVA, cranial measurements, excluding GLS.

S1.7. ANOVA, wing measurements, excluding FA.

S1.8. MANOVA, LDA scores.

Supplementary Information S2 (https://doi.org/10.6084/m9.figshare.22794326).—High resolution images showing useful characters to identify species of *Anoura*.

S2.1. Skulls and mandibles of *Anoura cultrata* showing geographic variation in the species.

S2.2. Skulls and mandibles of large species of *Anoura*.

S2.3. Skulls and mandibles of small species of *Anoura*.

S2.4. Study skins of large species of *Anoura* showing interspecific variation in the width of the interfemoral membrane.

S2.5. Study skins of small species of *Anoura* showing interspecific variation in the width and furriness of the interfemoral membrane.

S2.6. Study skins of the holotypes of *Anoura caudifer* and *A. luismanueli*.

S2.7. Photograph of the head of a live specimen of *Anoura cultrata*.

S2.8. Photographs of the heads of live specimens of *Anoura*.

S2.9. Photographs of live specimens of *Anoura latidens*, *A. peruana*, *A. luismanueli*, and *A. caudifer*.

S2.10. Live specimens of *Anoura caudifer* and *A. luismanueli* photographed together.

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Appendix 1: Specimens of *Anoura cultrata* included in the study

Bolivia: La Paz: Serranía Bellavista, 47 km by road N Caranavi (-15.72, -67.48), 1,350 m (LSUMZ 22960-22962).

Colombia: Cauca: Municipio El Tambo, Corregimiento La Gallera, Vereda El Cóndor (2.73, -77.00), 1,525 m (MHNUC-M 845, 846). Municipio Patía, Corregimiento El Estrecho, Vereda Las Tallas (2.12, 77.08), 600 m (MHNUC-M 654). Municipio Santa Rosa, Corregimiento San Juan de Villalobos, Vereda La Esmeralda (1.56, -76.31), 1,690 m (MHNUC-M 1513). **Cundinamarca:** Sesquile (5.05, -73.80), 2,650 m (ROM 84934). **Huila:** Cueva del Indio, Parque Nacional Natural Cueva de Los Guácharos (1.62, -76.10), 1,950 m (IAvH-M 2166–2176; examined by EEG). Municipio Timaná, Insp. Naranjal, Vereda Limoncillo (1.98, -75.87), 1,200 m (ICN 17746). **Nariño:** Municipio Barbacoas, Corregimiento de Junín, La Guarapería, 3 km W Junín (1.33, -78.15), 900 m (ICN 13639; examined by EEG). **Norte de Santander:** Gramalote (7.90, -72.80), 1,020 m (FMNH 62777; lost specimen, Nagorsen & Tamsitt 1981). **Risaralda:** Minas del Chaquiro, Parque Nacional Natural Los Nevados (4.82, -75.54), 2,244 m (CUS-M 22, 80–82). **Santander:** Cueva Del Indio, Chiracoca, Bochalema (7.62, -72.67), 1,280 m (ROM 85008–85014). Municipio Encino, Vereda Los Pericos, Finca Vegaleón (6.17, -73.13), 1,600 m (ICN 17513; examined by EEG). Municipio Encino, Vereda Río Negro, Finca El Aserradero, sitio Las Tapias (8.10, -73.10), 2,013 m (ICN 17512; examined by EEG). Municipio Suaita, Insp. Policía, San José de Suaita, Finca El Recreo (6.10, -73.45), 1,580 (ICN 15301; examined by EEG). **Tolima:** Vereda Boquerón, 5.5 km SE of Ibagué (4.40, -75.20), 1,130 (ROM 75256–75264, 75266, 75268–75273, 75277, 75328, 75329–75347, 75350–75352, 75355, 75356, 75359, 77232, 77233, 77236, 77237, 77239–77241, 77243, 77244, 77250–77252, 77254, 77256, 77261, 77263, 77264, 77267–77270, 77275, 77302, 77304, 77305).

Costa Rica: Alajuela: 4 km SSE Cariblanco, 27 km NE Naranjo (10.23, -84.17), 1,250 m (TTU 34281). Cantón de Upala, Bijagua, El Pilón, Parque Nacional Volcán Tenorio (10.70, -84.98), 750 m (KU 158393). Cariblanco, 28 km NE Naranjo (10.27, -84.18), 900 m (TCWC 9829). **Cartago:** Río Chitaría, on Turrialba-Siquirres highway (9.92, -83.60), 775 m (LSUMZ 12735). **Heredia:** 1 Km S, 11.5 Km E San Miguel, Parque Nacional Braulio Carrillo (10.30, -84.08), 700 m (USNM 562775–562785). 3.5 Km S, 11.5 Km E San Miguel, Parque Nacional Braulio Carrillo (10.28, -84.08), 1,000 (USNM 562774). Vara Blanca (10.17, -84.15), 1,850 (LSUMZ 13791; TTU 13171). **Puntarenas:** Finca Las Cruces, 6 km SE San Vito de Java (8.80, -82.95), 1,200 m (LACM 38682). **San José:** 11 km S Restaurant La Georgina (Villa Mills), 1 km N Chanchera (9.46, -83.72), 1,620 m (LACM 25438). Fila la Máquina, ca. 3 km E Canaan (9.45, -83.57), 2,000 m (LSUMZ 12734).

Ecuador: Azuay: Gaby-Papa Grande, Cantón Camilo Ponce Enríquez, Cordillera de Mollopongo (-3.05, -79.70), 550 m (MEPN 10349, 10355, 10377). **Carchi:** Río El Pailón, near confluence with Río San Juan (1.00, -78.25), 975 m (MEPN 871806). **Cotopaxi:** Reserva Otonga (-0.42, -79.00), 2,100 (QCAZ 2566). **El Oro:** Jardín Botánico on limits with Reserva Privada Jocotoco, Colegio Moro Moro (-3.66, -79.74), 910 m (QCAZ 8990). **Esmeraldas:** 10 km S Luis Vargas Torres, Río Santiago (0.88, -78.79), 65 m (MEPN 851374, 851374). 2 km S of Alto Tambo (0.90, -78.52), 700 m (ROM 105795). Alto Tambo, km 3 vía Lita-San Lorenzo (0.88, -78.48), 560 m (MEPN 84153). **Morona-Santiago:** Uuntsuants, Centro Shuar, Cordillera del Kutukú (-2.55, -77.90), 518 m (MEPN 5704, 9718). **Pastaza:** Cuevas de Mera, Vía Mera-Santa Rosa (-1.43, -78.10), 1,200 m (QCAZ 4869, 4947).

Mera (-1.43, -78.10), 1,160 m (MEPN RR400). **Pichincha:** Nanegal, Gavilán de Orongo (0.12,-78.67), 1,700 m (QCAZ 1971). Nanegal, Reserva Maquipucuna (0.12, -78.67), 1,400 (MEPN 944083). **Santo Domingo:** La Unión del Toachi, Otongachi (-0.31, -78.95), 890 m (QCAZ 4746). **Zamora-Chinchipe:** Vía Mayaycu (-4.07, -78.62), 950 m (MEPN 10033).

Panama: Bocas del Toro: Rancho Mojica, Río Changena, approx. 48 km W Almirante (9.03, -82.68), 1,463 m (USNM 319249). Río Changena Camp (9.10, -82.57), 762 m (USNM 319376). **Chiriquí:** Cerro Punta, Casa Tilley ['Hostal Cielito Sur Bed & Breakfast'] (8.85, -82.60), 1,725 m (USNM 323180). Cuesta de Piedra (8.67, -82.63), 914 m (USNM 331261). **Darien:** ca. 6 km NW Cana, E slope Cerro Pirre (7.93, -77.70), 1,200 m (LSUMZ 25504). Cerro Malí (8.12, -77.23), 1,433 m (USNM 337987–337989). Cerro Tacarcuna (8.17, -77.30), 1,250 m (USNM 337991). Head of Río Pucro, Cerro Malí (8.13, -77.25), 1,250 m (USNM 337990). Tacarcuna Village Camp, Río Pucro (8.17, -77.30), 975 m (USNM 309395–309402). **Los Santos:** Cerro Hoya (7.35, -80.65), 900 m (USNM 323181).

Peru: Amazonas: Headwaters of Río Kagka [of Río Cenepa] (-4.27, -78.15), 790 m (MVZ 154786). Provincia Luya, Río Utcubamba, 11 km by rd NW Pedro Ruiz (-5.92, -78.06), 1,097 m (FMNH 128637). **Ayacucho:** Huanhuachayo (-12.73, -73.78), 1,660 m (AMNH 233250–233255, 233261–233263, 233268, 233269). San José, Rio Santa Rosa (-12.73, -73.77), 1,050 (LSUMZ 16471). **Cuzco:** Cordillera Vilcabamba, W Side (-12.58, -73.67), 1,450 m (AMNH 214324). Cordillera Vilcabamba, W Side (-12.58, -73.65), 2,160 m (AMNH 233256, 233257). Provincia de La Convencion, E Cordillera Vilcabamba, 'Ridge Camp' (-11.77, -73.33), 500 m (USNM 588078). Provincia de La Convención, Tangoshiari (-11.78, -73.33), 1,000 m (USNM 588022). Provincia de Paucartambo, near Suecia (a roadside restaurant), km 138.5 carretera Paucartambo-Shintuya (-13.10, -71.57), 1,950 (FMNH 169829). **Huánuco:** 31 km SSE Tingo María (-9.56, -75.92), 850 m (TCWC 11882). Divisoria in Cordillera Azul, carretera Tingo María-Pucallpa (-9.18, -75.80), 1,600 m (LSUMZ 12490). Trail to Hacienda Paty, below Carpish Pass [carretera Huánuco-Tingo María] (-9.68, -76.15), 2,165 m (LSUMZ 17941). **Madre de Dios:** Cerro de Pantiacolla, E slope near summit, Manú (-12.60, -71.32), 1,030 m (FMNH 122086).

Venezuela: Aragua: Estación Biológica Rancho Grande, Parque Nacional Henri Pittier, 14 km NW Maracay (10.35, -67.68), 1,150 m (CVULA 3534, 3595; EBRG 79, 1968, 2249, 2250–2253, 3077, 3603, 4288, 4292, 28474, 28475; MBUCV 1073, 1074; USNM 517428, 517429, 517438, 517439). 4 Km NW, El Limón (10.32, -67.65), 550 m (EBRG 2615, 2616; USNM 517430–517437). **Barinas:** Pozo Azul, 5.7 km NE Calderas (8.94, -70.40), 1,232 m (MHNLS 12270). Quebrada El Molino, Calderas (8.95, -70.43), 1,515 m (MHNLS 12252, 12253). Quebrada La Bellaca, Sector San Ramón, 7 km NNE Altamira (8.87, -70.49), 1,040 m (CVULA 6849, 8616). Quebrada La Sorda, Calderas (8.88, -70.49), 1,240 m (MHNLS 12217). **Carabobo:** Camino a Cumbre de Valencia, San Esteban (10.40, -68.02), 350 m (MHNLS 1228–1230). **Lara:** Cafetales El Alto, 2.6 km S Guarico (9.60, -69.79), 1,333 (MCNG 3197). **Mérida:** 4 km ENE Santo Domingo (8.87, -70.63), 1,625 (CVULA 8749). Cueva de Loma de Benito, 4 km S Guaraque (8.12, -71.74), 2,380 m (CVULA 3629, 3749, 3750, 6886, 6987, 6990, 6998, 7107–7110; EBRG 27842). Cueva del Pirata, 0.6 km SE La Azulita (8.72, -71.44), 1,000 m (CVULA 8093). La Carbonera, 6 Km SE La Azulita (8.67, -71.45), 1,870 m (USNM 385796). Quebrada La Astillera, 6 km SSW Mérida (8.54, -71.15), 1,720 m (CVULA 3871). **Miranda:** Agua Blanca, Parque Nacional Guatopo (10.07, -66.47), 400 m (MBUCV 2930, 2931). Cueva Walter Dupouy, near Capaya (10.48, -66.27), 195 m (EBRG 6384, 6385, 28830; MHNLS 1743; USNM 419464, 491716). Embalse Agua Fría, Parque Nacional Macarao (10.39, -67.18), 1,735 m (EBRG 22283). La Macanilla, Parque Nacional Guatopo, 28 km SE Santa Teresa del Tuy (10.12, -66.52), 550 m (EBRG 22040). Río Marasmita, Toma de agua de Capaya (10.47, -66.28), 250 m (MHNLS 1727, 1728). **Táchira:** 'Las Piñas, La Paragua, Bolívar' [amended to Río Potosi, 14 km SE Pregonero] (7.95, -71.65), 1,100 m (CVULA 2250). **Trujillo:** Finca La Nona, 5.5 km ESE Boconó (9.25, -70.22), 2,040 m (MCNG 1034, 1035, 1052). Puesto de Guardaparques, Parque Nacional Guaramacal (9.25, -70.22), 2,000 m (EBRG 22630). Sierra de Portuguesa, 14.7 km SE Boconó (9.17, -70.16), 1,330 (MCNG 3282). **Vargas:** El Aguacatal, Hacienda El Limón (10.44, -67.27), 1,400 m (MHNLS 2334). **Yaracuy:** Sierra de Aroa, Capilla de Juan Milla, 11.3 km WNW San Felipe (10.37, -68.84), 1,777 m (CVULA 8750). Sierra de Aroa, Cerro El Tigre, Municipio Bolívar, Parque Nacional Yurubí, 13.5 km NW San Felipe (10.42, -68.83), 1,000 m (EBRG 26574). Serranía de Bobare, Finca El Jaguar, 16 km NW Aroa (10.55, -69.00), 750 m (EBRG 22335).

Appendix 2. Linear measurements (mm) and body masses (g) of *Anoura cultrata* specimens belonging to six geographic groups separated by topographic depressions (Fig. 2): Chorotega Volcanic Front and Azuero Peninsula Highlands (COPA: Costa Rica–W Panama); Darien Highlands (EPA: E Panama); Venezuelan Coast Range, Sierra de Aroa, and Serranía de Bobare (NVE: N Venezuela); Merida Cordillera (WVE: W Venezuela); Colombian Western, Central and Eastern Cordilleras, and Ecuadorian Andes (COEC: Colombia–Ecuador); and Central Andes (PEBO: Peru–Bolivia). Descriptive statistics are: mean ± standard deviation (minimum–maximum) [sample size].

Measurement	COPA	EPA	NVE	WVE	COEC	PEBO
Head and body length	72.9 ± 4.6 (62.0–78.0) [14]	80.4 ± 5.2 (72.0–94.0) [13]	72.9 ± 4.5 (64.0–83.0) [43]	71.2 ± 6.6 (59.8–90.0) [26]	67.9 ± 5.8 (52.0–81.0) [99]	62.7 ± 1.5 (61.0–64.0) [3]
Tail length	4.5 ± 2.1 (3.0–6.0) [2]	5.3 ± 1.5 (2.0–7.0) [12]	4.3 ± 1.1 (2.0–6.6) [36]	4.2 ± 1.2 (2.0–6.0) [17]	4.6 ± 1.9 (2.0–12.0) [65]	3.8 ± 0.9 (2.7–5.7) [12]
Hind-foot length	12.9 ± 0.9 (12.0–15.0) [14]	15.0 ± 1.2 (13.0–17.0) [13]	13.2 ± 1.3 (9.0–15.0) [43]	12.2 ± 1.2 (10.0–15.0) [26]	12.3 ± 1.5 (9.0–15.0) [93]	11.2 ± 1.3 (9.0–12.0) [5]
Ear length	13.5 ± 1.7 (11.0–17.0) [14]	16.4 ± 0.7 (15.0–17.0) [13]	15.0 ± 1.7 (7.0–17.0) [43]	13.5 ± 2.1 (10.0–19.0) [26]	14.3 ± 1.6 (10.0–17.0) [99]	14.5 ± 0.9 (14.0–15.5) [3]
Forearm length*	43.2 ± 0.9 (40.9–44.4) [16]	44.1 ± 0.9 (42.6–45.3) [11]	42.1 ± 1.1 (40.1–43.8) [34]	42.2 ± 1.2 (39.3–44.1) [27]	41.9 ± 1.0 (39.3–44.9) [96]	40.9 ± 1.6 (38.0–43.7) [18]
Digit 3, metacarpal length	42.1 ± 1.0 (40.2–43.8) [15]	42.3 ± 1.2 (41.1–44.1) [11]	40.9 ± 1.2 (37.6–43.1) [26]	41.2 ± 1.5 (37.8–44.9) [27]	41.2 ± 1.1 (38.8–43.5) [64]	39.1 ± 1.8 (35.7–41.7) [15]
Digit 3, phalanx 1 length	13.5 ± 0.9 (10.7–14.5) [15]	14.2 ± 0.4 (13.6–14.9) [11]	13.4 ± 0.4 (12.7–14.3) [26]	13.9 ± 0.6 (12.9–15.1) [27]	13.8 ± 0.7 (12.0–15.5) [63]	13.4 ± 0.6 (12.4–14.2) [15]
Digit 4, metacarpal length	40.1 ± 2.0 (35.5–42.2) [15]	41.5 ± 1.1 ± (39.9–43.3) [11]	39.2 ± 1.4 (36.7–42.0) [26]	39.4 ± 1.6 (36.2–42.3) [27]	39.8 ± 1.1 (36.7–42.5) [64]	36.9 ± 2.4 (30.2–40.3) [15]
Digit 4, phalanx 1 length	10.8 ± 0.9 (8.5–11.7) [15]	10.9 ± 0.5 (10.1–11.6) [11]	10.4 ± 0.7 (8.1–11.5) [26]	10.6 ± 0.8 (8.6–12.7) [27]	11.0 ± 0.7 (9.5–14.2) [63]	10.3 ± 1.0 (7.8–12.1) [15]
Digit 5, metacarpal length	34.8 ± 1.0 (32.0–36.6) [15]	36.2 ± 0.9 (34.4–37.5) [11]	34.0 ± 1.2 (32.1–36.8) [26]	34.2 ± 1.4 (31.8–36.6) [27]	34.2 ± 1.2 (32.2–40.6) [64]	31.5 ± 1.6 (29.6–35.8) [15]
Digit 5, phalanx 1 length	8.8 ± 0.5 (8.0–9.5) [15]	9.1 ± 0.3 (8.7–9.6) [11]	8.4 ± 0.4 (7.6–9.1) [26]	8.5 ± 0.4 (7.9–9.6) [27]	8.8 ± 0.5 (7.7–10.8) [63]	8.2 ± 0.4 (7.2–9.1) [15]
Tibia length	15.2 ± 0.7 (13.9–16.2) [15]	15.6 ± 0.3 (15.2–16.0) [11]	14.9 ± 0.6 (14.1–16.7) [26]	15.2 ± 0.9 (13.1–16.6) [26]	15.1 ± 0.7 (13.2–16.2) [56]	14.6 ± 0.8 (13.7–16.0) [15]
Calcar length	3.7 ± 0.4 (2.9–4.5) [15]	3.8 ± 0.5 (2.9–4.8) [11]	4.0 ± 0.4 (3.5–5.5) [26]	3.9 ± 0.5 (3.0–5.1) [27]	3.9 ± 0.6 (2.6–5.8) [63]	4.0 ± 0.5 (3.4–5.3) [14]
Greatest skull length*	26.0 ± 0.3 (25.3–26.6) [15]	26.4 ± 0.3 (25.9–26.8) [11]	25.7 ± 0.6 (24.1–26.9) [26]	24.9 ± 0.4 (24.1–25.5) [28]	24.5 ± 0.6 (23.0–26.0) [93]	23.7 ± 0.5 (23.1–24.5) [12]
Condylobasal length	25.3 ± 0.4 (24.6–26.0) [15]	25.5 ± 0.4 (24.9–25.9) [11]	24.7 ± 0.6 (22.8–25.7) [26]	24.1 ± 0.4 (23.3–24.9) [28]	23.7 ± 0.6 (22.0–24.8) [79]	22.9 ± 0.5 (22.1–23.7) [12]
Palatal length	13.4 ± 0.3 (12.8–13.7) [15]	13.3 ± 0.4 (12.6–13.9) [11]	13.3 ± 0.5 (11.9–14.2) [26]	12.5 ± 0.4 (11.8–13.8) [28]	12.5 ± 1.6 (11.5–24.0) [58]	11.8 ± 0.3 (11.2–12.1) [11]

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Appendix 2. (Continued)

Measurement	COPA	EPA	NVE	WVE	COEC	PEBO
C–M_3 length	9.1 ± 0.2 (8.7–9.4) [15]	9.2 ± 0.2 (8.8–9.4) [11]	8.8 ± 0.3 (8.4–9.3) [26]	8.6 ± 0.2 (8.2–8.9) [27]	8.5 ± 0.2 (8.0–9.0) [57]	8.1 ± 0.2 (7.8–8.4) [12]
Rostral breadth	4.6 ± 0.1 (4.4–4.8) [15]	4.5 ± 0.2 (4.1–4.8) [11]	4.6 ± 0.2 (4.1–4.9) [26]	4.5 ± 0.2 (4.2–4.8) [28]	4.4 ± 0.2 (4.0–4.9) [56]	4.4 ± 0.1 (4.2–4.6) [10]
Postorbital constriction	5.1 ± 0.2 (4.9–5.5) [15]	5.3 ± 0.2 (5.0–5.6) [11]	5.2 ± 0.2 (4.8–5.4) [25]	5.0 ± 0.2 (4.7–5.3) [28]	5.0 ± 0.1 (4.6–5.3) [56]	5.0 ± 0.2 (4.6–5.2) [12]
Zygomatic breadth	10.5 ± 0.3 (10.0–11.0) [15]	10.7 ± 0.2 (10.4–11.0) [10]	10.5 ± 0.3 (10.0–11.0) [25]	10.4 ± 0.3 (10.0–10.9) [23]	10.2 ± 0.3 (9.4–10.9) [52]	9.9 ± 0.3 (9.4–10.3) [12]
Braincase breadth	10.0 ± 0.2 (9.7–10.3) [15]	9.9 ± 0.2 (9.6–10.1) [11]	9.9 ± 0.3 (9.4–10.3) [26]	9.7 ± 0.2 (9.2–10.1) [28]	9.6 ± 0.2 (9.1–10.1) [60]	9.3 ± 0.2 (9.0–9.6) [12]
Mastoid breadth	10.6 ± 0.2 (10.3–10.8) [15]	10.4 ± 0.2 (10.1–10.6) [11]	10.5 ± 0.3 (9.9–11.0) [26]	10.4 ± 0.3 (9.8–11.0) [28]	10.2 ± 0.3 (9.4–11.0) [55]	9.8 ± 0.2 (9.3–10.1) [11]
Braincase height	8.8 ± 0.2 (8.5–9.3) [15]	8.8 ± 0.3 (8.5–9.4) [11]	8.4 ± 0.3 (7.8–8.8) [26]	8.4 ± 0.2 (7.9–8.8) [28]	8.3 ± 0.3 (7.7–9.0) [55]	8.0 ± 0.1 (7.8–8.2) [10]
C–C breadth	5.0 ± 0.2 (4.9–5.3) [15]	5.0 ± 0.2 (4.5–5.3) [11]	5.1 ± 0.3 (4.3–5.5) [26]	5.1 ± 0.2 (4.7–5.4) [27]	4.9 ± 0.3 (4.3–5.9) [53]	4.7 ± 0.2 (4.5–5.0) [12]
M_3–M_3 breadth	6.1 ± 0.2 (5.7–6.3) [15]	6.0 ± 0.2 (5.8–6.3) [11]	6.0 ± 0.2 (5.6–6.3) [26]	6.0 ± 0.2 (5.6–6.3) [27]	5.8 ± 0.2 (5.3–6.2) [57]	5.6 ± 0.2 (5.4–5.9) [12]
Mandibular length	18.0 ± 0.4 (17.2–18.8) [15]	18.6 ± 0.5 (18.0–20.0) [11]	17.8 ± 0.4 (16.8–18.6) [25]	17.1 ± 0.3 (16.6–17.6) [27]	16.4 ± 2.0 (8.4–17.7) [73]	16.2 ± 0.4 (15.6–16.8) [10]
c–m_3 length	9.6 ± 0.2 (9.3–9.9) [15]	9.8 ± 0.3 (9.3–10.2) [11]	9.3 ± 0.3 (8.6–9.8) [26]	9.1 ± 0.2 (8.6–9.4) [24]	9.0 ± 0.3 (8.5–9.8) [56]	8.6 ± 0.2 (8.2–8.9) [10]
Body mass	18.2 ± 1.5 (16.0–21.0) [12]		16.9 ± 2.1 (14.0–22.9) [29]	15.8 ± 2.0 (11.0–18.5) [21]	16.3 ± 2.2 (11.0–21.6) [53]	14.0 ± 1.3 (12.5–15.0) [3]

*Males vs. females (forearm lengths): EPA, 43.2 ± 0.7 (42.6–44.1) [4] vs. 44.5 ± 0.5 (43.9–45.3) [7]; WVE, 41.9 ± 1.1 (39.3–43.6) [20] vs. 43.1 ± 1.0 (41.5–44.1) [7]; PEBO, 42.2 ± 1.6 (40.2–43.7) [5] vs. 40.4 ± 1.3 (38.0–42.7) [13]. Males vs. females (greatest skull lengths): NVE, 25.9 ± 0.5 (25.2–26.9) [11] vs. 25.5 ± 0.6 (24.1–26.2) [15]. See Results for explanation.

Appendix 3. Specimens of *Anoura* and outgroups used in genetic analysis.

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 113886	*Glossophaga*	*soricina*	Suriname	JF435477
ROM 101333	*Choeroniscus*	*godmani*	El Salvador	ABCSA745-06
ROM 105779	*Anoura*	*aequatoris*	Ecuador	JF448524
ROM 105787	*Anoura*	*aequatoris*	Ecuador	JF448522
ROM 105794	*Anoura*	*aequatoris*	Ecuador	JF448523
TTU-M 102454	*Anoura*	*aequatoris*	Ecuador	OQ944941
ROM 104024	*Anoura*	*caudifer*	Ecuador	JF448527
ROM 104454	*Anoura*	*caudifer*	Ecuador	JF448531
ROM 105122	*Anoura*	*caudifer*	Ecuador	JF448525
ROM 105163	*Anoura*	*caudifer*	Ecuador	JF448526
ROM 105499	*Anoura*	*caudifer*	Ecuador	JF448529
ROM 105890	*Anoura*	*caudifer*	Ecuador	JF447868

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Appendix 3. (Continued)

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 105934	*Anoura*	*caudifer*	Ecuador	JF448528
ROM 106113	*Anoura*	*caudifer*	Ecuador	JF448530
ROM 106353	*Anoura*	*caudifer*	Ecuador	JF448533
ROM 118777	*Anoura*	*caudifer*	Ecuador	JF448534
ROM F37728	*Anoura*	*caudifer*	Ecuador	JF448532
TTU-M 85075	*Anoura*	*caudifer*	Ecuador	OQ944944
TTU-M 85208	*Anoura*	*caudifer*	Ecuador	OQ944943
ROM 106587	*Anoura*	*caudifer*	Guyana	EF079982
ROM 106588	*Anoura*	*caudifer*	Guyana	EF079983
ROM 106589	*Anoura*	*caudifer*	Guyana	EF079984
ROM 106590	*Anoura*	*caudifer*	Guyana	EF079985
ROM 114618	*Anoura*	*caudifer*	Guyana	JF452132
ROM 114649	*Anoura*	*caudifer*	Guyana	JF452130
ROM 114650	*Anoura*	*caudifer*	Guyana	JF452128
ROM 114651	*Anoura*	*caudifer*	Guyana	JF452141
ROM 114669	*Anoura*	*caudifer*	Guyana	JF452133
ROM 114734	*Anoura*	*caudifer*	Guyana	JF447869
ROM 114754	*Anoura*	*caudifer*	Guyana	JF452138
ROM 114755	*Anoura*	*caudifer*	Guyana	JF452120
ROM 114756	*Anoura*	*caudifer*	Guyana	JF452121
ROM 114768	*Anoura*	*caudifer*	Guyana	JF452122
ROM 114769	*Anoura*	*caudifer*	Guyana	JF452123
ROM 114770	*Anoura*	*caudifer*	Guyana	JF452124
ROM 114771	*Anoura*	*caudifer*	Guyana	JF452127
ROM 114776	*Anoura*	*caudifer*	Guyana	JF452140
ROM 114801	*Anoura*	*caudifer*	Guyana	JF452131
ROM 115210	*Anoura*	*caudifer*	Guyana	JF452125
ROM 115235	*Anoura*	*caudifer*	Guyana	BCBNC072-06
ROM 115255	*Anoura*	*caudifer*	Guyana	EF079987
ROM 115272	*Anoura*	*caudifer*	Guyana	EF079988
ROM 115297	*Anoura*	*caudifer*	Guyana	JF452137
ROM 115298	*Anoura*	*caudifer*	Guyana	JF452136
ROM 115299	*Anoura*	*caudifer*	Guyana	JF452135
ROM 115300	*Anoura*	*caudifer*	Guyana	JF452134
ROM 115332	*Anoura*	*caudifer*	Guyana	JF452139
ROM 115341	*Anoura*	*caudifer*	Guyana	JF452129
ROM 115342	*Anoura*	*caudifer*	Guyana	JF452126
ROM 115343	*Anoura*	*caudifer*	Guyana	EF079989
ROM 115344	*Anoura*	*caudifer*	Guyana	EF079990
ROM 115345	*Anoura*	*caudifer*	Guyana	JF447870
ROM 115346	*Anoura*	*caudifer*	Guyana	EF079991
ROM 115347	*Anoura*	*caudifer*	Guyana	EF079992
ROM 115362	*Anoura*	*caudifer*	Guyana	EF079981

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Appendix 3. (Continued)

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 115363	*Anoura*	*caudifer*	Guyana	EF079986
ROM 115864	*Anoura*	*caudifer*	Guyana	EF079993
ROM 115865	*Anoura*	*caudifer*	Guyana	EF079994
ROM 115962	*Anoura*	*caudifer*	Guyana	EF079995
ROM 113962	*Anoura*	*caudifer*	Suriname	JF447478
ROM 114123	*Anoura*	*caudifer*	Suriname	JF447477
ROM 119704	*Anoura*	*caudifer*	Suriname	JQ601426
CVULA 9081	*Anoura*	*caudifer*	Venezuela	OQ944953
CVULA 9111	*Anoura*	*caudifer*	Venezuela	OQ944954
CVULA 9112	*Anoura*	*caudifer*	Venezuela	OQ944955
TTU-M 33312	*Anoura*	*caudifer*	Venezuela	OQ944946
TTU-M 33313	*Anoura*	*caudifer*	Venezuela	OQ944945
QCAZ 18217	*Anoura*	*cultrata*	Ecuador	NC065675
ROM 105795	*Anoura*	*cultrata*	Ecuador	JF447871
LSUMZ 555	*Anoura*	*cultrata*	Panama	OQ944947
FMNH 128637	*Anoura*	*cultrata*	Peru	OQ944948
CVULA 6986	*Anoura*	*cultrata*	Venezuela	OQ944956
CVULA 6987	*Anoura*	*cultrata*	Venezuela	OQ944957
CVULA 6990	*Anoura*	*cultrata*	Venezuela	OQ944958
CVULA 8749	*Anoura*	*cultrata*	Venezuela	OQ944959
CVULA 8750	*Anoura*	*cultrata*	Venezuela	OQ944960
12A	*Anoura*	*geoffroyi*	Brazil	KT236265
TTU-M 85093	*Anoura*	*geoffroyi*	Ecuador	OQ944942
TTU-M 85106	*Anoura*	*geoffroyi*	Ecuador	OQ944940
ROM 126404	*Anoura*	*geoffroyi*	Grenada	OQ944951
ROM 126412	*Anoura*	*geoffroyi*	Grenada	OQ944952
ROM 106660	*Anoura*	*geoffroyi*	Guyana	EF080014
ROM 106692	*Anoura*	*geoffroyi*	Guyana	BCBNT049-06
ROM 106706	*Anoura*	*geoffroyi*	Guyana	EF080015
ROM 106707	*Anoura*	*geoffroyi*	Guyana	EF080016
ROM 106717	*Anoura*	*geoffroyi*	Guyana	EF080017
ROM 108828	*Anoura*	*geoffroyi*	Guyana	EF080011
ROM 111865	*Anoura*	*geoffroyi*	Guyana	EF080018
ROM 114735	*Anoura*	*geoffroyi*	Guyana	EF079999
ROM 114736	*Anoura*	*geoffroyi*	Guyana	EF080000
ROM 114765	*Anoura*	*geoffroyi*	Guyana	JF452142
ROM 114766	*Anoura*	*geoffroyi*	Guyana	EF080001
ROM 114767	*Anoura*	*geoffroyi*	Guyana	EF079997
ROM 114772	*Anoura*	*geoffroyi*	Guyana	JF452167
ROM 114874	*Anoura*	*geoffroyi*	Guyana	EF080019
ROM 115088	*Anoura*	*geoffroyi*	Guyana	EF080002
ROM 115171	*Anoura*	*geoffroyi*	Guyana	EF080003
ROM 115236	*Anoura*	*geoffroyi*	Guyana	EF080004

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Appendix 3. (Continued)

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 115237	*Anoura*	*geoffroyi*	Guyana	BCBNC074-06
ROM 115256	*Anoura*	*geoffroyi*	Guyana	EF080005
ROM 115258	*Anoura*	*geoffroyi*	Guyana	JF452162
ROM 115259	*Anoura*	*geoffroyi*	Guyana	JF452160
ROM 115260	*Anoura*	*geoffroyi*	Guyana	JF452171
ROM 115261	*Anoura*	*geoffroyi*	Guyana	JF452169
ROM 115273	*Anoura*	*geoffroyi*	Guyana	JF452164
ROM 115274	*Anoura*	*geoffroyi*	Guyana	JF452163
ROM 115301	*Anoura*	*geoffroyi*	Guyana	EF080006
ROM 115319	*Anoura*	*geoffroyi*	Guyana	JF452161
ROM 115320	*Anoura*	*geoffroyi*	Guyana	JF452159
ROM 115321	*Anoura*	*geoffroyi*	Guyana	JF452170
ROM 115322	*Anoura*	*geoffroyi*	Guyana	JF452168
ROM 115324	*Anoura*	*geoffroyi*	Guyana	JF452165
ROM 115325	*Anoura*	*geoffroyi*	Guyana	ABGYF657-06
ROM 115326	*Anoura*	*geoffroyi*	Guyana	EF080007
ROM 115327	*Anoura*	*geoffroyi*	Guyana	EF079998
ROM 115328	*Anoura*	*geoffroyi*	Guyana	JF447872
ROM 115329	*Anoura*	*geoffroyi*	Guyana	EF079996
ROM 115330	*Anoura*	*geoffroyi*	Guyana	EF080008
ROM 115331	*Anoura*	*geoffroyi*	Guyana	EF080009
ROM 115348	*Anoura*	*geoffroyi*	Guyana	EF080012
ROM 115352	*Anoura*	*geoffroyi*	Guyana	EF080013
ROM 115353	*Anoura*	*geoffroyi*	Guyana	JF452166
ROM 115361	*Anoura*	*geoffroyi*	Guyana	JF447874
ROM 116492	*Anoura*	*geoffroyi*	Guyana	EF080010
ROM 116522	*Anoura*	*geoffroyi*	Guyana	JF452173
ROM 116563	*Anoura*	*geoffroyi*	Guyana	JF452174
ROM 116581	*Anoura*	*geoffroyi*	Guyana	JF452153
ROM 116583	*Anoura*	*geoffroyi*	Guyana	JF452152
ROM 116602	*Anoura*	*geoffroyi*	Guyana	JF452172
ROM 116617	*Anoura*	*geoffroyi*	Guyana	JF452156
ROM 116623	*Anoura*	*geoffroyi*	Guyana	JF452151
ROM 116641	*Anoura*	*geoffroyi*	Guyana	JF452157
ROM 116646	*Anoura*	*geoffroyi*	Guyana	JF452158
ROM 116662	*Anoura*	*geoffroyi*	Guyana	JF452150
ROM 116666	*Anoura*	*geoffroyi*	Guyana	JF452148
ROM 116667	*Anoura*	*geoffroyi*	Guyana	JF452147
ROM 116668	*Anoura*	*geoffroyi*	Guyana	JF452146
ROM 116669	*Anoura*	*geoffroyi*	Guyana	JF452145
ROM 116670	*Anoura*	*geoffroyi*	Guyana	JF452144
ROM 116672	*Anoura*	*geoffroyi*	Guyana	JF452143
ROM 116692	*Anoura*	*geoffroyi*	Guyana	JF452155

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Appendix 3. (Continued)

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 116693	*Anoura*	*geoffroyi*	Guyana	JF452154
ROM 116707	*Anoura*	*geoffroyi*	Guyana	JF452149
ROM 116708	*Anoura*	*geoffroyi*	Guyana	JF447878
ROM 116715	*Anoura*	*geoffroyi*	Guyana	JF447873
ROM 116716	*Anoura*	*geoffroyi*	Guyana	JF452175
ROM 116723	*Anoura*	*geoffroyi*	Guyana	JF447877
ROM 116734	*Anoura*	*geoffroyi*	Guyana	JF447876
ROM 116746	*Anoura*	*geoffroyi*	Guyana	JF447875
ROM 114218	*Anoura*	*geoffroyi*	Suriname	JF447880
ROM 114225	*Anoura*	*geoffroyi*	Suriname	JF447479
ROM 117443	*Anoura*	*geoffroyi*	Suriname	EU096555
ROM 117483	*Anoura*	*geoffroyi*	Suriname	EU096556
ROM 117531	*Anoura*	*geoffroyi*	Suriname	EU096557
ROM 119554	*Anoura*	*geoffroyi*	Suriname	ABGYH062-12
ROM 119558	*Anoura*	*geoffroyi*	Suriname	ABGYH064-12
ROM 119566	*Anoura*	*geoffroyi*	Suriname	ABGYH069-12
ROM 119569	*Anoura*	*geoffroyi*	Suriname	ABSRA622-08
ROM 119582	*Anoura*	*geoffroyi*	Suriname	ABSRA635-08
ROM 119665	*Anoura*	*geoffroyi*	Suriname	ABGYH098-12
ROM 119678	*Anoura*	*geoffroyi*	Suriname	JQ601414
ROM 119695	*Anoura*	*geoffroyi*	Suriname	ABGYH112-12
ROM 119696	*Anoura*	*geoffroyi*	Suriname	ABGYH113-12
ROM 119700	*Anoura*	*geoffroyi*	Suriname	ABGYH115-12
ROM 120222	*Anoura*	*geoffroyi*	Suriname	HQ545675
ROM 120390	*Anoura*	*geoffroyi*	Suriname	HQ919742
ROM 120660	*Anoura*	*geoffroyi*	Suriname	JQ601250
CVULA 9084	*Anoura*	*geoffroyi*	Venezuela	OQ944961
CVULA 9113	*Anoura*	*geoffroyi*	Venezuela	OQ944962
ROM 107853	*Anoura*	*geoffroyi*	Venezuela	JF447879
ROM 108111	*Anoura*	*latidens*	Guyana	EF080022
ROM 115317	*Anoura*	*latidens*	Guyana	EF080023
ROM 115318	*Anoura*	*latidens*	Guyana	EF080020
ROM 115323	*Anoura*	*latidens*	Guyana	JF447882
ROM 115351	*Anoura*	*latidens*	Guyana	EF080021
ROM 115925	*Anoura*	*latidens*	Guyana	JF447881
CVULA 9087	*Anoura*	*luismanueli*	Venezuela	OQ944963
CVULA 9088	*Anoura*	*luismanueli*	Venezuela	OQ944964
CVULA 9089	*Anoura*	*luismanueli*	Venezuela	OQ944965
CVULA 9090	*Anoura*	*luismanueli*	Venezuela	OQ944966
CVULA 9110	*Anoura*	*luismanueli*	Venezuela	OQ944967
QCAZ 18218	*Anoura*	*peruana*	Ecuador	NC065676
ROM 101463	*Anoura*	*peruana*	El Salvador	JF446440
ROM 101464	*Anoura*	*peruana*	El Salvador	JF446441

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Appendix 3. (Continued)

Sample ID	Genus	Species	Country	Genbank or BOLD
ROM 101527	*Anoura*	*peruana*	El Salvador	JF446442
ROM 99831	*Anoura*	*peruana*	Guatemala	JF446614
ROM 99832	*Anoura*	*peruana*	Guatemala	JF446615
LSUMZ 556	*Anoura*	*peruana*	Panama	OQ944949
ROM 104299	*Anoura*	*peruana*	Panama	JF447340
LSUMZ 5933	*Anoura*	*peruana*	Peru	OQ944950
ROM 125160	*Anoura*	*peruana*	Peru	OQ944972
CVULA 9095	*Anoura*	*peruana*	Venezuela	OQ944968
CVULA 9114	*Anoura*	*peruana*	Venezuela	OQ944969
CVULA 9115	*Anoura*	*peruana*	Venezuela	OQ944970
CVULA 9117	*Anoura*	*peruana*	Venezuela	OQ944971