New Species of *Anoura* (Chiroptera: Phyllostomidae) from Colombia, with Systematic Remarks and Notes on the Distribution of the *A. geoffroyi* Complex

Hugo Mantilla-Meluk and Robert J. Baker

Abstract

A new species of nectar-feeding tailless bat in the genus *Anoura* (Chiroptera: Phyllostomidae) is described from the highlands of the Colombian Andes and the independent mountain system of the Sierra Nevada de Santa Marta. Complete zygomatic arches, a relatively wide uropatagium, and wide first upper molars with poorly developed paracones are proposed as synapomorphies of the new species and *A. geoffroyi geoffroyi*. However, the two taxa are allopatrically distributed, and the new species is morphologically distinguished from *A. g. geoffroyi* by a smaller skull and body size, more massive and squared molars with wider hypoconal basins, smaller P4 that are not laterally compressed, reduced anterobasal cusps, and medial internal cusps that are enlarged. Based on morphological analysis the distributional ranges of *A. geoffroyi* subspecies were interpreted as follows: *A. g. lasiopyga* is restricted to Central America from Costa Rica north to Mexico; *A. g. peruana* is restricted to the mid to high elevations of the Andean system from Bolivia to Colombia; and *A. g. geoffroyi* is restricted to the mid and low elevations of eastern versant of the Andes from Brazil to northern South America, including the island of Trinidad. Further, the morphological affinities between *A. g. apolinari* and members of the *A. geoffroyi* complex support its current recognition as a junior synonym of *A. g. peruana*. Based on the morphological distinction observed between *A. g. peruana* and *A. g. geoffroyi*, including the absence of complete zygomatic arches, a more delicate rostrum, less massive molars, and overall darker coat coloration, as well as the ecological differentiation of the areas inhabited by these two taxa, we recommend the elevation of *A. peruana* to specific level.

Key words: *Anoura*, bats, Colombia, new species

Resumen

Se describe una nueva especie de murciélago nectarívoro sin cola del género *Anoura* (Chiroptera: Phyllostomidae) proveniente de los Andes y el sistema montañoso independiente de la Sierra Nevada de Santa Marta en Colombia. La presencia de arcos zigomáticos completos, un uropatagio relativamente amplio y molares superiores amplios, son propuestos como sinapomorfías para la nueva especie y *A. geoffroyi geoffroyi*. Sin embargo, estos dos taxa se encuentran alopátricamente distribuidos y la nueva especie se distingue morfológicamente de *A. g. geoffroyi* por tener un menor tamaño de cráneo y menor tamaño corporal, molares más masivos y cuadrados, con las fosas de los hipoconos más amplias, los P4 de un tamaño menor, no lateralmente comprimidos y cúspides anterobasales de mayor tamaño. Basados en análisis morfológicos interpretamos la distribución de las subespecies de *A. geoffroyi* como sigue: *A. g. lasiopyga* es restringida a las elevaciones medias y altas de Centro América desde Costa Rica hasta México; *A. g. peruana* es restringida a las elevaciones medias y altas del sistema Andino desde Bolivia hasta Colombia; y *A. g. geoffroyi* es restringida a las tierras medias y bajas de la vertiente oriental de los Andes desde Brasil hasta el norte de Sur América, incluyendo la isla de Trinidad. Adicionalmente, las afinidades morfológicas entre *A. g. apolinari* y los miembros del complejo *A. geoffroyi* apoyan su actual reconocimiento como sinónimo menor de *A. g. peruana*. Basados en las diferencias morfológicas observadas entre *A. g. peruana* y *A. g. geoffroyi*, incluyendo la ausencia de arcos zigomáticos completos, rostro más delicado, molares menos masivos y una coloración del pelaje más oscura, así como también la diferenciación ecologica entre las áreas habitadas por estos dos taxa recomendamos la elevación de *A. peruana* a estado específico.

Palabras clave: *Anoura*, Colombia, murciélagos, nueva especie

INTRODUCTION

Nectarivorous bats of the genus *Anoura* Gray 1838 (Glossophaginae: Choeronycterini) (Baker et al. 2003) currently are recognized as eight species: *A. caudifer* (Geoffroy St.-Hilaire 1818); *A. geoffroyi* Gray 1838; *A. aequatoris* (Lönnberg 1921); *A. cultrata* Handley 1960; *A. latidens* Handley 1984; *A. luismanueli* Molinari 1994; *A. fistulata* Muchhala, Mena, and Albuja 2005; and *A. cadenai* Mantilla-Meluk and Baker 2006. *Anoura geoffroyi* is the most widely distributed and morphometrically variable species in the genus and includes three recognized subspecies: *A. g. geoffroyi* Gray 1838, from Rio de Janeiro, Brazil (type locality accompanied by a question mark in the description), restricted to Rio de Janeiro by C. O. C. Vieira (1942:324); *A. g. peruana* (Tschudi 1844), from Junín, Peru; and *A. g. lasiopyga* Peters 1868, type locality "Mexico" restricted to the state of Veracruz, Mexico, by Arroyo-Cabrales and Gardner (2003:740). The uncertainty of the geographic origin of some of the holotypes has made it difficult to define the geographic boundaries of the subspecies, or to validate potential new taxa within the *A. geoffroyi* complex. Two junior synonyms exist for *Anoura g. peruana*: *A. g. apolinari* (Allen 1916), described from Boquerón de San Francisco, near Bogotá, Cundinamarca, Colombia; and *A. g. antricola* Anthony 1921, described from Loja, Ecuador. Although *A. geoffroyi* has been documented in Colombia (Mantilla-Meluk et al. 2009), the hypothesized presence of *A. geoffroyi* geographic variants in northern South America often has lacked a detailed systematic analysis, and their geographic limits remain poorly defined. In a recent examination of *Anoura* specimens deposited in the Colombian collections of the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, we discovered a distinctive and undescribed species of *Anoura* previously identified as *A. geoffroyi*. Herein, we describe this new species of *Anoura* and use multivariate methods to evaluate the phenetic similarities among recognized taxa within the *A. geoffroyi* complex (*A. g. geoffroyi*, *A. g. lasiopyga*, and *A. g. peruana*). Due to the unique opportunity to conduct systematic analyses of a relatively large number of *A. geoffroyi* voucher specimens from Cundinamarca, Colombia, we also re-examine the taxonomic status of *A. g. apolinari*. Further, we evaluate the presence of *A. g. geoffroyi* and *A. g. lasiopyga* in Colombia and take advantage of the wide geographic extent of the available specimens to further refine the distributional limits of these two taxa in Central America.

MATERIALS AND METHODS

Data collection.—We examined 268 adult *A. geoffroyi* specimens (149 males and 119 females), from Bolivia (2), Brazil (3), Colombia (155), Costa Rica (2), Ecuador (6), Guatemala (8), Mexico (27), Peru (33), and Trinidad (31), deposited in the following institutions: American Museum of Natural History (AMNH); Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN); Field Museum of Natural History (FMNH); Musée D'Histoire Naturelle de Geneve (MHNG); Museo de Historia Natural de la

Universidad del Cauca (MHNUC); Museo de la Universidad Distrital Francisco José de Caldas (MUD); Southwestern Biology Collection of the University of New Mexico (MSB); and the Museum of Texas Tech University (TTU) (Appendix). Relative age of each specimen was determined based on the degree of ossification of phalangeal epiphyses and the completeness of ossification of the basisphenoid suture. For each specimen, we recorded 12 craniodental measurements with digital calipers to the nearest 0.01 mm as follows: greatest length of the skull (GLS), greatest distance from the anteriormost projection of the nasal bones to the posteriormost portion of the occipital bone; condylobasal length (CB), distance from the anteriormost projection of the premaxillae to the posteriormost projection of the exoccipital condyles; palatal length (PAL), distance from the anteriormost point of the premaxilla (excluding incisors) to the posterior margin of the horizontal process of the palatine, just in the midline of the horizontal process of the palatine; postorbital constriction (PO), least width across the interorbital constriction at a right angle to the longitudinal axis of the cranium; mastoid breadth (MB), greatest breadth across the lateral margins of the parietal at the posterior region to the suture coronalis (measured at a right angle to the longitudinal axis of the cranium); anterior braincase breadth (BCW); braincase height (BCH), distance from the juncture of the midline and frontal–parietal sutures to the inferiormost point of the glenoid fossae; maxillary toothrow length (LTR); M3 breadth (M-M), greatest breadth across the lateral margins of M3 at a right angle to the longitudinal axis of the tooth; greatest breadth across the canines (C-C), distance between the externalmost point of the canine alveoli; mandibular condylocanine length (ML), greatest distance from the anteriormost point of the alveolus of the lower canines to the posteriormost point of the mandibular condyles; and mandibular toothrow length (MTR), greatest distance from the anteriormost surface of i1 to the posteriormost surface of m3. Although for this work only dry skins were analyzed, we recorded the relative size of the uropatagium (UL), relative size of the vibrissae (VL), and the relative size of the thumb (TL).

Sexual dimorphism.—To identify those measurements that contribute the most to skull variation among large *Anoura*, we performed a Principal Components Analysis (PCA) among 234 *Anoura* specimens (125 males and 109 females) with complete data in this work, including all recognized *A. geoffroyi* subspecies and the newly described taxon; then, a MANOVA was performed on six craniodental variables that accounted for most of the variation (GLS, CB, PAL, M-M, C-C, ML) between male and female *A. geoffroyi* to test for sexual dimorphism in the R statistical package, script available at: http://facultybiol.ttu.edu/strauss/Multivar/R/SampleDFAManova.R.txt.

Multivariate analysis.—To investigate and describe the morphometric variation and phenetic similarity between the new species and other representatives of *A. geoffroyi* across its geographic range, we applied Principal Component Analyses to the twelve craniodental variables listed above of 260 *A. geoffroyi* specimens (143 males and 117 females) in the statistical package PAST, http://folk.uio.no/ohammer/past/download.html. Due to the existence of missing data within the sample (0.99%), the "missem" MATLAB function, available at www.ttu.edu/strauss/Matlab/Matlab.htm, was applied to find the most likely values for those missing data. Female and male measurements were analyzed separately because of significant differences observed in skull size in our MANOVA.

RESULTS

Sexual dimorphism.—Sexual dimorphism was confirmed among 234 *A. geoffroyi* specimens in this study (125 males and 109 females). A MANOVA performed on the six craniodental variables that contributed the most to skull variation in this analysis (GLS, CB, PAL, M-M, C-C, ML), show significant differences ($F = 9.33$; $p < 0.001$) between *A. geoffroyi* males and females.

Principal Component Analyses.—Principal Component Analyses revealed high levels of intrasubspecific morphological variation for both male and female *A. geoffroyi*. All subspecies of *A. geoffroyi* extensively overlapped in morphospace. *Anoura g. peruana* had the widest range of morphometric variation with *A. g. geoffroyi* and *A. g. lasiopyga* present within the morphospace of *A. g. peruana* (Fig. 1). The greater

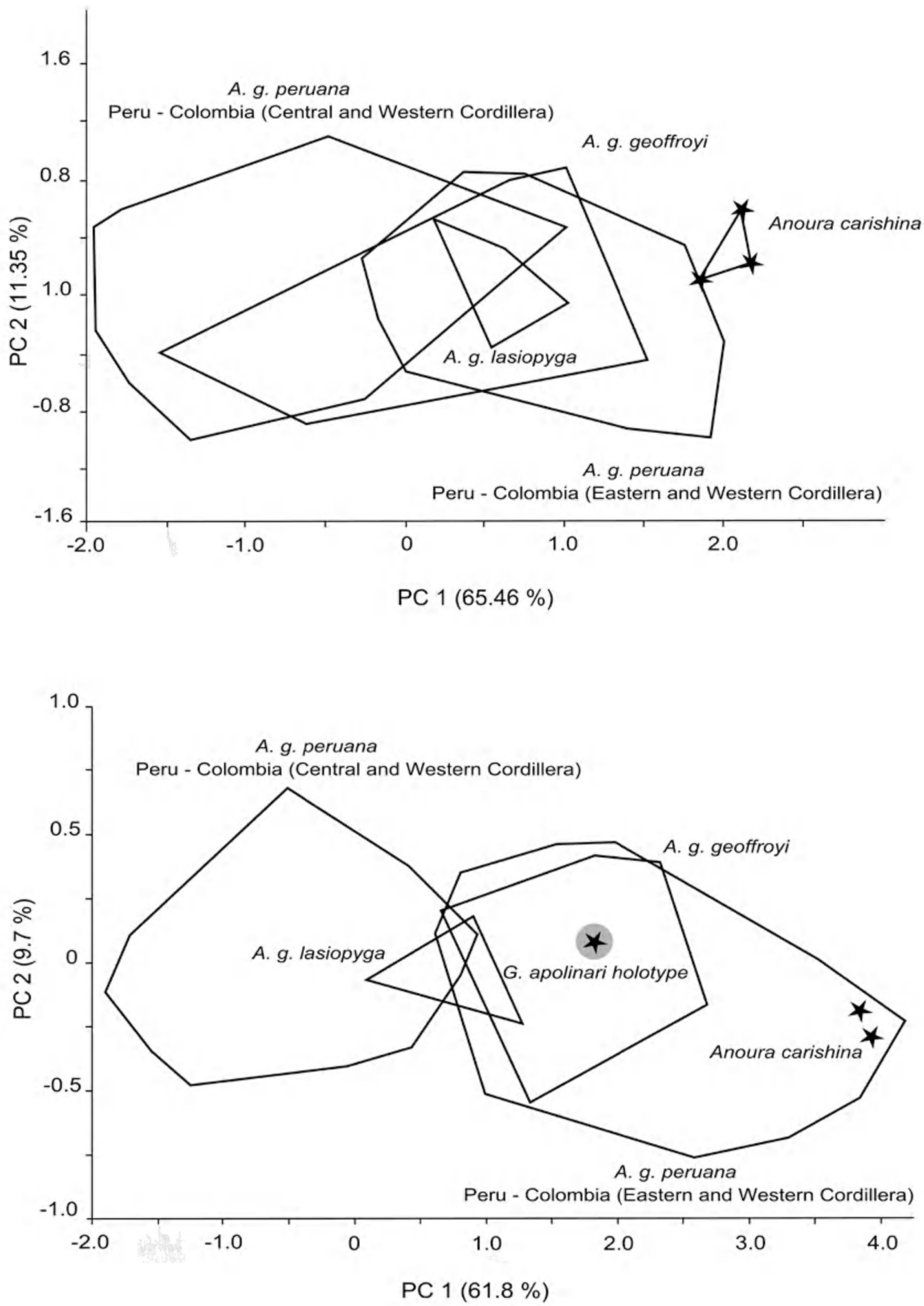

Figure 1. Scatter plot showing the results of Principal Component Analyses applied to 12 craniodental measurements of adult males (top) and adult females (bottom) representing: new species *Anoura carishina* (black stars), holotype *A. g. apolinari* AMNH 37376 (star in grey circle), *A. g. peruana*, *A. g. lasiopyga*, and *A. g. geoffroyi*.

Table 1. Principal component scores of the percentage of variation explained by the first two components and loadings of the analyzed variables for both A. geoffroyi (sensu lato) *males and females. GLS: Greatest length of skull; CB: Condylobasal length; PAL: Palatal length; PO: Post orbital constriction width; MB: Mastoid breadth; BCW: Braincase width; BCH: Braincase height; LTR: Tooth-row length; M-M: Distance across upper molars; C-C: Distance across upper canines; ML: Mandible length; MTR: Longitude of the mandibular tooth-row.*

	♀		♂	
	PC1	PC2	PC1	PC2
% Variation	61.8	9.7	65.466	11.35363
GLS	-0.4848	0.237	-0.2478	0.4858
CB	-0.5252	0.1312	-0.3028	0.5304
PAL	-0.4763	-0.6418	0.8558	0.4518
PO	-0.0071	0.132	-0.057	0.03148
MB	-0.0485	0.3904	0.05467	0.0784
BCW	-0.0242	0.298	0.08931	0.07177
BCH	0.01131	0.4585	0.1636	0.03369
LTR	-0.1987	0.05901	-0.1708	0.186
M-M	-0.0442	0.02493	-0.0548	0.05301
C-C	-0.0318	0.09404	-0.0214	0.09798
ML	-0.4099	0.1659	-0.1096	0.4082
MTR	-0.2207	0.07332	-0.1703	0.2267

variation found among *A. g. peruana* can be also related to its larger sample size in this analysis.

Palatal length accounted for most of the variation among males and females, followed by condylobasal length and greatest length of the skull, with all having negative loadings in females and positive loadings in males (Table 1).

Anoura g. peruana from the departments of Ayacucho, Huánuco, and Ollantaytambo in Peru, Pichincha in Ecuador, and Caldas and Quindío in Colombia were characterized by a larger average size (GLS > 25.5 mm) in comparison with specimens of *A. g. peruana* from other localities, including specimens from Cundinamarca, Colombia. Differences in size between *A. g. peruana* from Peru and *A. g. peruana* from Cundinamarca, Colombia, were more evident among females than in males (Fig. 1).

Some specimens from the mid- to high elevations in the departments of Magdalena, Nariño, and Valle del Cauca were among the smallest representatives of the *A. geoffroyi* complex (GLS < 24.5 mm). The above mentioned specimens shared the complete zygomatic arches (or evidence of this condition) and relatively large uropatagia of *A. g. geoffroyi* from the lowlands.

DISCUSSION

Taxonomic remarks.—The systematics of the genus *Anoura* has been a source of debates on the validity of morphology to identify independent evolutionary units (Sanborn 1933; Cabrera 1957; Mantilla-Meluk and Baker 2006; Jarrín-V and Kunz 2008). The observed morphological variation among large *Anoura* in the *A. geoffroyi* complex has been interpreted as geographic variants, resulting in the designation of three subspecies: *A. g. geoffroyi*, *A. g. lasiopyga*, and *A. g. peruana*. Up to date, it has been difficult to establish the geographic boundaries of *A. geoffroyi* geographic variants. Geographic distributions of these three taxa have been established based primarily on the indiscriminate usage of available Linnean epithets. In addition, two currently recognized subspecies, *A. g. peruana* and *A. g. lasiopyga,* were described before 1868 in different genera than *Anoura* (*Choeronycteris peruana* and *Glossonycteris lasiopyga*), making difficult the identification of diagnostic characters to separate them from other members of the genus. We used morphological criteria derived from the study of the holotypes of *Glossophaga apolinari* Allen 1916 (*A. g. apolinari*) and *Glossonycteris lasiopyga* Peters 1868 (*A. g. lasiopyga*) to reassess the taxonomic status of *A. peruana* and these two taxa and to define their geographic ranges.

Taxonomic status of Anoura g. apolinari.—*Anoura g. apolinari* is currently considered a junior synonym of *A. g. peruana* (Simmons 2005). This taxon, with type locality in Boquerón de San Francisco, near Bogotá, Cundinamarca, Colombia, was described based on six specimens (sex not defined by the author Allen 1916). However, the holotype of *G. apolinari* (AMNH 37376, GLS = 26.0 mm) has the long and delicate rostrum, the smaller and less laterally divergent canines, and less pronounced zygomatic processes typical of Peruvian female specimens of *A. g. peruana* (Fig. 2). Sexual dimorphism was observed among *A. g. peruana* specimens included in this work, with females having an overall larger size than males in all analyzed measurements (Table 2). Based on the morphology observed, as well as morphometric ranges documented, we concluded that specimen AMNH 37376 used by Allen (1916) as holotype of *G. apolinari* is within the measurements of female *A. g. peruana*. In our PCA, the holotype of *G. apolinari* was within the morphospace of *A. g. peruana*. Based on the observed similarities in discrete characters, as well as the overlapping morphometric ranges, it is difficult to distinguish *G. apolinari* from *A. g. peruana*. Therefore, we recommend maintaining *G. apolinari* as junior synonym of *A. g. peruana* and the application of the epithet *A. g. peruana* for *A. geoffroyi* Colombian specimens characterized by a large skull (GLS > 25.5), incomplete zygomatic arches, reduced uropatagium, and dark coat color, ranging from Mummy-Brown to Black (Ridgeway 1912) as well as long hair lengths.

Geographic distributions.—The most recent works including distributional maps for *A. geoffroyi* subspecies in northern South America differ in their interpretation of the geographic limits of *A. g. peruana* and *A. g. lasiopyga* in Colombia (Gardner 2008 [2007]; Ortega and Alarcón-D 2008). Gardner (2008 [2007]) reported *A. g. peruana* for the Colombian territory and mentioned that *A. lasiopyga*, only reported for Ecuador in South America (Albuja 1983), is potentially present on the western side of Colombia. In contrast, although Ortega and Alarcón-D (2008) accepted *G. apolinari* (holotype from Cundinamarca, Colombia) as a synonym of *A. g. peruana*, the taxon was excluded from Colombia in their distribution map. In addition, Ortega and Alarcón-D (2008) extended the distribution of *A. g. lasiopyga* to the entire Andean region in Colombia. We did not find support for the hypothesis of Ortega and Alarcón-D (2008) in the morphology observed in our specimens examined. In our samples, the Colombian specimens of *A. geoffroyi* with incomplete zygomatic arches matched the description of *A. g. peruana*. Compared with the *G. lasiopyga* holotype (MHNG 515.88), Colombian samples presented a more acute palatal angle, a darker coat color, and relatively longer hair (Figs. 2 and 3). The same characteristics were observed in specimens from Ecuador analyzed in this work (N = 6; GLS mean = 25.58 mm, StDv = 0.51) (Appendix).

Until 1957, *A. g. lasiopyga* was known only from 41 specimens, all from localities north of Guatemala (Goodwin 1934). Anderson (1957) extended the distribution of *A. g. lasiopyga* into Costa Rica based on one specimen (KU 39249) from San Rafael, Canton de Tarrazú (misspelled on tag as Terrazi), 30 km S from San José (1300 m). Anderson (1957) compared specimen KU 39249 with a series of 13 specimens (KU 60635-46, KU 60978-61076) from Teopisca, Chiapas, and mentioned that despite differences in external color and cranial measurements, specimen KU 39249 was within the ranges proposed for *A. g. lasiopyga*. In addition, specimen KU 39249 was paler than typical *A. g. peruana* from South America and both the Costa Rican and the Mexican specimens averaged smaller than those of *A. g. peruana* in all analyzed measurements (Anderson 1957) (Table 2). Among *A. geoffroyi* from Middle America examined in this work, two color phases were distinguished: a) pale phase (Sanborn 1933) (Light-Gray to Light-Drab, Ridgeway 1912), also characterized by short hair, represented in our samples

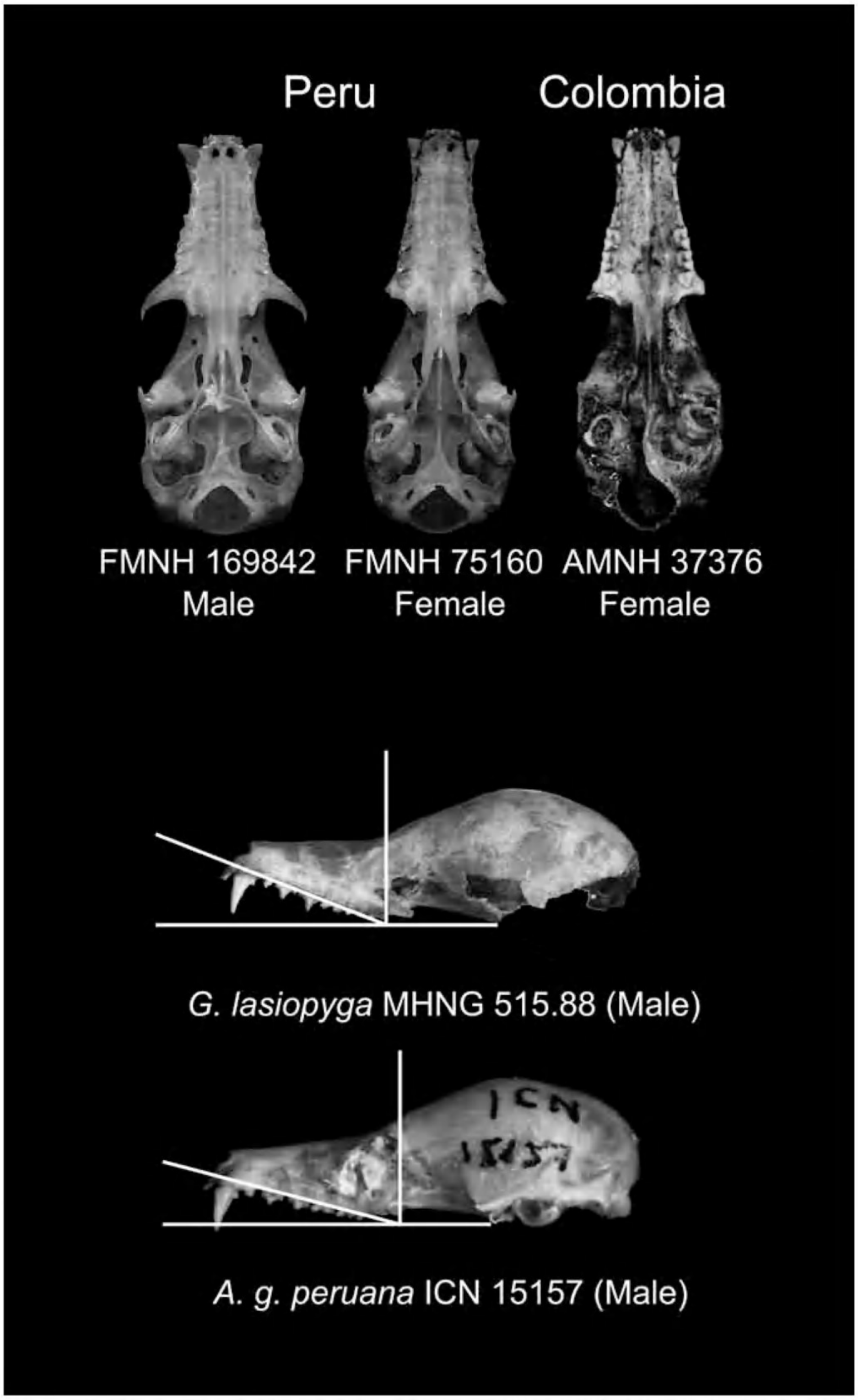

Figure 2. Comparison between *A. g. peruana* (FMNH ♂ 169842, Pucataitambo, Peru; FMNH ♀ 75160, Andahuaylas, Peru) and the holotype of *A. g. apolinari* (Allen 1916) (AMNH ♀ 37376, San Francisco, Bogotá, Colombia) (upper row). Difference in palatal angle between holotype of *Glossonycteris lasiopyga* (MHNG 515.88 ♂) and *A. g. peruana* from Colombia (ICN 15157 ♂) (lower row).

Table 2. Average values of the 12 analyzed craniodental measurements (mm) of large Anoura *specimens. Abbreviations: GLS: Greatest length of skull; CB: Condylobasal length; PAL: Palatal length; PO: Postorbital constriction width; MB: Mastoid breadth; BCW: Braincase width; BCH: Braincase height; TR: Tooth-row length; M-M: Distance across upper molars; C-C: Distance across upper canines; ML: Mandible length; MTR: Longitude of the mandibular tooth-row. StDv = Standard Deviation.*

♀		GLS	CB	PAL	PO	MB	BCW	BCH	TR	M-M	C-C	ML	MTR
A. geoffroyi		24.94	24.20	13.19	5.05	9.21	9.75	7.35	9.41	6.10	4.44	17.39	9.59
N = 33	StDv	0.451	0.48	0.51	0.18	0.21	0.21	0.33	0.26	0.23	0.17	0.33	1.10
A. lasiopyga		25.16	24.45	13.02	5.06	9.01	9.71	7.18	9.53	6.03	4.44	17.67	9.90
N = 4	StDv	0.60	0.50	0.69	0.09	0.17	0.08	0.09	0.24	0.13	0.07	0.34	0.23
A. peruana		25.45	24.25	13.33	4.95	9.13	9.67	7.21	9.53	6.06	4.29	17.50	9.80
N = 78	StDv	0.65	1.19	1.51	0.19	0.23	0.21	0.44	0.31	0.19	0.16	0.66	0.43
A. carishina		24.04	23.31	11.98	4.86	8.88	9.55	7.22	8.98	5.99	4.11	16.58	9.47
N = 2	StDv	0.00	0.04	0.29	0.19	0.27	0.35	0.37	0.07	0.15	0.06	0.12	0.03
♂													
A. geoffroyi		25.00	24.25	13.24	5.05	9.18	9.76	7.48	9.39	6.11	4.66	17.29	9.87
N = 43	StDv	0.51	0.53	0.57	0.17	0.22	0.20	0.24	0.22	0.25	0.38	0.44	0.34
A. lasiopyga		25.05	24.30	13.08	4.95	9.09	9.54	7.17	9.38	6.18	4.62	17.26	9.81
N = 13	StDv	0.70	0.70	0.38	0.20	0.21	0.38	0.20	0.32	0.12	0.23	0.57	0.33
A. peruana		25.07	24.06	13.31	4.89	9.07	9.76	7.37	9.37	6.06	4.28	17.04	9.55
N = 88	StDv	0.57	0.65	0.78	0.17	0.21	0.22	0.41	0.29	0.22	0.23	0.51	0.32
A. carishina		24.31	23.37	12.29	5.12	9.27	9.83	7.52	9.20	6.11	4.45	16.67	9.53
N = 3	StDv	0.20	0.12	0.24	0.23	0.23	0.11	0.12	0.09	0.18	0.06	0.14	0.12

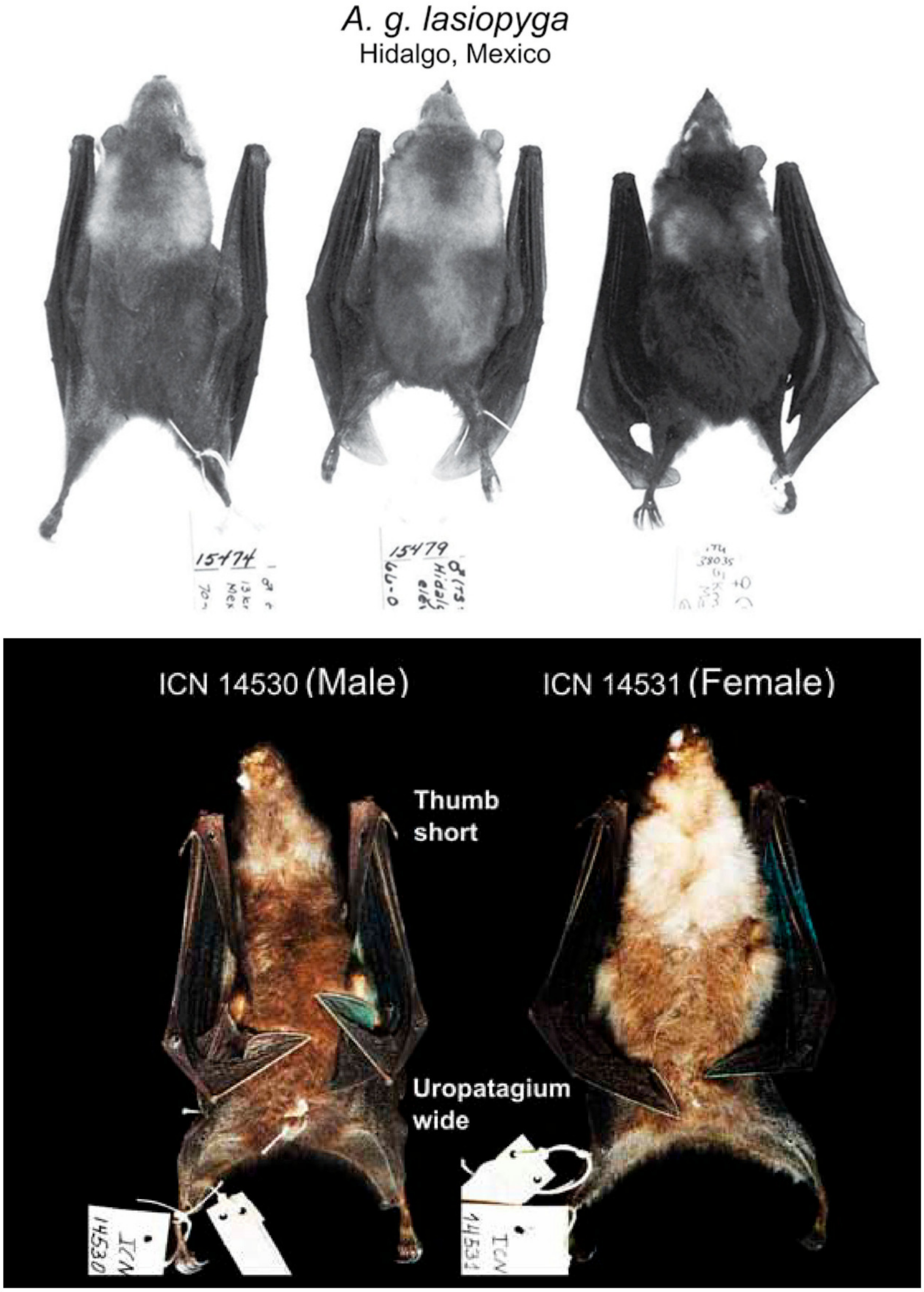

Figure 3. Differences in coat color and hair length among *A. g. lasiopyga* from Mexico (TTU 15474 ♂, TTU 15479 ♂, and TTU 38035 ♀) (top). Skin of *A. carishina* holotype (ICN 14530 ♂) and a female (ICN 14531 ♀) of the type series (bottom).

by specimens from the Mexican state of Hidalgo; and b) dark phase (dusky-brown to blackish-brown, Ridgeway 1912), also characterized by longer hair, represented in our sample by specimens from the Mexican states of Hidalgo, Tamaulipas, Tlaxcala, and Veracruz, as well as samples from Olancho, Honduras, and Punta Arenas, Costa Rica that to some extent resemble the typical coat color pattern observed in *A. g. geoffroyi* (Fig. 3) (Appendix). Further analyses using datasets other than morphology will be necessary to elucidate the taxonomic affinities between Middle American *A. geoffroyi* populations and *A. g. geoffroyi* from the lowlands to mid-elevations on the eastern versant of the Andes and the island of Trinidad.

Although *A. g. peruana* had the largest range of variation in skull size among samples in this work, specimens from Bolivia, Colombia, Ecuador, and Peru were clearly distinguishable from typical *A. g. geoffroyi* from the lowlands along eastern South America, including specimens from Brazil, by the absence of zygomatic arches, more delicate rostrum, less massive molars and premolars, and a darker general coat color from Mummy-Brown to Black (Ridgeway 1912), with no intermediate forms. Based on the morphological distinction between *A. g. peruana* and *A. g. geoffroyi* we support the elevation of *A. peruana* (Tschudi 1844) to specific status.

Size variation in Anoura peruana.—Samples of *Anoura peruana* in this work included the widest ranges of size variation for all the measurements analyzed (Table 2). Greatest length of the skull (GLS), representing the measurement that accounted for most of the variation among all taxa analyzed, ranged from 24.05 to 26.51 mm (mean = 25.04; StDev = 0.61) in *A. peruana*. Among our samples, large and small *A. peruana* were found sympatrically in some localities on the Eastern Cordillera of the Colombia Andes as well as the northernmost range of the Central Cordillera; in contrast, *A. peruana* from Peru and the southern portion of the Central and Western Cordilleras of the Colombia Andes only included specimens characterized by skulls larger than 25.05 mm. *Anoura peruana* had the widest range of geographic distribution including contrasting ecosystems across the Andean range. We suggest that size variation in *A. peruana* may be interpreted as an adaptive response of this taxon to the heterogeneity of the environments included in its distributional range. Nonetheless, a more detailed analysis including independent data sets is necessary to clarify the taxonomic affinities of *A. peruana* specimens with small skull size (GLS < 25.5) from the Eastern Cordillera and the northern range of the Colombian Andes.

Undescribed morphological variation in our samples.—Among the smaller *A. geoffroyi* specimens (GLS < 24.5 mm) examined in our morphological assessment we found an unrecognized taxon characterized by complete zygomatic arches and relatively wide uropatagium from the mid- and high elevations of the Colombian Andes and from the geographically isolated range of the Sierra Nevada de Santa Marta. A formal description of this taxon is presented below.

Family Phyllostomidae Gray 1825
Genus *Anoura* Gray 1838
Anoura carishina sp. nov.

Holotype.—Adult male ICN 14530 from Taminango, corregimiento de Remolino, department of Nariño, collected by A. Albesiano, C. Ariza, J. Alvarez, and H. Mantilla-Meluk (in the field notes the holotype of *A. carishina* was identified with group field collection number 21). The holotype, preserved as a skin-and-skull voucher specimen in excellent condition (Figs. 3 and 4) (Table 3), was collected on 5 December 1996.

Paratypes.—The type series consists of four individuals prepared as skin-and-skull voucher specimens as follows: an adult female (ICN 14531), collected by A. Albesiano, C. Ariza, J. Alvarez, and H. Mantilla-Meluk (collectors number 36) on 9 December 1996 at the type locality; an adult male (ICN 5224) collected at San Pedro de La Sierra, finca Tierra Grata, department of Magdalena, Colombia (10°54′06″N, 74°02′00″W) at 1320 m, on 26 May 1976 by A. Cadena García (collector number ACG 1147); an adult female (ICN 5225) from the same locality collected at 1320 m by A. Cadena García, M. Romer, and B. Moreno (without an assigned field number and date); and an adult male (ICN 5938) from Pance, department of Valle del Cauca, Colombia (3°19′42″N, 76°38′19″W), collected at 1200 m, on 5 February 1947 by M. Thomas (collector number 3299) (Fig. 5, Table 3).

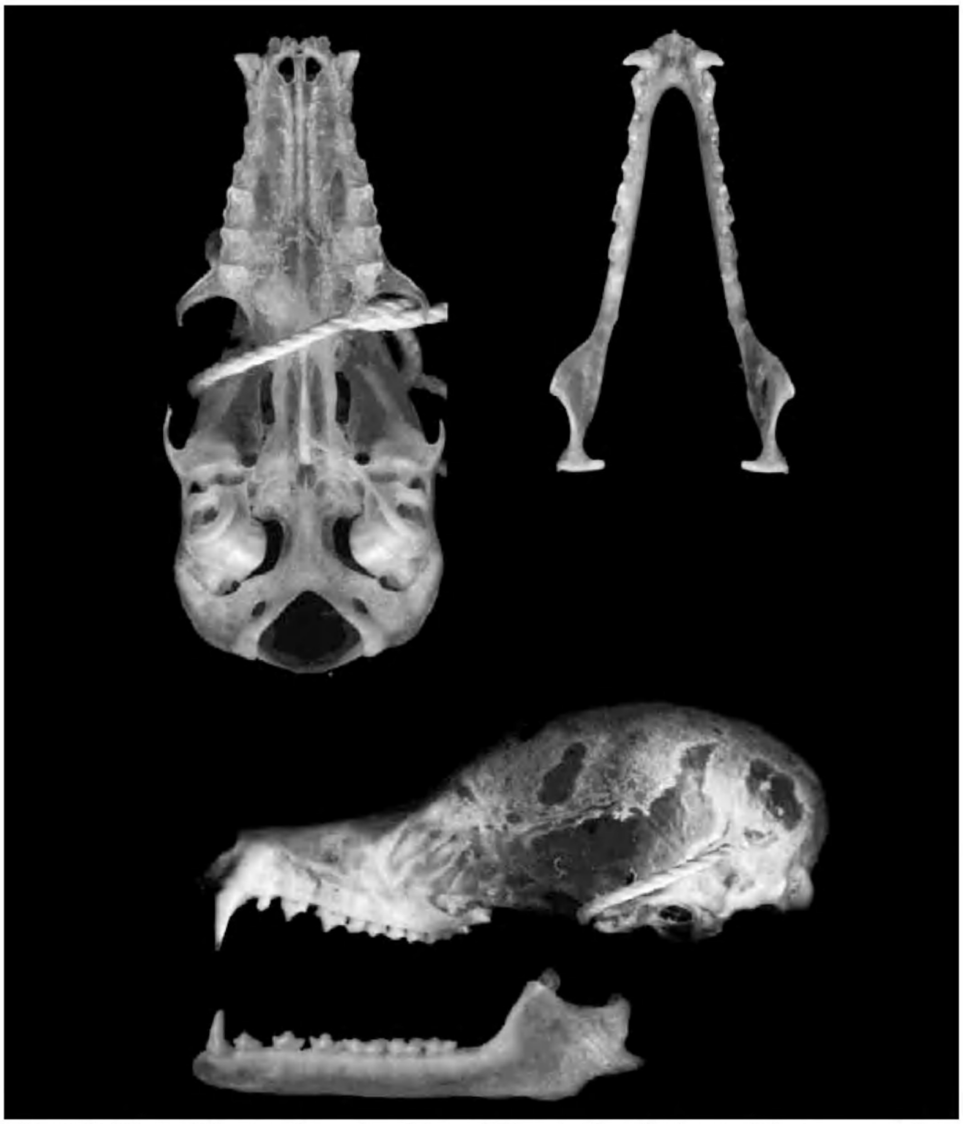

Figure 4. Ventral (upper photos) and lateral (lower photo) views of *Anoura carishina* holotype skull and mandibles.

Table 3. Average values of the 12 craniodental measurements analyzed for Anoura carishina *holotype (*) and the type series. Abbreviations: GLS: Greatest length of skull; CB: Condylobasal length; PAL: Palatal length; PO: Postorbital constriction width; MB: Mastoid breadth; BCW: Braincase width; BCH: Braincase height; TR: Tooth-row length; M-M: Distance across upper molars; C-C: Distance across upper canines; ML: Mandible length; MTR: Longitude of the mandibular tooth-row.*

ICN	Sex	GLS	CB	PAL	PO	MB	BCW	BCH	TR	M-M	C-C	ML	MTR
14530*	♂	24.52	23.5	12.05	4.88	9.03	9.77	7.65	9.3	6.06	4.38	16.58	9.65
5224	♂	24.13	23.3	12.3	5.33	9.48	9.96	7.49	9.12	6.31	4.48	16.83	9.41
5938	♂	24.27	23.3	12.52	5.16	9.29	9.77	7.41	9.18	5.97	4.5	16.61	9.52
14531	♀	24.04	23.28	11.77	4.99	9.07	9.8	7.48	8.93	6.09	4.15	16.66	9.49
5225	♀	24.04	23.34	12.18	4.72	8.69	9.3	6.69	9.03	5.88	4.07	16.49	9.45

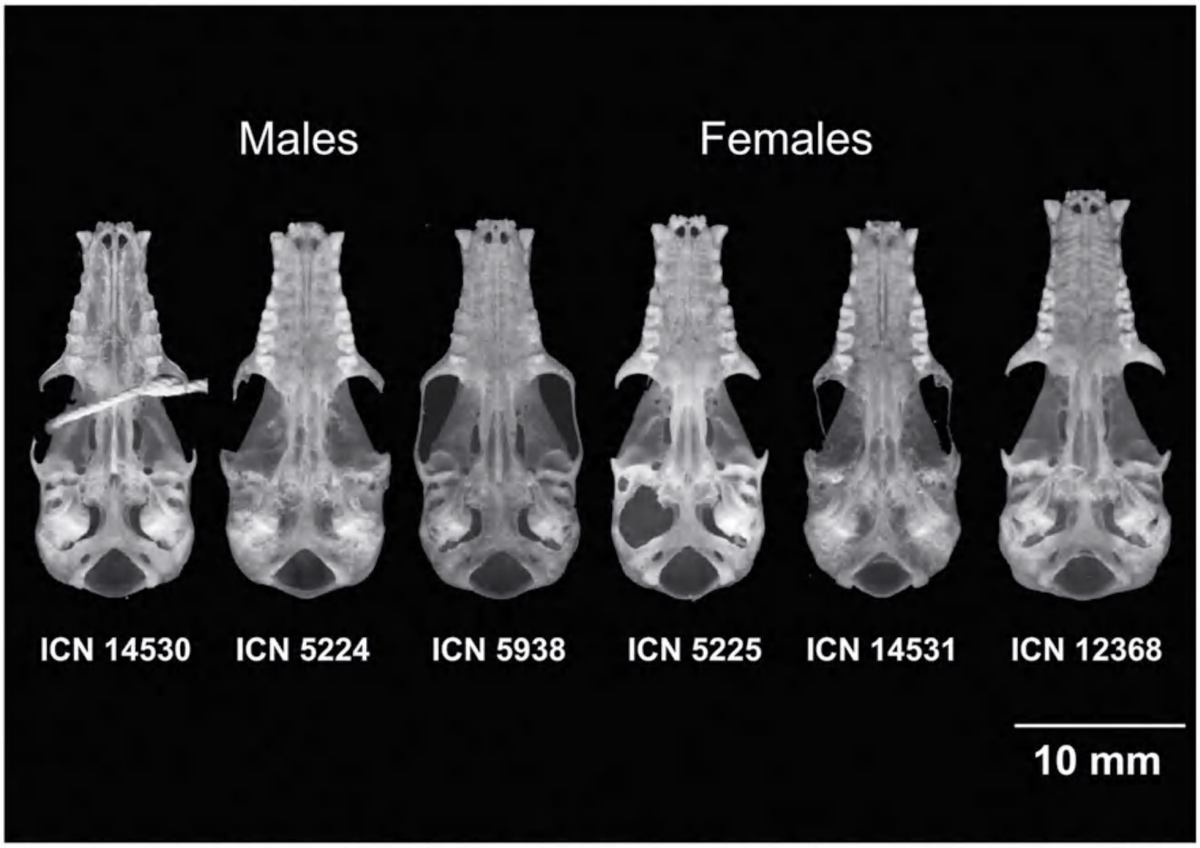

Figure 5. Type series of *A. carishina*: Holotype ICN 14530 ♂ from Taminango, Nariño; ICN 5224 ♂ from San Pedro de la Sierra, Magdalena; ICN 5938 ♂ Pance, valle del Cauca; ICN 5225 ♀ San Pedro de la Sierra, Magdalena; ICN 14531 ♀ from Taminango, Nariño; and *A. g. peruana* ICN 12368 ♂ from Quindio.

Diagnosis.—The new form can be distinguished from other species in the genus by the following characteristics: small skull (GLS < 24.5 mm); presence of complete fragile zygomatic arches (sometimes broken); small canines; P4 massive with a triangular base; paracone poorly developed on the first upper molar; large, wide, and squared upper molars, with a well-developed hypoconal basin; and rostrum wide in its base at the area between M3 and the P4, which is particularly noticeable from a dorsal view (Fig. 6). Externally, *A. carishina* can be distinguished from other species in the *A. geoffroyi* complex by relatively short lateral vibrissae (VL < 7.0 mm); reduced thumb (TL < 5.24 mm); and absence of tail.

Description.—*Anoura carishina* is among the smallest representative of the *A. geoffroyi* complex, best indicated by cranial measurements, including GLS, CBL, and PAL (Table 2) and its shorter thumb size (TL < 5.24 mm). General coloration is cinnamon-brown (Ridgway 1912) resembling that of *A. g. geoffroyi*. The dorsal and ventral pelage typically is long and bicolored. Individual hairs are basally white for two thirds of the length of the hair and cinnamon-brown (Ridgway 1912) on their distal edge. Ears and membranes average paler than in *A. g. geoffroyi*. Although all specimens included in this work correspond to dry skins likely to have modifications in some of the external characters, mystacial vibrissae in *A. carishina* appeared to be shorter than in other representatives of the *A. geoffroyi* complex, and the uroptagium was clearly more developed in the holotype and specimens in the type series of *A. carishina* when compared with *A. g. peruana* specimens (UW >3.5). Uropatagium of *A. carishina* is hairy on both ventral and dorsal surfaces, with a well-developed whorl of hairs on the edge.

Skull, mandible, and teeth are similar to those of *A. geoffroyi*, but the rostrum is shorter and the braincase is more globoid, particularly in males; the zygomata is complete, but thin and sometimes broken; the canines are small, not projected laterally, and are almost parallel

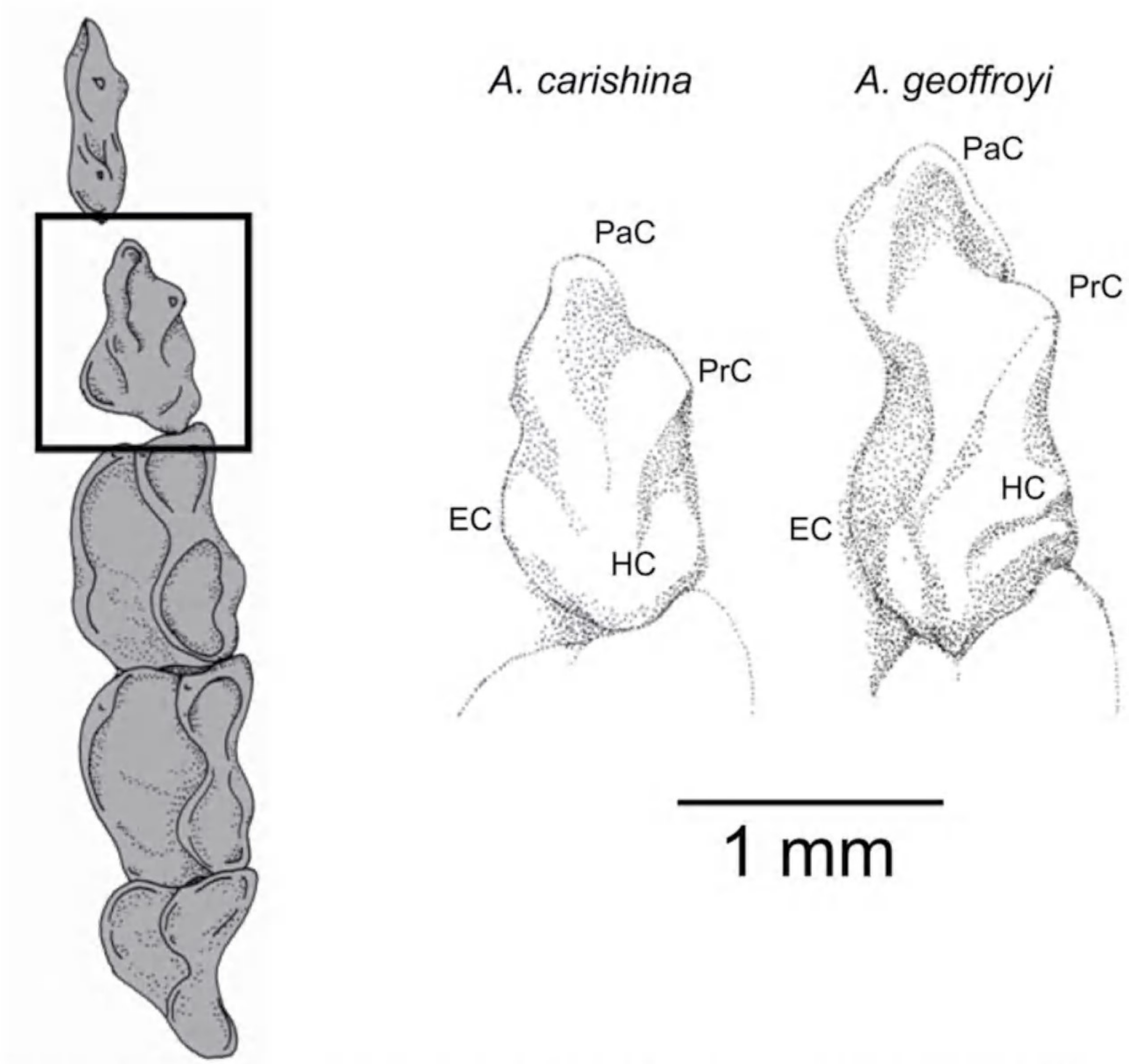

Figure 6. Differences in size and development of the cusps of the second upper premolar (P4) between *A. carishina* and *A. geoffroyi*. Praconid (PaC); Protoconid (PrC); Hypoconid (HC); Entoconid (EC). Lingual side on the left of the drawing.

to the tooth row; the posterolateral edges of the palate are pointed; the P3 and P4 are relatively wide in comparison to those in *A. geoffroyi*, *A. lasiopyga*, and *A. g. peruana*; the new species has a reduced, thick, and shorter anterobasal cusp on the P4, while the medial internal cusp of the P4 is enlarged, rendering the basal outline of the tooth to be approximately triangular; the molars are thick and squared, with a wide hypoconal basin; the posterior portion of the rostrum is wide; and the maxillae are slightly projected laterally, making them visible from a dorsal view.

Type locality.—The holotype was collected in Taminango, corregimiento de Remolino, department of Nariño. This area of Taminango is part of the xerophitic enclave of the Patía River, where local arid conditions are the results of a rain-shadow effect created by the transversal position of the Patía depression. The Patía region is located in southwestern Colombia between the Western and Central Cordilleras (Fig. 7), in the upper Patía River basin, Department of Nariño, Colombia (1°34′23″N, 77°16′59″W). The average annual temperature is 25.2°C, and the average relative humidity is 79%. The annual average precipitation is 809.3 mm distributed in a bimodal-tetraseasonal pattern. Rainfall is greatest between March and May, and between October and December. In this zone, the shrubs *Lippia origanoides*, *Lantana canescens,*

Figure 7. Type locality of *Anoura carishina* in Taminago, Nariño, Colombia (1°34′23″ N, 77°16′59″ W) at 1,465 m. Inset; geographic location of type series (site 1 designates holotype locality).

and *Senna pallida*, and the cacti *Stenocereus griseus*, *Pilosocereus* sp., and *Opuntia dillenii* are abundant. Pollen of *S. griseus*, *Pilosocereus* sp., and *O. dillenii* was found on the fur of two nectarivorous bats captured in the area (*A. carishina* and *Choeroniscus godmani*). Other bat species found locally included *Artibeus jamaicensis*, *Carollia perspicillata*, *Phyllostomus discolor*, *P. hastatus*, *Micronycteris megalotis*, *Desmodus rotundus*, *Sturnira erythromos*, *S. lilium*, *Enchistenes hartii*, and *Chiroderma salvini*.

Distribution.—*Anoura carishina* is widely distributed in Colombia from the department of Nariño on the border with Ecuador to the piedmonts of the Sierra Nevada de Santa Marta in the department of Magdalena in the Colombian Caribbean. There is no evidence of *A. carishina* on the eastern versant of the Eastern Cordillera in the Colombian Andes. Based on the wide variety of ecosystems included in the distribution of *A. carishina*, it is probable that this taxon may extend its distribution along the Andes southward into Ecuador (Fig. 7).

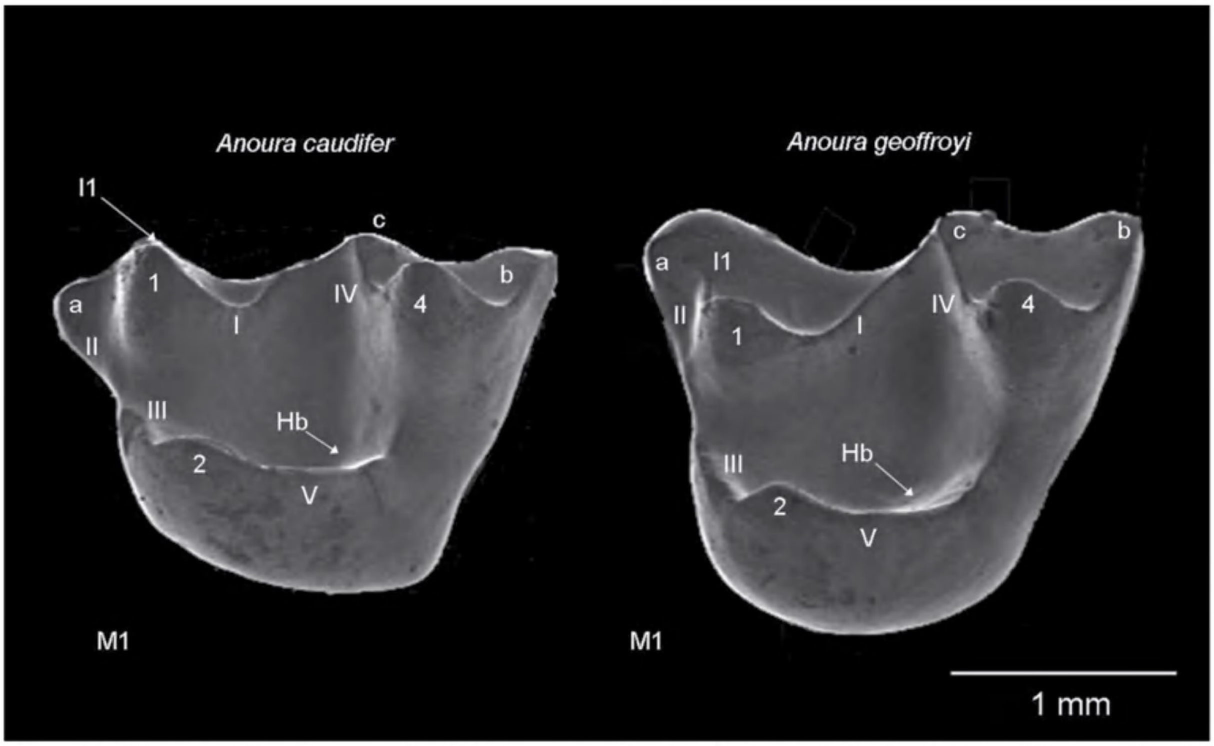

Figure 8. Electron microphotograph of first upper molars (M1) (lingual view) of *A. caudifer* complex (*A. aequatoris*, *A. cadenai*, *A. caudifer*, and *A. fistulata*) (left) and *A. geoffroyi* sensu lato (*A. g. geoffroyi*, *A. g. lasiopyga*, and *A. g. peruana*) (right). We followed the nomenclature system for dental homologies on M1 proposed by Hershkovitz (1977): eocone or paracone (1); protocone (2); metacone (4); parastyle (a);metastyle (b); epiconule or protoconule (c); precentrocrista (I); paracrista (I1); preprotocrista (III); postcentrocrista (IV); postprotocrista (entocrista) (V); hypoconal basin (Hb). Images obtained by B. Strack, FMNH.

Comparisons.—*Anoura carishina* is sympatric at sampling localities with three other recognized taxa in *Anoura (A. cadenai*, *A. cultrata*, and *A. g. peruana*). The new species is easily distinguished from *A. cadenai* by the triangular shape of P4 (in contrast with the laterally compressed P4 of *A. cadenai*) and the absence of a well-developed paracone (eocone) on M1, which is always well-developed in all species within the *A. caudifer* complex (*A. aequatoris*, *A. cadenai*, *A. caudifer*, *A. fistulata*, and *A. luismanueli*) (Fig. 8). *Anoura carishina* lacks the robust and knife-shaped canines as well as the blade-shaped lower first premolar of *A. cultrata*. *Anoura carishina* also is found near localities where *A. g. peruana* is present in the elevations of the Sierra Nevada de Santa Marta, although the two taxa occur at different altitudes. *Anoura carishina* is easily distinguished from *A. g. peruana* by its paler color (Ridgway 1912), smaller size (Table 2), shallow notch on the posterior edge of the palatal bones (sometimes erroneously called fossa mesopterigoydea), smaller thumb, shorter lateral vibrissae, and relatively large uropatagium; these characteristics along with the complete zygomata and the longer hair, also differentiate *A. carishina* from *A. lasiopyga*. Traits separating *A. carishina* from *A. lasiopyga* also apply to distinguish it from *A. latidens*.

Etymology.—*Anoura carishina* takes its name from the Quichua word "carishina" which means "woman who resembles a man" (Cordero 2003). Carishina in the Inca culture is a male character who wears female clothes as a costume in festivities. We consider the Quichua word carishina appropriate to highlight the following significant aspects of the new species: 1) its geographic origin - the *A. carishina* holotype was collected in the Andes of southern Colombia originally inhabited by ethnic groups that speak Quichua; and 2) its smaller size with respect to other species within the *A. geoffroyi* complex and lower degree of sexual dimorphism. We chose this name as a tribute to the senior author's father who has dedicated his life to the study of the Inca culture, and to our colleagues who have been dedicating their efforts to the understanding of the Andean mammalian chiropterofauna, particularly Alfred L. Gardner, Bruce D. Patterson, Victor Pacheco, René M. Fonseca, Luis Albuja, Luis Fernando Aguirre, Paúl Velazco, and Sergio Solari.

This work would not be possible without the many efforts of collectors who generously have enriched scientific collections through the years, providing in this way the evidence that feeds the always healthy scientific discussion. Through our work we would like to encourage the community of scientists interested in this fascinating group of organisms to validate the museological work by contributing with specimens that would be a valuable asset to present and coming generations of mammalogists.

ACKNOWLEDGMENTS

We thank Y. Muñoz-Saba, and the staff of the ICN; A. Rodríguez-Bolaños and the staff of the MUD; M. Rodríguez-Posada, M. Ruedi and the MHNG for access to the images of *G. lasiopyga* holotype; the AMNH for making available images of the holotype of *G. apolinari*; H. E. Ramírez-Chaves for valuable comments on the taxonomy of the group; and H. Garner and the staff of the NSRL Museum of TTU museum. This work would not have been possible without the generous cooperation of B. D. Patterson, L. R. Heaney, W. B. Stanley, B. Starck, and the staff of the Field Museum of Natural History. We thank all of them for their support and assistance. Financial support was provided by the Thomas J. Dee and Karl P. Schmidt Funds of the Field Museum's Scholarship Committee, the Texas Tech University Horn Professors Scholarship Award, and the Department of Biological Sciences. We thank A. Daugherty, R. Marchán, L. Siles, M. Pinto, C. Gomes de Sotero Caio, and L. Bradley for valuable editorial assistance.

LITERATURE CITED

Albuja, V., L. 1983. Murciélagos del Ecuador. Escuela Politécnica Nacional, Departamento de Ciencias Biológicas, Quito, Ecuador. 285 pp.

Allen, J. A. 1916. New South American mammals. Bulletin of the American Museum of Natural History 35:83–87.

Anderson, S. 1957. New records of the bat, *Anoura geoffroyi lasiopyga*. Natural History Miscellanea, Chicago Academy of Science 159:1-3.

Anthony, H. E. 1921. Preliminary report on Ecuadorian mammals. No. 1. American Museum of Natural History Novitates 20:1-6.

Arroyo-Cabrales, J., and A. L. Gardner. 2003. The type specimen of *Anoura geoffroyi lasiopyga* (Chiroptera: Phyllostomidae). Proceedings of the Biological Society of Washington 116:737-741.

Baker, R. J., S. Hoofer, C. A. Porter, and R. A. van Den Busche. 2003. Evolutionary relationships and classification of New World leaf-nosed bats inferred from DNA sequence. Occasional Papers, Museum of Texas Tech University 230: 1-32.

Cabrera, A. 1957. Catálogo de los Mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Tomo 4. No. 1.

Cordero, L. Diccionario Quichua Castellano y Castellano Quichua. Corporación Editora Nacional, Quito, Ecuador. 427 pp.

Gardner, A. L. 2008 [2007]. Mammals of South America, Vol. 1, Marsupials, Xenarthrans, Shrews, and Bats. University of Chicago Press, Chicago, Illinois. 669 pp.

Geoffroy St. Hilaire, É. 1818. Sur de nouvelles chauve-souris, sous le nom de Glossophages. Memoires Musee d' Histoire Naturelle de Paris 4:411-18, pls. 17-18.

Goodwin, G. G. 1934. Mammals collected by A. W Anthony in Guatemala, 1924-1928. Bulletin of American Museum of Natural History 68:1-60.

Gray, J. E. 1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species. Magazine of Zoology and Botany 2:483-505.

Handley, C. O. Jr. 1960. Descriptions of new bats from Panama. Proceedings of the United States National Museum 112:459-479.

Handley, C. O. Jr. 1984. New species of mammals from northern South America: A long-tongued bat genus *Anoura* Gray. Proceedings of the Biological Society of Washington 97:513-21

Hershkovitz, P. 1977. Living New World Monkeys (Platyrrhini), with an introduction to Primates, Volume 1. The University of Chicago University Press, Chicago and London. 1117 p.

Jarrín-V, P. and T. H. Kunz. 2008. Taxonomic history of the genus *Anoura* (Chiroptera: Phyllostomidae) with insights into the challenges of morphological species delimitation. Acta Chiropterologica 10(2):257-269.

Lönnberg, E. 1921. A second contribution to the mammalogy of Ecuador with some remarks on Caenolestes. Arkiv För Zoologi. 14: 1-104.

Molinari, J. 1994. A new species of *Anoura* (Mammalia Chiroptera Phyllostomidae) from the Andes of northern South America. Tropical Zoology 7:73-86.

Mantilla-Meluk, H., and R. J. Baker. 2006. Systematics of small *Anoura* (Chiroptera: Phyllostomidae) from Colombia, with description of a new species. Occasional Papers, Museum of Texas Tech University 261:1-17.

Mantilla-Meluk, H., A. M. Jiménez-Ortega, and R. J. Baker. 2009. Phyllostomid bats of Colombia: annotated checklist, distribution, and biogeography. Special Publications, Museum of Texas Tech University 56:1-37.

Muchhala, N. P. Mena V., and L. Albuja V. 2005. A new species of *Anoura* (Chiroptera: Phyllostomidae) from the Ecuadorian Andes. Journal of Mammalogy 86:457-61.

Ortega, J., and I. Alarcón-D. 2008. *Anoura geoffroyi* (Chiroptera:Phyllostomidae). Mammalian Species 818:1-7.

Peters, W. 1868. Über die zu Glossophagae gehörigen Flederthiere und über eine neue Art der gattungen Colëura. Monatsber. Akademie der Wissenchaften von Berlin 1868:361-68.

Ridgway, R. 1912. Color standards and nomenclature. Published by the author, Washington, DC. 273 p.

Sanborn, C. C. 1933. Bats of genera *Anoura* and *Lonchoglossa*. Field Museum of Natural History (Zoological Series) 27:23-28.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312-529 in Mammal species of the World, a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds). 3rd ed. John Hopkins University Press, Baltimore, Maryland.

Tschudi, J. J. von. 1844. Therologie. Pp. 1–262 in Untersuchungen über die Fauna Peruana. Scheitlin and Zollikofer, St. Gallen, Germany.

Vieira, C. O. C. 1942. Esaio monográfico sobre os quirópteros do Brasil. Arquivos de Zoología. Estado São Paulo 4:219-471.

Addresses of authors:

HUGO MANTILLA-MELUK

Department of Biological Sciences
Texas Tech University
Lubbock, TX, 79409
hugo.mantilla@ttu.edu

ROBERT J. BAKER

Department of Biological Sciences
Texas Tech University
Lubbock, TX, 79409
rjbaker@ttu.edu

APPENDIX

List of specimens examined. Acronyms are described in the text.

Anoura carishina (n = 5): COLOMBIA: Magdalena,Pedro de La Sierra, Finca Tierra Grata, ICN 5224 ♂ and ICN 5225 ♀; Nariño, Taminango, ICN 14530 ♂ and 14531♀; and Valle del Cauca, Pance ICN 5938 ♂.

Anoura geoffroyi apolinari (n = 1): COLOMBIA: Cundinamarca: Boquerón de San Francisco, near Bogotá AMNH 37376 ♀.

Anoura geoffroyi geoffroyi (n = 52): BRAZIL, Ceara FMNH 116852-54 ♀; COLOMBIA: Caquetá: Rio Mesay, Puerto Abeja, (Vorizal - Tepuy), southeastern, Serrania de Chiribiquete, ICN 14538 ♀, ICN 14539-40 ♂; Parque Natural Nacional Chiribiquete, Río Cuñare, Raudal El Tubo, southeastern, Serrania de Chiribiquete, ICN 14711 ♂; Parque Natural Nacional Chiribiquete western side Serranía Norte, ICN 12769 ♂; Meta: Acacías, Vereda San José, ICN 9700-01 ♂; Restrepo, Caney Alto, ICN 8060 ♂, ICN 8061 ♀, ICN 8062 ♂, ICN 8063 ♀, ICN 10110 ♂, ICN 10111-13 ♀; Restrepo, Surroundings CREAD, Caño Seco, ICN 10932 ♂; La Macarena, souther portion of the Serrania de La Macarena, Caño Cristales, ICN 7727-28 ♂; Restrepo, Caney Alto, Villavicencio, Pozo Azul Cave, ICN 9750 ♂; TRINIDAD: Blanchisseuer, TTU 5463 ♀, TTU 5370 ♂, TTU 5403 ♂; Maracas Valley, TTU 5363 ♂; San Rafael, TTU 5384 ♂, TTU 5823 ♂, TTU 5826 ♂, 37665-66 ♂; Saint Andrew, TTU 5464 ♂, TTU 8977 ♀, TTU 8979 ♂, TTU 26463-65 ♀, TTU 26466 ♂, TTU 26467-68 ♀, TTU 26469-70 ♂, TTU 26471-72 ♀, TTU 26473-76 ♂, TTU 26788 ♀; Saint George, TTU 26780 ♀, TTU 26787 ♂, TTU 37664 ♀.

Anoura geoffroyi lasiopyga: (n = 36): Color phase a) MEXICO: Hidalgo, TTU 15465-68 ♂, TTU 15470 ♂, TTU 15471 ♀, TTU 15472 ♂,TTU 15473 ♀, TTU 15474 ♂, TTU 15476 ♀, TTU 15477-81 ♂; Veracruz, TTU 10029 ♀, FMNH 34162 ♀; MHNG 515.88 ♂; Color phase b) COSTA RICA: Punta Arenas, Finca Las Cruces County, MSB 26789-90 ♀; GUATEMALA: Santa Elena, FMNH 41654 ♂, FMNH 41832-33 ♀, FMNH 41834-35 ♂, FMNH 41837-38 ♂; Jalapa, FMNH 73362 ♀; MEXICO: Hidalgo, TTU 36704 ♂, TTU 38035 ♀; Tamulipas, TTU 7345-46 ♂, TTU 7347-48 ♀; San Luís Potosi TTU 9931 ♀; Tehuetlán, TTU 5469 ♂; Tlaxcala, TTU 25342 ♀.

Anoura peruana (n = 172): BOLIVIA: La Paz, 0.5 km Río Zongo MSB 70293 ♂; San Matías, FMNH 39294 ♂; COLOMBIA: Antioquia: ICN, 8753 ♂; Jardín, Vereda La Linda, Quebrada La Linda, ICN 16454 ♂; San Luís Corregimiento El Prodigio, Vereda Las Confusas, Quebrada Corinto, Las Confusas Cave, ICN 13316 ♀, ICN 13317 ♂; ICN 16502 ♀; Urrao, Páramo de Frontino, FMNH 72191 ♂; FMNH 72192-96 ♀; Venecia, Santa Catalina Caves; Boyaca: ICN 1704 ♀, ICN 5314 ♀; ICN 5315 ♂; ICN 5420 ♂; Caldas: MHNUC, 450-51 ♂, MHNUC 460 ♂, MHNUC 462; Manizalez, Alto del Laurel, La Navarra, ICN 16730 ♀, MNHUC 452 ♀; Cauca: Inza, Vereda Tierras Blancas, school surroundings, ICN 8439 ♀, ICN 8440 ♂; El Retiro, Reserva Río Blanco, ICN 15157 ♂; Cundinamarca: ICN 8048 ♂, ICN 12971 ♂; MUD, 162-65 ♂, MUD 170-72 ♂, MUD 177 ♂, MUD 184 ♂, MUD 189 ♂; ICN 5274 ♀, ICN, 17694 ♀; Cabrera, Granja Experimental Agropecuaria, ICN 9552 ♂; Cabrera, Vereda Peñas Blancas, El Infiernito Cave, ICN12629 ♂, ICN 12630-31 ♀, ICN 12632 ♂, ICN 12633 ♀, ICN 12634 ♂; Choachí, Vereda Ferralara, Peña Fonte, ICN 8854 ♀; La Calera, Los Patios, ICN 8850-51 ♀; Tena, Laguna de Pedro Palo, ICN 5494 ♀, ICN 8367 ♂; Villapinzón, headwaters Bogotá River, ICN 17675 ♀, ICN 17677-78 ♂; Ubalá, Exit to Bogotá, ICN 15100 ♀; Zipaquira, Páramo de Guerrero, FMNH 72204 ♂, FMNH 72206-07 ♂, FMNH 72208-13 ♀; Huila: Las Cuevas Parque, Indian Cave, 160m from exit, FMNH 58678 ♀, FMNH 58680-81 ♀; FMNH 58679 ♂; Magdalena: Serranía San Lorenzo, Inderena Station, ICN 5353 ♀, Serranía San Lorenzo, Inderena Station ICN 5354-55 ♂; Serranía San Lorenzo, Hacienda La Victoria ICN 5356 ♂; Serranía San Lorenzo, Hacienda La Victoria ICN 5357-60 ♀; Nariño: La Victoria FMNH 113482 ♂; Llorente, FMNH 113449 ♀, FMNH 113489 ♀, FMNH 113490 ♂, FMNH 113491 ♀; FMNH 223492 ♀; FMNH 114029 ♂; Quindío: Salento; Natural Reserve Cañón Quindío, frente de reforestacion La Montaña, ICN 12368

APPENDIX (CONT.)

♂, 12369-70 ♀, ICN 12371-73 ♂, ICN 12374 ♀, ICN 12375-78 ♂; Natural Reserve Cañón Quindío, frente de reforestacion La Romelia, ICN 12380-83 ♀, ICN 12385-87 ♂; Natural Reserve Cañón Quindío, frente de reforestacion La Picota, ICN 12388-90 ♀; Risaralda: ICN 12538 ♂; Santuario, Verada, Los planes, ICN 11791 ♀; Santuario, Verada, El Campamento, ICN 11833-34 ♀; Santander: MUD, 641-43 ♂; Charalá, Vereda El Salitre, finca El Mirador, Aida Cave, ICN 17498 ♀, ICN 17499 ♂; Encino, Vereda Río Negro, sitio Las Tapias, finca El Aserradero, ICN 17515 ♀, ICN 17517 ♂, ICN 17518 ♀, ICN 17519 ♂; Ocamonte, Finca Macanal, La Virgen Cave, ICN 17632 ♀; Ocamonte, Vereda Miraflorez, finca Macanal, La Virgen Cave, ICN 17633 ♂, ICN 17634 ♀; Tolima: Km. 140 carretera Libano-Murillo, Hacienda Casas Viejas, ICN 8380 ♂; Herveo, Vereda Albania, ICN 3470 ♀; Icononzo, El Tigre Caves, ICN 8812 ♀, ICN 8681 ♂, ICN 8682-83 ♀; ECUADOR: Chimborazo, Pallatngo, USNM 513439 ♂, USNM 513440 ♀: Guayas, Balao, Guertas Negras, USNM 498832 ♂, USNM 534301 ♂; Pichincha, Zapadores, USNM 513437-38 ♂; PERU: Amazonas: Bongara, Road Utcubamba, between Churuja y Pedro Ruiz, FMNH 128643 ♂, FMNH 128645 ♂; Chachapoyas, Balsas, 19 km by road E, FMNH 128639 ♂; Apurimac: Abancay, Bosque Ampay, FMNH 110922 ♀, FMNH 110923 ♂; Andahuaylas, FMNH 75178 ♀, FMNH 75179-80 ♂, FMNH 75159-62 ♀, FMNH 75163-64 ♂, Hacienda La Laguna, FMNH 75157-58 ♂, FMNH 75177 ♂; Ayacucho: La Mar, Ocros, Hacienda Pajonal, FMNH 75165 ♀, FMNH 75166-69 ♂, FMNH 75170-71 ♀, FMNH 75181 ♀; Huánuco: Tingo María Las Lechuzas Cave, MSB 49924-28 ♂; Junín, Cueva de Guarapo, ca. 35 km Tarma, MSB 53085 ♀, San Ramon, USNM 507176 ♂, USNM 507177 ♀; Ollantaytambo, USNM 195127 ♂; UNDETERMINED LOCALITY: ICN 18052 ♀, ICN 18053 ♂, ICN 18054 ♀.