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A new species of *Anoura* Gray, 1838 (Chiroptera: Phyllostomidae) from Peru, with taxonomic and biogeographic comments on species of the *Anoura caudifer* complex

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Anoura is a Neotropical genus of long-tongued bats containing at least 10 species, whose taxonomy has been revised substantially in recent years. Herein, we describe a new species of *Anoura* from the Cordillera Oriental of the Peruvian Andes, inhabiting montane forests (Yungas) at 1900–3450 m altitude, along the Río Cosñipata valley in Manu Biosphere Reserve, Cuzco; where it is sympatric with *A. peruana*, *A. cultrata*, and *A. caudifer*. This new species is most similar to *A. caudifer* and *A. aequatoris*, but it is distinguished from them by a unique combination of morphological characters: pelage dark; uropatagium narrow with margins densely furred; foot claws whitish; skull with a long and narrow rostrum; zygomatic arches complete and straight (in lateral view); posterolateral margins of palate without processes; braincase smoothly rounded; first upper premolar (P²) peg-like and separated from the upper canine by a wide gap; second upper premolar (P³) without anterobasal cusp; mandible long, straight, thin and delicate with a large symphysis. Principal Component Analysis separated well the new species from *A. aequatoris* and *A. caudifer*. In MANOVA analyses, followed by Bonferroni post-hoc test, the new species differed significantly from *A. aequatoris* and *A. caudifer* in six and 11 characters, respectively. The new species and *A. aequatoris* have montane distributions, whereas *A. caudifer* occurs at lower elevations. In Peru, the new species and *A. aequatoris* show disjunct distributions: the former in the central and southern regions, and the latter in the north-central region of the country. This suggests a vicariant effect probably related to the deep Río Apurímac. Finally, we comment on the taxonomy of the *A. caudifer* complex, discuss the biogeographical implications of the discovery of the new species, and suggest the recognition of a new region of endemism for small mammals in the southern Yungas, south of the Río Apurímac to Bolivia.

Key words: Andes, bats, biogeography, Cusco, new species, Peru, taxonomy, Yungas

INTRODUCTION

The nectar-feeding bats of the genus *Anoura* Gray, 1838 are medium to small-sized members of the Phyllostomidae that lack or have a short tail completely encased in a narrow interfemoral membrane. Griffiths and Gardner (2008) recognized seven species of *Anoura*: *A. cadenai* Mantilla-Meluk and Baker, 2006, occurring in southwestern Colombia; *A. caudifer* (É. Geoffroy St.-Hilaire, 1818) occurring from Venezuela and the Guianas southward to NW Argentina; *A. cultrata* Handley, 1960, occurring from Costa Rica southwards to Bolivia; *A. fistulata* Muchhala, Mena, and Albuja 2005, restricted to Ecuador; *A. geoffroyi* Gray, 1838, from southern Mexico southwards to SE Brazil, and Trinidad and Grenada in the Lesser Antilles; *A. latidens* Handley, 1984, occurring from Guyana and Venezuela to central Peru; and *A. luismanueli*

Molinari 1994, occurring in Venezuela. These authors considered that *A. aequatoris* (Lönnerberg 1921), which was separated from *A. caudifer* using discriminant analyses by Mantilla-Meluk and Baker (2006), was not adequately diagnosed and retained *A. c. aequatoris* as a subspecies. Similarly, Jarrín-V. and Kunz (2008) challenged the methodological approach on how species of *Anoura*, including *A. aequatoris*, have been described and diagnosed.

After Griffiths and Gardner (2008), numerous changes have occurred in the genus. Pacheco *et al.* (2009) accepted *A. aequatoris* as a valid species and reported additional specimens from Pasco Department, central Peru. Mantilla-Meluk *et al.* (2009) further differentiated *A. aequatoris* from *A. luismanueli*; however, detailed comparisons with *A. cadenai*, *A. caudifer*, and *A. fistulata* are still lacking. A recent revision by Mantilla-Meluk and Baker (2010) involved the recognition of *A. peruana*

(Tschudi, 1844), a former synonym of *A. geoffroyi*, and the elevation of *A. g. lasiopyga* (Peters, 1868) to species level. However, *A. g. lasiopyga* was not recognized as a valid species in a recent summary of Neotropical bats (Díaz *et al.*, 2016). Mantilla-Meluk and Baker (2010) described the new species *Anoura carishina* Mantilla-Meluk and Baker 2010, from the Colombian Andes, and suggested that *A. aequatoris*, *A. cadenai*, *A. caudifer*, *A. fistulata*, and *A. luismanueli* are members of the *A. caudifer* complex. The distributions of some species have also been extended: *A. aequatoris* ranges now to Bolivia (Mantilla-Meluk *et al.*, 2012) and *A. fistulata* ranging now from southern Colombia to southern Bolivia (Mantilla-Meluk *et al.*, 2014), and *A. luismanueli* to northern Colombia (Mantilla-Meluk and Baker, 2006).

In the course of a study of the mammalian community from the upper zone of the Manu Biosphere Reserve, along the Río Cosñipata Valley, Cusco, Peru in 1989, we captured three specimens of *Anoura* that were considerably distinct from any other *Anoura* species known from Peru. Three additional specimens were collected in expeditions from 1995 to 1996, and 1999 to 2001, and reported in several papers as *Anoura* sp. nov. (Pacheco *et al.*, 1993; Patterson *et al.*, 1996; Solari *et al.*, 2006) or *Anoura* sp. (Pacheco *et al.*, 1995). This new taxon belongs to the *A. caudifer* complex (*sensu* Mantilla-Meluk and Baker, 2010) and has a narrow and densely haired uropatagium that closely resembles to *A. aequatoris*; but also has several skin and craniodental features that clearly differentiate it from *A. aequatoris* and other congeners. These differences convince us that the Manu population corresponds to an unnamed species which we diagnose and describe in this work.

MATERIALS AND METHODS

Specimens and Study Area

The specimens of *Anoura* sp. nov. were collected in the Province of Paucartambo, Department of Cusco, Peru, in the Manu Biosphere Reserve, a protected area (18,812 km²) in south-central Peru that encompasses a unique range and diversity of habitats, from lowland tropical forests at 150 m to all stages of premontane, lower and upper montane forest, and moist puna grassland up to 4200 m altitude (Patterson *et al.*, 2006). The type locality of *Anoura* sp. nov. is in dense and humid upper montane forest, where the slopes are steep and rocky, and often more than 40 degrees. Forest canopy is approximately 8 to 20 m high and is formed by trees of the genera *Brunellia*, *Clethra*, *Hedyosmum*, *Miconia*, *Ocotea*, *Polylepis*, and *Weinmannia*; usually individuals of *Polylepis pauta* with

40–70 cm diameter at breast height (DBH) are the dominant canopy species. Forest understory is heterogeneous, with shrubs and small trees of the genera *Cestrum*, *Clusia*, *Hedyosmum*, *Miconia*, *Myrsine*, *Oreopanax*, *Prunus*, *Psychotria*, *Schefflera*, *Solanum*, and *Symplocos*; a locally abundant *Chusquea* bamboo; and herbs of *Oxalis* and *Pilea*, in addition to several genera of terrestrial ferns, including *Pteris* and *Thelypteris* (León, 1991). Large tree trunks and branches often support dense mats of mosses, hepatics, and bromeliads.

One specimen of the new bat species was collected at lower elevation in La Esperanza (2880 m) which was slightly more xeric than the type locality at Trocha Ericsson. Netting efforts took place in dry open slopes or bushy slopes near small streams. A specimen was collected in Pillahuata (2600 m above sea level [a.s.l.]) and another in Suecia (1900 m a.s.l.); the last two sites are in montane forests where nets were set on both sides of the road along deep ravines.

Qualitative Morphologic Assessment

Our descriptive terminology for tooth morphology follows Phillips (1971). Descriptions of morphological characters follow Handley (1984), Molinari (1994), Sanborn (1933, 1943), and Carstens *et al.* (2002). Color pelage was described following Smith (1975). The specimens we examined are listed in Appendix. Qualitatively, 118 specimens were analyzed, including the holotype of *Anoura* sp. nov. For comparisons, species of the *Anoura caudifer* complex were directly examined, except for *A. cadenai* and *A. luismanueli*, which we did not have access to specimens. For these species, we relied on characteristics taken from the literature (Molinari, 1994; Mantilla-Meluk and Baker, 2006, 2010; Griffith and Gardner, 2008). We used some additional characteristics of *A. caudifer* from Oprea *et al.* (2009).

Morphometrics

External variables (ToL, total length; TaL, tail length; HFL, hind foot length; Ear, ear length, TrL, tragus length) and weight (W) were taken mainly from field labels. The head and body length (HBL) was estimated by subtracting TaL from ToL. Forearm length (FAL) was taken also from field labels or in a few cases measured from dry specimens when the value was missing. This was measured from the olecranon process to the shallow notch proximal to the thumb including carpals. All variables were measured to the closest 0.01 mm using digital calipers. The following craniomandibular measurements were used: greatest skull length (GSL), condylobasal length (CBL), palatal length (PALTL), maxillary toothrow length (MXTRL), zygomatic width (ZYGW), braincase width (BRW), postorbital width (POW), palatal width at third molar (M³M³), palatal width at canines (C¹C¹), braincase height (BRH), dentary length (DENL), mandibular toothrow length (MANDL), dentary height (DENT). Most of the variables are described and illustrated in Pacheco and Patterson (1992) or Simmons and Voss (1998). Only adults were measured, as determined by the complete fusion of the basisphenoid-basioccipital suture and the phalangeal epiphyses.

Analysis of sexual dimorphism for the new species was not attempted because of small sample size; however, based on the observation that the smallest specimen in the series is a female (Table 1), which could indicate the existence of sex dimorphism on size variables, results of morphometric analyses are given only for males. All measurements are considered dependent

TABLE 1. Measurements (mm) and body masses (g) of the type series of *A. javieri* sp. nov., including the holotype (*)

Character	MUSM					
	6734 ♂	6736* ♂	8749 ♂	16559 ♂	19602 ♂	11753 ♀
Head and body length	69.00	61.00	68.00	69.00	62.00	65.00
Tail length	0.00	0.00	0.00	8.00	4.00	0.00
Hind foot length	12.00	10.00	10.00	13.00	11.00	12.00
Ear length	13.00	13.00	13.00	12.00	13.00	13.00
Tragus length	5.00	5.00	—	6.00	6.00	6.00
Forearm length	38.00	37.00	37.00	37.00	38.00	37.00
Greatest skull length	24.15	23.65	24.72	24.81	24.15	23.70
Condylobasal length	23.35	22.85	24.04	24.21	23.65	23.11
Palatal length	13.45	12.65	13.00	13.16	12.63	12.29
Maxillary tooththrow length	9.25	8.75	9.05	9.29	8.83	8.59
Zygomatic width	8.95	9.00	9.35	9.12	9.16	8.63
Braincase width	8.80	8.85	9.07	8.94	8.72	8.96
Postorbital width	4.40	4.60	4.62	4.45	4.70	4.49
Palatal width at third molar	5.40	5.35	5.40	5.40	5.48	5.35
Palatal width at canines	3.92	3.78	3.78	3.79	3.89	3.59
Braincase height	6.55	6.35	6.80	6.65	6.58	6.39
Dentary length	17.70	16.95	18.49	18.21	17.51	17.22
Mandibular tooththrow length	9.60	9.15	9.32	9.54	9.22	8.94
Dentary height	1.55	1.40	1.50	1.49	1.51	1.45
Body mass	11.00	10.00	10.00	11.00	10.00	10.00

variables and normality was assessed using a Shapiro-Wilk Test. To identify the variables that significantly differ among species of the *A. caudifer* complex present in Peru, a MANOVA with Bonferroni post-hoc test was performed to avoid false positives resulting from multiple tests. Results were considered significant at $P \leq 0.05$. We also used principal components analysis (PCA) to assess species differences in the data. Principal components were extracted from the correlation matrix of the log-transformed measurements (forearm length and craniodental variables). The sample for these analyses consisted of *A. caudifer* ($n = 18$), *A. aequatoris* ($n = 16$), *A. fistulata* ($n = 11$), and *Anoura* sp. nov. ($n = 5$). Missing values ($< 1\%$ of measurements) were replaced with the corresponding average of specimens from the same locality. For descriptive statistic comparisons, measurements of *A. luismanueli* and *A. cadenai* were retrieved from Molinari (1994), and Mantilla-Meluk and Baker (2006), respectively. All morphometric analyses were done using SPSS Statistics ver. 20 for Mac.

SYSTEMATIC ACCOUNT

Family Phyllostomidae Gray, 1825

Subfamily Glossophaginae Bonaparte, 1845

Tribe Choeronycterini Solmsen, 1998

Subtribe Anourina Baker, Solari, Cirranello, and Simmons 2016

Genus *Anoura* Gray 1838

Anoura javieri, sp. nov.

Figs. 1 and 2

Anoura sp. nov. Pacheco et al. (1993).

Anoura sp. Pacheco et al. (1995).

Holotype

A male adult specimen catalogued in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM 6736). The holotype is a skin and skull in good condition, collected by Víctor Pacheco (field number VPT 887) on 5 September 1990. External and craniodental measurements for the holotype and paratypes are provided in Table 1.

Type locality

Trocha Ericsson (13°11'47''S, 71°37'11''W), District of Challabamba, Province of Paucartambo, Department of Cusco, Peru, 3350–3450 m a.s.l. This locality is on the southern border of the Manu National Park at km 110 on the Paucartambo-Pillcopata road, in the headwaters of Río Cosñipata, a tributary of the Río Alto Madre de Dios (Fig. 3).

Paratypes

Two adult males from the same locality: MUSM 6734, collected on 3 September 1990; and MUSM 8749, collected on 19 July 1991. Other designated paratypes are from nearby localities: adult male, MUSM 19602 (= FMNH 174510), from La Esperanza, 2880 m; adult female, MUSM 11753, from Pillahuata, 2600 m; and adult male, MUSM 16559 (= FMNH 169821) from Suecia, 1900 m. All the type specimens were collected along the Paucartambo-Pillcopata road in the Río Cosñipata valley. Vouchers are preserved in good condition.



FIG. 1. Dorsal, ventral and lateral views of cranium and mandible of *A. javieri* sp. nov. (MUSM 6736, holotype). The scale represents 10 mm

All are skins and skulls except MUSM 16559, which is an alcoholic specimen (fixed in formalin, and then transferred to ethanol) with skull removed, and MUSM 19602 that consists of a dry skin, skull and carcass in ethanol.

Distribution

Anoura javieri is known only from the upper montane forests of Manu Biosphere Reserve (1900–3450 m a.s.l.), Department of Cusco, Peru (Fig. 3).

Diagnosis

A small-sized *Anoura* that can be distinguished from other congeners by the following combination of characters: pelage dark brown overall with no distinct demarcation between dorsum and venter; tail present in two of six specimens; uropatagium narrow (< four mm at femur level) and densely furred with long hairs; and whitish claws on the hindfeet. Skull small with a long and narrow rostrum (GSL 23.7–24.8 mm); zygomatic arch complete; and lambdoid crest poorly developed. Upper incisors small and peg-like; first upper premolar (P²) also peg-like and separated from the upper canine by a wide gap; second upper premolar (P³) with anterobasal cusp absent; third upper premolar (P⁴)

without a posterolingual shelf; and paracone and metacone well developed in M¹. Mandible with long, thin, and delicate ramus; mandibular symphysis larger than canine width; and infra-angular process ventral to the middle part of the sigmoid notch.

Description

Anoura javieri is a small-size bat (HBL 61.0–69.0 mm). Dorsal pelage is long (about 6–7 mm), dark brown, and woolly throughout; individual hairs are white at the base (80%) contrasting with dark brownish tips (20%). The ventral fur is dark brown and not contrasting with the dorsal coloration; chin is dark brown as well, but the hairs have two bands, white in the base and dark brown in the tips. The mystacial vibrissae are dark brown, robust and comparatively long. The supra and infralabial vibrissae are present and long. The genal and interramal vibrissae are present and relatively long. The tragus is long (5–6 mm) with a rounded tip. The forearm is moderately long (37–38 mm) and densely haired. The interfemoral membrane is reduced to a narrow band (1.1–1.9 mm, measured in dry skins) with its edge densely furred with long hairs (4.3 mm average, some reaching up to 5.4 mm). The femur is barely haired or naked on the proximal half, becoming densely furred on the distal half. The tibia is densely haired. The tail is present in two of six specimens (absence could be an artifact of preparation). The feet are long and have whitish claws.

The skull has comparatively short and smoothly rounded braincase, and a long and comparatively narrow rostrum (GSL, 23.7–24.8 mm). The zygomatic arch is complete, straight and slender. The palate is moderately depressed, with posterolateral margins shallow and without palatal processes. The lambdoid crest is weakly developed. The paraoccipital processes are conspicuous, slender, and medially oriented. The upper incisors are notably weak, peg-like, and subequal. The surface of the upper canines is smooth, without a conspicuous sulcus. P² is peg-like, without the anterobasal cusp, but has a low posterobasal cusp. P² is separated from the upper canine by a wide gap, which is almost twice the length of P². P³ lacks the anterobasal cusp, and is separated from P⁴ by a distinct gap. The postero-lingual cingulum on P⁴ is absent or notably reduced, lacking a shelf. The molars have well developed paracones and metacones. The first upper molars are rectangular and have a weakly developed hypoconal basin; and the postprotocrista does not make an angle with the metacone. The lower premolars and molars are

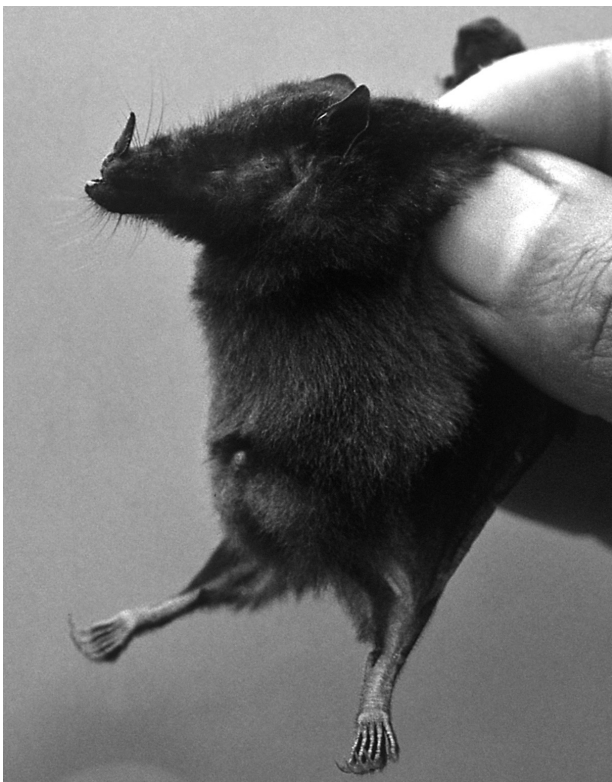


FIG. 2. Live photograph of the holotype of *A. javieri* sp. nov. (MUSM 6736). Photograph by V. Pacheco

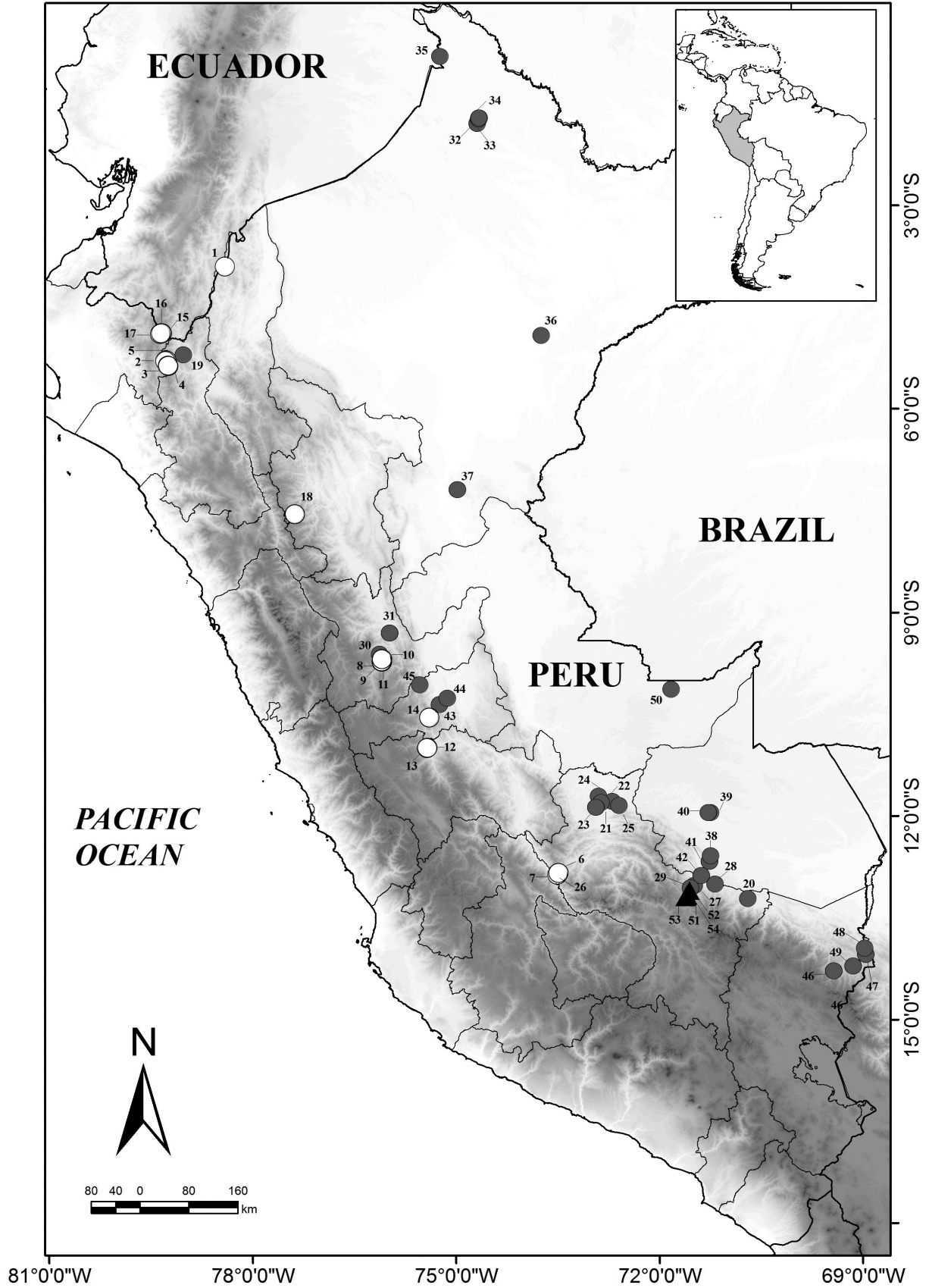


FIG. 3. Map showing the collecting localities of: *A. aequatoris* (○), *A. caudifer* (●), and *A. javieri* sp. nov. (▲) from Peru. Numbers are cross-referenced in Appendix

narrow, laterally compressed, and have well developed cusps. The paraconid on M_1 is comparatively elongated. The trigonid and talonid of lower molars are separated by a narrow constriction, and the trigonid is longer than the talonid. The mandibular ramus is long, thin, delicate, straight, and markedly low; and the mental foramen is comparatively small. The mandibular symphysis is large, usually subequal to the length of the lower canine or larger. The coronoid process is low, almost in line with the condylar process. A posterior process on the ventral surface of the mandible is well developed, and just ventral or postero-ventral to the sigmoid notch (Fig. 1).

Comparisons

Anoura javieri is a small bat that differs external, cranial and dentally from any other known species of *Anoura*. It is easily separated from the larger

species *A. carishina*, *A. geoffroyi*, *A. latidens*, *A. peruana* or *A. cultrata* by smaller size (forearm length < 40 mm), zygomatic arches always present, paracone and metacones well developed, tail sometimes present (see below), rostrum unusually long, canines small and without sulcus, and P_1 not blade-like (Tamsitt and Nagorsen, 1982; Mantilla-Meluk and Baker, 2010).

The new species can be confused with species of the *A. caudifer* complex, especially with *A. caudifer* and *A. aequatoris*, and with *A. fistulata*, present also in the Cosñipata valley (Tables 2 and 3; and Figs. 4, 5, 6, and 7). *Anoura javieri* and *A. caudifer* are similar in cranial and dental features; however, *A. javieri* can be distinguished by its larger body size (FA = 37.4 versus 35.27 mm on average), a longer and narrow rostrum (GSL = 24.3 vs. 22.0 mm on average), a depressed or smoothly rounded brain-

TABLE 2. Comparison of morphological differences among *A. fistulata*, *A. caudifer*, *A. aequatoris*, and *A. javieri* sp. nov.

Character	<i>A. fistulata</i>	<i>A. caudifer</i>	<i>A. aequatoris</i>	<i>A. javieri</i>
Pelage coloration	Dark brown close to black	Brown	Dark brown	Dark brown close to black
Fringe of hairs in uropatagium	Sparse fringe of hairs in the center of interfemoral membrane	Little, almost naked	Dense fringe of hairs bordering the interfemoral membrane	Dense fringe of hairs bordering the interfemoral membrane
Interfemoral membrane width	Wide, 4 to 7.5 mm	Wide, about 4 mm	Narrow, less than 4 mm	Narrow, much less than 4 mm
Posterior claws	Dark brown	Dark brown	Dark brown	Pale brown to whitish
Braincase shape	Rounded	Rounded	Rounded	Less rounded
Rostrum	Comparatively wide	Comparatively wide	Comparatively wide	Narrow
Rostrum length	Short	Short	Short	Long
Zygomatic arch in lateral view	Curved	Curved	Slightly curved	Relatively straight
Palatal shape	Shallow	Slightly depressed	Slightly depressed	Slightly depressed
Posterior border of palate	Palatal process present	Palatal process present	Palatal process present	Palatal process absent
Lambdoid crest	Distinct	Distinct	Reduced	Reduced
Paraoccipital process	Wide	Wide	Usually wide	Narrow
Paraoccipital process orientation	Relatively straight	Relatively straight	Barely curved	Curved
Incisors size	Outer longer than inner incisors	Outer longer than inner incisors	Incisors generally subequal	Incisors generally subequal
Sulcus in canine	Distinct	Distinct	Distinct	Absent
C-P ² gap	Small, about 1/2 the length of P ² or less	Small, about 1/2 the length of P ²	Moderate, from 1/2 to 1 of the length of P ²	Large, twice or more the length of P ²
p ³ -P ⁴ gap	Small	Small	Usually small	Distinct
P ³ anterior cusp	Usually reduced	Present	Present or reduced	Reduced or absent
P ⁴ lingual cusp	Present	Present	Reduced or absent	Absent
M ¹ hypoconal basin	Shallow	Shallow	Forming a less obtuse angle	Shallow
M ₁ width	Comparatively broad	Comparatively broad	Narrow	Narrow
M ₁ trigonid	Subequal to talonid	Subequal to talonid	Slightly longer than talonid	Slightly longer than talonid
Mandible symphysis	Greater than length of canine	Equal or less than the length of canine	Equal or slightly more the length of canine	Greater than length of canine
Mandible ventral margin	Slightly curved	Slightly or markedly curved	Slightly curved or straight	Straight
Mental foramen	Large	Small	Small	Small
Symphysis foramen	Large	Small	Small	Small

case, a zygomatic arch mostly horizontal in lateral view, and absence of a palatal process. In *A. javieri*, the outer incisors are barely longer than the inner, whereas in *A. caudifer* they are longer. *Anoura javieri* lacks a sulcus in the upper canine, which is distinctly present in *A. caudifer*. The anterior cusp of P³ is reduced or absent in *A. javieri*, but is always conspicuous in *A. caudifer*. In *A. javieri*, there are large gaps between C and P², and between P³ and P⁴, whereas in *A. caudifer* the gaps are small. In *A. javieri*, the ventral margin of the mandible is straight vs. slightly or markedly bowed in *A. caudifer*. In *A. javieri*, the mandibular symphysis is larger than

the length of the lower canine, whereas in *A. caudifer* it is shorter. The first lower molar of *A. javieri* has a large, conspicuous paraconid, the trigonid is larger than the talonid, and both structures are well separated by a narrow constriction, whereas in *A. caudifer* the paraconid is smaller, the trigonid and talonid are subequal, and the constriction between them is not as narrow. Additionally, *A. javieri* has darker coloration, paler hindfeet claws, shorter calcar, and a densely furred uropatagium reduced to a narrow band in comparison to *A. caudifer*, which has paler brown pelage, darker hindfeet claws, longer calcar, and wider and sparsely haired

TABLE 3. External and craniodental measurements (in mm) of male bats of the genus *Anoura*. Body mass is given in grams. Mean and standard deviation are followed by observed range size (in parentheses) and sample size (in italics)

Character	<i>A. aequatoris</i> Peru	<i>A. caudifer</i> Brazil	<i>A. caudifer</i> Peru	<i>A. javieri</i> Peru	<i>A. fistulata</i> Peru and Ecuador
Head and body length	57.83 ± 3.64 (54.00–65.00) 12	63.33 ± 3.06 (60.00–66.00) 3	62.16 ± 3.62 (57.50–70.00) 16	65.80 ± 3.96 (61.00–69.00) 5	63.30 ± 6.8 (54.00–70.00) 4
Tail length	1.43 ± 2.06 (0.00–5.00) 14	0.0	4.00 ± 1.37 (0.00–6.00) 16	2.40 ± 3.58 (0.00–08.00) 5	3.00 ± 2.65 (0.00–6.00) 3
Hind foot length	10.54 ± 1.18 (9.00–13.00) 14	11.33 ± 1.53 (10.00–13.00) 3	9.06 ± 1.24 (7.00–11.00) 16	11.20 ± 1.30 (10.00–13.00) 5	11.00 ± 1.63 (9.00–13.00) 4
Ear length	13.15 ± 1.34 (10.00–14.50) 13	12.50 ± 2.12 (11.00–14.00) 2	14.44 ± 1.36 (12.00–16.00) 16	12.80 ± 0.45 (12.00–13.00) 5	15.80 ± 1.26 (14.00–17.00) 4
Tragus length	5.82 ± 0.83 (5.00–7.00) 13	8.0	6.43 ± 1.16 (5.00–9.00) 14	5.50 ± 0.58 (5.00–6.00) 4	7.00 ± 1.41 (6.00–8.00) 2
Forearm length	35.80 ± 1.02 (34.00–37.34) 16	36.05 ± 0.07 (36.00–36.10) 2	35.27 ± 1.26 (33.30–38.00) 17	37.40 ± 0.55 (37.00–38.00) 5	37.70 ± 1.42 (35.00–40.00) 10
Greatest skull length	21.95 ± 0.43 (21.17–22.59) 16	22.64 ± 0.22 (22.50–22.89) 3	21.98 ± 0.42 (21.26–22.78) 18	24.30 ± 0.48 (23.65–24.81) 5	24.0 ± 1.17 (22.60–26.00) 11
Condylbasal length	21.28 ± 0.49 (20.37–22.09) 16	21.84 ± 0.23 (21.68–22.10) 3	21.30 ± 0.52 (20.36–22.25) 18	23.62 ± 0.55 (22.85–24.21) 5	23.50 ± 1.14 (22.10–25.30) 11
Palatal length	11.14 ± 0.41 (10.41–11.91) 16	12.18 ± 0.34 (11.79–12.43) 3	11.45 ± 0.39 (10.76–12.12) 18	12.98 ± 0.35 (12.63–13.45) 5	12.50 ± 0.79 (11.50–14.00) 11
Maxillary tooththrow length	8.10 ± 0.35 (7.47–8.89) 16	8.34 ± 0.12 (8.23–8.47) 3	8.14 ± 0.25 (7.67–8.56) 18	9.03 ± 0.24 (8.75–9.29) 5	9.20 ± 0.46 (8.40–9.80) 11
Zygomatic width	9.04 ± 0.38 (8.25–9.63) 16	9.57 ± 0.05 (9.52–9.61) 3	9.69 ± 0.25 (9.31–10.05) 16	9.12 ± 0.16 (8.95–9.35) 5	9.90 ± 0.29 (9.40–10.30) 7
Braincase width	8.74 ± 0.20 (8.40–9.11) 16	9.13 ± 0.04 (9.09–9.16) 3	8.84 ± 0.22 (8.34–9.20) 18	8.88 ± 0.13 (8.72–9.07) 5	9.30 ± 0.27 (8.92–9.83) 11
Postorbital width	4.44 ± 0.13 (4.21–4.71) 16	4.61 ± 0.04 (4.57–4.65) 3	4.57 ± 0.15 (4.29–4.78) 18	4.55 ± 0.12 (4.40–4.70) 5	4.70 ± 0.16 (4.43–4.95) 11
Palatal width at M ³	5.30 ± 0.19 (4.97–5.69) 16	5.65 ± 0.15 (5.54–5.82) 3	5.61 ± 0.21 (5.33–6.06) 17	5.41 ± 0.05 (5.35–5.48) 5	5.70 ± 0.28 (5.30–6.27) 11
Palatal width at canines	3.83 ± 0.18 (3.54–4.25) 16	4.09 ± 0.07 (4.04–4.17) 3	4.23 ± 0.11 (3.94–4.44) 18	3.83 ± 0.07 (3.78–3.92) 5	4.30 ± 0.10 (4.16–4.48) 11
Braincase height	6.59 ± 0.22 (6.21–7.11) 16	7.34 ± 0.20 (7.12–7.52) 3	6.95 ± 0.31 (6.39–7.58) 18	6.59 ± 0.16 (6.35–6.80) 5	7.10 ± 0.27 (6.77–7.45) 8
Dentary length	15.65 ± 0.56 (14.61–16.68) 16	16.21 ± 0.30 (16.00–16.56) 3	15.71 ± 0.41 (14.92–16.41) 18	17.77 ± 0.60 (16.95–18.49) 5	17.60 ± 1.15 (16.20–19.50) 11
Mandibular tooththrow length	8.41 ± 0.27 (7.90–8.81) 16	8.54 ± 0.09 (8.45–8.62) 3	8.44 ± 0.23 (7.99–8.91) 18	9.37 ± 0.20 (9.15–9.60) 5	9.40 ± 0.59 (8.53–10.34) 11
Dentary height	1.64 ± 0.13 (1.45–1.89) 16	1.69 ± 0.23 (1.51–1.95) 3	1.86 ± 0.13 (1.56–2.07) 18	1.49 ± 0.06 (1.40–1.55) 5	2.00 ± 0.15 (1.81–2.25) 8
Body mass	8.89 ± 0.68 (7.00–9.75) 12	10.5	9.16 ± 1.17 (6.60–11.50) 14	10.40 ± 0.55 (10.00–11.00) 5	12.80 ± 0.28 (12.60–13.00) 2

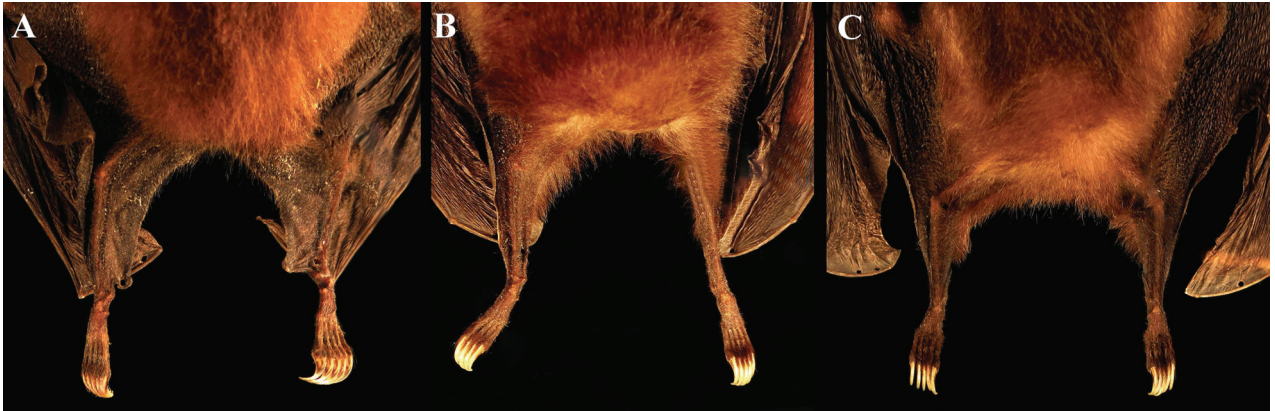


FIG. 4. Dorsal view of the uropatagia of: A — *A. caudifer* (MUSM 11754), B — *A. aequatoris* (MUSM 14916), and C — *A. javieri* sp. nov. (MUSM 19602). The uropatagium of *A. javieri* sp. nov. is narrower and hairy than the other species, but most similar to *A. aequatoris*. Not at scale

uropatagium. In *A. javieri*, the upper and lower labial vibrissae are longer.

Anoura javieri and *A. cadenai* are of similar size (FA = 37.0–38.0 mm vs. 36.1–37.0 mm;

GSL = 23.7–24.8 mm vs. 23.1–23.8 mm), but the skull and rostrum is much slender and delicate in the former species. In *A. javieri*, the upper canines are small without trace of a sulcus, whereas

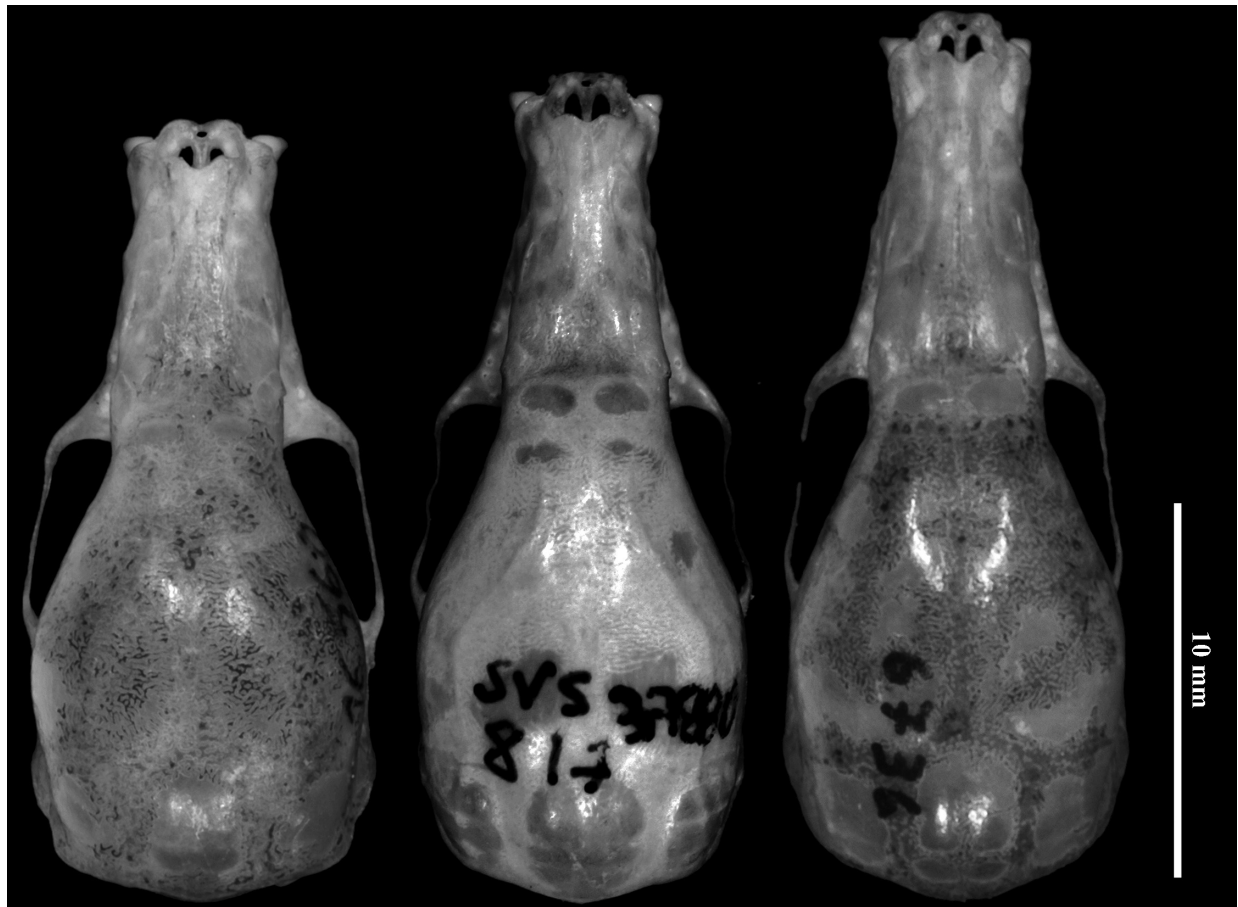


FIG. 5. Dorsal view of the skull of: *A. caudifer* (MUSM 16560), *A. aequatoris* (MUSM 37880), and *A. javieri* sp. nov. (MUSM 6736, holotype). Note the larger size of *A. javieri* sp. nov.

in *A. cadenai*, they is a moderate deep sulcus. In *A. javieri*, the upper incisors are separated when viewed from below (Fig. 6), whereas in *A. cadenai*, they are in contact. In addition, *A. javieri* exhibits a distinct keel at the mandibular symphysis whereas *A. cadenai* has a reduced or absent keel. At present, *A. cadenai* is known only from western Colombia.

Compared to *A. luismanueli*, *A. javieri* is larger (FA = 37.0–38.0 mm vs. 33.6–36.9 mm; GSL = 23.7–24.8 mm vs. 20.4–21.6 mm), with longer rostrum and a longer palatal length (PAL = 12.6–13.5 mm vs. 9.6–11.0 mm). Other measurements that show no overlap between these two species are condylobasal length, maxillary toothrow length, dentary length, dentary height, and mandibular toothrow length. P2 is very small and widely separated from the canine in *A. javieri*. Hairs on the margin of the uropatagium of *A. javieri* are longer and denser than those found in *A. luismanueli*. In ventral view of the skull, toothrows converge anteriorly in *A. javieri*, in contrast to the more parallel

toothrows of *A. luismanueli*. At present, *A. luismanueli* is known to occur only in Venezuela and Colombia.

Anoura aequatoris and *A. javieri* are more similar and could be confused because both have dark pelage and hairy uropatagia. However, *A. javieri* is on average larger (GSL = 24.3 mm vs. 22.0 mm; FA = 37.4 mm vs. 35.8 mm), has a longer slender rostrum, and a smoothly rounded braincase. Additionally, *A. javieri* is characterized by a small P² that is widely separated from the canine, a M¹ with well-reduced hypoconal basin, and a shallow angle between the postprotocrista and metacone. Other differential characters of *A. javieri* are absence of palatal process, smooth anterior surface of upper canines, lower molars laterally compressed, m1 larger than the other molars, well developed paraconid, and lower molars with a deep constriction between the trigonid and the talonid. The mandibular symphysis in *A. javieri* is also larger than in most specimens of *A. aequatoris*, and the uropatagium is more densely haired.

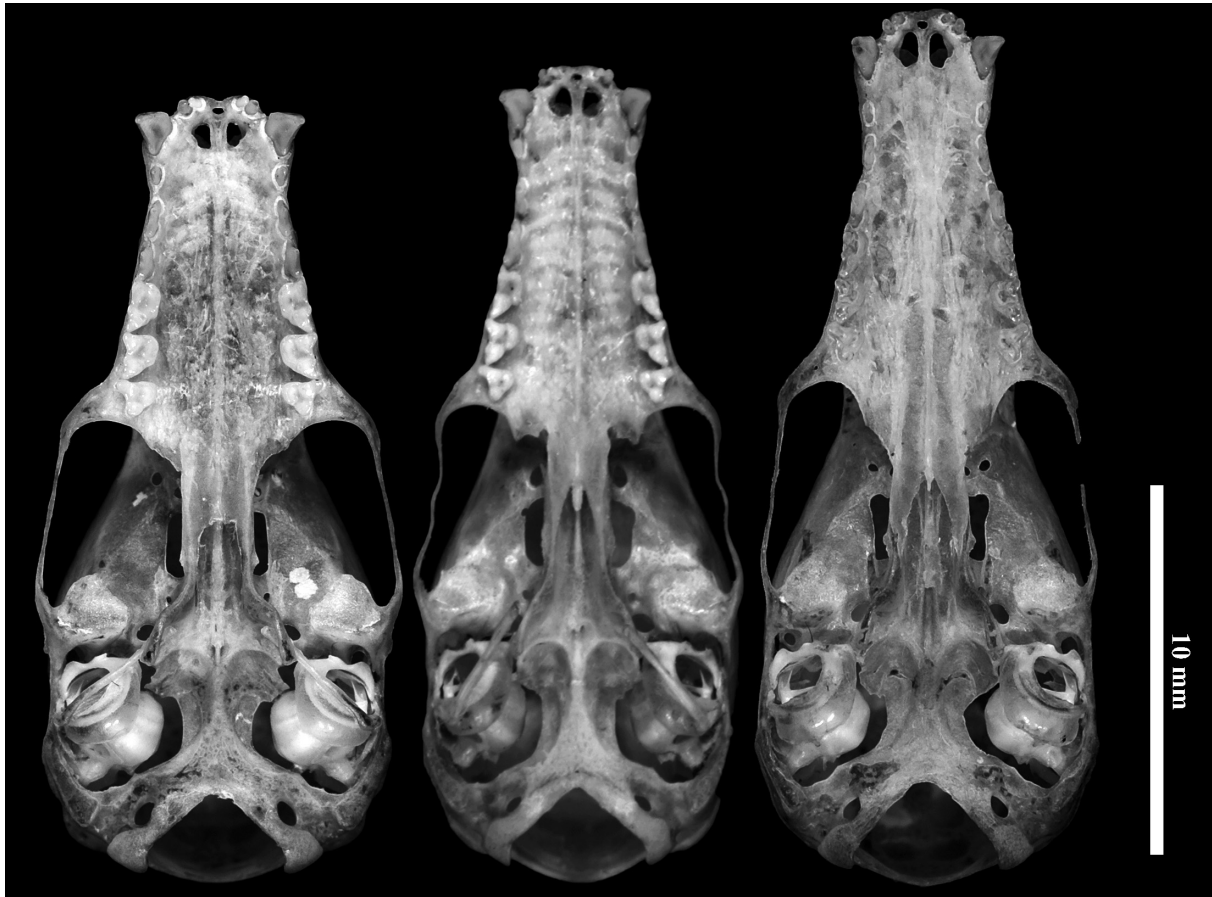


FIG. 6. Ventral view of the skull of: *A. caudifer* (MUSM 16560), *A. aequatoris* (MUSM 37880), and *A. javieri* sp. nov. (MUSM 6736, holotype)



FIG. 7. Lateral view of the skull and mandible of *A. caudifer* (MUSM 16560), *A. aequatoris* (MUSM 37880), and *A. javieri* sp. nov. (MUSM 6736, holotype)

Compared to *A. fistulata*, *A. javieri* has a much narrower and densely haired uropatagium, usually less than two mm in width vs. a broader, not as well haired membrane (4.0–7.5 mm). Foot claws are pale brown to whitish in *A. javieri* vs. dark brown in *A. fistulata*. *Anoura javieri* and *A. fistulata* average about the same size (GSL = 24.3 vs. 24.0 mm; FA = 37.4 vs. 37.5 mm), but the higher range of measurements shows that *A. fistulata* can attain larger size (Table 3). *Anoura javieri* has a narrow and slender rostrum and a smoothly and rounded braincase, whereas *A. fistulata* has a rectangular and broader rostrum and a more globular braincase with more distinct lambdoid crests. The palate in *A. javieri* is slightly domed in the midline and post-molar palatal processes are absent; in contrast to the flatter palate and distinctive palatal processes in *A. fistulata*. In *A. javieri*, the upper incisors are sub-equal in length vs. a distinctly larger outer incisor in *A. fistulata*. In *A. javieri*, the upper canines lack a posterior cusp on the cingulum and a sulcus on the anterior surface, which are distinct in *A. fistulata*. The lower molars of *A. javieri* are narrow and the trigonid is larger than the talonid; in contrast, the molars are comparatively broader, and the trigonid and talonid are subequal in *A. fistulata*. The mental foramen is small in *A. javieri*, vs. large in *A. fistulata*.

Etymology

It is a pleasure to dedicate this species to Javier Ortiz de la Puente Denegri (1928–1952), one of the first Peruvian mammalogists (Fig. 8). Javier had been highly interested in the natural sciences since childhood, and became a professor at Universidad Nacional Mayor de San Marcos at an early age. Unfortunately, he died young at the age of 24 in a tragic automobile accident, thus was unable to complete several planned publications and could not have the opportunity to prepare students in mammalogy. However, his legacy continues among Peruvian biologists because of his charisma, talent and his few, but significant contributions. Surviving contemporaneous colleagues recall him as an enthusiastic, talented and devoted student of the natural sciences. The late professors Luz Sarmiento and Hernando de Macedo often talked about Javier as a talented young scientist. Javier Ortiz de la Puente inspired the senior author to follow him in the study of mammals. Both, the late Philip Hershkovitz and Karl K. Koopman personally knew Ortiz de la Puente and also expressed their admiration for him to the senior author. His monograph ‘Estudio

Monográfico de los Quirópteros de Lima y Alrededores’ (Ortiz de la Puente, 1951) is still a benchmark for anybody interested in the study of the Peruvian bat fauna. Additional notes, with photographs, on Javier’s life have been published by Aguilar-Fernández (2009) and Franke (2007, 2012).

Ecology and habitat

Anoura javieri has been collected in upper montane forest habitat, but only from July to September during the typical dry season; none has been collected during the rainy season expeditions in spite of similar mist-netting efforts at the same sites. *Anoura javieri* has been collected in sympatry with the following bat species: *A. caudifer*, *A. cultrata*, *A. peruana*, *Chiroderma salvini*, *Artibeus glaucus*, *Enchisthenes hartii*, *Micronycteris megalotis*, *Sturnira erythromos*, *S. magna*, *Platyrrhinus albericoi*, *P. masu*, *Tadarida brasiliensis*, *Eptesicus brasiliensis*, *Lasiurus blossevillii*, *Myotis keaysi*, and *M. oxyotus* (Pacheco *et al.*, 1993; Solari *et al.*, 2006).

The analysis of one stomach of *A. javieri* revealed an abundance of pollen of diverse forms, and vegetative remains that appears to be anthers. Neither arthropods nor endoparasites were found. No ectoparasites have been collected on any of the reported specimens.

Morphometric analysis

The 13 craniodental and forearm length variables exhibited a normal distribution with the Shapiro-Wilk test. Multivariate tests of MANOVA showed an overall significant difference among species ($P = 0.000$ for Pillai’s Trace and Wilks’ Lambda). Bonferroni post-hoc test identified the variables that significantly differentiated species in multiple comparisons (Table 4). *Anoura javieri* differed significantly from *A. aequatoris* in six variables, from *A. caudifer* in 11 variables, and from *A. fistulata* in six of 14 variables. A Principal Component Analysis (PCA) of the measurements of *A. caudifer*, *A. aequatoris*, *A. fistulata*, and *A. javieri*, found two components with eigenvalues larger than 1.0. These two components (PC1 and PC2) accounted for 79.1% of total variance (56.3% and 22.8%, respectively — Table 5). The third component had an eigenvalue of 0.79 (5.7%), and therefore was ignored. In the plot of PC 1, usually considered to be a ‘size’ component, vs. PC 2, *A. javieri* is clearly separated in morphospace. This plot shows that *A. javieri* is larger than *A. aequatoris* and *A. caudifer*, and suggests that ‘shape’ is an important factor to differentiate *A. javieri* from *A. fistulata*. *Anoura*



FIG. 8. A photograph of Javier Ortiz de la Puente Denegri, taken from Franke (2012) with permission of the author

caudifer and *A. aequatoris* show some degree of mutual overlap, but *A. fistulata* is also clearly separated from the other species (Fig. 9). The variables that accounted for the greatest proportion of variance are CBL, GSL, MANDL, DENL, MXTRL, BRW, and PALTL, for the first component; and C¹C¹, ZYGW, and DENT for the second component.

DISCUSSION

Anoura javieri sp. nov. likely represents a member of the *A. caudifer* species complex (Mantilla-Meluk and Baker, 2010); however, the genus still lacks a formal phylogenetic assessment to clarify the nature of the species groups. Nevertheless, *A. javieri* has several of the characteristics of the proposed *A. caudifer* species complex, such as a well-developed paracone and a reduced paracrista on the first upper molar (Mantilla-Meluk and Baker, 2010; Mantilla-Meluk *et al.*, 2012). In addition, the metacone is also well-developed, and the parastyle is enlarged as confirmed by us in *A. javieri* and other species of the *A. caudifer* species group we have examined. These characters might prove to be

synapomorphies of the *A. caudifer* species complex, revealing the existence of a monophyletic group, in which case a subdivision of the genus *Anoura* is warranted. If that was the case, the taxon *Lonchoglossa* Peters 1868 would be available for the *A. caudifer* species complex. Surprisingly, neither a morphological nor a molecular phylogeny has been attempted for the complete genus. Some sequences are available, but are limited and have been used mainly in higher level evaluations of relationships. Mitochondrial DNA and nuclear RAG2 sequences were obtained for *A. geoffroyi* (Baker *et al.*, 2003). Also, sequences of *cyt b* for *A. caudifer* and *A. geoffroyi* have been used in a molecular phylogeny (Hoffmann *et al.*, 2008), and were found closely related (Agnarsson *et al.*, 2011).

Solari *et al.* (2006) reported four sympatric species of *Anoura* in the Cosñipata Valley, *A. javieri* (as *Anoura* sp. nov.), *A. peruana* (as *A. geoffroyi*), *A. cultrata*, and *A. caudifer*; but one more species was overlooked. One unidentified specimen of *Anoura* (MUSM 8750) was collected in the same valley at 1550 m a.s.l. in San Pedro, in 1992, but because it was not confidently assigned to any known species of *Anoura*, it was left as *Anoura* sp. in the MUSM collection. Later, the species *A. fistulata* was

TABLE 4. MANOVA followed by Bonferroni post-hoc test among species for the entire sample of 13 cranial variables and forearm length for adult males of *A. aequatoris* ($n = 16$), *A. caudifer* ($n = 18$), *A. fistulata* ($n = 11$), and *A. javieri* sp. nov. ($n = 5$). Values in bold represent statistical difference at 5% in Bonferroni test. All F -values in MANOVA are statistically significant at $P \leq 0.05$

Variable	MANOVA F	Bonferroni post-hoc test					
		<i>aequatoris</i> - <i>caudifer</i>	<i>aequatoris</i> - <i>fistulata</i>	<i>aequatoris</i> - <i>javieri</i>	<i>caudifer</i> - <i>fistulata</i>	<i>caudifer</i> - <i>javieri</i>	<i>fistulata</i> - <i>javieri</i>
FORL	12.047	1.000	0.001	0.057	0.000	0.005	1.000
GSL	38.191	1.000	0.000	0.000	0.000	0.000	1.000
CBL	38.186	1.000	0.000	0.000	0.000	0.000	1.000
PALTL	28.527	0.517	0.000	0.000	0.000	0.000	0.724
MXTRL	35.813	1.000	0.000	0.000	0.000	0.000	1.000
ZYGW	29.104	0.000	0.000	1.000	0.094	0.002	0.000
BRW	13.786	1.000	0.000	1.000	0.000	1.000	0.011
POW	6.544	0.068	0.000	0.710	0.241	1.000	0.614
M ³ M ³	11.99	0.000	0.000	1.000	0.545	0.369	0.025
C ¹ C ¹	44.025	0.000	0.000	1.000	1.000	0.000	0.000
BRH	13.977	0.001	0.000	1.000	0.136	0.048	0.001
DENL	30.126	1.000	0.000	0.000	0.000	0.000	1.000
MANDL	28.135	1.000	0.000	0.000	0.000	0.000	1.000
DENT	29.34	0.000	0.000	0.137	0.029	0.000	0.000

described (Muchhala *et al.*, 2005) and we found that our specimen MUSM 8750 corresponded exactly to that description. Therefore, this specimen is the first record of *A. fistulata* for the Cuzco region and for Manu Biosphere Reserve. *Anoura fistulata* has been found at 1690 m, in Chacaneque, Puno department (Garate-Bernardo and Carrasco-Rueda, 2011) and up to 2285 m a.s.l. at Abiseo National Park, San Martín (Pacheco *et al.*, 2009), suggesting that the upper range of *A. fistulata* might likely overlap with the lower range of *A. javieri*. Another species, *A. latidens*, is also present in the Cuzco region, but their southernmost record is at La Convención, district of Echarate, 2445 m a.s.l., in the Cordillera de Vilcabamba (Solari *et al.*, 2001), some 200 km north of the Cosñipata valley, but future work might determine if *A. latidens* is also present in the Cosñipata valley. Nonetheless, it is impressive that at least five species of *Anoura* are sympatric in a single river drainage, posing the question of what ecological and physiological differences might exist among them to allow this pattern within nectarivorous bats. Little is known of the ecology of these species to understand this distribution. Diverging roosting behavior has been proposed for other bats (Velazco *et al.*, 2014).

With respect to *A. caudifer*, Koopman (1978) mentioned that all Peruvian localities are on the Amazonian side of the Andes, from 150 m to 2825–2845 m a.s.l. (Cordillera Vilcabamba, Cuzco); however, all our examined specimens of *A. caudifer* from Peru set the upper range of the species to 2286 m a.s.l. in Cajamarca, Tabaconas, San Ignacio. It is very likely that Koopman's (1978) records for

higher elevations are in fact representatives of *A. javieri*. Similarly, Medina *et al.* (2012a) claimed that *A. caudifer* is distributed in the Río Cosñipata, from 1300 m to 2870 m a.s.l., in contrast to the reported range of 340 m to 1920 m a.s.l. in the same river drainage (Solari *et al.*, 2006). Since Medina *et al.*'s (2012a) specimens that were collected at higher elevations overlap the elevational distribution of *A. javieri* (from 1900 m to 3450 m), a confirmation of their identifications is needed to test whether both

TABLE 5. Factor loadings of the first two axes of a PCA based on the correlation matrix of 13 cranial variables and forearm length for adult males of *A. aequatoris* ($n = 16$), *A. caudifer* ($n = 18$), *A. fistulata* ($n = 11$), and *A. javieri* sp. nov. ($n = 5$)

Variable	Principal component	
	PC 1	PC 2
CBL	0.900	-0.379
GSL	0.892	-0.386
MANDL	0.876	-0.344
DENL	0.844	-0.427
MXTRL	0.843	-0.371
BRW	0.823	0.197
PALTL	0.822	-0.411
M ³ M ³	0.707	0.495
POW	0.672	0.397
BRH	0.619	0.558
FORL	0.599	-0.486
C ¹ C ¹	0.549	0.678
ZYGW	0.665	0.668
DENT	0.548	0.635
Eigenvalue	7.9	3.2
Variance %	56.3	22.8
Accumulated variance	56.3	79.1

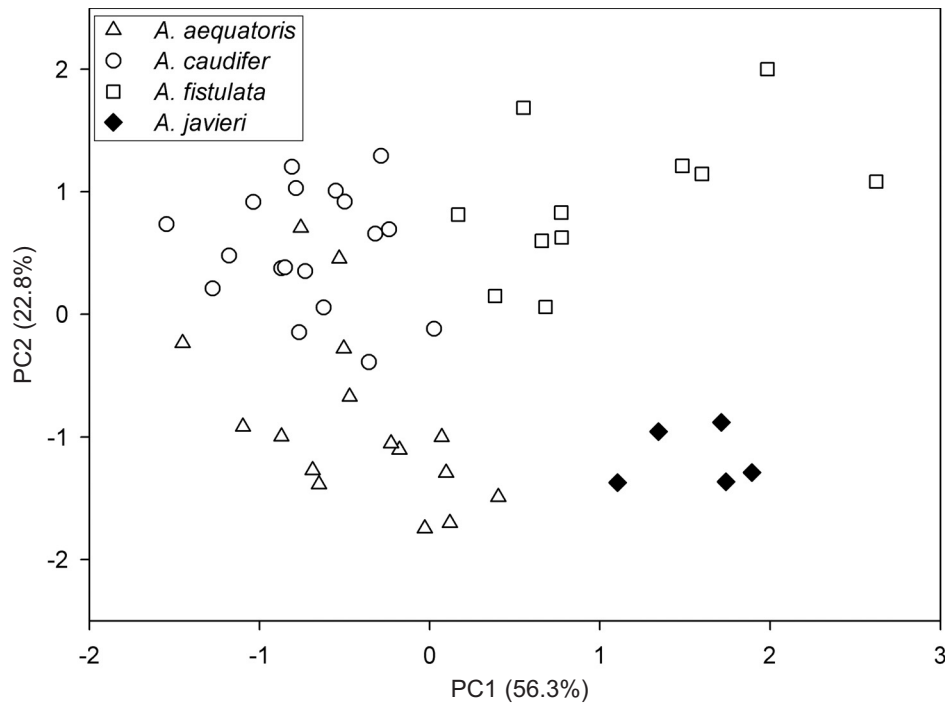


FIG. 9. Projection of specimen scores for axes 1 and 2 of PCA, applied to 13 craniodental variables and forearm length of adult males of *A. aequatoris* ($n = 16$), *A. caudifer* ($n = 18$), *A. fistulata* ($n = 11$), and *A. javieri* sp. nov. ($n = 5$). See Table 5 for variable correlations and explanation of percent variance

species really overlap extensively in elevational distribution in the Yungas.

Other species of *Anoura* are known to reach high elevations. *Anoura cultrata* has been recorded from 50 m, in very humid forest in Ecuador (Albuja, 1989), to at least 2600 m a.s.l. in montane rain forest of Costa Rica (Nagorsen and Tamsitt, 1981), but reaches up to 2826 m a.s.l. at Bosque de Carpish, Huánuco (MUSM 18553). Also, *A. latidens* has been recorded at 2600 m in Pasco, Oxapampa, San Alberto (Solari *et al.*, 1999). *Anoura javieri* appears to be the nectarivorous bat with a high upper distribution limit, second only to *A. peruana* which has been found up to 3774 m a.s.l. *Anoura javieri* has not been collected at lower elevations despite extensive surveys carried out in the Cosñipata valley and nearby, suggesting that the distribution of *A. javieri* at upper montane forests is not a sampling artifact. Few bat species are restricted or have a high preference for montane habitats, suggesting the existence of a group of montane bat species that includes: *Platyrrhinus ismaeli* with a range from 1600 m to 3498 m a.s.l., *Carollia manu* from 850 m to 2250 m a.s.l., and *Eptesicus andinus* from 1219 m to 3380 m a.s.l., among others (V. Pacheco, unpublished, based on MUSM records). Without doubt, more surveys are needed to proof whether this group

of montane bat species is real or rather it is just an artifact produced by insufficient collections.

Tamsitt and Valdivieso (1966) reviewed the taxonomic status of *A. caudifer*, concluding that the species was monotypic. Molinari (1994) showed this species to be a composite taxon when he described *A. luismanueli*. Although he compared *A. luismanueli* with *A. caudifer*, he did not compare it with the similar *A. aequatoris*, probably because Tamsitt and Valdivieso (1966) had concluded that it was a junior synonym of *A. caudifer*. However, Molinari (1994) noted that the lower extremes of *A. caudifer* given by Tamsitt and Valdivieso (1966) were below those given by other authors, and thus suggested their samples to consist of a mixture of specimens of *A. caudifer*, *A. luismanueli*, and probably another small unrecognized *Anoura*. In this sense, both *A. aequatoris* and *A. luismanueli* were recently compared by Mantilla-Meluk and Baker (2006), and Mantilla-Meluk *et al.* (2009), through a morphological and morphometric analysis that showed *A. luismanueli* to occur in the Cordillera Oriental of Colombia, and *A. aequatoris* to occur in the Cordillera Central and Cordillera Occidental of Colombia, and in the wet forests of north-western and eastern Ecuador. This is at odds with the distribution of *A. aequatoris* in Peru, which appears

to be restricted to the montane forests of the eastern side of the Andes. This pattern of distribution on both sides of the Andes of Ecuador suggests that *A. aequatoris* needs to be further characterized (Jarín-V. and Kunz, 2008). It might represent a species complex.

Although we provide a detailed morphological characterization of *A. aequatoris* based on northern Peruvian samples, it does not yet constitute a species revision. To complete that, further comparisons are needed with Ecuadorean populations, especially with the type series from Illambo (including topotypes), and with Colombian populations. Some key characters to identify *aequatoris*, such as the densely haired uropatagium (Lönnberg, 1921), are also found in *A. javieri*, and *A. luismanueli*. Therefore, this character is no longer diagnostic; on the contrary, it might represent a synapomorphy for a group that includes these species. Lönnberg (1921) mentioned the absence of a tail as one of the diagnostic characteristics of *A. aequatoris* (based on two specimens), but a tail was present in five of our 16 measured samples. Molinari (1994) found a short (3.0–6.0 mm) tail to be present in 39 Venezuelan specimens of *A. luismanueli*, but Mantilla-Meluk and Baker (2006) found its presence to be variable in samples from Colombia. Similarly, a tail was present in only two of six specimens of *A. javieri*. Therefore, presence of a tail in the *caudifer* complex is variable and is not a good taxonomic character to rely on. Because the absence of tail could be an artifact of study skin preparation, a study of this structure should be based on the examination of specimens preserved as fluid.

Mantilla-Meluk *et al.* (2012) provided the first record of *A. aequatoris* from Bolivia based on a specimen from Chijchijpa, La Paz, Bolivia. They based its determination on an assessment of cranial characteristics and a principal component analysis of 54 specimens of the *A. caudifer* complex. However, their figure 1 shows unusually large canines and first upper and lower premolars, a first upper premolar very close to the canine, an incomplete zygomatic arch, and a very narrow basisphenoid bone. These characteristics are absent in all the specimens of *A. aequatoris* that we have examined. Therefore, the identification of the Bolivian specimen of *A. aequatoris* needs to be confirmed. In any case, this Bolivian specimen clearly is not *A. javieri*, although the species may be present in Bolivia.

The Yungas in the central and southern Peruvian Andes is considered in a broad sense homogeneous regarding mammalian composition. However, our

report of *A. javieri* in the southeastern Yungas is coincidental with the known distribution of several other mammalian species that are present only in the Yungas of southern Peru and Bolivia. These species are: the bat *Carollia manu* (Pacheco *et al.*, 2004), the didelphid marsupials *Gracilinanus aceramarcae* and *Marmosa andersoni* (Creighton and Gardner, 2008); the paucituberculate marsupial *Lestoros inca* (Myers and Patton, 2008), and the rodents *Akodon mimus*, *A. surdus*, *A. torques*, and *A. lutescens* (Pardiñas *et al.*, 2015), *Oxymycterus hiska* and *O. juliacae* (Oliveira and Goncalves, 2015), *Nephelomys levipes* (Percequillo, 2015), *Neacomys vargasillosai* (Hurtado and Pacheco, 2017), *Rhipidomys ochrogaster* (Tribe, 2015), *Thomasomys daphne* and *T. ladewi* (Pacheco, 2015), *Cuscomys ashaninka* and *C. oblativa* (Emmons, 2015), and *Isothrix barbara-brownae* (Emmons and Patton, 2015). This fauna suggests that a region of endemism for small mammals exists in the southern Yungas, roughly south of the Apurímac river, and that at least in Peru the Yungas are geographically structured (V. Pacheco, unpublished). This provides a strong argument for the conservation of the Yungas based on the composition of species, not only from an ecosystemic perspective.

The known diversity of bats in Peru has increased from 165 (Pacheco *et al.*, 2009) to 181 species up to November 2017. This makes Peru the third country in the Neotropics with the most bats species after Colombia and Brazil. The recent additions to the bat fauna of Peru are: *Cyttarops alecto*, from Huánuco (Velazco *et al.*, 2011); *Artibeus bogotensis*, from Jenaro Herrera, Loreto (Calderón and Pacheco, 2012); *Sturnira bakeri*, from Tumbes (Sánchez and Pacheco, 2016); *Eumops patagonicus*, from Cuzco (Medina *et al.*, 2012b); *Eumops delticus*, from San Juan, near Iquitos, Loreto (Díaz, 2011); *Histiotus macrotus*, from Tacna (Aragón A. and Aguirre Q., 2014); and *Rhogeessa hussoni* and *R. io*, from Pampas del Heath (Medina *et al.*, 2016). Some new names were the result of revisionary work: *Anoura peruana* (Mantilla-Meluk and Baker, 2010), *Glossophaga valens* (Pari *et al.*, 2015), *Lophostoma occidentalis* (Velazco and Cadenillas, 2011), *Artibeus aequatorialis* (Larsen *et al.*, 2010), *Pteronotus rubiginosus* (Pavan and Marroig, 2016), *Promops davisoni* (Gregorin and Chiquito, 2012), and *Myotis caucensis* (Moratelli *et al.*, 2013). Based on these revisions, four species reported for Peru by Pacheco *et al.* (2009) are no longer listed for the country: *Anoura geoffroyi*, *Artibeus jamaicensis*, *Promops nasutus*, and *Pteronotus parnelli*. Other

names represent new species: *Peropteryx pallidoptera* (Lim *et al.*, 2010), *Hsunycteris dashe* (Velazco *et al.*, 2017), *Platyrrhinus angustirostris* (Velazco *et al.*, 2010), *Thyroptera wynneae* (Velazco *et al.*, 2014), and *Eumops chiribaya* (Medina *et al.*, 2014). *Micronycteris schmidtorum* was not listed for Peru by Días *et al.* (2016) probably following Williams and Genoways (2008), but it is listed here based on two specimens reported from Manu Biosphere Reserve (Solari *et al.*, 2006). The species richness for the country is increasing rapidly, indicating that the real number of bat species is still far from being known.

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APPENDIX

Specimens examined. Species and specimens examined are housed in the following institutions: Escuela Politécnica Nacional, Quito (EPN); Field Museum of Natural History, Chicago (FMNH); Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM); Museo de Zoología de la Pontificia Universidad Católica, Quito (QCAZ). Specimens marked with an asterisk (*) were measured. Coordinates for unique localities are included. Locality numbers (in bold) appear in Fig. 3.

Anoura aequatoris ($n = 39$) — PERU: Amazonas (1) Condorcanqui, El Cenepa, Cordillera del Cóndor, R. Comaina, P. V. 3 Alfonso Ugarte, 03°54'S, 78°25'W, 1138 m (MUSM 10626). Cajamarca (2) San Ignacio, Tabaconas, Anexo Cerro Grande-Sector Puchua, 05°17'40.8"S, 79°17'34.5"W, 2100 m (MUSM 37880*); (3) San Ignacio, Tabaconas, Palmas Pampa, 05°21'43.4"S, 79°15'11.8"W, 1785 m (MUSM 37881); (4) San Ignacio, Tabaconas, Palmas Pampa, 05°21'53.6"S,

79°15'2.8"W, 1733 m (MUSM 37823*, 37882*); (5) San Ignacio, Tabaconas, Tierra Blanca; 05°17'0.4"S, 79°16'44.1"W, 2407 m (MUSM 24993). Cusco (6) La Convención, Echerate, Quimbiri, Campamento Wayrapata, 12°50'9.6"S, 73°29'42.0"W, 2445 m (MUSM 14483*, 14484*, 14485, 14486); (7) La Convención, Quimbiri, Campamento Lactahuaman, 12°51'54.0"S, 73°30'46.8"W, 1710 m (MUSM 14480*). Huánuco, (8) Huánuco, Chinchao, Bosque de Carpish, 09°43'59.9"S, 76°6'23.0"W,

APPENDIX. Continued

2826 m (MUSM 18552*); **(9)** Chinchao, Caserío de San Pedro de Carpish, 09°43'28"S, 76°05'58"W, 2757 m (MUSM 18252*, 18253); **(10)** Chinchao, Caserío de San Pedro de Carpish, 09°41'4.8"S, 76°05'47.5"W, 1982 m (MUSM 18884–18887, 18888*, 18889–18892, 18893*, 18894, 18895); **(11)** Chinchao, Cordillera de Carpish, 09°43'37.0"S, 76°6'7.0"W, 2760 m (MUSM 18411). *Junín*, **(12)** Chanchamayo, Chanchamayo, Santuario Nacional Pampa Hermosa Los Cedros, 10°59'43.1"S, 75°25'37.2"W, 1540 m (MUSM 41319); **(13)** Chanchamayo, Chanchamayo, Santuario Nacional Pampa Hermosa Podocarpus, 10°58'37.2"S, 75°25'57.1"W, 1890 m (MUSM 41320*). *Pasco*, **(14)** Oxapampa, Oxapampa, San Alberto (límite oeste del P. N. Yanachaga Chemillen), 10°33'S, 75°24'W, 2600 m (MUSM 10119*, 14915, 14916*). *Piura*, **(15)** Huancabamba, El Carmen de la Frontera, Quebrada el Gallo, 04°53'1.0"S, 79°20'30.6"W, 2121 m (MUSM 23358); **(16)** El Carmen de la Frontera, Quebrada el Gallo-Campamento Bomba Quemada 1, 04°53'10"S, 79°21'08"W, 2757 m (MUSM 23459); **(17)** El Carmen de la Frontera, Minera Majaz Campamento Nueva York, 04°54'16.1"S, 79°22'38.2"W, 3100 m (MUSM 23602). *San Martín*, **(18)** Mariscal Cáceres, P. N. Río Abiseo, Las Palmas, 07°33'S, 77°23'W, 2045–2250m (MUSM 7214, 7219*, 7223*, 7228*).

Anoura caudifer ($n = 57$) — BRAZIL: *Sao Paulo*, Ilha da Cardoso, 25°11'6"S, 47°59'43"W, 10 m (FMNH 141597*); Primeiro Morro, 24°22'S, 47°50'W (FMNH 94700); Quadro Penteado, 24°23'S, 48°12'W, 50 m (FMNH 94701*). PERU: *Cajamarca*, **(19)** San Ignacio, San Ignacio, Chirinos Nuevo Chalaquito "El Chaupe", 05°12'18.0"S, 79°1'30.8"W, 2100 m (MUSM 12627). *Cusco*, **(20)** Huajyumbé, Quincemil, 13°13'S, 70°42'W, 630 m (FMNH 93541*); **(21)** La Convención, Camisea Konkari, 11°48'S, 72°52'W, 450 m (MUSM 14681); **(22)** La Convención, Echerate, Camisea-San Martín, 11°46'60.0"S, 72°42'W, 487 m (MUSM 13464*); **(23)** La Convención, Echerate, Camisea Las Malvinas, 11°52'10.2"S, 72°56'22.5"W, 400 m (MUSM 14682–14684); **(24)** La Convención, Echerate, Camisea Pagoreni, 11°42'22.0"S, 72°54'9.0"W, 450 m (MUSM 13462); **(25)** La Convención, Echerate, Camisea Segakiato, 11°50'42.1"S, 72°35'58.5"W, 460 m (MUSM 14685); **(26)** La Convención, Quimbiri, Campamento Llactahuaman, 12°51'54.0"S, 73°30'46.8"W, 1710 m (MUSM 14477–14479); **(27)** Paucartambo, Kosñipata, Consuelo km #165 17 km by rd W of Pilcopata, 13°01'25.0"S, 71°29'30.7"W, 1200 m (MUSM 9467, 9468); **(28)** Paucartambo, Kosñipata, Tono, 5 km S of Río Tono and 18 road km W of Patria, 13°0'S, 71°10'60.0"W, 900 m (MUSM 9472); **(29)** Paucartambo, Kosñipata, Estación Biológica Bosque Nublado, San Pedro, 13°3'16.8"S, 71°32'46.4"W, 1480 m (MUSM 11754). *Huánuco*, **(30)** Huánuco, Chinchao, Hacienda Paty pasando Carpish, 09°37'S, 76°08'W, 2195 m (MUSM 1209); **(31)** Leoncio Prado, Rupa Rupa, ca Tingo María, 09°18'S, 75°59'W, 600 m (MUSM 2753–2758). *Loreto*, **(32)** Maynas, Torres Causana, 12 km S. del P. V. Arcadia (en cuevas), 01°47'27.7"S, 74°41'33.7"W, (MUSM 20992*); **(33)** Maynas, Torres Causana, 2 km E del P. V. Arcadia (Platanal), 01°42'58.1"S, 74°40'18.1"W (MUSM 20993*); **(34)** Maynas, Torres Causana, P. V. Arcadia Río Napo, 01°42'33.3"S, 74°39'59.4"W (MUSM 20994*, 20997*, 20998*, 20999); **(35)** Maynas, Torres Causana, P. V. Castaña Río Aguarico, 00°48'13.0"S, 75°14'24.0"W (MUSM 21000*); **(36)** Requena,

Jenaro Herrera, Centro de Investigación Jenaro Herrera, 04°55'1.2"S, 73°45'W (MUSM 5585); **(37)** Ucayali, Contamana, Aguas Calientes (Cerros de Contamana), 07°11'20.1"S, 74°58'59.9"W, 150 m (MUSM 699, 700). *Madre de Dios*, **(38)** Cerro de Pantiacolla, E. slope NR Summit, ca. 4 km NNE Shintuya, 12°34'60"S, 71°15'00"W (FMNH 138891*); **(39)** Manu, Pakitza, 11°56'47.0"S, 71°15'W, 350 m (MUSM 480); **(40)** Manu, Pakitza, 11°56'47.0"S, 71°16'59.9"W, 340 m (MUSM 6826, 6827*); **(41)** Manu, Madre de Dios, Quebrada Aguas Calientes a 2.75 km al Este de Shintuya, 12°40'6.0"S, 71°16'8.0"W, 400 m (MUSM 16560*, 16562, 16563*); **(42)** Manu, Madre de Dios, Hacienda Amazonia R. Alto Madre de Dios frente a Atalaya, 12°52'38.3"S, 71°23'11.4"W, 500–780 m (FMNH 125422*, MUSM 8747*). *Pasco*, **(43)** Oxapampa, Palcazú, Campamento R. Lobo (P.N. Yanachaga Chemillen), 10°21'30.0"S, 75°14'46.0"W, 500 m (MUSM 10117*, 10118*); **(44)** Oxapampa, Palcazú, Shiringamazu carretera a Iscosazin, 10°15'40.8"S, 75°7'46.7"W, 450 m (MUSM 10120*); **(45)** Oxapampa, Pozuzo, Palmira, 10°3'46.3"S, 75°32'12.6"W, 830 m (MUSM 10799*). *Puno*, **(46)** Sandia, Sandia, Río Huacamay, 14°16'58.8"S, 69°25'58.8"W, 805 m (MUSM 11503, 11504); **(47)** Sandia, San Pedro de Putinapunco, Curva Alegre, 14°2'30.0"S, 68°57'41.0"W, 950 m (MUSM 26631, 26632); **(48)** Sandia, San Pedro de Putinapunco, San Fermín, 13°56'37.0"S, 68°58'34.0"W, 850 m (MUSM 26633); **(49)** Sandia, San Juan del Oro, Challohuma, 14°12'35.0"S, 69°8'56.0"W, 1200 m (MUSM 26775, 26776). *Ucayali*, **(50)** Purús, Purús, Balta, Río Curanja, 10°7'48.0"S, 71°49'59.9"W, 300 m (MUSM 1210).

Anoura fistulata ($n = 16$) — ECUADOR: *Cotopaxi*, Cantón Sigchos, Reserva Integral Otonga, 0°25'8.04"S, 79°00'14.04"W, 2200 m (QCAZ 2567*). *Santo Domingo*, Cantón Santo Domingo, Reserva Ecológica Río Guajalito, 0°13'44.18"S, 78°47'50.64"W, 1900 m (QCAZ 2740*), Cantón Santo Domingo, Reserva Ecológica Río Guajalito, 0°18'41.08"S, 79°10'15.96"W, 2000 m (QCAZ 3424*, 3427). *Morona Santiago*, Morona, Domono-Lundije, Parroquia San Isidro, 02°13'02.42"S, 78°07'35.26"W, 1170 m (EPN 11035). *Napo*, El Chaco, Alto Coca, El Salado, 00°15'N, 77°41'W, 1800 m (EPN 4631*). *Zamora Chinchipe*, Chinapinza, La Herradura, 04°02'02"S, 78°34'12"W, 1750 m (EPN 9714); Paquisha, Loma Emperadora, Cordillera del Cóndor, 03°54'57.31"S, 78°29'30.05"W, 1800–2000 m (EPN 10667, 11847*), Destacamento Militar Cóndor Mirador, 03°44'S, 78°23'W, 1725 m (EPN 9711*, 9713*).

PERU: *Cajamarca*, San Ignacio, Tabaconas, Palma Pampa, 5°21'53.57"S, 79°15'2.84"W, 1733 m (MUSM 37883*). *Cuzco*, San Pedro, 13°03'16.81"S, 71°32'46.43"W, 1550 m (MUSM 8750). *San Martín*, P.N. Río Abiseo, Las Palmas 07°33'S, 77°23'W, 2045–2285 m (MUSM 7215*, 7221*), La Meseta, 06°53'42.43"S, 71°23'28.18"W, 1707 m (MUSM 24363*).

Anoura javieri ($n = 6$) — PERU: *Cusco*, **(51)** Paucartambo, Challabamba, P. V. (Acjanaco), 13°12'0"S, 71°37'12"W, 3350–3450 m (MUSM 6734*, 6736*, 8749*); **(52)** Suecia 138.5 km Carretera Shintuya, 13°6'S, 71°34'12.0"W, 1900 m (MUSM 16559*); **(53)** La Esperanza, 13°10'48.0"S, 71°36'36.0"W, 2880 m (MUSM 19602*); **(54)** Paucartambo, Pillahuata, 13°9'36.0"S, 71°34'12.0"W, 2600 m (MUSM 11753).