Original study

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Morphology and genetics concur that *Anoura carishina* is a synonym of *Anoura latidens* (Chiroptera, Glossophaginae)

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Abstract: *Anoura carishina* was described based on cranial and dental morphology, but the original analyses did not include *Anoura latidens*, a similar species of *Anoura*. We used morphological, morphometric, and genetic analyses to evaluate the taxonomic identity of *A. carishina*. We performed a principal components analysis to evaluate the correspondence between morphological and taxonomic groups for 260 specimens of large-bodied *Anoura* (*A. carishina*, *Anoura geoffroyi*, *A. latidens*, and *Anoura peruana*), and statistically analyzed traits diagnostic for *A. latidens*, including (1) morphology of the third upper premolar (P^4), (2) size of the second (P^3) and third (P^4) upper premolars, and (3) angle formed by the maxillary toothrows. We find that *A. latidens* and *A. carishina* are indistinguishable, and share several characters lacking in *A. geoffroyi*, including a P^4 with triangular shape, an under-developed anterobasal cusp in the P^3, a smaller braincase, and a shorter rostrum. Phylogenetic analyses using ultra-conserved elements infer that the holotype and two paratype specimens of *A. carishina* are paraphyletic and nested within *A. latidens*, while one paratype diagnosable by morphology as *A. geoffroyi* nests within *A. geoffroyi* samples. We demonstrate that *A. carishina* should be considered a junior synonym of *A. latidens*, updating the distribution of the latter.

Keywords: broad-toothed tailless bat; South America; systematics; taxonomy; ultra-conserved elements.

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1 Introduction

Anoura is one of the most speciose genera in the phyllostomid subfamily Glossophaginae. It is currently comprised of 11 species, although not all are widely accepted (Griffiths and Gardner 2007; Handley 1984; Jarrín and Kunz 2008; Mantilla-Meluk and Baker 2006, 2010; Pacheco et al. 2018; Tamsitt and Valdivieso 1966). The genus can be subdivided into two groups and an additional single species based on size, dental morphology, and presence/absence of a tail (Allen 1898; Griffiths and Gardner 2007; Handley 1960): a group of six tailed and small-bodied species [*A. caudifer* (Geoffroy Saint-Hilaire 1818), *A. aequatoris* (Lönnberg 1921), *A. cadenai* Mantilla-Meluk and Baker 2006, *A. fistulata* Muchhala et al. 2005, *A. javieri* Pacheco et al. 2018 and *A. luismanueli* Molinari 1994], four tailless and large-bodied species [*A. carishina* Mantilla-Meluk and Baker 2010, *Anoura geoffroyi* (Gray 1838), *A. peruana* (Tschudi 1844) and *Anoura latidens* Handley 1984], and one tailed and large-bodied species (*A. cultrata* Handley 1960) with unique lower premolar shape. Mantilla-Meluk and Baker (2010) reviewed the taxonomy of three of the four large-bodied tailless *Anoura*, recognizing *A. peruana* as a species distinct from *A. geoffroyi* and describing the new species *A. carishina* from several localities in Colombia. However, because the diagnostic characters of *A. latidens* are similar to the diagnostic characters of *A. carishina*, comparison between these species is necessary to clarify species boundaries.

Anoura carishina is known from the five specimens of the type series deposited at the Mammal Collection Alberto Cadena García at Instituto de Ciencias Naturales (ICN, Universidad Nacional, Bogotá, Colombia). Its distribution is limited to three localities: the holotype specimen ICN 14530 and paratype ICN 14531 are from Taminango,

department of Nariño (1.67°, −77.32°), in an arid valley in the western slopes of the southern Colombian Andes, two paratypes (ICN 5224, 5225) are from San Pedro de La Sierra, department of Magdalena (10.90°, −74.04°) in the Sierra Nevada de Santa Marta, a mountain system isolated from the Andes in northern Colombia, and the final paratype (ICN 5938) is from Cali, Pance, department of Valle del Cauca (3.32°, −76.63°), in the upper inter-Andean valley of the Cauca river. *Anoura carishina* was described as a large-bodied *Anoura* with the following diagnostic characters: greatest length of skull less than 24.5 mm, small canines, P^4 teeth with a wide triangular base, and complete zygomatic arches [although they are broken in several of the type series collections (Mantilla-Meluk and Baker 2010)].

Anoura latidens was described as a large-bodied species of *Anoura*, distinguishable from *A. geoffroyi* by a relatively short rostrum, an inflated braincase, nearly parallel maxillary toothrows, and smaller and more robust premolars which have a quadrangular appearance when viewed from above (Handley 1984). More specifically, Handley (1984) states that the third upper premolar (P^4) has a medial-internal cusp enclosed in the triangular base of the tooth (rather than an abruptly protruding cusp as in *A. geoffroyi*) and that the second upper premolar (P^3) possesses a reduced anterobasal cusp. The holotype is from Pico Ávila, Caracas, Venezuela, and the species has been reported for at least 14 localities in Venezuela (Handley 1976, 1984; Linares 1986, 1998) where it occupies a variety of ecosystems with an altitudinal range from 50 to 2600 m above sea level (m a.s.l.). *Anoura latidens* is also reported from a handful of localities outside of Venezuela, in Bolivia, Colombia, Guyana, and Peru (Calderón-Acevedo and Muchhala 2020; Handley 1984; Lim and Engstrom 2001; Linares 1998; Solari et al. 1999), suggesting a wide yet discontinuous distribution.

In Colombia, *Anoura latidens* has been recorded in the Andean region (eastern, central, and western mountain ranges) and the inter-Andean valleys (Alberico et al. 2000; Solari et al. 2013). The first record for the country was mentioned in the species description (Handley 1984) as collected by Nicéforo María in 1923 in San Juan de Rioseco, department of Cundinamarca, on the western slope of the Cordillera Oriental (eastern mountain range) above the inter-Andean valley of the Magdalena river at a height of 1000 m a.s.l. Later Muñoz (2001) incorrectly attributed the first record to Wilson and Reeder (1993) and added a new locality in the Cordillera Oriental in the municipality of Gramalote, department of Norte de Santander, however Muñoz did not give a catalog number for this specimen supposedly located in the Museo de Ciencias Naturales de La Salle. Two other localities were reported by Rivas-Pava et al. (2007) based on three specimens deposited at Museo de Historia Natural de la Universidad del Cauca (MHNUC-M) from the municipalities of Acevedo (department of Huila) and Argelia (department of Cauca). The most recent reported locality was Reserva Forestal Bosque de Yotoco (Department of Valle del Cauca) in the southwestern Andes, with one specimen deposited in the Instituto de Ciencias Naturales (ICN) mammal collection (Mora-Beltrán and López-Arévalo 2018). With only five localities, the knowledge of *A. latidens* in Colombia is scarce, which impacts the understanding of its conservation threats.

In this study we used morphological, morphometric and molecular phylogenetic approaches to evaluate the taxonomic status of *A. carishina*. We focused on the extent to which *A. carishina* and *A. latidens* are distinguishable from each other and other large-bodied *Anoura*. We also examined all known Colombian records of *A. latidens* to evaluate its distribution within the country.

2 Materials and methods

We conducted a taxonomical revision of *Anoura* to assess the morphological variation and geographical distribution of *A. latidens*. We reviewed the published records and examined the skulls of specimens labeled as *A. geoffroyi* and *Anoura caudifer* in the following collections: Colección de Mamíferos Alberto Cadena García at Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (ICN), Instituto de Investigación en Recursos Biológicos Alexander von Humboldt (IAvH), Museo de Historia Natural Universidad Distrital Francisco José de Caldas Colección de Mamíferos (MHNUD-M), Museo de Historia Natural de la Universidad del Cauca (MHNUC-M), Colección Teriológica Universidad de Antioquia (CTUA), Colección de Mamíferos Museo de Ciencias Naturales de la Salle (CSJ-m) National Museum of Natural History, Smithsonian Institution (USNM), Muséum d'Histoire Naturelle de la Ville de Genève (MHNG), American Museum of Natural History (AMNH), and Field Museum of Natural History (FMNH).

We measured 260 specimens, including 5 *A. carishina*, 48 *A. peruana*, 59 *A. latidens*, and 148 *A. geoffroyi* (106 *A. g. geoffroyi* and 42 *A. g. lasiopyga*) (See Supplementary Appendix S1 for the complete list of revised specimens). We measured 12 cranial and 11 postcranial variables to the nearest 0.01 mm. Craniodental characters included: greatest length of skull (GLS, distance from the most posterior point of the skull to the most anterior point of the premaxilla not including incisors); condylobasal length (CBL, distance from the most posterior point of the condyles to the most anterior point of the premaxilla not including incisors); postorbital breadth (PB, minimum interorbital distance measured across the frontals); braincase breadth (BB, greatest breadth of the braincase, not including the mastoid and paraoccipital processes); height of braincase (HB, distance from the ventral border of the foramen magnum to the parietal); mastoid breadth (MB, greatest width at the mastoid processes); maxillary tooth-row length (C-M^3, distance from the most posterior point of the third upper molar to the most anterior point of the upper canine); palatal length (PL); breadth across third upper molars (M^3–M^3); breadth across upper canines (C–C); mandibular length (ML, distance

from the condyles to the anterior face of the mandible); and mandibular tooth-row length (C–M_3, distance from canine to the third mandibular molar). Postcranial measurements included: forearm (FA, measured from the olecranon to the articulation of the wrist); length of 3rd (D3mt), 4th (D4mt), and 5th (D5mt) metacarpals; length of the 1st and 2nd phalanxes of 3rd (D3p1, D3p2), 4th (D4p1, D4p2), and 5th (D5p1, D5p2) digits; and length of the tibia (Tib). Measurements were selected based on their frequent use in bat taxonomy (Calderón-Acevedo and Muchhala 2018; Handley 1960, 1984; Mantilla-Meluk and Baker 2006, 2010; Nagorsen and Tamsitt 1981; Velazco 2005; Velazco and Patterson 2008; Velazco and Simmons 2011). Note that our measurement of the greatest length of the skull differs from that in the description of *Anoura carishina* by Mantilla-Meluk and Baker (2010). We measured the greatest length of the skull from the posterior-most point of the occipital to the anterior-most point in the premaxilla (excluding incisors), the measurement used in all *Anoura* descriptions (Handley 1960, 1984; Molinari 1994; Muchhala et al. 2005) except in *A. carishina* when Mantilla-Meluk and Baker (2010) measured all specimens from the posterior-most point of the occipital to the anterior-most point of the nasal bones. Table 1 summarizes our measurements for the type series of *A. carishina* and the holotype of *A. latidens*. To analyze the morphospace of *Anoura* and explore the morphometric variation of measured traits, we performed a principal component analysis (PCA) with two data sets including representatives of *A. carishina*, *A. geoffroyi*, *A. latidens*, and *A. peruana*. The first dataset (n = 125) included all 23 craniodental and postcranial measurements; the second dataset (n = 202) included only the 12 craniodental measurements.

To test the reliability of dental characters distinguishing tailless large-bodied *Anoura* species, we traced the contour of the premolars from digital photographs of the ventral view of the skull of 70 *A. latidens*, 36 *A. geoffroyi*, seven *A. peruana* and five *A. carishina*. We took each photograph next to a band of millimeter paper in order to standardize measurements. We selected the contour of the P^3 and P^4 using the software ImageJ (Schneider et al. 2012) and obtained the area of the contour of each tooth using the "Measure" function. To quantify the shape of the P^4 (irrespective of size) we transformed every contour image of the P^4 to a binary image in Image J and then employed an elliptical Fourier transformation on these images. Using the software SHAPE v1.3 (Iwata and Ukai 2002) this contour was transformed into chain code, assigning a string of code that represents the perimeter of every image of the third upper premolar, which was then used to create a harmonic or elliptical Fourier descriptor (EFDs) series. This approach allowed us to quantify the shape using 20 harmonics, which were used as input for a PCA.

Aside from tooth morphology, another character cited by Handley (1984) as important in distinguishing *A. latidens* from *A. geoffroyi* is that the former has nearly parallel maxillary toothrows. To quantify this, we used ImageJ to overlay lines over images of the occlusal view of the maxillae for 5 *A. carishina*, 34 *A. geoffroyi*, 4 *A. peruana* and 66 *A. latidens*. Specifically, these lines connected the metastyle of the third upper molar (M^3) to the most anterior point of the canines for each toothrow (see Supplementary Data SD2, Supplementary Figure S3). We then measured the angle between these lines.

We tested for significant differences between *A. geoffroyi*, *A. latidens*, *A. peruana* and *A. carishina* in (1) craniodental measurements (including those related to rostrum length and an inflated braincase);

Table 1: Craniodental measurements (mm) of the type specimen of *Anoura latidens*, and the type series of *A. carishina*.

	***A. latidens* type USNM 370119**	***A. carishina* type ICN 14530**	***A. carishina* ICN 5224**	***A. carishina* ICN 5225**	***A. carishina* ICN 14531**	***A. carishina* ICN 5938**
GLS	24.05	24.08	24.44	24.05	23.90	24.12
CBL	23.27	23.35	23.65	23.53	23.45	23.52
PB	4.81	5.24	4.91	4.86	5.19	5.15
BB	9.50	10.03	9.81	9.35	9.82	9.88
HB	7.54	8.30	8.04	7.91	7.83	7.72
MB	9.99	10.11	9.75	10.02	10.17	10.22
C–M^3	9.06	9.09	9.32	9.18	9.01	9.28
PL	13.44	12.27	12.52	12.71	12.87	13.11
M^3–M^3	5.94	6.31	6.22	5.91	6.09	6.06
C–C	4.09	4.46	4.39	4.06	4.16	4.52
ML	16.89	17.15	17.46	17.00	17.27	17.36
C–M_3	9.35	9.71	9.48	9.48	9.39	9.63
FA	42.69	43.09	44.15	43.79	41.14	41.07
D3mt	39.53	39.32	39.24	39.86	38.22	39.11
D3p1	13.21	13.69	13.48	13.00	13.47	12.81
D3p2	21.18	20.42	20.50	21.18	21.01	20.47
D4mt	37.88	37.09	38.97	38.37	36.43	37.73
D4p1	9.73	9.64	10.20	10.07	10.26	9.97
D4p2	13.32	14.24	13.65	15.03	14.11	14.08
D5mt	33.57	32.64	33.56	33.07	30.89	32.62
D5p1	7.81	8.20	8.20	8.00	8.68	8.06
D5p2	11.92	11.62	12.65	13.22	12.34	12.61
Tib	14.97	13.64	15.05	15.40	14.73	14.34

See Section 2 for measurement abbreviations. All measurements used in this study were taken by the authors.

(2) the centroids of PC1 and PC2 of the craniodental dataset; (3) P^4 and P^3 size (e.g. total surface area); (4) the shape of P^4 (EFD principal components) and (5) the toothrow angle using a multivariate analysis of variance (MANOVA) followed by a Bonferroni-corrected and a Fisher's least significant difference post-hoc tests to account for significant differences in the central tendency of morphometric variables between each species. Pillai's Trace and Wilk's Lambda to indicate which effects contributed more to the models.

To complement our morphological assessment of *A. latidens* and *A. carishina* we inferred a phylogenetic tree using ultra-conserved elements (UCEs). Taxonomic coverage included *A. carishina* (four specimens including the holotype), *A. geoffroyi* (five specimens), *A. latidens* (two specimens), *A. caudifer* (four specimens), and *Glossophaga longirostris* (one specimen) as an outgroup. We extracted genomic DNA from preserved tissues and museum skins using the Puregene DNA isolation kit (Gentra System, Minneapolis, MN, USA). We subjected the tissue samples of the type series of *A. carishina* to a series of ethanol and distilled water washes to remove contaminants. Samples were immersed and vortexed in 99% ethanol with a subsequent 70% ethanol wash for four consecutive days (Giarla and Esselstyn 2015; Velazco and Patterson 2013). Genomic DNA extractions were then sent to RAPiD Genomics LLC (Gainesville, FL) for library preparation and target enrichment of over 2386 UCEs in the tetrapod 2.5K probe set (Faircloth et al. 2012), followed by paired-end sequencing (2 × 100 bp) of the UCEs on Illumina HiSeq 3000 PE100 machines. We processed and assembled the resulting reads using the program phyluce v1.6 (Faircloth 2016). After matching UCE contigs to the probes in phyluce, we created an alignment using only the UCE contigs shared between our samples using MAFFT v7 (Katoh and Standley 2013). Our final dataset contained 741 UCE loci shared by all 16 individuals. We concatenated UCE loci into a matrix, and used it to infer the 'best' maximum-likelihood (ML) tree in RAxML-NG (Kozlov et al. 2019) using the GTR + Γ model with 500 bootstrapping iterations. Ultra-conserved elements provide a reliable and robust tool for inferring phylogenetic relationships and has already been tested both at shallow population levels (Andermann et al. 2019; Giarla and Esselstyn 2015; Jackson et al. 2017; Lima et al. 2018; Morales et al. 2017), as well as in relationships among the orders of placental mammals (McCormack et al. 2012). The raw reads used during this research are available under BioProject PRJNA529738, accessible at http://www.ncbi.nlm.nih.gov/bioproject/529738.

3 Results

3.1 Morphological identification

The holotype specimen of *A. carishina* (ICN 14530) has the same dental characters used for describing and diagnosing *A. latidens*. Four specimens (ICN 14530,14531, 5224, 5225) were identifiable as *A. latidens* in the *A. carishina* type series, because these have second upper premolars (P^3) with a reduced anterobasal cusp and the medial-internal cusp of the third upper premolars (P^4) enclosed in a triangular base. Specimen ICN 5839 possesses neither of these characters, and is instead diagnosable as *A. geoffroyi*: it has narrow upper and lower last premolars, and while it has a developed medial-internal cusp in the P^4 it is not enclosed in the base of the tooth, lacking the characteristic triangular base found in *A. latidens* (Figure 1).

3.2 Morphometric analyses

The type series of *A. carishina* overlaps with other analyzed *Anoura* species in most of its measurements (Figure 2; Supplementary Data SD1). In the principal component analysis with all the measurements (Figure 2A) 33.24 and 10.68% of the variation is explained by the first two principal components. Results were similar when only craniodental measurements (Figure 2B) were used (PC1 40.01%, PC2 17.19%).

P^4 shape variation was explained by the first two principal components of 20 EFDs (PC1 71.83% and PC2 13.07%, Figure 3). The holotype of *A. carishina* (ICN 14530) is in the center of the morphospace occupied by *A. latidens*, with the paratype diagnosable as *A. geoffroyi* (ICN 5938) closer to the morphospace of *A. geoffroyi*. Despite evidencing different morphological clusters corresponding to *A. geoffroyi* plus *A. peruana* and *A. latidens*, the morphospace of the shape of P^4 does not show a full separation between them (Figure 3).

The multivariate analysis of variance (MANOVA) on morphometric measurements shows overall significant differences for each measurement (Pillai's Trace and Wilks' Lambda $P < 0.001$); however, differences in postorbital breadth ($F_{3,121} = 1.023$, $P = 0.385$) and forearm length ($F_{3,121} = 0.223$, $P = 0.881$) were not significant across all species comparisons (Table 2). Bonferroni corrected P values show significant differences between *A. latidens* and *A. carishina* only in height of braincase ($P = 0.030$), while variables are significantly different between *A. geoffroyi* and *A. latidens*, with the exception of postorbital breadth ($P = 1.0$), height of braincase ($P = 0.166$), and forearm length ($P = 1.0$). Specifically, *A. latidens* has a shorter greatest length of skull, palate length, maxillary toothrow length, braincase breadth, and mastoid breadth in comparison to *A. geoffroyi* and *A. peruana* (Table 2, Supplementary Data SD2). There is no statistical difference between *A. latidens* and *A. carishina*.

The MANOVA on the centroids of PC1 and PC2 of the craniodental dataset shows similar results to the analysis on morphometric measurements. PC1 shows no significant differences (Bonferroni corrected $P = 1.0$) between *Anoura latidens* (PC1 $X = -0.0732$) and *A. carishina* (PC1 $X = -0.0886$); *A. geoffroyi* and *A. peruana* are significantly different from *A. latidens* and putative *A. carishina* ($P = 0.001$, $X = -0.0732$). Similarly, PC2 also shows no significant differences ($P = 0.120$) between *A. latidens* (PC2

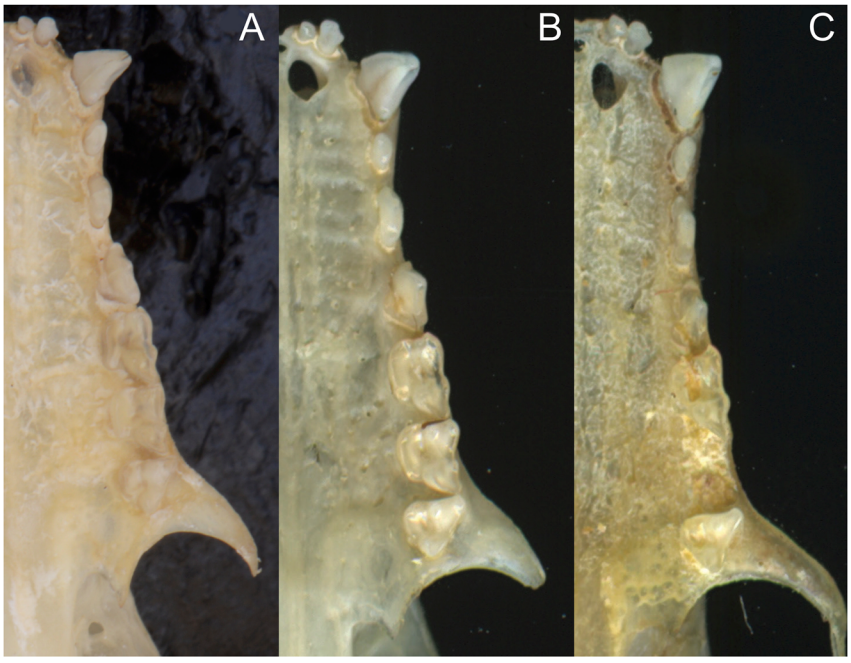

Figure 1: Skull morphology of (A) *Anoura latidens* holotype USNM 370119, (B) *A. carishina* holotype ICN 14530 and (C) *A. carishina* paratype ICN 5938. Note the robust molars and premolars in the first two, in contrast to the slender premolars of the *A. carishina* paratype ICN 5938.

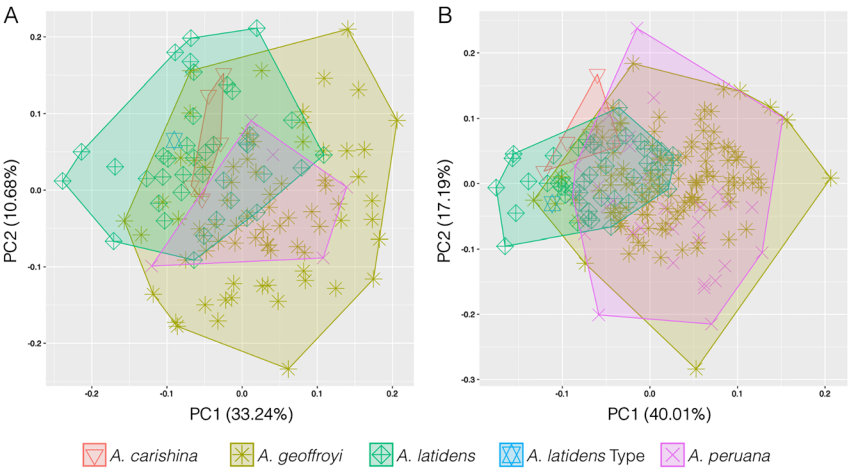

Figure 2: (A) PCA analyses using 12 craniodental and 11 postcranial measurements, and (B) using only the 12 craniodental measurements of *Anoura carishina*, *A. geoffroyi*, *A. latidens*, and *A. peruana*. Note how the morphospace of all species extensively overlaps in both datasets.

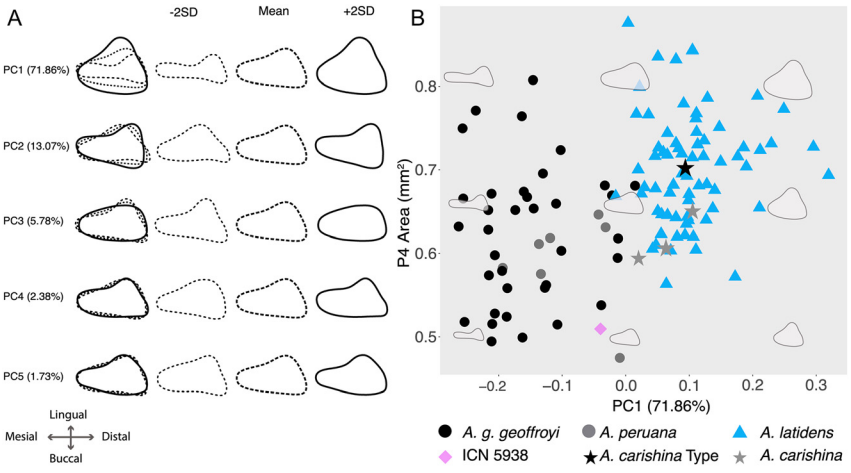

Figure 3: (A) Mean (long-dashed lines), −2SD (short-dashed lines), and + 2SD (solid line) contour shapes of the third upper premolar (P^4) in our sample (with all three superimposed to the left), showing the variation explained by each of the elliptical Fourier descriptor (EFD) principal components. (B) Scatterplot of EFD PC1 vs. P^4 area. Note that the *Anoura carishina* type specimen (ICN 14530) is nested well within the morphospace of *A. latidens*.

Table 2: MANOVA *F* values and *P*-values, with statistics for Bonferroni-corrected post-hoc tests of morphometric variables between *Anoura peruana* ($n = 5$), *A. carishina* ($n = 5$), *A. geoffroyi* ($n = 75$) and *A. latidens* ($n = 40$), with significant *P*-values in bold.

Variables	MANOVA *F*	MANOVA *P*	*A. latidens–A. carishina*	*A. geoffroyi–A. carishina*	*A. peruana–A. carishina*	*A. geoffroyi–A. latidens*	*A. peruana–A. latidens*	*A. geoffroyi–A. peruana*
GLS	**33.013**	**0.000**	1.000	**0.001**	**0.001**	**0.000**	**0.000**	1.000
CBL	**25.771**	**0.000**	1.000	**0.001**	**0.006**	**0.000**	**0.001**	1.000
PB	**1.023**	0.385	1.000	1.000	0.867	1.000	1.000	0.607
BB	**5.587**	**0.001**	1.000	1.000	1.000	**0.001**	1.000	0.354
HB	**5.625**	**0.001**	**0.030**	0.295	**0.005**	0.166	0.500	**0.043**
MB	**9.297**	**0.000**	1.000	**0.047**	1.000	**0.000**	1.000	0.255
C–M^3	**9.982**	**0.000**	1.000	0.087	0.120	**0.000**	**0.003**	0.415
PL	**21.262**	**0.000**	1.000	**0.001**	**0.001**	**0.000**	**0.000**	0.787
M^3–M^3	**3.094**	**0.030**	1.000	1.000	1.000	**0.021**	0.902	1.000
C–C	**17.085**	**0.000**	1.000	0.058	1.000	**0.001**	1.000	0.387
ML	**5.034**	**0.003**	1.000	0.515	0.211	**0.009**	0.850	1.000
C–M_3	**14.744**	**0.000**	1.000	**0.012**	**0.002**	**0.000**	**0.000**	0.417
FA	**0.223**	0.881	1.000	1.000	1.000	1.000	1.000	1.000

See Section 2 for measurement abbreviations.

$X = 0.007$) and *A. carishina* (PC2 $X = 0.0591$). Differences between *A. carishina* and *A. geoffroyi* are also significant ($P = 0.028$, PC2 $X = -0.044$).

The MANOVA on premolar shape and toothrow angle (Table 3) shows significant differences between species for the area of P^4 ($F_{3,105} = 14.878$, $P < 0.001$), PC1 of P^4 shape ($F_{3,105} = 103.508$, $P < 0.001$) and toothrow angles ($F_{3,105} = 3.157$, $P = 0.028$). Bonferroni-corrected post-hoc tests show that *A. latidens* has a larger P^4 area ($X = 0.69$ mm^2) than *A. carishina* ($X = 0.61$ mm^2, $P = 0.049$), *A. geoffroyi* ($X = 0.61$ mm^2, $P < 0.001$), and *A. peruana* ($X = 0.56$ mm^2, $P = 0.002$). The first principal component of the P^4 shape showed significant differences between *A. geoffroyi* and both *A. carishina* and *A. latidens*, and between *A. peruana* and *A. latidens* ($P < 0.001$), while *A. peruana* was not different from *A. geoffroyi* ($P = 0.112$) or *A. carishina* ($P = 0.079$). Notably, *A. carishina* is not significantly different from *A. latidens* for any of these traits except P^4 area, and the four specimens of *A. carishina* diagnosable as *A. latidens* fall completely within the range of *A. latidens* variation in P^4 area (Figure 3). Even though toothrow angle was significantly different overall ($F_{3,105} = 3.157$, $P = 0.028$) only a Fisher's least significant difference post-hoc test showed differences between *A. geoffroyi* and *A. latidens* ($P = 0.011$). In light of the lack of statistical evidence supporting the morphological diagnosis of *A. carishina*, the holotype and three of the paratypes are diagnosable as individuals of *A. latidens*.

3.3 Phylogenetic analysis

Our maximum likelihood phylogenetic analysis shows that *A. carishina* is not monophyletic. The type series of *A. carishina* is split between *A. latidens* and *A. geoffroyi*, with sequences from specimens that are morphologically

Table 3: MANOVA *F* and *P*-values, with statistics for Bonferroni-corrected post-hoc tests of P^3 and P^4 area, toothrow angles (TRA) and principal components 1 and 2 of P^4 shape between *Anoura peruana* ($n = 4$), *A. carishina* ($n = 5$), *A. geoffroyi* ($n = 34$) and *A. latidens* ($n = 66$), with significant *P*-values in bold.

Variables	MANOVA *F*	MANOVA *P*	*A. latidens–A. carishina*	*A. geoffroyi–A. carishina*	*A. peruana–A. carishina*	*A. geoffroyi–A. latidens*	*A. peruana–A. latidens*	*A. geoffroyi–A. peruana*
P^3 area	0.952	0.418	1.000	1.000	1.000	0.641	1.000	1.000
P^4 area	14.878	**0.000**	**0.049**	1.000	1.000	**0.000**	**0.002**	**1.000**
P^4 shape PC1	103.508	**0.000**	0.678	**0.000**	0.079	**0.000**	**0.000**	0.122
P^4 shape PC2	0.340	0.797	1.000	1.000	1.000	1.000	1.000	1.000
TRA	3.157	**0.028**	1.000	1.000	1.000	0.066	0.407	1.000

See Section 2 for measurement abbreviations.

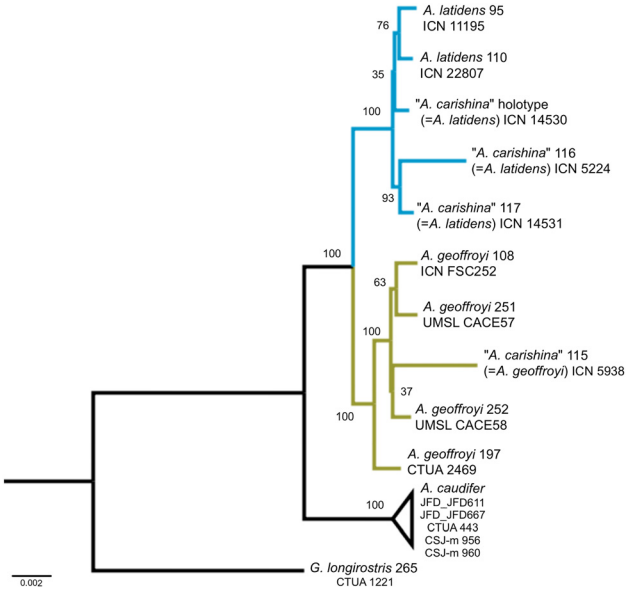

Figure 4: Maximum likelihood phylogenetic tree of *Anoura* showing the position of the holotype and paratypes of *Anoura carishina*. The holotype specimen of *A. carishina* (ICN 14530) and two paratypes (ICN 14521, 5224) are nested within *A. latidens* specimens while specimen ICN 5938 is nested within *A. geoffroyi* specimens from Colombia and the Lesser Antilles.

diagnosable as *A. latidens* nested among *A. latidens* sequences, and sequences from the specimen diagnosable as *A. geoffroyi* nested among sequences from *A. geoffroyi* specimens from Colombia and Trinidad and Tobago (Figure 4; Table 4). This phylogenetic hypothesis based on 741 UCE loci supports the position of *A. latidens* as the sister taxa of *A. geoffroyi*. Bootstrap support is high for the clusters subtending the three species of *Anoura* (*A. caudifer, A. geoffroyi* and *A. latidens*), and low within each species (Figure 4).

4 Discussion and conclusion

Morphology, morphometrics and genetics indicate that the type series of *A. carishina* represents a mixed group, with four individuals corresponding to *A. latidens* and one to *A. geoffroyi*. Our analyses of craniodental measurements and premolar shape find no support for *A. carishina* as a morphologically distinct taxon from *A. latidens*. This conclusion is further backed by our phylogenetic analyses, which evidence *A. latidens* as the sister taxon of *A. geoffroyi*, a phylogenetic pattern inferred by previous phylogenetic hypotheses for the genus (Dávalos et al. 2014; Rojas et al. 2016). Our results also clarify the characters that distinguish *A. latidens* from *A. geoffroyi* (shorter rostrum, less inflated braincase, less parallel toothrows) and expand the known distribution of *A. latidens* in Colombia, raising issues regarding the conservation of this species in the country.

In our review of previously-published records of *A. latidens* in Colombia, we find that only two are valid, including specimen AMNH 69187 used in the species description (Handley 1984) and ICN 22807 from Reserva Forestal Bosque de Yotoco, municipality of Yotoco, department of Valle del Cauca (Mora-Beltrán and López-Arévalo 2018). The *A. latidens* specimens reported by Rivas-Pava et al. (2007) from the municipalities of Acevedo (department of Huila; MHNUC-M 0722, 0723) and Argelia (Department of Cauca; MHNUC-M 1552) actually correspond to individuals of *A. geoffroyi* based on their narrow molars and premolars and the lack of the triangular base of P^4, while there is no record of the *A. latidens* specimen reported by Muñoz (2001) in the mammal collection of Colegio San Jose de la Salle. The two putative records of *A. latidens* that we did find in this collection were both captured in Gramalote (department of Norte de Santander, Colombia) and are diagnosable as *Glossophaga soricina*, having well developed and crowded lower incisors (Griffiths and Gardner 2007).

On the other hand, among all of the collections we reviewed, we found a total of three *Anoura latidens* specimens that were misidentified as other *Anoura* species. Specimens ICN 4398, ICN 11195, and MHNUD-M 587 coincide with the dental characters of *A. latidens* proposed by Handley (1984). ICN 4398 is an adult male, preserved as a skin and extracted skull. This record is located in the inter-Andean valley of the Cauca River, between the Cordillera Central and Cordillera Occidental (central and western mountain ranges). ICN 11195 is an adult male, preserved as a skin and extracted skull. It was collected in Parque Regional Natural Ucumarí, Vereda la Suiza, city of Pereira, department of Risaralda. This locality is situated in the protected area Santuario de Fauna y Flora Otún Quimbaya and resides in the western slope of the Cordillera Central (central mountain range) at an elevation of 1900 m a.s.l. MNHUD-M 587 is an adult male, preserved as a skin and extracted skull. It was collected in Vereda La Huerta, municipality of La Vega, department of Cundinamarca on the western slope of the Cordillera Oriental at an elevation of 980 m a.s.l.

4.1 Taxonomic identity of *Anoura carishina*

Our results clearly support *Anoura carishina* being a junior synonym of *A. latidens*. First, the triangular base of the third upper premolar P^4 of the holotype specimen of *A. carishina* (ICN 14530) and three paratypes is

Table 4: Catalog and GenBank accession numbers of samples and UCE reads used in this study.

Species	Catalog no.	Sequence code	GenBank accession no.	Country	Province	Municipality	Latitude	Longitude
Anoura caudifer	JFD_JFD611	A.caudifer214	KCZH00000000.1	Colombia	Antioquia	Urrao	6.52	−76.25
Anoura caudifer	JFD_JFD667	A.caudifer215	KCZG00000000.1	Colombia	Antioquia	Urrao	6.52	−76.25
Anoura caudifer	CTUA 443	A.caudifer259	KCZF00000000.1	Colombia	Antioquia	Medellín	6.19	−75.55
Anoura caudifer	CSJ-m 956	A.caudifer260	KCZE00000000.1	Colombia	Antioquia	Urrao	6.54	−76.24
Anoura caudifer	CSJ-m 960	A.caudifer261	KCZD00000000.1	Colombia	Antioquia	Urrao	6.54	−76.24
Anoura geoffroyi	ICN 5938	A.carishina115	KCZL00000000.1	Colombia	Valle del Cauca	Santiago de Cali	3.33	−76.64
Anoura geoffroyi	CTUA 2469	A.geoffroyi197	KCYS00000000.1	Colombia	Tolima	Cajamarca	4.48	−75.50
Anoura geoffroyi	UMSL CACE57	A.geoffroyi251	KCYR00000000.1	Trinidad and Tobago	Sangre Grande		10.47	−61.18
Anoura geoffroyi	UMSL CACE58	A.geoffroyi252	KCYQ00000000.1	Trinidad and Tobago	Sangre Grande		10.47	−61.18
Anoura geoffroyi	ICN FSC252	A.geoffroyi108	KCYT00000000.1	Colombia	Meta	Vista Hermosa	2.73	−73.75
Anoura latidens	ICN 11195	A.latidens95	KCYO00000000.1	Colombia	Risaralda	Pereira	4.73	−75.57
Anoura latidens	ICN 22807	A.latidens110	KCYN00000000.1	Colombia	Valle del Cauca	Yotoco	3.83	−76.33
Anoura latidens	ICN 14530	A.carishina holotype	KCZI00000000.1	Colombia	Nariño	Taminango	1.68	−77.33
Anoura latidens	ICN 5224	A.carishina116	KCZK00000000.1	Colombia	Magdalena	San Pedro de la Sierra	10.91	−74.05
Anoura latidens	ICN 14531	A.carishina117	KCZJ00000000.1	Colombia	Nariño	Taminango	1.68	−77.33
Glossophaga longirostris	CTUA 1221	G.longirostris265	KCYF00000000.1	Colombia	La Guajira	Barrancas	10.93	−72.75

Museum acronyms: CTUA, Colección Teriológica Universidad de Antioquia; CSJ-m, Colección de Mamíferos Museo de Ciencias Naturales de la Salle; ICN, Colección de Mamíferos Alberto Cadena García. Catalog numbers with the acronym UMSL belong to the tissue collection of the Muchhala Lab at University of Missouri St. Louis, and numbers with the acronym JFD correspond to specimens hosted at the Díaz Lab in Universidad EAFIT, Medellín, Colombia.

indistinguishable from *A. latidens*. Second, all these specimens lack a developed anterobasal cusp in the second upper premolar (P^3). Third, none of the 18 morphological measurements differ between *A. latidens* and the *A. carishina* specimens with the exception of height of the brain case and P^4 area, which extensively overlap. The fourth paratype (ICN 5938) presents a developed anterobasal cusp in the second upper premolar (P^3) and lacks a medial internal cusp enclosed in the base of the third upper premolar (P^4), supporting its diagnosis as *A. geoffroyi*. In our review of the type material, we also discovered that the specimen labeled as the holotype in Figure 4 presented by Mantilla-Meluk and Baker (2010) is in fact the paratype ICN 5225 (see Supplementary Data SD2, Supplementary Figure S1).

4.2 Diagnosis of *Anoura latidens* and *A. geoffroyi*

Of the traits mentioned by Handley (1984) to diagnose *A. latidens* from *A. geoffroyi*, we confirm the reliability of: a more robust and more triangular third upper premolar (P^4, Figure 3), a reduced anterobasal cusp of second upper premolar (P^3), and a shorter rostrum (Table 2; Supplementary Data SD1). We add the mastoid breadth and mandibular tooth row length, which are also smaller in *A. latidens* (Table 2; Supplementary Data SD1). Contrary to Handley (1984) we found that *A. geoffroyi* has more paralleled toothrows (X = 13.39°) than *A. latidens* (X = 14.01°), and that *A. latidens* has a less inflated braincase than *A. geoffroyi* and *A. peruana* (Table 2; Supplementary Data SD1).

4.3 Distribution and implications for bat conservation in Colombia

By combining the two valid previously-published records of *Anoura latidens* in Colombia (Handley 1984; Mora-Beltrán and López-Arévalo 2018) with the seven records we found here, we report *A. latidens* in seven localities across the country (Figure 5; Supplementary Appendix S1). With the exception of the Sierra Nevada de Santa Marta, all localities fall within highly altered ecosystems (Etter et al.

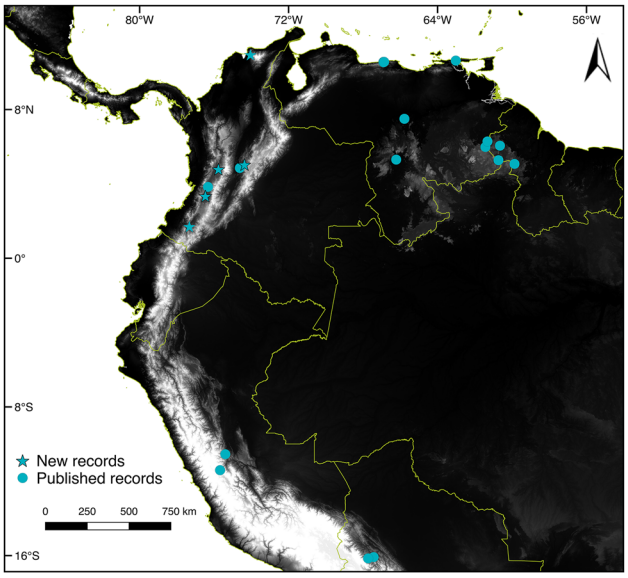

Figure 5: Distribution of *Anoura latidens* in South America. Stars indicate new records in Colombia, while dots indicate all other previously published records.

2006). Vereda El Hormiguero (ICN 4398) is located in a sugar cane agricultural system, even at the time of the capture of the specimen (Arata et al. 1967). San Juan de Rioseco (AMNH 69187) and Vereda La Huerta (MHNUD-M 587) are mountainous areas with a landscape composed of ranching pastures, small agricultural fields, and fragments of natural forests. Vereda La Suiza (ICN 11195) presents a heterogeneous forest cover composed of fragments of natural forests, secondary forests, and reforested areas; it is part of the Santuario de Fauna y Flora Otún Quimbaya, registered in the Colombian National System of Protected Areas (SINAP) (Estrada-Villegas et al. 2010). Reserva Forestal Bosque de Yotoco (ICN 22807) is a protected reserve in the department of Valle del Cauca on the eastern slopes of the Western Cordillera. All records are located in the Andean region and the Sierra Nevada de Santa Marta between 590 and 1690 m a.s.l.

In Venezuela, *A. latidens* has a similar elevational distribution, with records from 50 to 2240 m a.s.l., the majority (81%) located between 1000 and 1500 m a.s.l. and in a variety of ecosystems from lowland forests to highland Andean forests, but with a preference for moist evergreen forests (Handley 1984; Linares 1986; Soriano et al. 2002). In Guyana, *A. latidens* occurs in the lowland Neotropical rain forests of the protected area Iwokrama Forest, a bat diversity hotspot in South America (Lim and Engstrom 2001). In Peru it is reported between 840 and 2600 m a.s.l., in the Peruvian Yungas forests, which mark a transition between high altitude Andean forests and Amazonian moist forests (Handley 1984; Solari et al. 1999). Recently *A. latidens* was reported from Bolivia, where it occurs in the Yungas forests on the southeastern Andes between 1224 and 1857 m a.s.l. (Calderón-Acevedo and Muchhala 2020). The Bolivian Yungas are humid forests that transition from the Andean highlands to the eastern lowlands, and are characterized by being some of the most diverse ecosystems in Bolivia containing 48% of the bat diversity of the country (Vargas et al. 2010; Vargas and Patterson 2007).

Assessing the conservation status of *A. latidens* under the IUCN criteria is challenging given its discontinuous distribution across highly transformed environments. Local abundances are also unknown, although its rarity in Colombian mammal collections suggests a low abundance in the Colombian Andes. Further challenges stem from the sympatry of *A. latidens* and *A. geoffroyi*, which can only be identified by craniodental characters, and are then commonly misidentified during fieldwork. The use of small magnifying lenses can help in identifying the last upper premolar, we also suggest the use of wing punches to take tissue samples of potential *A. latidens* individuals to corroborate their identity using genetic barcodes. It is crucial to coordinate future strategies with the different bat conservation programs in South America, and encourage researchers to work on *A. latidens* to be able to accurately estimate population trends and develop effective conservation strategies.

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Conflict of interest statement: The authors declare no conflicts of interest regarding this article.

Compliance with ethical standards: This research only used museum specimens and previously collected tissue samples; procedures are in accordance with national laws. Genetic sequences used during this research are available in GenBank (http://www.ncbi.nlm.nih.gov) under BioProject PRJNA529738, accessible at http://www.ncbi.nlm.nih.gov/bioproject/529738. Voucher specimens used in the phylogenetic analyses are deposited in museum collections or university laboratories (see Table 4.).

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