

Geographic variation in select species of the bat genus *Platyrrhinus*

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The taxonomy of Neotropical bats is constantly changing, with new species being described and junior synonyms elevated, while other taxa are relegated to junior synonyms or subspecies. The genus *Platyrrhinus* has followed this trend, with some issues persisting about the current status of its subspecies. Here we evaluate variation in cranial shape and size based on geometric morphometric analyses of *Platyrrhinus dorsalis* and *P. umbratus*. *P. dorsalis* occurs at elevations from sea level to above 2,000 m and is found from southern Panama southward into Colombia and along both slopes of the Andes in Ecuador. *P. umbratus* occurs at elevations from 400 m to above 3,150 m in the Andean from Colombia south through Bolivia and Caribbean Mountain systems of Venezuela and Colombia. Our analyses did not support the recognition of subspecies in either species. The difference in skull size and shape between populations of *P. dorsalis* is associated with elevation, suggesting that this species exhibits an altitudinal clinal variation, with individuals being larger in the lower elevation and smaller in higher elevations. In *P. umbratus* the difference in skull size and shape between populations is associated with a latitudinal cline, with individuals tending to be larger in the northern part of their range. Our analyses did not reveal the existence of secondary sexual variation in *P. dorsalis* nor in *P. umbratus*.

La taxonomía de murciélagos Neotropicales está en un estado de constante cambio, con algunas especies siendo descritas, sinónimos menores siendo elevados o especies siendo reconocidas como sinónimos menores o subspecies. El género *Platyrrhinus* no ha sido la excepción a esta tendencia, y presenta una larga historia de cambios taxonómicos persistiendo algunas dudas acerca del estado actual de sus subspecies. Evaluamos la variación en forma y tamaño del cráneo en *Platyrrhinus dorsalis* y *P. umbratus* basándonos en análisis de morfometría geométrica. *P. dorsalis* se encuentra presente en elevaciones desde el nivel del mar hasta por encima de los 2,000 m y se distribuye desde Panamá al sur hasta Colombia, y a lo largo de ambas vertientes de los Andes en Ecuador. *P. umbratus* se encuentra presente en elevaciones desde 400 m hasta los 3,150 m, con distribución en los Andes de Venezuela a Bolivia y el Sistema Montañoso del Caribe de Venezuela y Colombia. Nuestros análisis no apoyan el reconocimiento de subspecies en *P. dorsalis* o *P. umbratus*. La diferencia en el tamaño y forma del cráneo entre poblaciones de *P. dorsalis* está asociada con la elevación, sugiriendo que esta especie presenta una variación clinal altitudinal, con individuos grandes a elevaciones menores y pequeños en las altas. En *P. umbratus* también el tamaño y forma del cráneo está asociada con una clina latitudinal, con los más grandes en la parte septentrional de la distribución. Nuestros análisis no revelan la presencia de variación sexual secundaria en ninguna de las dos especies.

Keywords: Andes, cline, neotropics, *Platyrrhinus dorsalis*, *Platyrrhinus umbratus*, subspecies, taxonomy.

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Introduction

The Neotropical bat genus *Platyrrhinus* is one of the most speciose phyllostomid genera (Simmons and Cirranello 2022). Members of the genus, also known as broad-nosed bats, are widely distributed from Mexico to northern Argentina, with most species found in the Andes region (Velazco and Patterson 2008; Velazco and Gardner 2009; Velazco and Lim 2014; Velazco et al. 2018; Palacios-Mosquera et al. 2020). Over the past two decades, numerous taxonomic changes have been made within the genus, and only since 2005, recognized diversity increased from ten to nineteen species, nearly doubling the number of taxa (Simmons 2005; Simmons and Cirranello 2022; Velazco 2005; Velazco and Gardner 2009; Velazco and Lim 2014; Velazco et al. 2018; Palacios-Mosquera et al. 2020).

Simmons (2005) recognized subspecies in three *Platyrrhinus* species (e. g., *helleri* [*helleri* and *incarum*], *lineatus* [*lineatus* and *nigellus*], and *umbratus* [*aquilus*, *oratus*, and *umbratus*]). However, after several revisionary studies, all of those subspecies were elevated to full species, except for *P. umbratus oratus* which was regarded as a junior synonym of *P. umbratus* (Velazco 2005; Velazco and Gardner 2009; Velazco and Patterson 2008). Velazco et al. (2018) used phylogenetic, linear morphometrics, and ecological niche modeling analyses to review the systematics and taxonomy of *Platyrrhinus nigellus* and *P. umbratus*. The authors suggested that *nigellus* should be recognized as a junior synonym of *umbratus*. Nonetheless, populations of *nigellus* and *umbratus* can be differentiated by subtle external and craniodental morphological differences indi-

cating the possible existence of subspecies or clinal geographic variation (Velazco and Gardner 2009). On the other hand, currently, only subspecies in *Platyrrhinus dorsalis* (*P. d. dorsalis* and *P. d. chocoensis*) are recognized in the genus, but their subspecific status is still controversial. *Platyrrhinus dorsalis* is polytypic, with *chocoensis* and *dorsalis* recognized based on the geographic structure of the morphological variation (Palacios-Mosquera et al. 2020).

Neotropical bat distribution ranges sometimes encompass a variety of biomes, which expose these species to a variety of environments (e. g., climate, vegetation, elevation, etc). Due to this variety of factors some of these species present different degrees of geographic variation throughout their distribution range. These patterns of geographic variation have been suggested to be the result of subspecies (e. g., Molinari et al. 2017; Garbino et al. 2020; Pavan et al. 2021; Tavares et al. 2022), altitudinal (e. g., Moratelli et al. 2013; Castillo-Figueroa 2022), or latitudinal clines (e. g., Nargosen and Tamsitt 1981; Kelly et al. 2018; Méndez-Rodríguez et al. 2021).

Herein we analyzed 2D geometric morphometric data to evaluate whether the populations of *P. dorsalis* and *P. umbratus* deserve subspecific recognition or that the external and craniodental morphological differences between the populations of these two species is the result of an altitudinal or latitudinal cline.

Material and methods

Specimens examined. Our assessment of the taxonomy of *Platyrrhinus dorsalis* and *P. umbratus* was based on the 2D geometric morphometric analyses of the skulls of museum specimens from the following museums: Field Museum of Natural History (FMNH), Chicago, Illinois, United States; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Villa de Leyva, Boyacá, Colombia; Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá, Colombia; Muséum National d'Histoire Naturelle (MNHN-CG), Paris, France; Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru; Museum of Zoology (UMMZ), University of Michigan, Ann Arbor, Michigan, USA; National Museum of Natural History (formerly U.S. National Museum—USNM), Smithsonian Institution, Washington, D.C., United States; and Sección de Zoología, Departamento de Biología, Universidad del Valle (UV), Cali, Colombia.

Geometric morphometrics analyses. We used 376 skulls of adult individuals from the entire distribution range of *Platyrrhinus dorsalis* and *P. umbratus* (Appendix 1). Dorsal and ventral pictures of the skulls were taken with a Konica Minolta DiMAGE Z6 digital camera. The images were processed with Adobe Photoshop CC. Coordinates of the morphological landmarks (Figure 1) were recorded for each image using tpsDIG version 2.31 (Rohlf 2001). We defined the landmarks based on homology, consistency of relative position, coverage of the form, and repeatability (Zelditch

et al. 2012). Specimens of *P. dorsalis* and *P. umbratus* were grouped into two set of populations (*dorsalis* and *chocoensis* or *nigellus* and *umbratus*) based on external and craniodental morphological differences that distinguished those taxa (Velazco 2005; Velazco and Gardner 2009; Velazco et al. 2018; Palacios-Mosquera et al. 2020). Hereafter, we use *dorsalis* and *chocoensis* or *nigellus* and *umbratus* to refer to the morphological diagnosable groups within each species.

We analyzed a total of 281 images (dorsal view) of *Platyrrhinus dorsalis* (61 from populations assigned to *dorsalis* and 114 from populations assigned to *chocoensis*) and *P. umbratus* (58 from populations assigned to *nigellus* and 48 from populations assigned to *umbratus*; Appendix 1). Dorsal-view landmark definitions were as follows: (1) anteriormost point of the premaxilla; (2) medial point of the anterior edge of the nasal bones; (3) most distal point of the postorbital process; (4) meeting point between the braincase and the anterior edge of the posterior root of the zygomatic arch; (5) posteriormost point of the zygomatic arch opening; (6) meeting point between the braincase and the posterior edge of the posterior root of the zygomatic arch; and (7) posteriormost point of the occipital region (Figure 1A). Landmarks were digitized on the right side of each dorsal image of the skulls, and all the analyses were performed using this configuration.

We analyzed a total of 382 images (ventral view) of *Platyrrhinus dorsalis* (52 from populations assigned to *dorsalis* and 145 from populations assigned to *chocoensis*) and *P. umbratus* (56 from populations assigned to *nigellus* and 129 from populations assigned to *umbratus*; Appendix 1). Ventral view landmark definitions were as follows: (1) anteriormost point of the premaxilla; (2) most posteromedial point on the margin of the incisive foramen; (3) most antero-internal point on M1; (4) most anterolabial point on M2; (5) most antero-internal point on M2; (6) most anterior point on the posterior edge of the palatine; (7) meeting point between

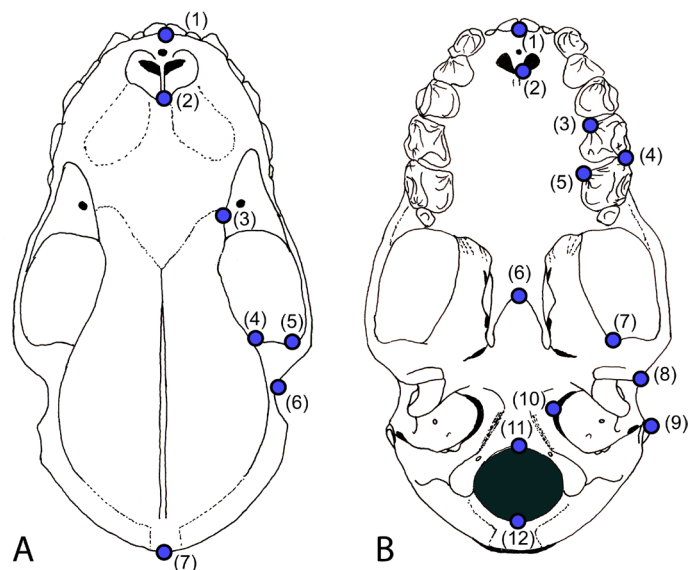


Figure 1. Dorsal (A) and ventral (B) views of a *Platyrrhinus* cranium illustrating the landmarks used in geometric morphometric analyses.

the anterior section of the glenoid fossa and squamosal; (8) most external point on the posterior section of the postglenoid fossa; (9) squamosal lateral extremity, behind the auditory region; (10) most medial point on the margin of the basicochlear fissure; (11) anteriormost point on the margin of the foramen magnum; (12) posteriormost point on the margin of the foramen magnum (Figure 1B). Landmarks were digitized on the left side of each ventral image of the skulls, and all the analyses were performed using this configuration.

The landmark coordinates datasets were converted into Procrustes distances using a Generalized Procrustes Analysis (GPA) that removes undesirable effects of scale, position, and orientation using the *gpagen* function in the R package 'geomorph' (Adams et al. 2021; Baken et al. 2021). We acquired Procrustes shape coordinates, and a size proxy called centroid size (CS) as the square root of the sum of squares of the distance of each landmark to the centroid (mean of all coordinates) of the configuration (Bookstein 1997). Additionally, consensus shapes summarizing the dorsal and ventral views of the skull shape variation among groups were generated. Here, each individual was compared against the consensus shape, which allowed us to visualize differences between groups. Afterwards, we checked the GPA for outliers using the *plotOutliers* function in the 'geomorph' package. Outliers were removed from the analysis and the GPA's were rerun.

Differences in centroid size between females and males (sexual dimorphism) and also among groups were graphically summarized using a series of boxplots in each view. The effects of size, sex, and groups on the dorsal and ventral views of the skull shape and its interactions was tested by evaluating the fit of models using the randomized residual permutation procedure (RRPP) with the *lm.rpp* function in the R package 'RRPP' (Collyer and Adams 2018, 2022). Using the same function, we quantified the differences in size among groups, employing the (log) centroid size of the specimens as the response variable, and sex and groups as independent predictors. All models were fit using the type-II (hierarchical) sum of squares, and its significance was based on 10,000 permutations of residual randomization. We used the *anova.lm.rpp* function to compute analysis of variance (ANOVA) tables for each model, which are based on random statistical distributions and use the F distribution to calculate effect sizes. Pairwise comparisons were conducted on significant factors using the *pairwise* function in the R package 'RRPP' (Collyer and Adams 2018, 2022).

Differences in the dorsal and ventral views of the skull shape among groups were also explored using ordination methods. First, we performed principal component analyses (PCA) on the Procrustes-aligned data using the *gm.prcomp* function in the R package 'geomorph' (Adams et al. 2021; Baken et al. 2021). Of the PCs produced, we chose those that contained significant cumulative variance of shape in each view. Then we generated deformation grids with the extremes (maximum and minimum) of shape

variation along the principal components 1 and 2 (PC1 and PC2). Second, we used a linear discriminant analysis (LDA) using the *lda* function in the R package 'MASS' to determine whether the groups could be reliably distinguished (Venables and Ripley 2002). Jackknife cross-validation was used to estimate the probability of a specimen belonging to any of the predefined groups. Matrices and scripts associated with analyses in this study have been deposited on GitHub (https://github.com/pvelazco/Platyrrhinus_GM.git). The LSID for this publication is: urn:lsid:zoobank.org:pub:4D40F6B2-A27E-461B-8087-401702F7757A.

Results

Platyrrhinus dorsalis variation in skull size. We did not find evidence of sexual dimorphism in size in any of the views examined (Table 1; Figure 2A, B). The two-sample t-test between male and female specimens assigned to *chocoensis* found no statistically significant differences ($t = -0.701$, $d. f. = 112$, $P = 0.484$ [dorsal view]; $t = -0.035$, $d. f. = 143$, $P = 0.971$ [ventral view]). Similarly, the two-sample t-test between male and female specimens assigned to *dorsalis* found no statistically significant differences ($t = 0.046$, $d. f. = 56$, $P = 0.963$ [dorsal view]; $t = 0.233$, $d. f. = 50$, $P = 0.816$ [ventral view]). Finally, the two-sample t-test using all the specimens from both groups found no statistically significant differences between male and females of *P. dorsalis* ($t =$

Table 1. ANOVA results regarding effects of sex, groups, and their interaction on centroid size (log CS).

	Df	SS	MS	R ²	F	Z	P
Centroid Size (CS)							
(A) Dorsal view – <i>Platyrrhinus dorsalis</i>							
Sex	1	0.273	0.273	0.002	0.329	-0.149	0.563
Groups	1	20.718	20.718	0.129	24.923	3.580	< 0.01
Sex x Groups	1	0.162	0.162	0.001	0.195	-0.447	0.672
Residuals	168	139.660	0.831	0.867			
Total	171	161.040					
(B) Ventral view – <i>Platyrrhinus dorsalis</i>							
Sex	1	0.009	0.009	0.000	0.009	-1.506	0.924
Groups	1	0.872	0.872	0.005	0.889	0.453	0.350
Sex x Groups	1	0.049	0.049	0.000	0.050	-1.002	0.821
Residuals	193	189.315	0.981	0.995			
Total	196	190.236					
(C) Dorsal view – <i>Platyrrhinus umbratus</i>							
Sex	1	1.083	1.083	0.014	1.674	0.878	0.206
Groups	1	9.236	9.236	0.121	14.273	2.919	< 0.01
Sex x Groups	1	1.280	1.280	0.017	1.978	1.027	0.160
Residuals	100	64.713	0.647	0.846			
Total	103	76.531					
(D) Ventral view – <i>Platyrrhinus umbratus</i>							
Sex	1	0.128	0.128	0.001	0.137	-0.592	0.714
Groups	1	27.719	27.719	0.142	29.636	3.887	< 0.01
Sex x Groups	1	1.515	1.515	0.008	1.619	0.876	0.204
Residuals	177	165.555	0.935	0.848			
Total	180	195.321					

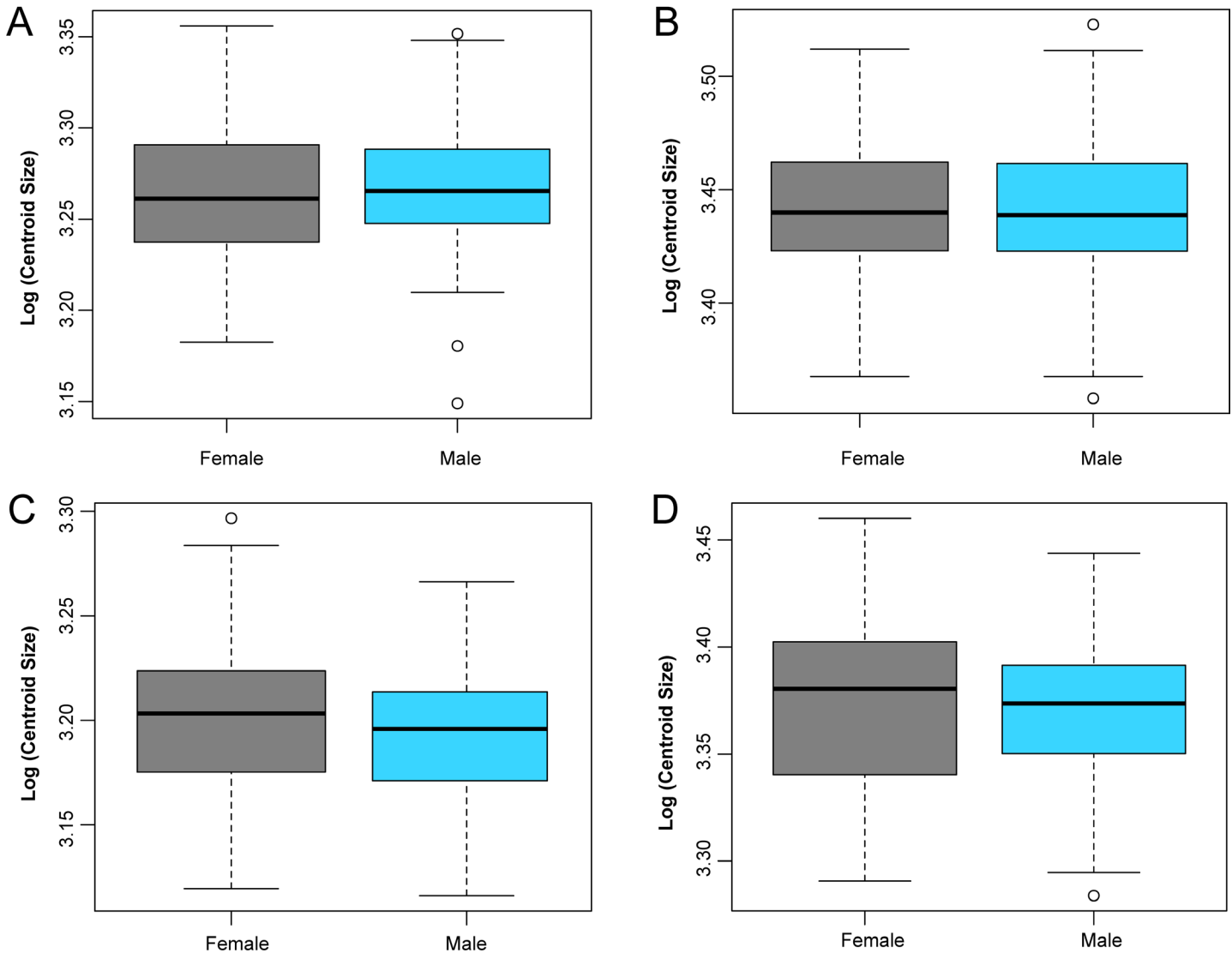


Figure 2. Box plots of the centroid size by species/sex. (A) dorsal view of *Platyrrhinus dorsalis*, (B) ventral view of *P. dorsalis*, (C) dorsal view of *P. umbratus*, and (D) ventral view of *P. umbratus*. Sex: females = gray and males = light blue. Color box limits indicate the first (25%) and third (75%) quartile, the thick black line indicates the median centroid size, and open circles represent outliers.

-0.732, $d. f. = 170$, $P = 0.465$ [dorsal view]; $t = 0.009$, $d. f. = 195$, $P = 0.992$ [ventral view]). The centroid size (CS) in the dorsal view of the cranium was significantly different between the two groups, showing that individuals of *dorsalis* are smaller than *chocoensis* ($P < 0.01$; Table 1; Figure 3A). The variance of the factors tested, represented by mean squares value and the R^2 , showed that most of the variance in cranium size is found between groups (Table 1). However, the centroid size (CS) in the ventral view of the cranium was not significantly different between the two groups ($P = 0.350$; Table 1; Figure 3B).

Platyrrhinus dorsalis variation in skull shape. The ANOVA did not find evidence of sexual dimorphism in cranium shape in either view (Table 2). There were significant differences on both views of the cranial shape variation in the entire Procrustes shape space between the two groups ($P < 0.05$; Table 2). Fitted linear models exhibited significant effect of size on the shape variation in both views; however, the morphological variation explained by size was low

(< 3% in all cases; Table 2) so the allometric effect was not considered, and analyses and graphical representations were carried out on the original shape coordinates.

The PCA showed a clear ordination in both views of the cranium (Figure 4). The first three PC scores accounted for 73% (dorsal view) and 47% (ventral view) of total shape variation. Results are shown from the first two PCs, which accounted for 64% (dorsal view) and 37% (ventral view) of the variation respectively (Figure 4).

The DFA showed a small overlap between the groups indicating that they are different in the shape of the cranium. Specimens were correctly assigned in high percentages to *chocoensis* (93% – dorsal view and 97% – ventral view) and *dorsalis* (71% – dorsal view and 90% – ventral view).

Platyrrhinus umbratus variation in skull size. We did not find evidence of sexual dimorphism in size in any of the views examined (Table 1; Figure 2C, D). The two-sample t-test between male and female specimens assigned to *nigellus* found no statistically significant differences ($t = -0.897$, $d. f. =$

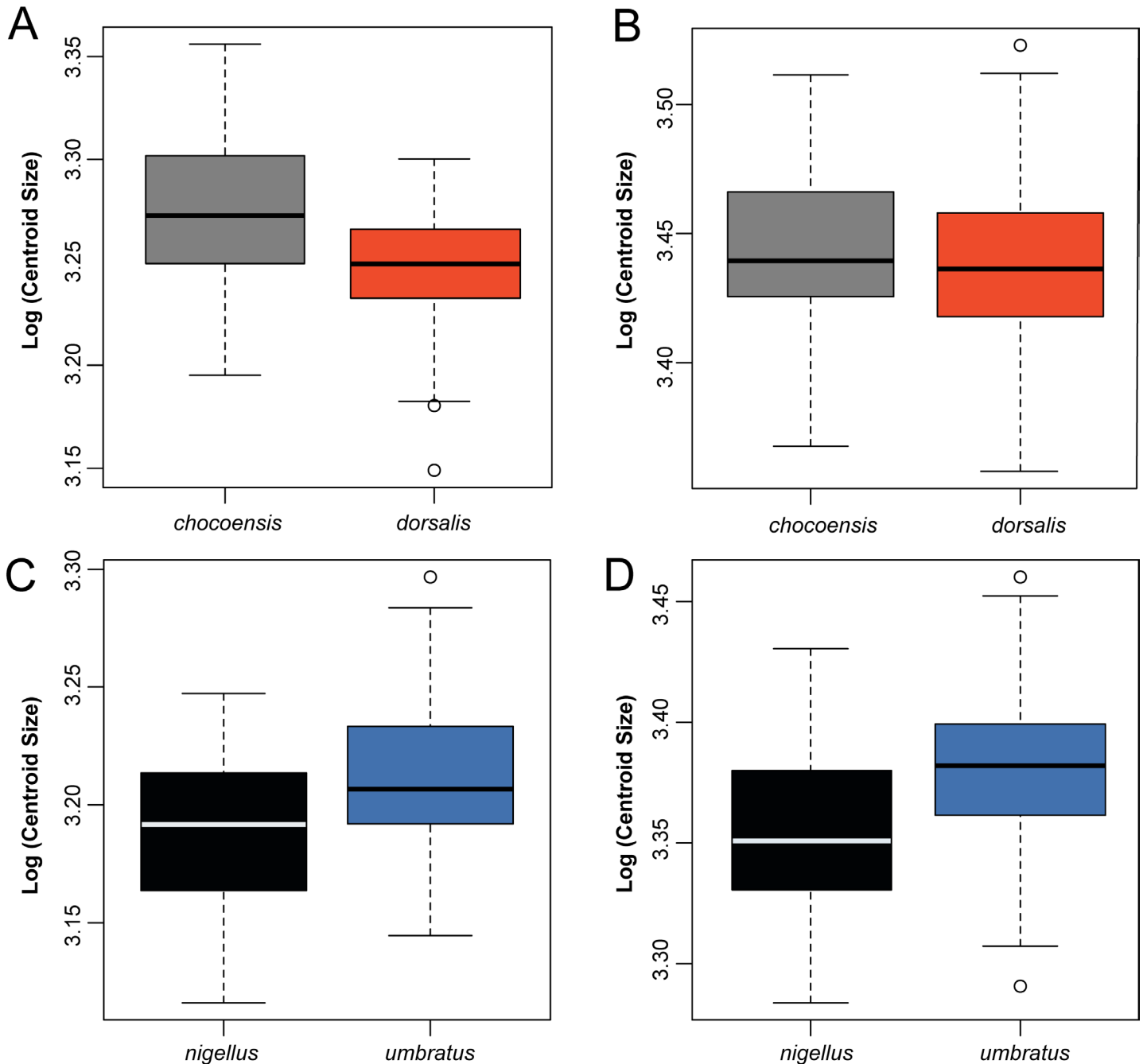


Figure 3. Box plots of the centroid size by groups, showing dorsal (A) and ventral (B) views of *Platyrrhinus dorsalis*, and dorsal (C) and (D) ventral views of *P. umbratus*. Groups: *chocoensis* = gray, *dorsalis* = red, *nigellus* = black, and *umbratus* = blue. Color box limits indicate the first (25%) and third (75%) quartile, the thick black line indicates the median centroid size, and open circles represent outliers.

54, $P = 0.374$ [dorsal view]; $t = -0.832$, $d. f. = 54$, $P = 0.409$ [ventral view]). Similarly, the two-sample t-test between male and female specimens assigned to *umbratus* found no statistically significant differences in the ventral view of the cranium ($t = 0.983$, $d. f. = 123$, $P = 0.328$). We were not able to run a similar test for the dorsal view since we did not have enough male specimens ($n = 1$) of *umbratus*. The two-sample t-test using specimens from both groups found no statistically significant differences between males and females of *P. umbratus* ($t = 1.161$, $d. f. = 101$, $P = 0.248$ [dorsal view]; $t = 0.650$, $d. f. = 179$, $P = 0.516$ [ventral view]). The centroid size (CS) in the dorsal and ventral views of the cranium were significantly different

between the two groups showing that individuals of *umbratus* are larger than *nigellus* ($P < 0.01$ in both views; Table 1; Figure 3C, D). The variance of the factors tested, represented by mean squares value and the R^2 , showed that most of the variance in cranium size is found between groups (Table 1).

Platyrrhinus umbratus variation in skull shape. The ANOVA did not find evidence of sexual dimorphism in cranium shape in either view (Table 2). There were significant differences on both views of the cranial shape variation in the entire Procrustes shape space between the two groups ($P < 0.05$; Table 2). Fitted linear models exhibited significant effect of size on the shape variation in the dorsal view of the

Table 2. ANOVA results regarding effects of size (allometry), sex (sexual dimorphism), groups and their interactions on shape.

	Df	SS	MS	R ²	F	Z	P
Shape							
(A) Dorsal view – <i>Platyrrhinus dorsalis</i>							
Size	1	0.003	0.003	0.017	3.215	1.999	0.025
Sex	1	0.000	0.000	0.003	0.564	-0.498	0.694
Groups	1	0.013	0.013	0.084	15.964	4.382	< 0.01
Size x Sex	1	0.000	0.000	0.003	0.583	-0.435	0.665
Size x Groups	1	0.002	0.002	0.010	1.983	1.345	0.097
Sex x Groups	1	0.001	0.001	0.004	0.719	-0.136	0.550
Size x Sex x Groups	1	0.001	0.001	0.005	0.991	0.337	0.361
Residuals	164	0.134	0.001	0.863			
Total	171	0.155					
(B) Ventral view – <i>Platyrrhinus dorsalis</i>							
Size	1	0.004	0.004	0.029	6.716	5.234	< 0.01
Sex	1	0.001	0.001	0.004	0.974	0.092	0.466
Groups	1	0.020	0.020	0.147	34.584	9.196	< 0.01
Size x Sex	1	0.000	0.000	0.003	0.808	-0.361	0.641
Size x Groups	1	0.001	0.001	0.007	1.660	1.482	0.066
Sex x Groups	1	0.000	0.000	0.003	0.641	-0.946	0.828
Size x Sex x Groups	1	0.001	0.001	0.005	1.190	0.598	0.275
Residuals	189	0.108	0.001	0.805			
Total	196	0.135					
(C) Dorsal view – <i>Platyrrhinus umbratus</i>							
Size	1	0.002	0.002	0.025	2.760	2.028	0.022
Sex	1	0.000	0.000	0.002	0.260	-1.864	0.969
Groups	1	0.002	0.002	0.033	3.677	2.575	0.005
Size x Sex	1	0.000	0.000	0.006	0.669	-0.388	0.652
Size x Groups	1	0.000	0.000	0.006	0.700	-0.306	0.621
Sex x Groups	1	0.001	0.001	0.010	1.145	0.518	0.299
Residuals	97	0.054	0.001	0.873			
Total	103	0.062					
(D) Ventral view – <i>Platyrrhinus umbratus</i>							
Size	1	0.001	0.001	0.007	1.430	1.074	0.141
Sex	1	0.001	0.001	0.008	1.600	1.419	0.079
Groups	1	0.004	0.004	0.040	7.655	5.887	< 0.01
Size x Sex	1	0.001	0.001	0.007	1.402	1.038	0.149
Size x Groups	1	0.001	0.001	0.011	2.063	2.077	0.019
Sex x Groups	1	0.001	0.001	0.007	1.380	1.012	0.155
Size x Sex x Groups	1	0.001	0.001	0.005	1.012	0.196	0.424
Residuals	173	0.102	0.001	0.898			
Total	180	0.113					

cranium; however, the morphological variation explained by size was low (< 3 %; Table 2) so the allometric effect was not considered, and analyses and graphical representations were carried out on the original shape coordinates.

The PCA did not show a clear ordination in both views of the cranium (Figure 5). The first three PC scores accounted for 68 % (dorsal view) and 42 % (ventral view) of the cranium total shape variation. Results are shown from the first

two PCs, which accounted for 55 % (dorsal view) and 32 % (ventral view) of the variation respectively (Figure 5).

The DFA showed a small overlap between the groups indicating that they differ in cranial shape. Specimens were correctly assigned to *nigellus* (73 % – dorsal view and 46 % – ventral view) and *umbratus* (75 % – dorsal view and 90 % – ventral view) in high percentages.

Discussion

In the past decade, recognized bat diversity has increased due to new species descriptions and taxa raised from synonymy (Burgin et al. 2018). Within Phyllostomidae, examples include *Lophostoma nicaraguae* (Esquivel et al. 2022), *Glossophaga bakeri* (Velazco et al. 2021), *Tonatia bakeri*, and *T. maresi* (Basantes et al. 2020). In a few other cases, species have been downgraded to junior synonyms or subspecies (e. g., *Chiroderma vizottoi* [Garbino et al. 2020]; *Vampyressa sinchi* [Tavares et al. 2022]; *Lophostoma yasuni* [Camacho et al. 2016]). This was the case of *Platyrrhinus chocoensis* that was regarded as a subspecies of *P. dorsalis* based on linear morphometrics and genetic analyses (Palacios-Mosquera et al. 2020), and *P. nigellus* that was regarded as a junior synonym of *P. umbratus* based on linear morphometrics, genetic data, and ecological niche modeling analyses (Velazco et al. 2018). Our geometric morphometric analyses support the recognition of two morphological groups in *P. dor-*

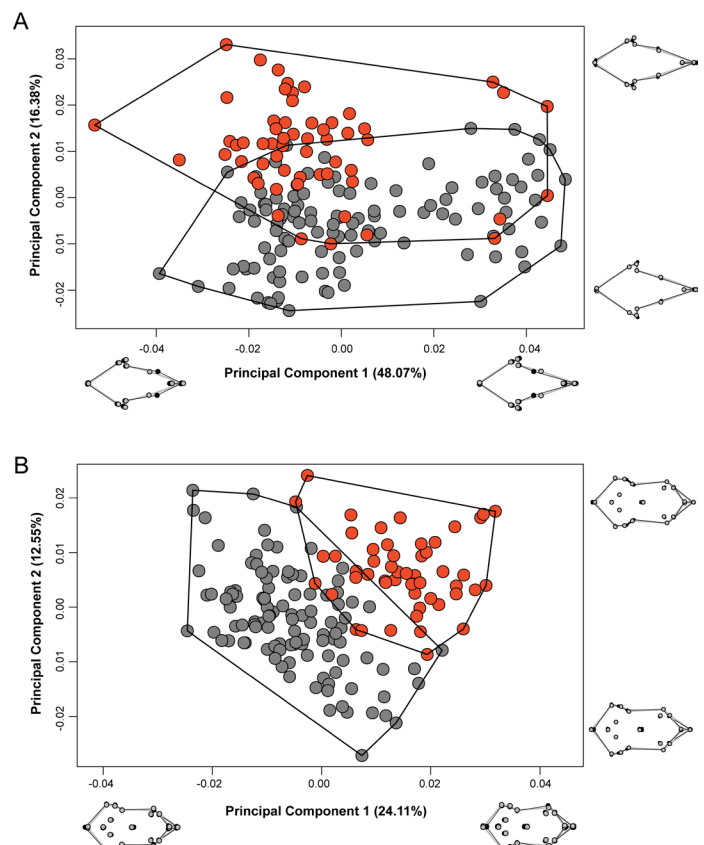


Figure 4. Principal Component Analysis (PCA) of *Platyrrhinus dorsalis* obtained from the (A) dorsal and (B) ventral views of the cranium. Specimens of each group is represented by a dot (*chocoensis*: gray; *dorsalis*: red).

salis (*chocoensis* and *dorsalis*) and in *P. umbratus* (*nigellus* and *umbratus*), but does not support the recognition of these groups as subspecies.

The recognition of subspecies in phyllostomid species has been on the rise in recent years. To mention some examples, [Garbino et al. \(2020\)](#) performed a comprehensive revision of *Chiroderma* and recognized subspecies in *Chiroderma doriae* (*doriae* and *vizottoi*) and *C. villosum* (*jesupi* and *villosum*); [Molinari et al. \(2017\)](#) described *Sturnira adrianae* with two subspecies (*adrianae* and *caripana*) from montane populations in Colombia and Venezuela; and more recently, [Tavares et al. \(2022\)](#) suggested that *Vampyressa sinchi* be recognized as a subspecies of *V. melissa* and not as a separate species based on genetic analyses. One characteristic that all of the aforementioned cases have in common is that the subspecies in each species are not reciprocally monophyletic ([Molinari et al. 2017](#); [Garbino et al. 2020](#); [Tavares et al. 2022](#)). However, [Patten \(2015\)](#) proposed that a morphologically diagnosably distinct, geographically circumscribed group that does not form a distinct genetic clade or is not reciprocally monophyletic in relation to other such clades in the same species could be considered a subspecies. The two morphological groups in *P. dorsalis* (*chocoensis* and *dorsalis*) and *P. umbratus* (*nigellus* and *umbratus*) fulfill all the requirement for subspecies proposed by [Patten \(2015\)](#), with the exception that the groups are geographically circumscribed from each other. In both species there is some overlap in the geographic ranges of both group pairs.

The recognition of *chocoensis* as a subspecies of *Platyrrhinus dorsalis* as suggested by [Palacios-Mosquera et al. \(2020\)](#) was not supported by our analyses. Genetic analyses did not recover the two groups of *dorsalis* to be reciprocally monophyletic ([Palacios-Mosquera et al. 2020](#)). The linear and geometric morphometric analyses showed that populations of *chocoensis* and *dorsalis* are statistically significantly different, with individuals of *dorsalis* being smaller than *chocoensis*. However, *chocoensis* and *dorsalis* occur in sympatry in several localities in Colombia in the departments of Boyacá, Cundinamarca, Meta, Santander, and Valle del Cauca ([Velazco and Gardner 2009](#); [Palacios-Mosquera et al. 2020](#)), precluding their recognition as subspecies of *P. dorsalis*. We found that the difference in skull size and shape between the two groups is associated with elevation, suggesting that this species exhibits an altitudinal clinal variation, with populations of *chocoensis* (larger individuals) being distributed in lowland habitats and *dorsalis* (smaller individuals) in mid to high elevations habitats. Both groups, *chocoensis* and *dorsalis*, exhibit some external and craniodental differences (see below). Furthermore, the linear and geometric morphometric analyses did not reveal the existence of secondary sexual variation among populations of *P. dorsalis* or its groups (this study; [Palacios-Mosquera et al. 2020](#)).

Our results also do not support the recognition of subspecies in *P. umbratus*. As in *P. dorsalis*, the genetic analyses did not recover the two groups of *umbratus* to be reciprocally

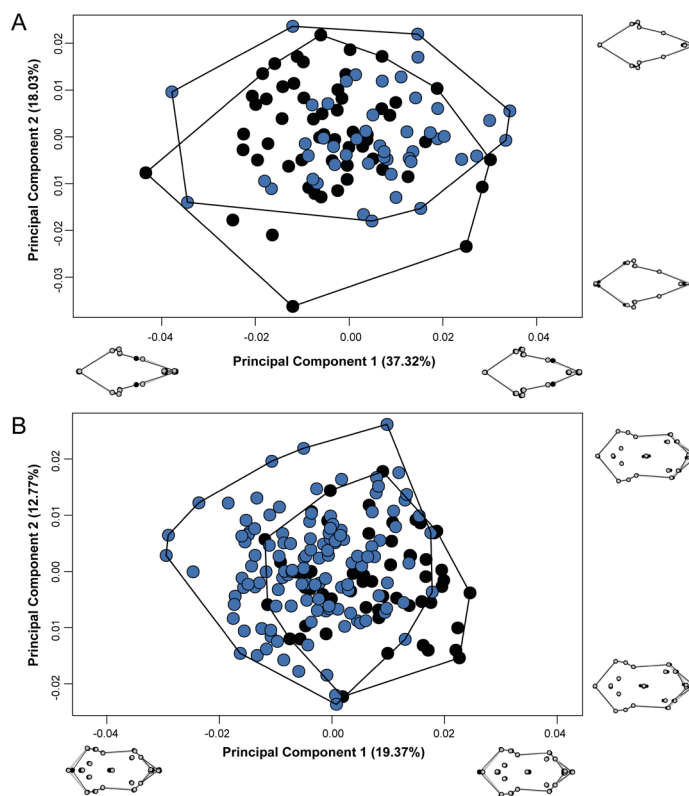


Figure 5. Principal Component Analysis (PCA) of *Platyrrhinus umbratus* obtained from the (A) dorsal and (B) ventral views of the cranium. Specimens of each group is represented by a dot (*nigellus*: black; *umbratus*: blue).

ally monophyletic ([Velazco et al. 2018](#)). The geometric morphometric analyses showed that populations of *nigellus* and *umbratus* are statistically significantly different, with individuals of *umbratus* being larger than *nigellus*. This indicates that *P. umbratus* tend to be larger in the northern part of their range, suggesting that this species exhibits a latitudinal clinal variation. Both groups exhibit some external and craniodental differences (see below). Furthermore, the linear and geometric morphometric analyses did not reveal the existence of secondary sexual variation among populations of *P. umbratus* or its groups (this study; [Velazco et al. 2018](#)).

Our findings indicate that the features used to delineate subspecies within *P. dorsalis* and *P. umbratus* were not phylogenetically relevant but rather represented geographical variation along a cline. Clinal variation in bats has been subject of debate and it has been reported in several neotropical species such as *Myotis nigricans* ([Moratelli et al. 2013](#)), *M. albescens* ([Moratelli and Oliveira 2011](#)), *Anoura cultrata* ([Nagorsen and Tamsitt 1981](#)), *Carollia perspicillata* and *Artibeus lituratus* ([Castillo-Figueroa 2022](#)) among others. Nevertheless, its presence in morphology along environmental gradients must be interpreted with caution, due to the taxonomy of many groups may be heavily impacted by this phenomenon.

Taxonomy. Based on the results of this contribution and other articles (e. g., [Velazco and Gardner 2009](#); [Velazco et al. 2018](#); [Palacios-Mosquera et al. 2020](#)) we present a revised taxonomy of *Platyrrhinus dorsalis* and *P. umbratus*.

Platyrrhinus dorsalis (Thomas, 1900)*Synonyms*

Vampyrops dorsalis Thomas, 1900:269. Type locality: "Paramba, [Imbabura,] N. Ecuador. Alt. 1,100 m."

Platyrrhinus chochoensis Alberico and Velasco, 1991:238. Type locality: Quebrada El Platinerio, 12 km W Istmina (by road), Department of Chocó, Colombia.

Distribution. *Platyrrhinus dorsalis* occurs at elevations from sea level to above 2,000 m from southern Panama southward into Colombia and along both slopes of the Andes in Ecuador.

Diagnosis. Lowland populations assigned to *chochoensis* are medium-size bats (FA [forearm length] 46.9–50.7 mm; CIL [condyloincisive length] 24.3–26.6 mm; Velazco and Gardner [2009]: table 3) characterized by a pale brown dorsal coloration, brownish and bicolored ventral fur; well-marked folds in the pinnae; fossa on the squamosal end of the zygomatic arch lateral to the glenoid fossa absent or almost imperceptible; styler cusp on the lingual face of the M2 metacone absent; only the labial cingulid present on the second lower premolar; and stylid cusp between the metaconid and protoconid of the m2 usually absent. In contrast, mid to high elevation populations assigned to *dorsalis* are medium-size bats (FA 46.6–49.5 mm, CIL 24.1–26.3 mm; Velazco and Gardner [2009]: table 3) characterized by a dark brown dorsal coloration, brownish and tricolored ventral fur; poorly marked but distinguishable folds in the pinnae; deep fossa on the squamosal end of the zygomatic arch lateral to the glenoid fossa; styler cusp on the lingual face of the M2 metacone present; both labial and lingual cingulids present on the second lower premolar; and stylid cusp between the metaconid and protoconid of the m2 present.

Remarks. Linear morphometric analyses did not reveal secondary sexual variation among populations of *chochoensis* or *dorsalis* (Palacios-Mosquera *et al.* 2020). The PCA showed that populations of *chochoensis* and *dorsalis* form two clusters in morphospace (Palacios-Mosquera *et al.* 2020: fig. 2), with individuals of *chochoensis* being larger than *dorsalis*. Molecular analyses recovered specimens of *chochoensis* nested within a larger clade that included specimens only of *dorsalis* (Palacios-Mosquera *et al.* 2020).

Platyrrhinus umbratus (Lyon, 1902)*Synonyms*

Vampyrops umbratus Lyon, 1902:151. type locality: "San Miguel," La Guajira, Colombia.

Vampyrops oratus Thomas, 1914:411. type locality: "Galifari, Sierra del Avila, [Distrito Federal] N. Venezuela. Alt. 6500' " [emend to "Galipán (10° 33' N, -66° 54' W, 1,980 m), Cerro Ávila, 5.7 km NE Caracas, Vargas, Venezuela"].

Vampyrops nigellus Gardner and Carter, 1972:1. type locality: "Huanhuachayo (12° 44' S, -73° 47' W), about 1,660 m, Departamento de Ayacucho, Peru."

Distribution. *Platyrrhinus umbratus* occurs at elevations from 400 m to above 3,150 m in the Andean and Caribbean Mountain systems of Venezuela and Colombia, and along the Andes in Ecuador, Peru, and Bolivia.

Diagnosis. Southern and some northern populations (*nigellus*) of the species are medium-size bats (FA 40.6–48.0 mm, CIL 21.9–25.2 mm; Velazco and Gardner [2009]: table 4) characterized by a tricolored ventral fur; densely haired fringe on the edge of the uropatagium; postorbital process absent or poorly developed; M1 protocone moderately developed; styler cusp on the lingual face of the M2 metacone absent; m2 hypoconid absent; and stylid cusp between the metaconid and protoconid of the m2 present. In contrast, northern populations (*umbratus*) of the species are medium-size bats (FA 42.0–47.8 mm, CIL 23.4–25.1 mm; Velazco and Gardner [2009]: table 4) characterized by a bicolored ventral fur; margin of the uropatagium usually hairy, sometimes sparsely haired; postorbital process moderately developed; M1 protocone well developed; styler cusp on the lingual face of the M2 metacone present; m2 hypoconid present; and stylid cusp between the metaconid and protoconid of the m2 absent.

Remarks. Analyses of linear measurements of *nigellus* populations did not reveal secondary sexual variation among populations (Velazco and Solari 2003). Linear morphometric analyses recovered a high overlap between specimens of *nigellus* and *umbratus*, indicating similarities in size and shape (Velazco *et al.* 2018). Molecular analyses recovered specimens of *nigellus* and *umbratus* clustering together, forming non monophyletic groups (Velazco *et al.* 2018). Ecological niche modeling analyses found that the potential distributions of *umbratus* and *nigellus* in the geographic space were highly similar, suggesting that both groups exhibit broadly overlapping climatic niches with no ecological differentiation (Velazco *et al.* 2018).

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Appendix 1

List of *Platyrrhinus dorsalis* and *P. umbratus* voucher specimens used in the geometric morphometric analyses and their associated localities. Collection acronyms are provided in the material and methods section.

Platyrrhinus dorsalis [*chocoensis*] ($n = 122$) — COLOMBIA: **Chocó** (IAvH 3316; UV 3645, 3647, 3648, 3817–3823, 7446, 7447, 7449, 10100–10103, 11289, 11302, 11310, 11332). **Nariño** (USNM 309018). **Valle del Cauca** (MNHN_CG 1989-1; USNM 339395, 339396, 483533–483552, 483554–483567, 483569–483572; UV 281, 972, 2153, 2162–2164, 2167, 2287–2291, 2294, 2810–2812, 3183–3185, 3707–3709, 4257, 4259, 5566–5575, 5748–5751, 5754, 5755, 10539, 10540). PANAMA: **Darién** (USNM 309601–309616).

Platyrrhinus dorsalis [*dorsalis*] ($n = 62$) — COLOMBIA: **Cauca** (IAvH 3313; UV 2165). **Chocó** (UV 4559–4561, 4571, 4575, 7448, 10034, 10035, 10837). **Cundinamarca** (ICN 8742). **Meta** (UV 3851). **Nariño** (UV 2942, 2943, 2947, 2948, 2950, 2953–2955, 2957, 3050, 3052–3055). **Quindío** (IAvH 7040). **Risaralda** (UV 2519). **Santander** (ICN 17502, 17503, 17583). **Valle del Cauca** (UV 806, 1243, 3419–3423, 3521, 3523, 3528, 7175, 7177, 7178, 7180, 7529, 7530, 10578–10580, 10833–10835, 11223, 11224, 11701, 11728, 11952, 12110, 12239, 12305).

Platyrrhinus umbratus [*nigellus*] ($n = 63$) — BOLIVIA: **La Paz** (UMMZ 127174). COLOMBIA: **Boyacá** (ICN 15066). **Cauca** (IAvH 3315). **Cesar** (FMNH 69484). **Cundinamarca** (ICN 5293). **Huila** (IAvH 3311). **Meta** (ICN 14800). **Norte de Santander** (IAvH 6631–6637, 6672, 6678, 6685, 6689, 6702, 6704, 6710, 6715, 6719, 6722, 6734, 6739). **Putumayo** (IAvH 6819, 6825). **Quindío** (ICN 12442, 12448). **Risaralda** (ICN 11934). **Santander** (ICN 8972, 17585–17587). **Valle del Cauca** (UV 12243, 12302, 12304, 12306, 12522, 12559). ECUADOR: **El Oro** (USNM 513465). **Pastaza** (USNM 548189, 548190, 548192, 548194). PERU: **Cuzco** (FMNH 93589, 93592, 93593, 93595–93597, 93599, 93600, 93604, 93606; MUSM 8857, 8858, 8860, 9975). **Madre de Dios** (MUSM 9955). **San Martín** (MUSM 7295, 7296).

Platyrrhinus umbratus [*umbratus*] ($n = 129$) — COLOMBIA: **Chocó** (UV 4149, 4150, 4152). **Cundinamarca** (ICN 5292, 5294, 5537, 5538). **Magdalena** (ICN 5388–5391). **Meta** (UV 3850). **Risaralda** (UV 2517, 2520). **Santander** (ICN 6695–6697). **Valle del Cauca** (UV 769, 1234). VENEZUELA: **Aragua** (USNM 370514, 370515, 517465, 517466). **Carabobo** (USNM 440651–440656). **Distrito Capital** (USNM 370407–370416, 370418, 370429, 370431–370433, 370435–370440, 370442–370444, 370446, 370447, 370452–370456, 370462, 370470, 370472, 370473, 370478, 370480–370492, 370494, 370500–370511, 372128, 408559, 408560, 408562–408564, 562985). **Mérida** (USNM 373837–373839, 387110–387114, 387117, 387118, 387129, 387132, 387137, 387138). **Miranda** (USNM 387126–387128, 387134–387136, 387139–387141; UV 11468). **Mona-gas** (USNM 408566–408568). **Trujillo** (USNM 373834–373836). **Yaracuy** (USNM 440647).