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Systematics of Small *Anoura* (Chiroptera: Phyllostomidae) from Colombia, with Description of a New Species

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Abstract

We analyzed the morphological variation of short tailless bats, *Anoura*, from Colombia in order to determine their phylogenetic affinities and to define their geographic structure. Our analysis confirmed the presence of *A. caudifer aequatoris* (Lönnberg 1921) as well as *A. luismanueli* (Molinari 1994) in Colombia and delimited their distributions in the country. Based on morphological and distributional differences between *A. caudifer caudifer* and *A. c. aequatoris*, we proposed the elevation of *A. aequatoris* to specific level. As a result of our morphological and geographic analyses we documented the presence in Colombia of an undescribed species of *Anoura*, *A. cadenai*, which is described in the present work.

Key words: *Anoura aequatoris*, *Anoura cadenai*, *Anoura caudifer*, *Anoura luismanueli*, bats, Colombia, phylogeography

Resumen

Se analizó la variación morfológica de poblaciones de los murciélagos pequeños sin cola del género *Anoura* en Colombia con el fin de determinar sus afinidades filogenéticas y definir su estructura geográfica. Nuestro análisis confirmó la presencia tanto de *A. caudifer aequatoris* (Lönnberg 1921) como también de *A. luismanueli* (Molinari 1994) en el país a la vez que se delimitan sus distribuciones dentro del territorio nacional. Basados en las diferencias halladas en términos morfológicos y de distribución entre *A. caudifer caudifer* y *A. c. aequatoris* proponemos la elevación de *A. aequatoris* al nivel de especie. Como resultado de nuestros análisis morfológicos y geográficos se documentó la presencia de una nueva especie de *Anoura*, *Anoura cadenai*, para Colombia, cuya descripción es incluida en este trabajo.

Palabras claves: *Anoura aequatoris*, *Anoura cadenai*, *Anoura caudifer*, *Anoura luismanueli*, Colombia, filogeografía, murciélagos

INTRODUCTION

Nectarivorous bats of the genus *Anoura* Gray 1838 (Phyllostomidae: Glossophaginae) presently represent six recognized species: *A. caudifer* Geoffroy (1818), *A. geoffroyi* Gray (1838), *A. cultrata* Handley (1960), *A. latidens* Handley (1984), *A. luismanueli* Molinari (1994), and *A. fistulata* Muchhala et al. (2005). With the exception of *A. fistulata* and *A. luismanueli*, all *Anoura* species have been recorded within Colombia (Muñoz 2001). Although the presence of both *A. luismanueli*, described from Venezuela, and *A. fistulata*, described from eastern Ecuador, has been suggested in Colombia (Molinari 1994; Muñoz 2001; Muchhala 2005), no formal study has confirmed their presence in Colombia. These two species are morphologically similar to *A. caudifer*, which exhibits the widest distribution within the genus in both Colombia (Muñoz 2001) and the Neotropics (Koopman 1981). Nonetheless, the habitat specificity and elevational distribution required by *A. caudifer*, a species primarily associated with high elevations, results in a smaller area of distribution than implied in range maps. Such habitat specificity often results in geographically isolated populations having reduced gene flow with contiguous population units, thus promoting differentiation. However, when morphological variation has been investigated among samples from different localities across its range of distribution, geographic structure has been difficult to determine.

Despite previous studies (Hershkovitz 1949; Tamsitt and Valdivieso 1966), the distributional range of *A. caudifer* within Colombia remains poorly investigated and phylogenetic relationships among its populations need to be clarified. Understanding the biodiversity of *Anoura* is important because bats of this genus are a key constituent of the chiropterofauna in the Andes of Colombia, which is considered one of the most threatened ecosystems of the world. The greatest complexity of the Andes occurs in Colombia, where the Andes are divided into three branches known as the Western, Central, and Eastern Cordilleras. This complexity is an important element in explaining the diversity of Colombian Andean fauna (Rangel 2000).

Distribution of Anoura caudifer *in the Neotropics*.—*Anoura caudifer* (Geoffroy 1818) inhabits the hilly and mountainous areas of the tropical part of South America, the lowlands of Peru, Ecuador, and Bolivia (Koopman 1981; Simmons 2005), but it is absent or rare in the lowlands of the Colombian and Venezuelan Llanos, the Brazilian Cerrados, and part of the Amazon basin (Tamsitt and Valdivieso 1966; Taddei 1975; Koopman 1981; Dois Reis 1984; Marques 1985; Ojeda and Mares 1989; Patterson et al. 2003; Simmons 2005).

Two subspecies have been recognized within the range of distribution of *A. caudifer*: *A. c. caudifer* (Geoffroy 1818) and *A. c. aequatoris* (Lönnberg 1921). *Anoura c. caudifer* was described from near Rio de Janeiro (Geoffroy 1818) and its distribution was extended to Colombia and Venezuela by Sanborn (1933, 1938, 1941) and to Surinam by Husson (1962). *Anoura c. aequatoris* was described from two individuals collected in Ilambo, Gualea, western Ecuador (Lönnberg 1921). Sanborn (1933) extended the distribution of *A. c. aequatoris* to Peru based on specimens collected in Vitoc, Junín, but erroneously reported the Valle de Vitoc to be on the western side of the Andes, when actually it is situated on the eastern versant. Cabrera (1957) agreed with Sanborn (1938) about the occurrence of *A. c. aequatoris* in both Ecuador and Peru.

Anoura caudifer *in Colombia*.—The first Colombian specimens of *Anoura caudifer* reported in the literature were collected in the Department of Cundinamarca, along the Eastern Cordillera (Sanborn 1938). Additional specimens were reported from Cúcuta, Department of Santander, from the southwestern Andes from Popayán, Department of Cauca (Sanborn 1941). Later, Hershkovitz (1949) extended the distribution of *A. caudifer* to the Colombian Caribbean Region (Pueblo Bello and Sierra Negra, Department of Magdalena). Hershkovitz (1949) classified samples from northern Colombia as *A. c. caudifer* but did not compare these to *A. c. aequatoris*. In spite of the detailed descriptions of Colombian *A. caudifer* by Sanborn (1938) and Hershkovitz (1949), a comprehensive analysis of the taxonomic relationships and distributional and ecological patterns within Colombia was not completed.

In the description of *Anoura c. aequatoris*, Lönnberg (1921) noted that specimens of *A. c. caudifer* were larger than specimens of *A. c. aequatoris*, and used the length of the fourth and fifth metacarpals as diagnostic for differentiating between these two subspecies. In a review of the morphology of the genus *Anoura*, Sanborn (1933) agreed with Lönnberg and also was able to separate *A. c. caudifer* from *A. c. aequatoris* based upon skull and forearm lengths. Comparative skull, forearm, and digit lengths reported as separating these two subspecies are presented in Table 1.

In contrast, Tamsitt and Valdivieso (1966) suggested that *A. caudifer* from throughout South America belonged to a single subspecies. In their analysis, specimens from the Andes of Colombia, Ecuador, Peru, and Venezuela were not significantly different from those from the Amazon basin of Brazil, Peru, and Ecuador. Tamsitt and Valdivieso (1966) also concluded that size was not a diagnostic character for geographic groups within *A. caudifer* because large specimens with forearms > 36 mm were widely distributed in Brazil, Colombia, Ecuador, Peru, and Venezuela. Similarly, individuals of *A. caudifer* with the shortest skulls (21.5-22.4 mm) were found partially overlapping the distribution of individuals with longest skulls (22.5-23.3 mm) in Brazil, Colombia, and Venezuela. However, the conclusions of Tamsitt and Valdivieso (1966) need to be revisited due to small sample sizes, small number of geographic samples, and failure to test for sexual variation. In addition, at the time Tamsitt and Valdivieso's paper was published, smaller individuals that could correspond to *A. luismanueli* also were included within *A. caudifer* (Molinari 1994), resulting in a wider range of morphometric variation.

Taking into account these observations, the widespread distribution of *A. caudifer* in Colombia (Koopman 1981), the basal phylogenetic position of *Anoura* within the Glossophaginae (Baker et al. 2000; Wetterer et al. 2000), and the great complexity of the Colombian mountainous system, greater diversification could be expected among *A. caudifer* populations in Colombia than suggested in the literature. These factors in combination with the evidence of morphometric differences among *A. caudifer* (sensu lato) populations were the motivational force of the present study.

The main objectives of this work were: 1) to test the existence of morphological variation among samples of *A. caudifer* from Colombia, 2) to define its geographic structure, and 3) to clarify differences between *A. caudifer* and other small species of *Anoura* in Colombia.

Table 1. Morphometric differences used as diagnostic characters between A. c. aequatoris *and* A. c. caudifer.

Characters	*Anoura c. aequatoris*	*Anoura c. caudifer*	Author
Skull length	22.5	23 – 23.5	Sanborn (1933)
Forearm length	34.3 – 35.9	35 – 36.3	Sanborn (1933) Lönnberg (1921)
4th metacarpal	3 mm shorter in *A. c. aequatoris* than in *A. c. caudifer*		Lönnberg (1921)
5th metacarpal	2 mm shorter in *A. c. aequatoris* than in *A. c. caudifer*		Lönnberg (1921)

METHODS

The Morphometric Isolines technique was used to visualize morphological variation suspected to be associated with geographic variation. The technique consists of the generation of an interpolated surface from georeferenced sample points (collecting localities of *A. caudifer* in Colombia) that are associated with a continuous variable (skull greatest length) by the application of a geographic interpolation method (Inverse Distant Weighted interpolation method, available at ArcGIS 9.0). Contour lines representing the geographic variation of the variable of interest were then derived by the application of the Contour tool of

the Spatial Analyst extension of ArcGIS 9.0. *Anoura caudifer* groups suggested by the Morphometric Isolines were used as hypothetical geographic morphogroups in Colombia. Specimens used in the analysis are deposited in the collections of the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia, Bogotá (Table 2).

In order to test for the statistical significance of geographic morphogroups suggested by the analysis of Morphometric Isolines, a discriminant analysis function of 13 post cranial and 13 skull measurements of 33 *A. caudifer* adult males from the localities used in the analysis of Morphometric Isolines was performed. Measurements used for the discriminant analysis are the same as those reported by Molinari (1994) and are listed in the Appendix. The discriminant function used was written in MATLAB and is available at: www.biol.ttu.edu/strauss/Matlab/Matlab.htm. Due to the existence of missing data within the sample (3.03%), the "missem" MATLAB function was applied to find the most likely values for those missing data. To determine the taxonomic status of Colombian specimens, specimens in each proposed geographic group were compared and contrasted against the descriptions of all small *Anoura* taxa.

Table 2. Sampling localities of A. caudifer *specimens deposited at the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia, Colombia.*

Group	ICN	Department	Locality	Altitude
1	5493	Cundinamarca	Tena, Pedro Palo Lake	2000 m
1	13786	Cundinamarca	Yacopi, Guadalito, Vereda	2100 m
1	13833	Meta	Acacias, Vereda Brisas del Guayaribo, Caño Chupas	1120 m
1	6603	Santander	Charalá, Virolin, left margin Oibita River	470 m
1	6605	Santander	Charalá, Virolín, left margin Oibita River	1766 m
1	6606	Santander	Charalá, Virolín, left margin Oibita River	1768 m
1	6608	Santander	Corregimiento de Virolín	1768 m
1	8123	Santander	Charalá, Virolin, left margin Oibita River	1700 m
1	8981	Santander	Charalá, Virolin, left margin Oibita River	No data
1	15295	Santander	Charalá, Virolin, left margin Oibita River	1750 m
2	8031	Antioquia	San Luis, Vereda San Pablo, San Antonio Creek	No data
2	98484	Antioquia	Jardin Vereda "La Linda", La Linda Creek	2000 m
2	16455	Caldas	Samaná, Vereda La Miel, nearby Tasajos camp	2100 m
2	14309	Caldas	Manizales, Guayabal Creek, Jardín de Mariposas	1120 m
2	16729	Risaralda	Pueblo Rico, road to La Boca Toma	470 m
2	11492	Risaralda	Mistrató, Corregimiento de Puerto de Oro	1766 m
2	11747	Risaralda	Santuario, Vereda El Campamento	1768 m
2	11832	Risaralda	Puerto Rico, Vereda Ciató, Los Pueblos Creek	1768 m
2	11868	Risaralda	Mistrató, 1.5 Km E San Antonio del Chairí	1700 m
2	12296	Risaralda	Mistrató, Vereda Empalado, Empalado Creek	No data
3	7615	Huila	Belén, Hacienda Meremberg	1800 m
3	8438	Huila	La Plata, Vereda El Patico, El Aguacatal Creek	2360 m
3	4393	Valle	Pichinde aprox 20 Km SE of Cali	No data
3	4391	Valle	2 Km N of Pance	1800 m
3	4400	Valle	2 Km N of Pance	1800 m
3	8892	Valle	Calima, Vereda Río Azul, left margin Calima River	No data
3	8893	Valle	Calima, Vereda Ríobravo, E Rio Bravo. Calima III	510 m
3	8894	Valle	Calima, Vereda Ríobravo, E Rio Bravo. Calima III	No data
3	9151	Valle	Calima, Darien, Río Bravo	No data
3	9152	Valle	Calima, Darien, Río Bravo	1000 m
3	9153	Valle	Calima, Darien, Río Bravo	1000 m
3	9154	Valle	Calima, Darien, Río Bravo	1000 m

RESULTS AND DISCUSSION

According to our analysis of morphometric isolines (Fig. 1), three distinct morphological units of *Anoura caudifer* (sensu lato) were revealed along the Colombian Andes. The three groups suggested by the analysis of Morphometric Isolines were confirmed by our discriminant analysis as follows: Group 1, populations from the Eastern Cordillera; Group 2, populations from the northern range of the Central and Western Cordillera; and Group 3, populations from the southern portion of the Western Cordillera (Table 2 and Figs. 1 and 2). Mean values of skull and forearm lengths of the three groups of *A. caudifer* differed (Table 3). Forearm and skull length were two of the criteria Sanborn (1933) used to separate *A. c. caudifer* and *A. c. aequatoris* (Table 3). The three geographic morphogroups are described in detail below.

Group 1: The smallest Anoura.—Specimens within Group 1 (Figs. 1 and 2) represent individuals with the smaller values for the measurements analyzed among samples in the present study. The smallest taxa within the genus are *A. luismanueli* from the Ven-

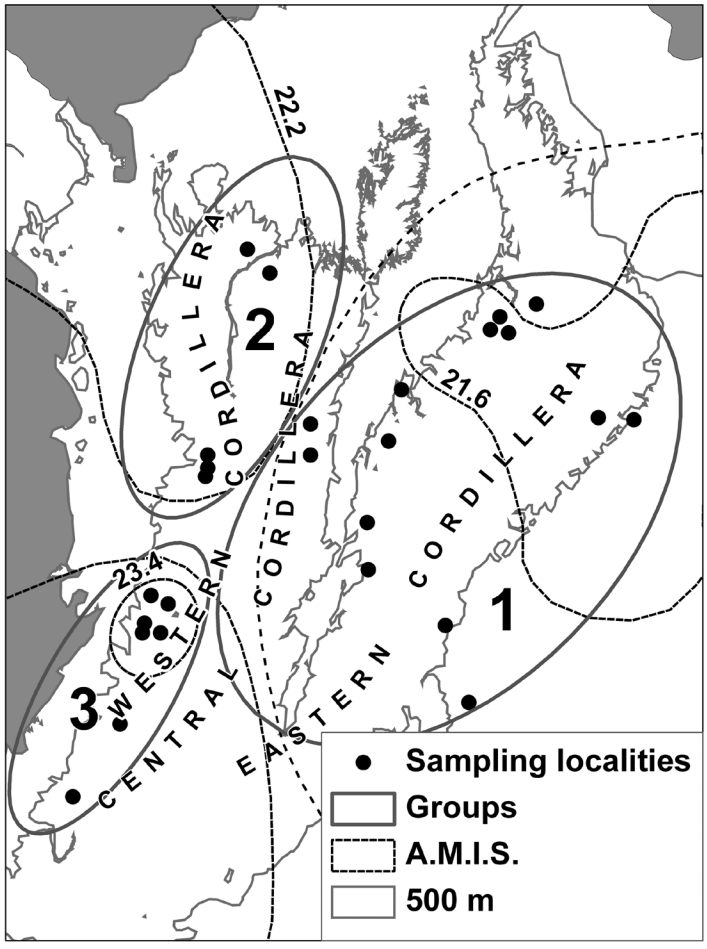

Figure 1. *Anoura caudifer* geographic groups (solid lines) used as hypotheses in our Discriminant Analysis function generated based upon the Analysis of Morphometric Isolines (A. M. I. S.) of geographic skull size variation (dashed lines).

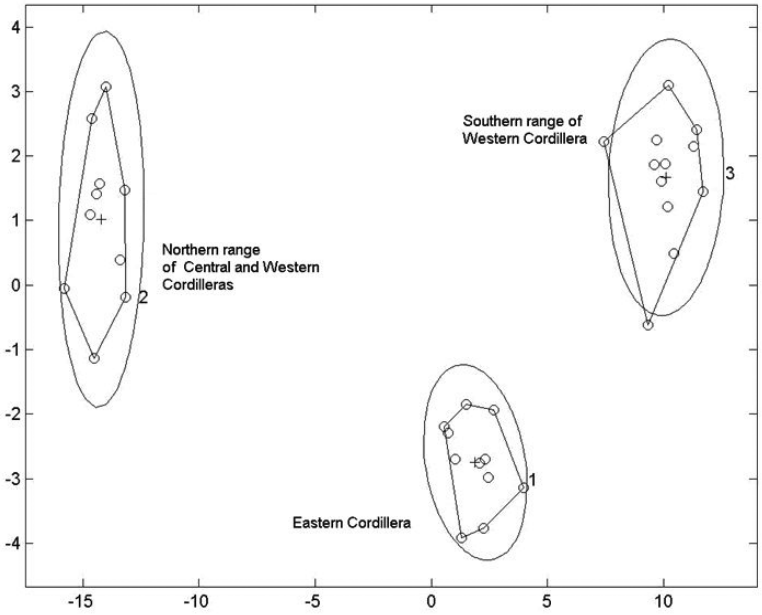

Figure 2. Scatter plot of the discriminant analysis function of *A. caudifer* specimens from Colombia documenting the pattern of morphometric variation by Andean Cordilleras.

Table 3. Comparison of ranges of skull and forearm length among A. c. caudifer *and* A. c. aequatoris *(Sanborn 1933), the holotype of* A. c. aequatoris *(Lönnberg 1921),* A. luismanueli *(Molinari 1994), and the three proposed geographic groups for Colombian* A. caudifer *(this study). Mean values are presented in parentheses below the ranges.*

	Skull length (mm)	Forearm length (mm)
Anoura c. caudifer	23.0 – 23.5	35.0 – 36.3
Anoura c. aequatoris	22.5	34.3 – 35.9
Anoura luismanueli	20.5	34.1
Eastern Cordillera	20.68 – 22.3 (21.56)	34.06 – 36.52 (35.18)
Northern range, Central and Western Cordillera	21.35 – 23.32 (22.14)	34.08 – 37.41 (35.49)
Southern range, Western Cordillera	21.29 – 23.81 (23.11)	34.86 – 38.1 (36.88)

ezuelan Andes (Molinari 1994) and the subspecies *A. c. aequatoris* described from the eastern Andes of Ecuador (Lönnberg 1921). It is difficult to establish differences between *A. c. aequatoris* and *A. luismanueli* because Molinari (1994) did not compare them, and diagnostic characters used by the authors did not provide enough details to confidently assign one of these names. Apparently *A. luismanueli* could be confused with *A. caudifer* as some of the measurements overlap (Molinari 1994), and those used as diagnostic may be influenced by geographic variation (Tamsitt and Valdivieso 1966). Besides size, few characters are useful to separate *A. luismanueli* from *A. caudifer*, as suggested by Molinari (1994). Molinari (1994) described the interfemoral membrane of *A. luismanueli* as moderately haired dorsally and densely furred medially on the ventral surface, in contrast with the virtually naked interfemoral membrane of *A. caudifer*.

To properly evaluate the characteristics of the uropatagium that may be useful to separate *A. luismanueli* from *A. c. aequatoris*, we analyzed six specimens from Ecuador deposited at the National Museum of Natural History (USNM 513436, 548070-71, 548075-77, and 548079-80), all of them being small individuals. Specimens within this series were characterized by dark coloration, a medium to narrow interfemoral membrane (3.0-3.5 mm), which is always densely furred with a fringe of hairs extending along the margin of the uropatagium. This trait clearly contrasts in length and density with the fringe present on the edge of the uropatagium of *A. caudifer* from Sao Paulo, Brazil, close to its type locality (Fig. 3). We considered those Ecuadorian individuals as typical *A. c. aequatoris* in our comparisons because they matched the description and their collecting localities were relatively closer to the type locality. In addition, we contrasted these *A. c. aequatoris* against two paratypes of *A. luismanueli* (USNM 581898 and 581899). Despite the latter specimens sharing the furred uropatagia present in *A. c. aequatoris*, the disposition and length of the hairs on the surface and the edge of the uropatagium was consistently different between *A. luismanueli* and *A. c. aequatoris*. Hairs on the edge of the uropatagium of *A. c. aequatoris* specimens were longer and denser mid ventrally than those found in *A. luismanueli*. At the same time, the uropatagia of the two *A. luismanueli* were more densely furred and hairs on the edge of the uropatagium were longer than those of *A. caudifer* from Brazil. Characteristics of the uropatagium are extremely variable within *A. caudifer* at least among the Colombian specimens included in the present work. Nonetheless, lightly haired uropatagia predominated among samples from Colombia, and densely furred uropatagia were common among small *A. caudifer* specimens in our Group 1.

A male specimen (ICN 13786) included in Group 1 (as well as a female [ICN 13787] not included in our discriminant analysis) from Yacopí, Cundinamarca, exhibits the free edge of the interfemoral membrane with a dense to sparse fringe of hairs on the margin, as well as a densely to sparsely furred mid ventral uropatagium, and externally noticeable tail. In addition, the latter specimens also presented the edge of the interfemoral membrane in a semicircular shape as mentioned in the *A. luismanueli* description (Molinari 1994). Based on their measurements and uropatagium characteristics, these two specimens appear to represent *A. luismanueli*. Nonetheless, the other eight individuals in Group 1 shared only some of the characteristics of the interfemoral membrane of *A. luismanueli*, varying in density and disposition of the hairs on the edge of the uropatagium. The ranges of the 13 measurements analyzed for both males and females within Group 1 overlapped the ranges presented by Molinari (1994) for *A. luismanueli* and coincided with 10 of the 12 measurements presented by Lönnberg (1921) in his description of *A. c. aequatoris*. When specimens of Group 1 were contrasted against the descriptions of both *A. c. aequatoris* (Lönnberg 1921) and *A. luismanueli* (Molinari 1994), they appeared to share discrete characteristics included in both descriptions, but features of their uropatagia closely resembled those exhibited by the two paratypes of *A. luismanueli*.

The combination of characters exhibited by samples of *A. caudifer* from the Eastern Cordillera in Colombia suggested that samples within Group 1 corresponded to *A. luismanueli*. An additional set of 21 *A. caudifer* females from the eastern side of the country from Charalá (ICN 6602, 6604, 6607, 8122, 8124, 8981), San José de Suaita (ICN 15296, 15298), Encino (ICN 17520-23, 17525-27, 17531, 17552-53), department of Santander and San Antonio de Tena (ICN 5272-73, 5492-93), department of Cundinamarca also were considered representatives of *A. luismanueli* populations in Colombia.

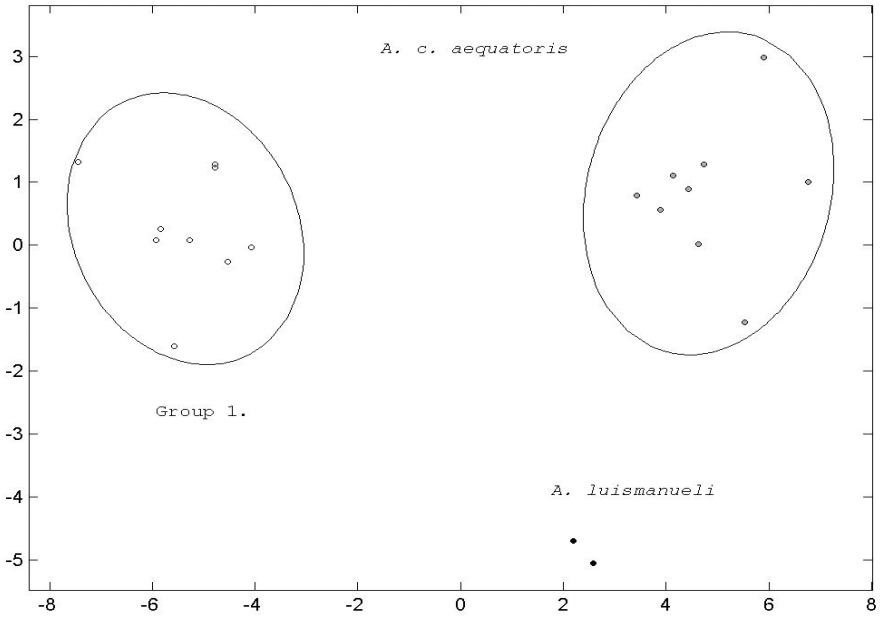

Figure 3. Discriminant function showing differences among small *Anoura* from Colombia included in Group 1 and specimens of *A. c. aequatoris* and *A. luismanueli*.

The presence of a tail, one of the diagnostic characters pointed out by Molinari (1994), was also variable within this subset of small individuals. In contrast to typical *A. luismanueli*, Lönnberg (1921) mentioned the absence of a tail as one of the characteristics of the only two specimens of *A. c. aequatoris* used in the description. The validity of tail presence as a good character to separate *A. caudifer* subspecies is still debatable and unfortunately our data do not provide enough information to clarify the evolutionary significance of tail presence within Colombian *A. caudifer*.

Group 2: Anoura caudifer *(sensu stricto) in Colombia.—Anoura caudifer* (sensu stricto) in Colombia includes all specimens within the geographic Group 2 (Figs. 1 and 2) that represents samples from the northern range of the central and western cordilleras with intermediate values for both skull and forearm lengths (Table 3). In addition to specimens of Group 2, some individuals from Group 3 were also identified as *A. caudifer*. Therefore, *A. caudifer* (sensu stricto) appears to be widely distributed across the central and western Andes in Colombia as well as the western versant of the Eastern Cordillera, where it is replaced by the smaller *A. luismanueli*. Southward, *A. caudifer* (sensu stricto) coexists with a larger form of *Anoura* and the small *A. aequatoris*.

Group 3: Small Anoura *from Group 3.*—Although Group 3 from the southwestern range of the Colombian Andes exhibited the largest average values for forearm and skull lengths, some individuals included within this range were relatively small. Populations of *A. caudifer* from the southwestern Colombian Andes were closer to the type locality of *A. c. aequatoris* Ecuador (Lönnberg 1921). The known distribution of *A. c. aequatoris* is restricted to a few localities from Ecuador and Peru; the subspecies is unknown in Colombia. However, Alberico et al. (2000) and Muñoz (2001) suggested the presence of *A. c. aequatoris* in Colombia, although no Colombian specimen has been reported. Some specimens from the southern part of the country, including a male from the department of Huila (ICN 7615) from Group 3 in our analysis, and specimens from Nariño (ICN 13634, 13635, 13636) and Valle del Cauca (ICN 8438) not included in our discriminant analysis, are small dark animals with no evidence of

tail, a densely furred uropatagium, and a long fringe of hairs along the edge. Although this subset from southern Colombia is represented by specimens with darker pelage than specimens of *A. c. aequatoris* from Ecuador, they are suggested to be representatives of that taxon in Colombia.

Taxonomic remarks.—A discriminant analysis including our typical *A. c. aequatoris* from Ecuador and Group 1 from eastern Colombia clearly separates the two groups (Fig. 3). We consider these documented differences in size between *A. c. caudifer* and Group 1, and the unique features of the uropatagium of *A. c. aequatoris* (Fig. 4b), as valid evidence to separate it from *A. caudifer*, thus supporting the recognition of *A. aequatoris* at the specific level. Figure 5 represents the distribution of identified taxa in this work.

A large and undescribed Anoura *from Colombia*.—Based only on skull length and forearm length, large individuals from the southwestern Colombian Andes did not appear to represent *A. c. aequatoris* despite their proximity to the type locality. In a comparison of skulls of *A. caudifer* from southwestern Colombia with skulls of *A. c. caudifer* from Sao Paulo, Brazil, the specimens from Colombia were distinctly larger and more massive.

Figure 4. a: Comparisons between skulls of *A. aequatoris* from Napo, Ecuador 68368 FMNH (left) and *A. caudifer* from Sao Paulo, Brazil 94700 FMNH (right). b: Uropatagia of *A. aequatoris* from Ecuador NMNH 574512 (left), and *A. caudifer* from Sao Paulo, Brazil 94700 FMNH (right).

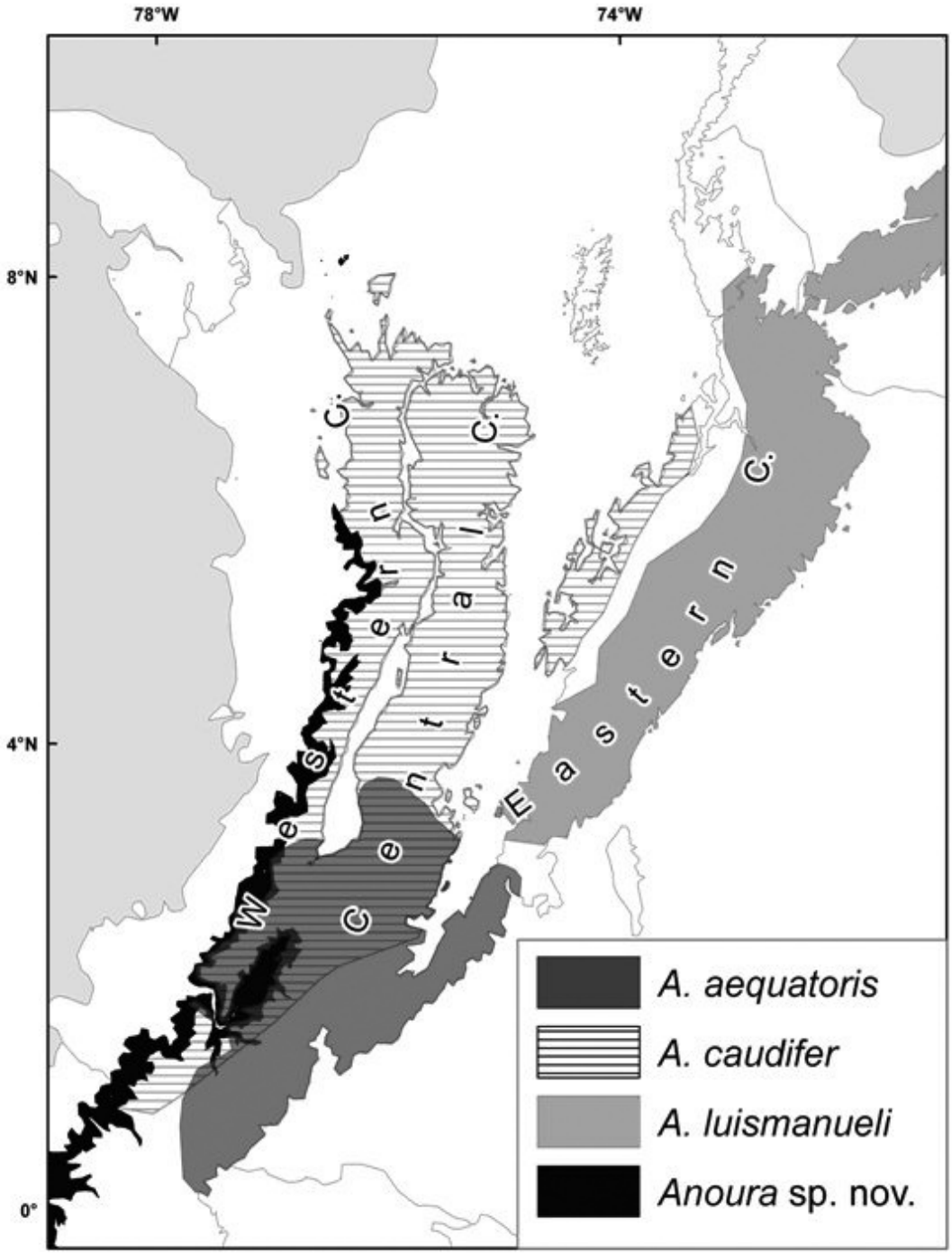

Figure 5. Distribution of small *Anoura* taxa identified in the present work.

In August 2000, the senior author reviewed the specimens deposited at the mammal collections of the Instituto de Ciencias Naturales (ICN). Several specimens classified as *A. caudifer* from southwestern Andes of Colombia were tentatively assigned as *A. cultrata* due to their larger size. These specimens all have a sulcus in the upper canines. Large size and the presence of the sulcus on the upper canines are two of the characters mentioned by Handley (1960) in his description of *A. cultrata*. However, other cranial characteristics are more similar to *A. caudifer* than to *A. cultrata*. These characteristics were also noted among specimens identified as *A. caudifer* from Pance, Valle del Cauca, Colombia deposited at the mammal collections of the USNM of the Smithsonian Institution.

Morphometry has been an important criterion used to separate species within *Anoura* (Handley 1984). The extent of variation for the characters we have analyzed in this study is similar to or exceeds that used to separate other species. Based on our morphometric analysis and other morphological evidence, we propose that the *A. caudifer*-like specimens from southwestern Colombian Andes represent an unrecognized taxon, which we describe below.

***Anoura cadenai*,** new species

Holotype.—Instituto de Ciencias Naturales (ICN 9152), an adult male, prepared as a museum study skin, with cranium and mandibles (Fig. 6), collected on 10 February 1984 by Dr. Alberto Cadena.

Type locality.—Field notes and original labels of specimens in the ICN collections indicate captures of *A. cadenai* took place between the municipios of Calima and Restrepo near the Rio Bravo at 1000 m elevation at 3º56′03″N, 76º29′18″W. These two municipios are located on the Calima River basin, which includes a transversal valley that runs almost perpendicular to the Western Cordillera of the Colombian Andes. Temperature in the area averages 18.4ºC and the mean annual precipitation approximates 1,050 mm. The Calima River basin includes different habitat zones from broad, level tropical lowlands up to the Páramo habitat at upper elevations (Instituto Geográfico Agustin Codazzi 1996). Most of the region is mountainous, with some level areas where three important rivers are present: Rio Azul, Rio Bravo, and Rio Calima. The area includes a mosaic of landscapes that are fragmented patches of agricultural plots, preserved forests, and xerophytic areas. The type locality is within a well-preserved Andean forest characterized by giant trees covered by epiphytes (Rangel 1987).

Distribution.—*Anoura cadenai* is thought to occur along the western versant of the southwestern Colombian Andes. In Colombia, the distribution of this species extends along an altitudinal belt between 800 and 1400 m. This altitudinal range constitutes the eastern boundary of the Chocó biogeographic province including the districts of Barbacoas, Micay, and Atrato-San Juan (Fig. 7).

Paratypes.—Other specimens in the type series include five males deposited in the collections of the Instituto de Ciencias Naturales (ICN 9151, 9153, and 9154 from Río Bravo, and ICN 8893 and 8894 from Pance, Valle del Cauca), five males deposited at the National Museum of Natural History of the Smithsonian Institution (USNM 486670, 48369, 48368, 48366, and 123442), and two females (USNM 48371 and 48367) collected by Arata and Thomas in 1966 from Pance, 20 km southwest Cali, Department of Valle del Cauca.

Description.—Coloration Blackish Brown-3 and Black (Ridgeway 1912) throughout; individual dorsal hairs are pale grayish on basal two thirds, brown tips; those of underparts black to base. Pelage short and crisp; interfemoral membrane narrow, with some hairs, external tail not visible. In size, averaging larger in body and cranial dimensions when compared with *A. caudifer* and *A. luismanueli*, but smaller than the other species within the genus. The skull is most like *A. caudifer* sensu stricto, although it resembles the more massive and square shaped skull of *A. cultrata*. Braincase tapered anteriorly; broad and heavy rostrum; zygomata complete but slender (broken in most specimens); braincase raising smoothly; broad and rounded occipital region; outer upper incisor enlarged; upper canine enlarged and projected, roughly triangular in cross-section at the base, with distinct anterointernal, anteroexternal, and posterior basal cusps; internal face anteroposteriorly concave, and anterior face flat, with a longitudinal sulcus from base of crown to near tip that resembles the sulcus of canines of *A. cultrata* but less prominent (Fig. 6).

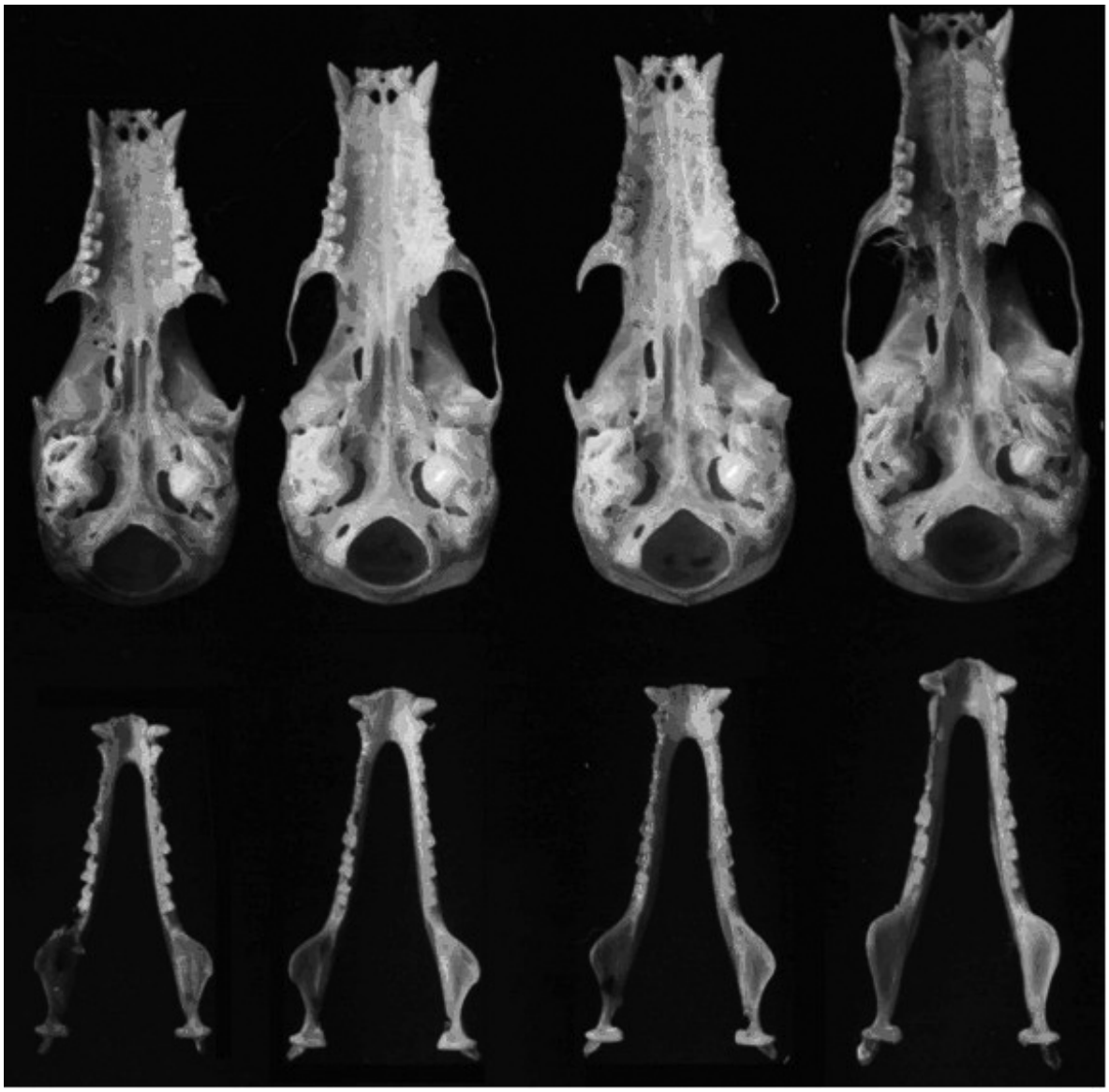

Figure 6. Skull and mandible comparison among sympatric species *A. caudifer*, *A. cadenai* (paratype ICN 9153), *A. cadenai* (holotype ICN 9152), and *A. cultrata* (left to right, respectively), at Calima, Valle del Cauca, Colombia.

Comparisons.—At the type locality, *Anoura cadenai* is sympatric with two other species of *Anoura*, *A. caudifer*, and *A. cultrata*. Although in general terms *A. cadenai* closely resembles *A. caudifer*, it shares characteristics with both *A. caudifer* and *A. cultrata*. *Anoura cadenai* is easily separated from *A. caudifer* y the combination of the following characteristics: larger size, lack of tail, and upper canines with a longitudinal sulcus. Compared to *A. cultrata*, *A. cadenai* is considerably smaller and its skull is much less robust. The upper canines of *A. cadenai* are smaller in comparison with the canines of *A. cultrata*, and the tail is absent. *Anoura cadenai* and *A. fistulata* exhibit a similar range of variation of the measurements analyzed in this work. However, *A. cadenai* appears to be smaller and less variable in size, in contrast to the wide range of variation in *A. fistulata* (Table 4). *Anoura cadenai* can also be distinguished externally by the absence of tail. Although we do not have fluid preserved material of *A. cadenai*, a detailed analysis of dry skins indi-

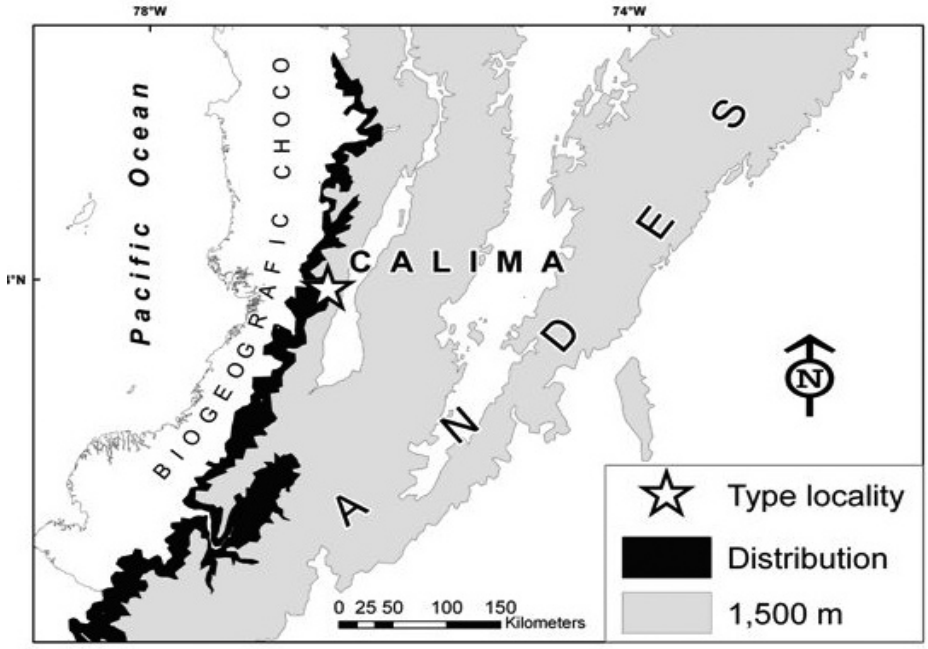

Figure 7. Type locality and potential distribution of *A. cadenai* in Colombia.

Table 4. Ranges of variation among species analyzed. Measurements labeled with (*) come from the original description.

External measurements	***A. luismanueli ****	**Small *A. caudifer***	***A. c. aequatoris***	***A. caudifer***	***A. cadenai***	***A. fistulata***
Total length	58.8 - 65.0	52.0 - 62.5	53.0 - 56.0	60.0 - 64.0	59.0 - 61.0	no data
Hind foot length	3.0 - 6.0	0.0 - 3.5	0.0	3.0 - 5.0	0.0	7.0 - 11.5
Ear length	10.0 - 12.0	8.17 - 13.0	14.0*	11.0 - 13.0	11.0 - 15.0	12.3 - 17.0
Tragus length	4.5 - 6.0	no data	no data	no data	no data	no data
Forearm length	33.6 - 33.9	34.06 - 36.52	no data	34.0 - 37.0	36.12 - 36.97	35.40 - 40.0
Tibia length	10.7 - 12.8	10.48 - 13.23	10.0	no data	no data	no data
Calcar length	2.5 - 3.5	2.64 - 4.47	no data	no data	no data	no data
Third digit:						
Metacarpal length	30.0 - 35.2	33.91 - 36.69	37.0	no data	36.05 - 36.99	no data
Length first phalanx	10.6 - 12.6	10.8 - 12.47	12.2*	no data	12.1 - 12.58	no data
Fourth digit:						
Metacarpal length	29.6 - 33.9	33.1 - 34.67	34.5	no data	32.83 - 35.01	no data
Length first phalanx	7.7 - 9.5	7.04 - 9.43	9.5*	no data	8.45 - 9.66	no data
Fifth digit:						
Metacarpal length	24.0 - 29.5	27.14 - 29.28	30.0	no data	29.29 - 30.41	no data
Length first phalanx	6.5 - 7.9	7.29 - 8.42	7.5*	no data	7.46 - 8.2	no data
Cranial measurements	***A. luismanueli ****	**Small *A. caudifer***	***A. c. aequatoris***	***A. caudifer***	***A. cadenai***	***A. fistulata***
Greatest skull length	20.4 - 29.5	27.14 - 29.28	22.5	21.2 - 22.5	23.1 - 23.8	22.9 - 26.1
Condylobasal length	19.6 - 20.9	17.71 - 19.34	22.0	20.5 - 21.5	19.8 - 20.79	22.3 - 25.1
Zygomatic width	8.3 - 9.4	no data	10.0	8.0 - 9.8	9.71 - 10.27	9.4 - 10.3
Greatest breadth of brain case	8.5 - 9.2	8.4 - 9.47	9.4	8.3 - 9.0	8.4 - 8.82	9.2 - 9.7
Interorbital breadth	4.1 - 5.4	4.35 - 4.73	5.0*	4.2 - 4.6	4.46 - 4.58	4.4 - 5.1
Maxillary tooth row	7.0 - 7.9	7.36 - 8.23	8.2	7.5 - 8.3	7.78 - 8.52	8.1 - 9.6
Breadth across the m2	5.0 - 5.7	5.3 - 5.8	5.5*	no data	no data	4.9 - 5.9

cates that the lower lip of *A. cadenai* does not have any evidence of the adaptations described for *A. fistulta* (Muchhala et al. 2005). *Anoura cadenai* can be separated from *A. fistulata* by the presence of a sulcus in the upper canines and by its upper incisors that are in contact when viewed from below, in contrast to the space present in *A. fistulata*. The occipitals in *A. fistulata* extend farther back (lateral view) in comparison with the flatter occipital region of *A. cadenai*. The mastoid region of *A. fistulata* is broader than the mastoid region in *A. cadenai*, and *A. fistulata* has a more conspicuous lambdoid crest. From a ventral view, *A. cadenai* differs from *A. fistulata* due to the presence of pointed projections of the palatal bone. In addition, *A. cadenai* is characterized by a reduced or absent keel at the mandible symphisis in comparison to the well developed mandible symphisis in *A. fistulata*; the presence of a well developed keel in *A. fistulata* is likely to be associated with the lower lip and tongue adaptations (Muchhala et al. 2005). The holotype of *A. fistulata* was collected on the eastern versant of the Ecuadorian Andes where the species seems to be widely distributed (Muchhala et al. 2005). Out of the nine collecting localities mentioned in the description of *A. fistulata*, just two of them (Bellavista and Guajalito) are located on the western versant of the Ecuadorian Andes. The Andes of Ecuador and Colombia have been suggested to be an effective barrier to gene flow between bat populations from the eastern and western versants (Baker et al. 2004). Due to similarities in size ranges between *A. fistulata* and *A. cadenai*, a revision of specimens of *A. fistulata* from western Ecuador is suggested to clarify their affinities.

Measurements.—Table 5 presents the external and cranial measurements of the holotype and three paratypes.

Etymology.—We name *Anoura cadenai* after Dr. Alberto Cadena, curator of the collection of mammals of the Instituto de Ciencias Naturales, who has dedicated his life to the study of the Colombian mammalian fauna. Dr. Cadena has not only contributed to the knowledge of Colombian mammals but also has mentored several generations of Colombian mammalogists. Both authors have had the privilege to share Dr. Cadena's knowledge and friendship.

Remarks.—At the type locality, *A. cadenai* occurs in sympatry with *A. caudifer*. Other bat species collected from the same locality include the Emballonurids *Balantiopteryx infusca* and *Peropteryx kappleri*, the furipterid *Furipterus horrens*, and the Phyllostomids *Artibeus jamaicensis*, *A. lituratus*, *Carollia perspicillata*, *Chiroderma salvini*, *Dermanura rava*, *D. glauca*, *D. phaeotis*, *Desmodus rotundus*, *Lonchophylla robusta*, *Mimon crenulatum*,

Table 5. External and cranial measurements of Anoura cadenai *holotype (*) and ICN paratypes. External and cranial measurements 1-26 are described in the Appendix.*

			External Measurements												
ICN	**Sex**	**Age**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
9152*	Male	Adult	59	0	11	12	36.85	12.04	36.46	12.37	35.01	8.45	30.41	7.96	4.9
9151	Male	Adult	60	0	10	14	36.97	12.43	36.99	12.11	32.83	9.66	29.91	7.98	4.22
9153	Male	Adult	60	0	10	12	36.7	11.28	36.05	12.1	35	8.48	30.07	8.2	4.33
9154	Male	Adult	61	0	10	10	36.12	10.19	36.46	12.58	34.14	8.57	29.29	7.46	5.33
	Average		**60**	**0**	**10**	**12**	**36.66**	**11.49**	**36.49**	**12.29**	**34.25**	**8.79**	**29.92**	**7.9**	**4.695**
			Cranial Measurements												
ICN	**Sex**	**Age**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
9152*	Male	Adult	23.8	8	12	4	4.53	9.71	8.66	9.69	4.27	20.4	ND	16.9	3.9
9151	Male	Adult	23.4	8	13	5	4.46	10.4	8.5	9.76	4.44	20.8	7.78	17.7	4.12
9153	Male	Adult	23.1	8	12	4	4.57	10.27	8.4	9.34	4.21	20.1	7.87	17.1	4.48
9154	Male	Adult	23.2	8	12	4	4.58	ND	8.82	9.66	4.33	20.1	8.52	16.4	4.2
	Average		**23.4**	**8**	**12**	**4**	**4.53**	**10.13**	**8.96**	**9.61**	**4.31**	**20.3**	**8.05**	**17.0**	**4.175**

Platyrrhinus chocoensis (endemic), *P. dorsalis*, *P. vittatus*, *Phyllostomus discolor*, *P. hastatus*, *Sturnira erythromos*, *S. lilium*, *S. ludovici*, and *Vampyressa thyone*. The Calima region, and in general the southwestern range of the Colombian Andes, is of crucial importance to the understanding of mammalian biogeography in the Neotropics. The region not only encloses one of the richest chiropterofaunas of the Neotropics but is also a center of speciation (Cadena et al. 1998). Handley (1966) described two new bat species for Colombia, *Rhinophylla alethina* and *Choeroniscus periosus* from Rio Raposo, near Buenaventura, and mentioned the biogeographic importance of the Pacific coast and Andean foot hills of northwestern Ecuador and Colombia as the continuation of a zone of endemism which extends into Panama.

CONCLUSIONS

Based on our analyses, we conclude that specimens considered to be *A. caudifer* in Colombia actually correspond to four taxa as follows: *A. caudifer* (Geoffroy 1818), *A. luismanueli* (Molinari 1994), *A. aequatoris* (Lönnberg 1921), and the new species *A. cadenai*. *Anoura caudifer* presents the broader distribution along the Colombian Andes and exists in sympatry with other *Anoura* species on the Central and Western Cordilleras. Although *A. luismanueli* and *A. aequatoris* were previously suggested in the country (Alberico 1998; Muñoz 2001), no formal analysis was conducted in order to confirm their presence in Colombia. We conclude that both taxa exist in Colombia. The distribution of *A. luismanueli* in Colombia can be extended southward to the Cordillera de Mérida in Venezuela on its eastern versant to the department of Cundinamarca, around 3°30′N being the southernmost locality for this species. Southward of 3°30′N, *A. luismanueli* is replaced by *A. aequatoris*, which extends southward from the department of Huila into Ecuador and Peru. The new species *A. cadenai* appears to be restricted to the southwestern portion of the Colombian Andes, possibly extending its distribution to northern Ecuador (Fig. 5).

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APPENDIX

List of external measurements presented in Table 5:

1) Total length, 2) Tail length, 3) Foot length, 4) Ear length, 5) Forearm length, 6) Tibial length, 7) Third digit metacarpal length, 8) Third digit phalangeal length, 9) Fourth digit metacarpal length, 10) Fourth digit phalangeal length, 11) Fifth digit metacarpal length, 12) Fifth digit phalangeal length, 13) Calcar length.

List of cranial measurements presented in Table 5:

14) Greatest skull length, 15) Cranium height, 16) Palatal length, 17) Rostrum width, 18) Post-orbital width, 19) Zygomatic width, 20) Cranium width, 21) Mastoid width, 22) Upper canine-canine distance, 23) Distance between the most anterior part of the foramen magnum and the most posterior part of the premaxillary bones (excluding incisors), 24) Mandible tooth row length, 25) Mandible length, 26) Mandible height.

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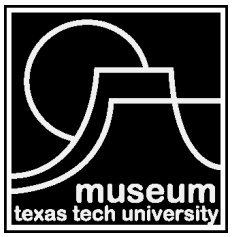

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