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ORIGINAL ARTICLE

Systematics and taxonomy of *Platyrrhinus chocoensis* (Chiroptera: Phyllostomidae) based on morphometric and genetic analyses: implications for biogeography and conservation

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Abstract

The Neotropical bat genus *Platyrrhinus* is one of the most speciose genera in the family Phyllostomidae. It includes 20 species of frugivorous bats that are endemic to the Neotropics. *Platyrrhinus chocoensis* is a species distributed from southern Panama southward into northern Ecuador on the lowlands and mid elevations of the Pacific coast of northern South America, across the Chocó Biogeographic region, a hot-spot of biodiversity, extending west of the Andes. Due to its association with the Chocoan rainforest, *P. chocoensis* was designated as one of the two species of bats included in the Red List of Colombian mammals. Another species of *Platyrrhinus*, *P. dorsalis*, also occurs in Colombia and Ecuador along both slopes of the Andes. In contrast with *P. chocoensis*, *P. dorsalis* is considered a relatively common bat species within the Least Concern category of the International Union for Conservation of Nature. We evaluate the systematics and taxonomy of both species, *P. chocoensis* and *P. dorsalis*, using a combination of morphometric and molecular analyses. Although our morphometric analyses support a consistent morphological differentiation between these two taxa, the analyses of mtDNA sequences of Cyt-*b* and ND2 revealed that *P. chocoensis* and *P. dorsalis* have no differentiation at the genetic level for the analyzed markers (0.7%); therefore, we recognize *P. chocoensis* as a junior synonym of *P. dorsalis*. In addition, our results support the recognition of two subspecies within *P. dorsalis*: the nominate *P. d. dorsalis* and *P. d. chocoensis*. Finally, we discuss the biogeographic implications of our findings, in particular the consequences of the synonymization of *P. chocoensis*, that also warrants the reevaluation of the taxonomic and conservation status of *P. dorsalis* populations from the Chocoan domain.

Keywords Allen's rule · Bergmann's rule · Chocó Biogeographic · Morphological evolution · Subspecies conservation

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Introduction

Platyrrhinus, with 20 currently recognized species, is one of the most diverse genera in the family Phyllostomidae (Velazco et al. 2018). Members of the genus occupy a wide variety of habitats, distributed from sea level to montane forests up to 3350 m (Velazco 2005). The phylogenetic relationships among species in *Platyrrhinus* have been evaluated using both morphological (Velazco 2005; Velazco and Gardner 2009) and molecular data (Velazco and Patterson 2008; Velazco et al. 2010, 2018; Velazco and Lim 2014). Out of the 20 currently recognized species, only *P. aquilus, P. chocoensis,* and *P. nitelinea* were not included in previous molecular analyses, due to the lack of tissue samples. *Platyrrhinus aquilus* is endemic to Panama (Velazco and Gardner 2009), while *P. nitelinea* and *P. chocoensis* are partly distributed in Colombia. *Platyrrhinus chocoensis* (= *Vampyrops chocoensis*) (Alberico and Velasco 1991) is considered an endemic of the Chocó Biogeographic region, with its type locality in Quebrada El Platinero (100 m), Itsmina, Chocó, Colombia (Alberico and Velasco 1991). *P. chocoensis* was described, based on 102 specimens collected from the lowlands of the Colombian Chocó Biogeographic region (Alberico 1990), and it is primarily considered a lowland tropical forests species, inhabiting environments between the sea level to 1000 m (Velazco and Gardner 2009; Valencia-Daza 2011; Burneo and Tirira 2014; Pozo-Rivera et al. 2018) from southern Panama (Darién) southward west of the Andes into northern Ecuador (Esmeraldas) (Gardner 2008). *P. chocoensis* has been registered for two localities in Panama, 22 localities in Colombia, and 30 localities in Ecuador. Due to its restricted distribution within the ecologically unique Chocó Biogeographic region, Rodrígez-Mahecha et al. (2006), included *P. chocoensis* as one of the three bats in the Red List of Colombian Mammals.

Platyrrhinus dorsalis (= *Vampyrops dorsalis*) occurs in sympatry with *P. chocoensis*. *P. dorsalis* was described by Thomas (1900) based on a single specimen collected in the town of Paramba (1100 m) on the western slope of the Andes in Ecuador. *P. dorsalis* is distributed in Colombia and Ecuador along both slopes of the Andes (between 150 and 2000 m) (Velazco and Gardner 2009). Alberico and Velasco (1991) support the distinction of *P. chocoensis* from *P. dorsalis* based on the following set of characteristics: (1) relatively short and broad upper central incisors, (2) M2 usually lacking an accessory cusp between the protoconid and metaconid, and (3) a small M3. In addition, *P. chocoensis* has a paler dorsal coloration and a less conspicuous dorsal stripe. This set of characteristics has been used by different authors to differentiate between these two species (Koopman 1993; Alberico and Velasco 1994;

Muñoz-Arango 2001; Velazco 2005; Velazco and Gardner 2009). Despite the recognition in the literature of these two taxa as valid species, some authors have mentioned that there are cases in which it is difficult to distinguish between them due to their similarity in size and morphology (Alberico 1990; Alberico and Velasco 1991).

The phylogenetic position of *Platyrrhinus dorsalis* has been evaluated using morphological characters (Velazco 2005; Velazco and Gardner 2009), as well as molecular data (Velazco and Patterson 2008; Velazco et al. 2018). Molecular phylogenies support its recognition as a valid species and include this taxon within a group conformed by the Andean species of the genus. On the other hand, phylogenetic analyses based solely on the evaluation of morphological characters (Velazco 2005; Velazco and Gardner 2009) placed *P. chocoensis* as sister to the clade that includes medium to large size species of the genus (*P. albericoi*, *P. aquilus*, *P. aurarius*, *P. dorsalis*, *P infuscus*, *P. ismaeli*, *P. lineatus*, *P. masu*, *P. nigellus*, *P. nitelinea*, *P. umbratus*, and *P. vittatus*); however, this association was weakly supported.

Considering: (1) the important biogeographic domain occupied by *P. chocoensis* on the western side of the Andes adjacent to Central America; (2) its sympatric occurrence with a morphologically similar taxon (*P. dorsalis*); and (3) its consideration as a focal species prioritized within the Colombian Red List of mammals; it is important to evaluate the systematics of *P. chocoensis*, using molecular data. We took advantage of new specimens with associated tissue samples available for the species, result of recent evaluations of the bat fauna of the Central Chocó, to evaluate the systematics of *P. chocoensis*.

Materials and methods

Specimens examined

Tissues and voucher specimens of *Platyrrhinus chocoensis* and *P. dorsalis* used in the molecular and morphological analyses are housed in the following scientific collections: British Museum (Natural History) (BMNH), London, UK; Colección Mastozoológica of the Universidad Tecnológica del Chocó (CMCH), Chocó, Colombia; Field Museum of Natural History (FMNH), Illinois, USA; National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C., USA; and Universidad del Valle (UV), Valle del Cauca, Colombia ("Appendix 1").

Molecular methods

We amplified and sequenced the entire cytochrome-*b* (1140 base pairs) and ND2 (1044 bp) genes for two Colombian specimens of *Platyrrhinus chocoensis* (CMCH 872, 1392).

DNA isolation and amplification were carried out in the Centro de Investigaciones Biomédicas, Laboratorio de Genética, Grupo de Investigación GEPAMOL at the Universidad del Quindío, following the protocol described by Velazco et al. (2010) with some modifications. DNA extraction was performed following the manufacturer's specifications. Whole genomic DNA was extracted from liver tissue (25 mg approximately, preserved in 96% alcohol) of two *P. chocoensis* specimens from Colombia using QIAamp DNA Mini Kit (Qiagen Inc., Valencia, California).

The amplification protocol included an initial DNA denaturation between 94 °C and 95 °C for 2 min, followed by 35 cycles of PCR (denaturation at 95 °C for 30 s, hybridization between 50 and 55 °C for 30 s, polymerization at 72 °C for 1 min), and a final extension at 72 °C for 10 min. The primers used for amplification and sequencing are indicated in Table 1. Finally, the products of the amplifications were visualized using a 1.5% agarose gel electrophoresis. The amplification products were sequenced using the ABI PRISM BigDye Terminators v. 3.1 sequencing kit 3.1 (Applied Biosystems, Foster City, CA). The protocol used involved a denaturation step at 96 °C for 60 s, followed by 25 cycles of denaturation at 96 °C for 10 s, annealing at 50 °C for 5 s, and a final extension at 60 °C for 4 min. The sequencing products were purified through an ethanol/EDTA precipitation protocol and sequenced in an ABI PRISM 3730 Genetic Analyzer sequencer (Applied Biosystems, Foster City, CA) using the amplification primers. The inspection of the chromatograms and the alignments were made with the software Codon Code Aligner 7.1.2. Additional Cyt-*b* and ND2 sequences from all other species of *Platyrrhinus* and outgroup were gathered from GenBank and were included for phylogenetic comparison ("Appendix 2"). We used MEGA7 to calculate the intraspecific and interspecific Cyt-*b* uncorrected sequence divergence ("*p*") (Kumar et al. 2016).

To evaluate the phylogenetic relationships of *Platyrrhinus chocoensis*, we used two methods of phylogenetic reconstruction. A total of 61 specimens was included in the phylogenetic analysis. Maximum Likelihood analysis (ML) were conducted using RAxML v 8.1 (Stamatakis 2014), using the option of fast resampling (rapid-bootstrapping, options −*f* and −*x*) for 10,000 replicates of nonparametric resampling. In addition, a Bayesian Inference (BI) analysis were performed using MrBayes v 3.2 (Ronquist et al. 2012), applying the nucleotide substitution models and parameters suggested by the AICc in ModelTest (Cyt-*b*: GTR + G + I; ND2: TVM + G + I). The BI analysis was started with a random tree, running 4 simultaneous Markov chains for 1×10^8 generations, recovering trees every 10,000 generations. The convergence of the chains was evaluated according to the Potential Scale Reduction Factor (PSRF) value close to 1.0 and Estimated Sample Size (EES) > 200 in Tracer 1.6 (Rambaut et al. 2014). A percentage of initial trees (25%) was discarded and the remaining trees were used to construct the consensus tree using majority rule (50%) and to calculate Bayesian posterior probabilities considering values ≥ 0.95 as significant. The trees obtained by both methodologies were visualized and edited in FigTree v 1.4.2 (Rambaut and Drummond 2015).

Morphometric analyses

A total of 163 specimens was used in the morphometric analyses, 147 of which had previously been assigned to *P. chocoensis* and 16 to *P. dorsalis* based on characteristics indicated by Velazco and Gardner (2009) ("Appendix 1"). Twenty-one external, cranial and dental measurements were recorded using a digital caliper with a 0.05 mm of accuracy. Description and abbreviations of the measurements are as follows:

Greatest length of skull (GLS), distance from the posterior-most point of the occiput to the anterior-most point of the upper incisors.
Condyloincisive length (CIL), distance between a line connecting the posterior-most margins of the occipital condyles and the anterior-most surface of the upper incisors.
Condylocanine length (CCL), distance between a line connecting the posterior-most margins of the occipital condyles and a line connecting the anterior-most surface of the upper canines.
Braincase breadth (BB), greatest breadth of the braincase, excluding the mastoid and paraoccipital processes.
Zygomatic breadth (ZB), greatest breadth across the zygomatic arches.
Postorbital breadth (PB), breadth at the postorbital constriction.
Palatal width at canines (C–C), least width across palate between the cingula of the upper canines.

Table 1 Primers used for amplification and sequencing of the fragments of interest in the samples of *P. chocoensis*

Gene	Primer name	Primer sequence	Source
Cyt-*b*	L14724	5′-CGA AGC TTG ATA TGA AAA ACC ATC GTT G-3′	Irwin et al. (1991)
	H15915	5′-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3′	
ND2	L-Met3841	5′-GGT CAG CTA AAT AAG CTA TCG GG-3′	Lloyd (2003)
	H-Asn5149	5′-GGA GAA GTA GAT TGA GC CAG TTG T-3	

Mastoid breadth (MB), greatest breadth across the mastoid region.

Palatal length (PL), distance from the posterior palatal notch to the anterior border of the incisive alveolus.

Maxillary toothrow length (MTRL), distance from the anterior-most edge of the upper canine crown to the posterior-most edge of the crown on M3.

Molariform toothrow length (MLTRL), posterior border of the M3 alveolus to the anterior border of P3.

Width at M1 (M1–M1), greatest width of palate across M1–M1.

Width at M2 (M2–M2), greatest width of palate across M2–M2.

Maxillary breadth (MXBR), least width across the maxilla, from the lingual sides of the two M2.

M1 width (M1W), greatest width of crown.

M2 width (M2W), greatest width of crown.

Dentary length (DENL), from the posterior-most point of the mandibular condyle to the anterior-most point of the dentary.

Mandibulary toothrow length (MANDL), distance from the anterior-most surface of the lower canine to the posterior-most surface of m3.

Coronoid height (COH), perpendicular height from the ventral surface of the mandible to tip of the coronoid process.

Width at mandibular condyles (WMC), greatest width between the inner margins of the mandibular condyles.

Width of m1 (m1W), greatest width of crown.

Forearm length (FA), distance from the olecranon process to anterior surface of carpals in the folded wing.

To evaluate the relationship between ecological variables and morphometric differences between *Platyrrhinus chocoensis* and *P. dorsalis*, the samples were discriminated according to landscape units based on topography, considering their relationship with the change in the floristic composition associated with the elevation. First, the following landscape units proposed by Poveda et al. (2004) were defined: Alluvial Plain (Lla), Piedmont (Pdm), Low Hills (CoB), Middle Hills (CoM), High Hills (CoA), and Andes mountain range (SaC). Subsequently, given the wide range of altitudinal distribution reported in the literature for *Platyrrhinus* (0–3000 m), the first four landscape units were grouped between 0 and 500, because they share more than 50% of their floristic composition, being differentiated from the high hills (500–1000 m) and the subandean mountain range forest (> 1000 m) that were considered as independent units, resulting in a grouping of the specimens in the present study in three elevation ranges (0–500 m, 501–1000 m, and 1001–2000 m). All the analyses were performed independently between females and males, to analyze the morphological variation associated with sex. The variables were

transformed to logarithm with base 10, and the normality of the measurements was evaluated (Shapiro–Wilk test, $p < 0.05$). Multiple principal component analyzes (PCA) were conducted to identify the main trends of morphometric variation within the species. For each main component, the correlation vector (Pearson correlation) between a variable and each main component was calculated. The first three components and the loads of each variable were retained; they were evaluated as an important measure to observe variations following Velazco and Solari (2003). To test the hypothesis of morphometric differentiation between *P. chocoensis* and *P. dorsalis*, a discriminant analysis was performed between the elevation record of each individual and the morphometric variables, followed by a MANOVA to test the significance of the groups found. All statistical analyses were performed using software R version 3.3.3 (2017). The principal component analyses were performed with the "factoextra" package (Kassambara and Mundt 2017) and the discriminant and MANOVA analysis were performed using the "MASS." Package (Ripley et al. 2017).

Results

Phylogenetic position of *Platyrrhinus chocoensis*

Maximum Likelihood and Bayesian Inference analyses of each marker independently and the combined mitochondrial (Cyt-*b* + ND2) partition matrix produced, similar topologies, with some strongly supported clades (Fig. 1). Eighteen different lineages were recovered. Both specimens of *Platyrrhinus chocoensis* were recovered nested within the *P. dorsalis* clade, clade that has high bootstrap and posterior probabilities values (Fig. 1). *Platyrrhinus dorsalis*, including *P. chocoensis*, was recovered sister to *P. infuscus* with high support in both analyses. Other relationships support the results of Velazco and Patterson (2008), Velazco et al. (2010, 2018), and Velazco and Lim (2014).

The average Cyt-*b* pairwise distances among all the specimens of the *Platyrrhinus dorsalis* clade, including *P. chocoensis*, is less than 0.7% (Table 2). The pairwise distance between *P. dorsalis* and its sister taxon *P. infuscus* is more than 5% (Table 2).

Morphometric analyses of *Platyrrhinus chocoensis* and *P. dorsalis*

The principal component analyses comparing *Platyrrhinus chocoensis* and *P. dorsalis* extracted eight components that accounted for 80% of the total variation. The first two components explained 44.5% of the variability in the sample. The PCA plot showed that *P. chocoensis* and *P. dorsalis* form two groups (Fig. 2). Although *P. chocoensis* and *P.*
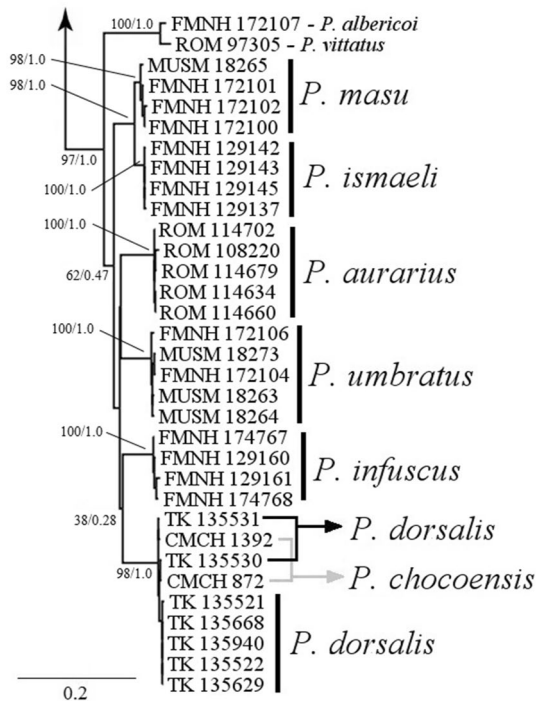
Fig. 1 Combined Cyt-*b* and ND2 Maximum Likelihood phylogram for *Platyrrhinus*. The support for each node is shown as ML bootstrap/Bayesian posterior probability (values greater than 50% are presented)
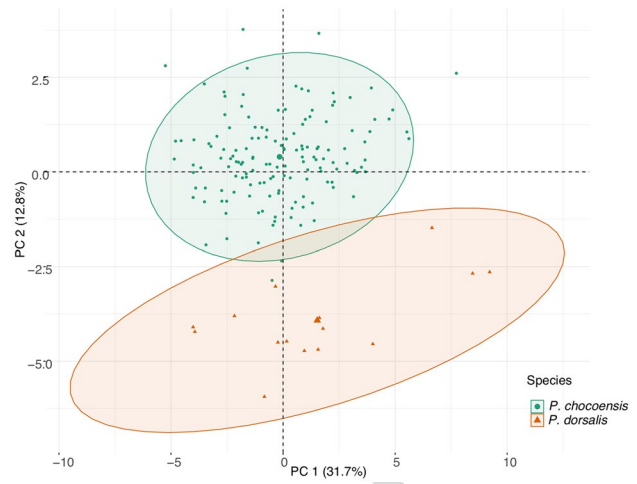

Fig. 2 Principal components analysis (PCA) with 95% prediction ellipses, from 22 characters, including individuals of *P. chocoensis* and *P. dorsalis*. Green dots represent *P. chocoensis*, and orange dots represent *P. dorsalis*

Table 2 Pairwise uncorrected percentage of Cyt-*b* sequence divergence among *P. chocoensis, P. dorsalis* and *P. infuscus*

		1	2	3
1	*Platyrrhinus chocoensis*	0.53		
2	*Platyrrhinus dorsalis*	0.49 ± 0.18	0.52 ± 0.16	
3	*Platyrrhinus infuscus*	5.50 ± 0.09	5.12 ± 0.09	4.88 ± 1.47

Table 3 Percentage of total variance explained and standardized coefficients of the first three self-vectors of 22 characters (acronyms defined in the text) of the analysis of Principal Components including individuals of *P. chocoensis* and *P. dorsalis*

Variables	PC1	PC2	PC3
%Explained	31.7	12.8	9.7
Eigenvalue	6.9	5.2	2.2
FA	-0.55	-0.48	0.43
GLS	-0.59	0.80	0.06
CIL	0.10	0.96	0.19
CCL	0.02	0.90	0.25
BB	-0.82	-0.49	-0.12
ZB	-0.64	-0.09	-0.46
PB	-0.52	-0.18	-0.08
C–C	-0.36	0.08	-0.21
MB	-0.75	0.15	-0.11
PL	0.34	0.24	0.27
MTRL	0.37	-0.20	0.22
MLTRL	1.08	-0.03	0.03
M2–M2	0.87	0.16	-0.38
M1–M1	0.76	0.24	-0.39
MXBR	0.52	-0.05	-0.70
M1W	-0.23	-0.83	0.39
M2W	0.21	-0.62	0.27
DENL	-0.06	0.59	0.35
MANDL	0.55	0.03	0.42
COH	-0.73	-0.19	-0.02
WMC	-0.54	-0.12	-0.44
m1W	0.97	-0.87	0.02

dorsalis have overlapping scores on PC1, these taxa are shown as distinct clusters on PC2 (Fig. 2). Factor loadings on PC2 suggest that this separation is primarily attributable to differences in three variables: GLS, CCL, and CIL (Table 3). In addition, the PCA plot of the scores of the two first PCs showed a high overlap between males and females, indicating secondary sexual dimorphism in size and shape to be absent in *P. chocoensis* + *P. dorsalis* (Fig. 3).

The discriminant analysis that evaluate the morphometric differences between the species with respect to elevation, indicated that 100% of the discrimination between groups was explained with only two canonical axes (Fig. 4). The first axis has 93.5% of the discriminatory power, being able to discriminate significantly the species according to their elevation (MANOVA, Wilks s $\lambda = 0.144$, $p \leq 2.2e-16$). The error rate (0.3%) in the classification,
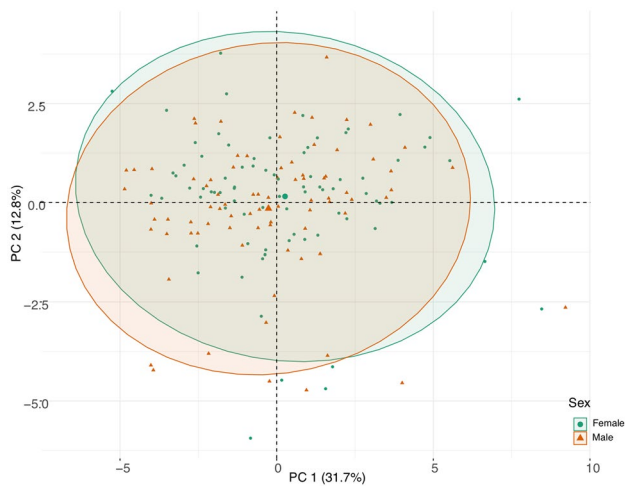
Fig. 3 Spatial position of the individuals of *P. chocoensis* and *P. dorsalis* from the analysis of principal components (PCA) with ellipses of 95% prediction, from 22 characters. Points in green represent females (*n* = 80), and orange ones, males (*n* = 82)
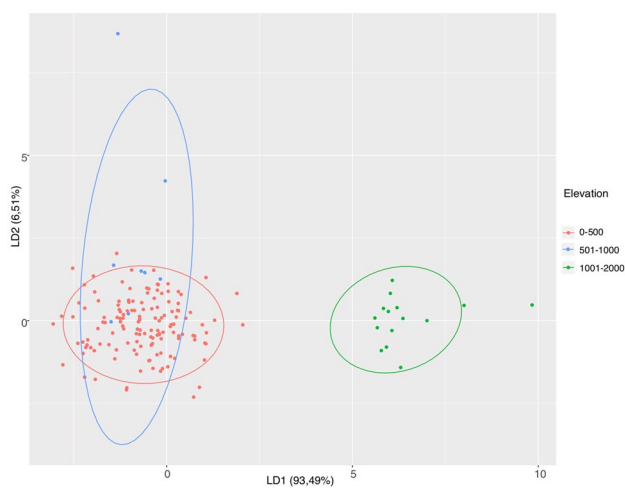

Fig. 4 Discriminant analysis between individuals *P. chocoensis* and *P. dorsalis*, obtained at different heights with an ellipse of 95% prediction. Where the points are individuals and the colors present the elevation ranges

327 showed that the individuals were correctly classified to
328 their groups, showing that there are significant differences
329 separating the specimens assigned to *P. chocoensis* from
330 *P. dorsalis*, which are found within the units of Andean
331 mountain range landscape > 1000 m, these in turn differ in
332 size in relation to those found in high and low hills. GLS
333 and CIL were the variables that presented the greatest dis-
334 criminatory capacity (Table 4). The MANOVA revealed
335 the presence of significant morphometric differences in
336 size (e.g., FA, GLS, BB, ZB, PB, CC, and MB) and the
337 shape of the jaw and the size of the teeth (e.g., MTRL,

Table 4 Contribution of the original variables to the discriminant capacity of the function (acronyms defined in the text)

Variables	LD1	LD2
FA	0.17	0.04
GLS	1.05	0.08
CIL	− 1.01	0.51
CCL	− 0.05	− 0.79
BB	0.14	0.20
ZB	− 0.02	0.09
PB	0.12	− 0.30
C–C	0.78	0.14
MB	0.02	− 0.03
PL	− 0.21	0.07
MTRL	0.05	− 0.84
MLTRL	− 0.50	0.30
M2–M2	− 0.46	− 0.27
M1–M1	0.34	− 050
MXBR	− 0.31	0.65
M1W	0.15	0.54
M2W	0.04	0.02
DENL	0.14	0.00
MANDL	− 0.17	0.46
COH	0.54	− 0.22
WMC	0.07	− 0.13
m1W	− 0.19	− 0.29

338 MLTRL, M2–M2, MXBR, M1W, COH, WMC, m1W)
339 (Table 5).

Discussion

Morphological distinction with lack of genetic differentiation

343 Due to the lack of tissues, *Platyrrhinus chocoensis* was not
344 included in previous molecular studies of the genus (Velazco
345 and Patterson 2008; Velazco et al. 2018). Our analysis of
346 Cyt-*b* and ND2 sequences found low genetic divergence
347 between the sequences of *P. chocoensis* and *P. dorsalis* (less
348 than 0.7%), which precludes their recognition as independ-
349 ent taxonomic units; therefore, we recognize *P. chocoensis*
350 as a junior synonym of *P. dorsalis*, reducing the number of
351 recognized species of *Platyrrhinus* to 19. The addition of
352 geographic records previously identified as *P. chocoensis*
353 as part of *P. dorsalis* represent a significant addition to the
354 distribution of the last. Previous molecular analyses found
355 *P. dorsalis* to be sister to a clade containing: *P. aurarius* + *P.*
356 *infuscus* + *P. ismaeli* + *P. masu* + *P. umbratus*, all of them
357 taxa with Andean distribution, with the exception of *P. infus-*
358 *cus* that is mostly distributed in western Amazonia.

359 In spite of the lack of genetic distinction among ana-
360 lyzed specimens of *Platyrrhinus chocoensis* + *P. dorsalis*,

Table 5 Results of multivariate analyses of variance (MANOVA) from 22 characters (acronyms defined in the text) including individuals *P. chocoensis* and *P. dorsalis*

Variable	Elevation	*F* value	Pr (> *F*)
FA	18.865	50.153	0.007724**
GLS	12.167	22.483	2.519e−09***
CIL	0.349	0.6772	0.5095
CCL	0.519	11.558	0.3174
BB	4.830	74.073	0.0008399***
ZB	9.176	13.298	4.568e−06***
PB	10.201	80.707	0.0004588***
C–C	36.287	28.78	2.15e−11***
MB	28.741	16.087	4.342e−07***
PL	0.911	12.742	0.2825
MTRL	4.421	83.084	0.0003699***
MLTRL	21.990	22.258	3.003e−09***
M2–M2	14.096	72.783	0.0009451***
M1–M1	0.3393	17.332	0.18
MXBR	0.4459	35.309	0.0316*
M1W	0.3434	55.357	0.004741**
M2W	0.0225	0.8463	0.4309
DENL	11.203	30.414	0.05056
MANDL	0.1315	0.6418	0.5277
COH	77.768	32.896	1.108e−12***
WMC	23.516	9.864	9.157e−05***
m1W	0.15719	14.777	1.3e−06***

Significance: ***$p < 0.01$; **$p < 0.05$; *$p < 0.1$

we documented a statistically significant decrease in skull size, and potentially body mass (not measured) according to elevation among analyzed specimens. The herein documented morphometric differences between subpopulations from the lowlands and mid elevations in the morphospace of both of the PCA and DFA, with no intermediate morphos, brings into consideration that these subpopulations may be in an early phase of speciation, with a rapid transmission of morphological features, that may be promoted by differential selective forces along the elevational gradient on the western slopes of the northwestern Andes of Colombia. Therefore, the geographic structure of the morphological variation, supported by our data, lead us to recognize two subspecies within *P. dorsalis*: the nominate *P. d. dorsalis* and *P. d. chocoensis*.

Size and elevation, biogeographic rules

It is known that bats have some of the highest metabolic rates among mammals, experiencing physiological restrictions for their establishment in high elevation ecosystems, characterized by low temperature and low oxygen concentration. Only four phyllostomid genera have been able to conquest the higher Andean elevations: the nectivore genus *Anoura*, and the frugivore genera *Sturnira*, *Artibeus*, and *Platyrrhinus*. Despite their contribution as pollinators and seed dispersers in the Andean environments, little is known on the adaptations that allow these bats to face the physiological challenges imposed by highland ecosystems. The Allen's and Bergmann's biogeographic rules have considered the effect of physiological constrains, inherent to colder environments, on warm-blooded vertebrate body size. It has been also suggested, that these morphological responses can led to distinct evolutionary fates among vertebrate populations (Assis et al. 2016). Bergmann's rule (Bergmann 1847), proposes that animals in cold habitats will be larger than those in warm habitats; on its part, the Allen's rule (Allen 1877), holds that in a warm-blooded species having distinct geographic populations, the limbs, ears, and other appendages of the individuals living in cold climates, tend to be shorter than in animals of the same species living in warm climates. Larger body-sizes are thought to favor the area/volume relationship, with a lower rate of heat dissipation among large individuals; in the same way, shorter appendages such as ears and extremities, dissipate less heat than larger ones. If these two rules apply for Neotropical chiropterans, we will expect to find larger individuals or species with shorter appendages in highland ecosystems, characterized by colder conditions. However, in an analysis of 22 mammalian families, Gohli and Kjetil (2016) found weak support for Bergmann's and Allen's rules among 101 phyllostomid species analyzed. The authors concluded that factors other than latitude and temperature are the major drivers of body mass evolution at the family level in mammals. Chiropteran species inhabiting the highlands of the Neotropics vary on both general body size and expression of their appendages. Although there is not an identified universal pattern that connects size and elevation among phyllostomid highland specialized genera, body size seems to play a role in the evolution of these taxa. While in the genus *Sturnira*, contrasting body sizes are found along the same elevations (e.g., *S. aratathomasi* GSL = 29.9 > 1600 m, *S. nana* GSL = 18.9; 1400–1600 m); *Artibeus* follows an opposite pattern of that established by the Bergmann's rule, with the small species of the subgenus *Dermanura* typically found in highland ecosystems, while the large body size of the subgenus *Artibeus* being common species of the lowlands in the Neotropics and apparently restricted to these environments. In our analyses, populations of *Platyrrhinus dorsalis* from the lowlands exhibit larger skulls in comparison with those from the mid and high elevations on the western slope of the Andes. Several macroecological studies (e.g., McCain 2007; López-González et al. 2012; Weier et al. 2017) agree that the distribution of bats in mountainous systems, is associated with the heterogeneity of the

vegetation cover, derived from changes in temperature, relative humidity and precipitation, across the gradient.

The Andes, was formed as a consequence of the subduction of the Pacific Plate under the western edge of the South American Continental Plate, generating on its north-westernmost and youngest portion, the so called *Anden Pacífico* (Pacific sidewalk), a stripe of continental land, that runs from south to north along the Pacific Coast supporting the Chocó Biogeographic region, one of the last coastal tropical rainforests on Earth and constituting the rainiest spot on the planet, reaching in its central portion, average mean annual precipitations of 14,000 mm/year. Because of its reduced width, the territory of the Biogeographic Chocoan region transversally turns from the sea level up to +3000 m, showing a great deal of environmental heterogeneity, resulting from climatic differences along the slopes of the Andean system in a very short distance (less than 100 km) (Rangel 2004). For Colombia, the Andean region appears as the most dynamic in terms of phyllostomid species turnover (Mantilla-Meluk et al. 2009). This change in species composition across the elevational gradient has been interpreted as a response to the rapid changes in environmental variables such as temperature, relative humidity, oxygen concentration and its effect on the constitution of the plant communities (Mantilla-Meluk et al. 2009). Little is known about the ecological boundaries of species in the genus *Platyrrhinus* but as the most diverse genus among Neotropical bats, it apparently have a high plasticity in morphology, that despite the mechanical restrictions of the stenodermatine skull rostrum, is represented by a large variation in skull sizes, ranging from 32.84 mm in *P. albericoi* to 20.44 in *P. brachycephalus* (Velazco 2005); no other phyllostomid genus has such a wide range in skull sizes. The herein documented variation in skull size for a single population inhabiting ecologically contrasting environments along an elevational gradient, opens the opportunity to develop a wide set of working hypotheses, explaining the success of *Platyrrhinus* in the Neotropics.

Lack of sexual dimorphism among analyzed subpopulations

Our morphometric analyses did not reveal the existence of secondary sexual variation among the examined individuals of the two taxa (Fig. 4). This is congruent with the patterns described by Velazco and Solari (2003) and Velazco et al. (2010, 2018), who did not find sexual dimorphism in other species of the genus. The presence of sexual dimorphism in bats has been associated with size, trophic differences related to carrying capacity during flight, segregation of niches and fecundity (de Camargo and de Oliveira 2012; Lisón 2012; Lisón et al. 2014). The presence of sexual dimorphism in phyllostomid has been documented for some species, such as *Uroderma bilobatum* (Baker et al. 1972), *Sturnira magna* (Tamsitt and Valdivieso 1986), *S. oporaphilum* and *S. ludovici* (Pacheco and Patterson 1992), *Phyllostomus discolor* (Power and Tamsltt 1973; Rodríguez-Posada and Sánchez-Palomino 2009), *Lophostoma silvicolum* (Dechmann et al. 2005), and *Artibeus lituratus* (López-Aguirre and Pérez-Torres 2015).

Conservation implications

Under the International Union for Conservation of Nature (IUCN) categorization inventory of the global conservation status of biological species, two species in the genus *Platyrrhinus* are categorized as Near Threatened (NT): *P. ismaeli* and *P. matapalensis*; three under the Data Deficient (DD) category: *P. aquilus*, *P. nitelinea*, and *P. umbratus*, while the rest of the species are under the Least Concerned (LC) category. Although, *P. chocoensis*, has been recorded in most of the public and private protected areas in Ecuador (Velazco 2005; Velazco et al. 2011), most of the Colombian localities in where this species has been reported are outside protected areas (Palacios-Mosquera and Garrido-Mosquera 2009).

The description of *P. chocoensis* was based on specimens from the Pacific Region of Colombia. Although not common at the time, the authors categorize *P. chocoensis* as a Data Deficient (DD) species (Alberico and Velasco 1991); later it was included in the Red List of Colombian Mammals, as Nearly Threatened (NT) (Rodríguez-Mahecha et al. 2006). Currently, *P. chocoensis* is the only species in the genus listed as Vulnerable (VU) due to its restricted distribution (< 20,000 km^2) in the Biogeographic Choco (Ramírez-Chaves and Suárez-Castro 2015).

Recently, the Central Area of the Biogeographic Chocó (locality of Pacurita), was designated as an Area of Importance for Bat Conservation in Colombia (RELCOM, 2018), based on its high diversity (Spp=51), and the presence of Chocoan endemic bats including: *Choeroniscus periosus*, *P. chocoensis,* and *Rhinophylla alethina*; highlighting its importance as a hotspot of diversity.

The recognition of *P. chocoensis* as a junior synonym of *P. dorsalis*, brings into consideration the need to reassess the conservation status of *P. dorsalis* geographic variants.

Reassessments of the conservation status, due to taxonomic changes have occurred among Colombian birds. During the elaboration of the first version of Red List of Birds of Colombia, Renjifo et al. (2002), included the tinamous *Cryturellus saltuarius* and *C. columbianus* as independent valid species. Based upon their habitat loss, *C. saltuarius* was identified as Critically Endangered (CR), while *C. columbianus* was categorized as Endangered (EN). In later versions of the Red List of Birds of Colombia (Renjifo et al. 2014, 2016), *C. saltuarius* and *C. columbianus*, were considered subspecies of *C. erythropus,* a

taxon that was excluded from new versions of the red list. The later may be one of the potential outputs in our case, with *P. dorsalis* Pacific Colombian populations categorized as LC. An alternative option, may be to consider *P. dorsalis* Pacific Colombian populations as a subspecies, and maintain its conservation status as VU. Similar cases were also considered for bird taxa in Colombia. Although the Red List of Birds of Colombia is constructed at the species level, the new versions have included the subspecies *Cryturellus obsoletus castaneus*, categorize under CR, as well as the subspecies of grasshopper sparrow *Ammodramus savanarum caucae*, categorized as EN (Renjifo et al. 2014, 2016). The Red List of Mammals of Colombia contains 31 subspecies, however, as we mentioned lines above, the number of bat species ($N = 2$) and subspecies ($N = 1$) evaluated for their conservation status in Colombia is very limited. The subspecific status was always very important in regional assessments of the mammalian diversity (Cabrera 1958). Unfortunately, after the second official list of Colombian mammals of Cuervo et al. (1986) subspecies were eliminated from this type of assessments, pattern followed by posterior efforts in Alberico et al. (2000), Solari et al. (2013), and Ramírez-Chaves et al. (2016).

Finally, we suggest further studies in which the implementation of other methods such as Landmark-based geometric morphometric analyses, as well as the use of other molecular markers evaluating other mechanisms of transmission, allow for a better evaluation of the morphological and molecular variation of *P. dorsalis* subpopulations on the western slope of the Andes, to consider the designation of *P. d. chocoensis* as a subspecies of special interest by the evolutionary process it represents and the ecological role these populations of bats play in a very unique environment, such it is the Biogeographic Choco, which currently is under high pressure.

Compliance with ethical standards

Appendix 1: Specimens examined

The following list includes all the specimens examined in this study with their respective localities. Refer "Materials and methods" for abbreviations.

Platyrrhinus chocoensis (147). **COLOMBIA**: *Cauca:* Alto Micay, Betania (FMNH 113745, 113821, 113824, 113828, 113829, 113831, 113833–113835). Nariño: La Guayacana (USNM 309018). *Valle del Cauca:* Concesión Bajo Calima, Cuartel BV83 (FMNH 140696, 140697); Río Raposo (USNM 339395, 339396); Río Zabaletas, 29 km SE Buenaventura (USNM 483533, 483535, 483537–483539); Río Zabaletas, approx. 30 km SE Buenaventura (USNM 483536). *Chocó:* Alto Baudó, Río Pato, Km 15, via Panamericana (UV 3823), El Afirmado (CMCH 151); Bahía Solano, Ensenada de Utría (UV 3645, 3646, 3647, 3648); Bajo Baudó-Pizarro Quebrada Señor Señorcito, Corregimiento Piliza (UV 11310), 2 km Nororiente (UV 11289); Casa máquinero confluencia, Río Angostura (UV 11332); Condoto, Opogodó (CMCH 703); Istmina, Quebrada el Platinero 12 km-Istmina (UV 3817–3822, 10100–10103); Primera Mojarra (CMCH 661); Medio Atrato, La Vuelta (CMCH 1817, 3019); Nuquí (CMCH 1846); Quibdó, Pacurita (CMCH 3017, 3018, 872, 970, 1092, 1245, 1247, 1256, 1263, 1330, 1912); Guarandó (CMCH 341); San José del Palmar, Quebrada la Guagua, 8 km al Oeste La Italia, Sub, Q. Toro Viejo (UV 7446, 7447, 7449); Unión Panamericana, Salero (CMCH 141, 171, 233, 639, 669, 674, 1392). *Risaralda:* Pueblorico, Casa Elias Parra Confluencia de las Q. Amurrupa y Amurrupacito, Área de Manejo Especial Étnico de Alto Amurrupa, Corr. Santa Cecilia (UV 14711, 14681, 14679). *Valle del Cauca:* Buenaventura (UV 13594, 14363, 14719), Instalación Base Naval, Bahía Málaga (UV 5434–5436, 5976, 5978–5982); Fuente de Materiales, Bahía Málaga (UV 5571, 5573, 5574, 5575); Granja Agr. R. Calima, 13 km N, 14 km E Buenaventura (UV 2810–2812, 3183–3185); Campamento Pulpapel, Concesión Bajo Calima (UV 5748, 5749, 10666); Cuartel BV-83- Concesión Bajo Calima (UV 5736, 5738, 5744, 5745, 5751, 5754, 5755, 10663, 10664, 10956, 10957); Cuartel BV-5- Concesión Bajo Calima (UV 10954, 10955, 10665); Embalse Represa Alto Anchícaya (UV 14823); Estación # 5 "El Mirador" Río Cajambre (UV 3707–3709); Estero el Bonguito, Bongo

puerto España (UV 13607); Finca San Pedro, Corr, Bazan Bocana (UV 13622); Río Zabaletas, 16 km S, 12 km E Buenaventura (UV 2162–2164, 2166, 2167, 10539, 10540); Quebrada San Joaquín, 8 km S., 3 km E, Bajo Calima (UV 2153); Quebrada Alegria, Bahía Málaga (UV 5359, 5360, 5566–5570, 5572); Río Zabaletas (UV 4257–4259); Río Zabaletas, 16 km S, 12 km E Buenaventura (UV 281, 972, 2287, 2288, 2290, 2291, 2294); Río Escalerete, Planta Acueducto (UV 3186); Tunel Murrapal, Represa Alto Anchicaya (UV 14358); Dagua, Qda. Pericos, via Cali-Buenaventura (UV 13749), Qda. El Oso, Vereda Saragosa, San Martin, via Cali-Buenaventura (UV 13596); Vereda el Placer; Corregimientola Cascada (UV 14838); Corregimiento Triana; via Cali-Buenaventura (UV 13795). **PANAMÁ:** *Darién:* Parque Nacional Darién, Rancho Frío (FMNH 128141).

Platyrrhinus dorsalis (15). **COLOMBIA:** *Cauca:* Charguayaco (FMNH 113538, 113539). *Huila:* Las Cuevas Parque, Upper Cabaña (FMNH 58740). *Valle del Cauca:* Dapa, 12 mi NW Cali (USNM 483573); Pichinde, 10 km SW Cali (USNM 483577); Pance, approx 20 km SW (USNM 483580–483585, 483593, 483598). **ECUADOR**: *Imbabura:* Paramba (BMNH 99.12.5.1 [Holotype of *Vampyrops dorsalis*]). **VENEZUELA**: *Vargas:* Galipán, Cerro Ávila, 5.7 km NE Caracas (BMNH 14.7.27.1 [Holotype of *Vampyrops oratus*]).

Appendix 2

Species, tissue collection number, and GenBank accession numbers for the *Platyrrhinus* and outgroup samples used in the study.

	Tissue/museum number	GenBank accession numbers	
		Cty-*b*	ND2
Carollia brevicauda	FMNH174595	FJ154120	FJ154186
Chiroderma villosum	FMNH174652	FJ154121.	FJ154187
Mesophylla macconelli	FMNH174719	FJ154122	FJ154188
Sturnira erythromos	FMNH174809	FJ154179	FJ154245
Uroderma magnirostrum	FMNH174907	FJ154180	FJ154246
Vampyriscus bidens	ALG14898	FJ154181	FJ154247
Vampyrodes caraccioli	FMNH174912	FJ154182	FJ154248
Vampyressa melissa	FMNH174910	FJ154185	FJ154251
Platyrrhinus albericoi	FMNH172107	FJ154123	FJ154189
Platyrrhinus angustirostris	FMNH129154	FJ154143	FJ154209

	Tissue/museum number	GenBank accession numbers	
		Cty-*b*	ND2
Platyrrhinus angustirostris	ROM105964	GQ184783	GQ184756
Platyrrhinus aurarius	ROM108220	FJ154125	FJ154191
Platyrrhinus aurarius	ROM114634	FJ154126	FJ154192
Platyrrhinus aurarius	ROM114660	FJ154127	FJ154193
Platyrrhinus aurarius	ROM114679	FJ154128	FJ154194
Platyrrhinus aurarius	ROM114702	FJ154129	FJ154195
Platyrrhinus brachycephalus	FMNH174746	FJ154131	FJ154197
Platyrrhinus brachycephalus	FMNH174748	FJ154132	FJ154198
Platyrrhinus chocoensis	CMCH 872	MT010326	MT017920
Platyrrhinus chocoensis	CMCH 1392	MT010327	MT017921
Platyrrhinus dorsalis	TK135521	FJ154133	FJ154199
Platyrrhinus dorsalis	TK135522	FJ154134	FJ154200
Platyrrhinus dorsalis	TK135530	FJ154135	FJ154201
Platyrrhinus dorsalis	TK135531	FJ154136	FJ154202
Platyrrhinus dorsalis	TK135629	FJ154137	FJ154203
Platyrrhinus dorsalis	TK135668	FJ154138	FJ154204
Platyrrhinus dorsalis	TK135940	FJ154139	FJ154205
Platyrrhinus fusciventris	AMNH267555	GQ184739	GQ184757
Platyrrhinus fusciventris	ROM112611	GQ184740	GQ184758
Platyrrhinus guianensis	ROM113991	KJ576930	KJ576939
Platyrrhinus guianensis	ROM114070	KJ576931	KJ576940
Platyrrhinus helleri	LSUM536	FJ154140	FJ154206
Platyrrhinus helleri	ROM99614	KJ576925	KJ576934
Platyrrhinus incarum	FMNH129156	FJ154144	FJ154210
Platyrrhinus incarum	USNM584494	GQ184735	GQ184753
Platyrrhinus infuscus	FMNH129160	FJ154148	FJ154214
Platyrrhinus infuscus	FMNH129161	FJ154149	FJ154215
Platyrrhinus infuscus	FMNH174767	FJ154150	FJ154216

	Tissue/museum number	GenBank accession numbers	
		Cty-*b*	ND2
Platyrrhinus infuscus	FMNH174768	FJ154151	FJ154217
Platyrrhinus ismaeli	FMNH129137	FJ154152	FJ154218
Platyrrhinus ismaeli	FMNH129142	FJ154153	FJ154219
Platyrrhinus ismaeli	FMNH129143	FJ154154	FJ154220
Platyrrhinus ismaeli	FMNH129145	FJ154155	FJ154221
Platyrrhinus lineatus	MVZ185596	FJ154156	FJ154222
Platyrrhinus lineatus	MVZ185602	FJ154159	FJ154225
Platyrrhinus lineatus	MVZ185603	FJ154160	FJ154226
Platyrrhinus masu	FMNH172100	FJ154161	FJ154227
Platyrrhinus masu	FMNH172101	FJ154162	FJ154228
Platyrrhinus masu	FMNH172102	FJ154163	FJ154229
Platyrrhinus masu	MUSM18265	FJ154164	FJ154230
Platyrrhinus matapalensis	TK134723	FJ154165	FJ154231
Platyrrhinus matapalensis	TK134726	FJ154166	FJ154232
Platyrrhinus umbratus	FMNH172104	FJ154169	FJ154235
Platyrrhinus umbratus	FMNH172106	FJ154170	FJ154236
Platyrrhinus umbratus	MUSM18263	FJ154171	FJ154237
Platyrrhinus umbratus	MUSM18264	FJ154172	FJ154238
Platyrrhinus umbratus	MUSM18273	FJ154173	FJ154239
Platyrrhinus recifinus	MVZ185604	KJ576962	KJ576935
Platyrrhinus recifinus	MVZ185605	FJ154174	FJ154240
Platyrrhinus recifinus	MVZ185610	FJ154176	FJ154242
Platyrrhinus vittatus	ROM97305	FJ154178	FJ154244

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