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Taxonomy of *Glossophaga valens* (Phyllostomidae, Chiroptera) from Arequipa, Peru

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Abstract: The common long-tongued bat, *Glossophaga soricina*, is a nectarivorous species, widely distributed in the Neotropics; it comprises five recognized subspecies, two of which are found in Peru: *G. soricina* occurs on the lower eastern slopes of the Andes as well as the Amazon, while *G. valens* that inhabits the western slopes of the Andes, extending south to the Arequipa region. Both taxa overlap in the arid Marañón valley, yet they exhibit notable morphological and genetic differentiation. The occurrence of *G. valens* in Arequipa raises questions regarding its taxonomic status, so in this study we combined cranial morphometrics with phylogenetic analyses based on two mitochondrial genes (cytochrome b and COI) and one nuclear gene (RAG2). Patterns of genetic variation suggest that *G. valens* is expanding its range into southern Peru. Morphometric analyses revealed that palate length contributed most strongly to group separation in morphometric space. Our findings support the recognition of *G. valens* as a distinct species and highlight the need for conservation efforts, given its restricted distribution along the western Andes and its nectarivorous diet —a case that parallels that of *Platalina genovensium*.

Key words:. Phylogenetic analysis, geographic distribution, morphometrics, morphology.

Resumen: Taxonomía de *Glossophaga valens* (phyllostomidae, chiroptera) en la región Arequipa. El murciélago longirostro común, *Glossophaga soricina*, es una especie nectarívora, ampliamente distribuida en el Neotrópico; con cinco subespecies documentadas, dos de ellas ocurren en Perú. *G. soricina* en las vertientes bajas de los Andes orientales además de la Amazonía y *G. valens* que habita al oeste de los Andes en la región costanera hasta Arequipa, no obstante, ambas confluyen en el valle seco del Marañón y mantienen ciertas diferencias morfológicas y genéticas. La presencia de *G. valens* en Arequipa plantea interrogantes sobre su estatus taxonómico, por ello este estudio combinó la morfometría craneal con la evaluación genética para el análisis filogenético de dos genes mitocondriales COI, Cyt b y RAG2 un gen nuclear. Con base en los patrones de variación genética, los resultados sugieren que se estaría ampliando el rango de distribución de *G. valens* hacia el sur del Perú y a nivel morfométrico, la longitud del paladar fue la medida que mayor contribución aportó a la distinción de la población en el morfoespacio. Estos datos respaldan el reconocimiento de *G. valens* como especie válida, resaltando la necesidad de su conservación, dada su restringida distribución en la vertiente occidental y su estilo de vida nectarívoro, similar al caso de *Platalina genovensium*.

Palabras clave: Análisis filogenético, distribución geográfica, morfometría, morfología.
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INTRODUCTION

The genus *Glossophaga* E´ Geoffroy St.-Hilaire, 1818 (Phyllostomidae, Glossophaginae) includes some of the most common and widely distributed neotropical bats (Miller, 1913). Their distribution is limited to elevations below 3000 meters above sea level (Webster, 1983). Recent taxonomic revisions have elevated four subspecies of *Glossophaga soricina* to the species level (Calahorra *et al.*, 2021). Two of these species occur in Peru: *G. valens*, which is distributed west

of the Andes in the coastal region, and *G. soricina*, found on the lower eastern Andean slopes and throughout the Amazon basin. These two species are sympatric in the arid *Marañón* Valley (Miller, 1913).

Although the number of chiropteran records in Peru has increased in recent years (Pacheco *et al.*, 2009; Pacheco *et al.*, 2021), knowledge of the *Glossophaga valens* on the western slope of southern Peru remains limited. Previous studies by Hoffmann & Baker (2001) and Calahorra *et al.*, (2021), characterized *G. valens* at the molecular level using samples from northwestern Peru only, without addressing potential variation in other regions. This has left a gap in our understanding of the species' geographic variation *G. valens* on the department of Arequipa in southern Peru. Likewise, Pari *et al.* (2015) conducted taxonomic surveys focused on the fauna of Arequipa, recognizing *G. valens* as a valid species, yet providing no further information regarding its morphological or genetic relationships with northern populations. The aim of this study is to clarify the taxonomic status of the *G. valens* population in Arequipa through an integrative analysis of morphometric and molecular data.

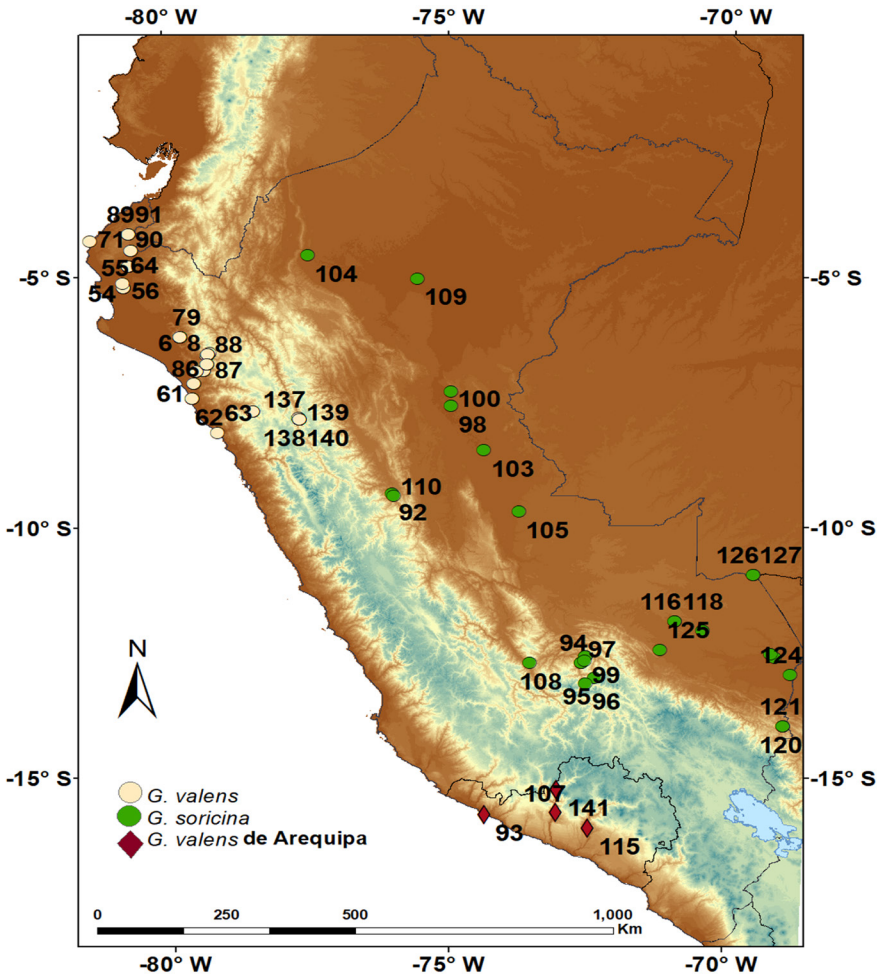

Fig. 1. Map. Explain explain explain

MATERIAL AND METHODS

This study was based on the analysis of morphometric and molecular datasets. Taxonomic decisions followed the phylogenetic species concept, with species delimitation based on monophyly and molecular diagnostic characters.

Specimens examined

A total of 142 specimens were examined (Fig. 1), representing both eastern and western regions of Peru (see Appendix). This material included additional specimens from key localities in the tropical Andes of southern Peru, such as Quechualla, Arequipa (15°19′31.23″ S, 73°3′32.29″ W), and El Oso, La Libertad (7°51′31.69″ S, 77°37′42.73″ W), which are situated within the semiarid inter-Andean Marañón valleys—an area of known sympatry between the two species. Additional specimens were collected to obtain fresh tissue for molecular sequencing, thereby expanding the available genetic dataset for Glossophaga populations in southern Peru.

Fieldwork followed the Guía de inventario de la fauna silvestre (MINAM, 2015), and euthanasia procedures complied with the guidelines of the American Society of Mammalogists (ASM, 1998) (Gannon *et al.*, 2007). All *Glossophaga* specimens from Peru analyzed in this study, including newly collected material, are deposited in the Natural History Museum of the National University of San Agustín (MUSA), Arequipa.

Molecular analyses

DNA was extracted from liver tissue preserved in 96% ethanol using the phenol–chloroform protocol (Longmire *et al.*, 1997). Gene sequencing was performed by Functional Biosciences Inc. (Madison, WI, USA). The mitochondrial cytochrome b (Cyt b) gene was amplified for three individuals using primers (5′ CAY CGT TGT ATT TCA ACT RTA AGA AC 3′) and glo6H (5′ CGGTGTAATGRATATACTACATRG 3′), following PCR conditions described by Hoffmann & Baker (2001). The thermal cycling profile consisted of an initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 15 s, annealing at 48 °C for 20 s, and extension at 72 °C for 1 min, with a final extension at 72 °C for 2 min. PCR products were purified using the QIAquick® PCR Purification Kit (Qiagen), following the manufacturer's instructions.

The mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified for four individuals using primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'), and the PCR protocol of Hebert *et al.*, (2003). The thermal regime consisted of an initial denaturation at 94 °C for 1 min; five cycles of 94 °C for 1 min, 45 °C for 1.5 min, and 72 °C for 1.5 min; followed by 35 cycles of 94 °C for 1 min, 50 °C for 1.5 min, and 72 °C for 1 min; and a final extension at 72 °C for 5 min. PCR products were purified from agarose gels using the QIAEX® II Gel Extraction Kit (Qiagen).

The nuclear recombination-activating gene 2 (RAG2) was amplified for three individuals using primers RAG2F220 (5′-GATTCCTGCTA(CT)CT(TC)CCTCCTCT-3′) and RAG2R995 (5′-CCCATGTTGCTTCCAAACCATA-3′) (Teeling *et al.*, 2000). PCR conditions followed Koubínová *et al.*, (2013), with an initial denaturation at 95 °C for 2 min, followed by 33 cycles of denaturation at 94 °C for 30 s, annealing for 60 s with a temperature gradient from 60 °C to 58 °C, then held at 57 °C, and extension at 72 °C for 90 s. A final extension was performed at 72 °C for 10 min. All newly generated sequences were deposited in GenBank (see Appendix). Outgroup taxa and the full list of sequenced specimens are provided in Días *et al.* (2017) and detailed in the Appendix.

Phylogenetic analysis

We examined the mitochondrial DNA (Cyt b) sequences to evaluate the systematic relationships within the *Glossophaga soricina* species complex and to assess the taxonomic placement of spe-

cimens from western and eastern Peru. The three newly sequenced *Glossophaga* specimens from Peru were added to the 71 *Glossophaga* sequences analyzed by Días *et al.* (2017), resulting in a dataset of 74 *Glossophaga* individuals. Six additional sequences from *Carollia perspicillata*, *Lionycteris spurrelli*, *Lonchophylla robusta*, *Chrotopterus auritus*, *Phyllostomus hastatus*, and *Tonatia saurophila* were included as outgroups. Sequence alignment was performed in MEGA 11 (Tamura *et al.*, 2021) using the MUSCLE algorithm (Edgar, 2004) with the UPGMA clustering method. The optimal substitution model for Cyt b was selected based on the Bayesian Information Criterion (BIC) in MEGA 11, which identified GTR+G+I as the best-fit model (Rodríguez & Ochoa, 1992; Kimura, 1980; Tavaré, 1986). This model accounts for rate heterogeneity across sites by incorporating a gamma distribution and invariant sites.

Genetic distances were estimated in MEGA 11 using Kimura's two-parameter model (K2P), which calculates the proportion of nucleotide differences between pairs of sequences (Kimura, 1980). Phylogenetic relationships were inferred using Bayesian Inference (BI) in MrBayes v.3.4 (Ronquist & Huelsenbeck, 2003), applying the Markov Chain Monte Carlo (MCMC) method. Four simultaneous Markov chains were run for 1,000,000 generations, with trees sampled every 1,000 generations. The first 10% of trees were discarded as burn-in, and posterior probabilities were calculated from the consensus of the remaining trees.

Convergence was assessed using Tracer v1.6.0 (Rambaut *et al.*, 2013), ensuring effective sample

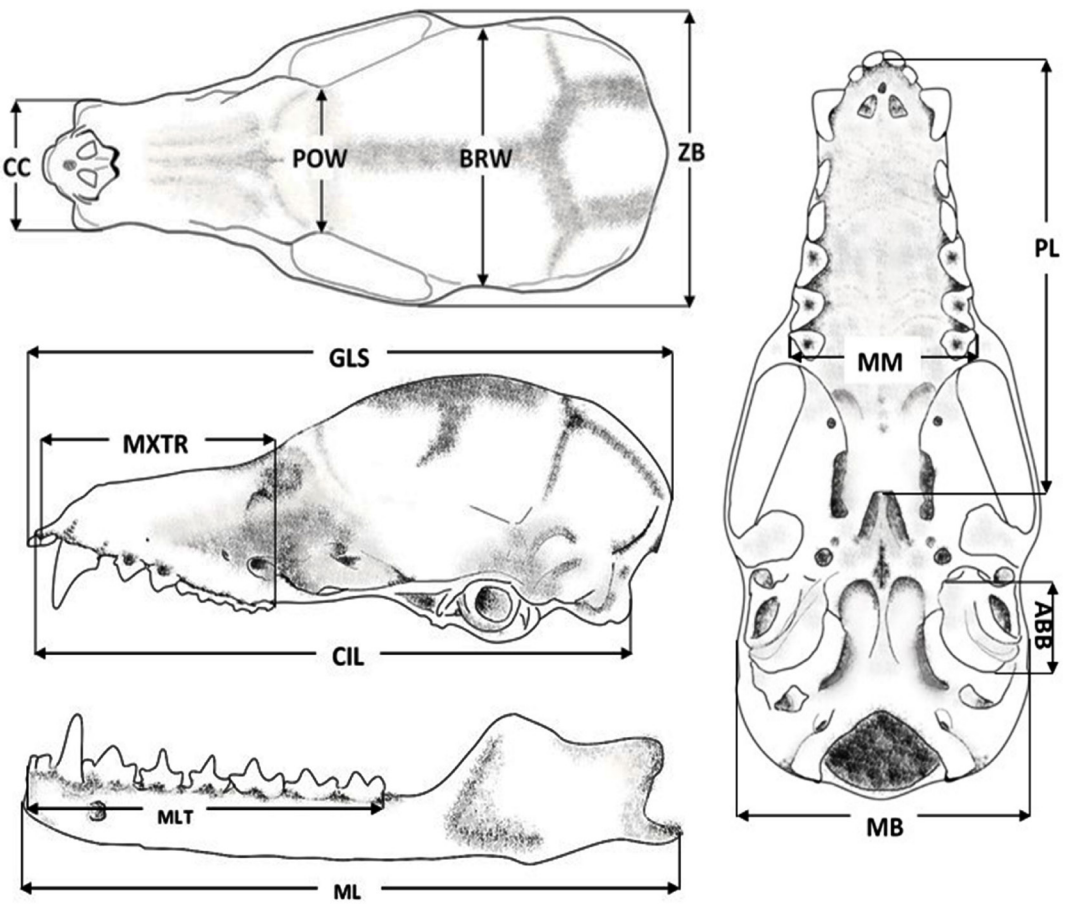

Fig. 2. Skull. Explain explain explain

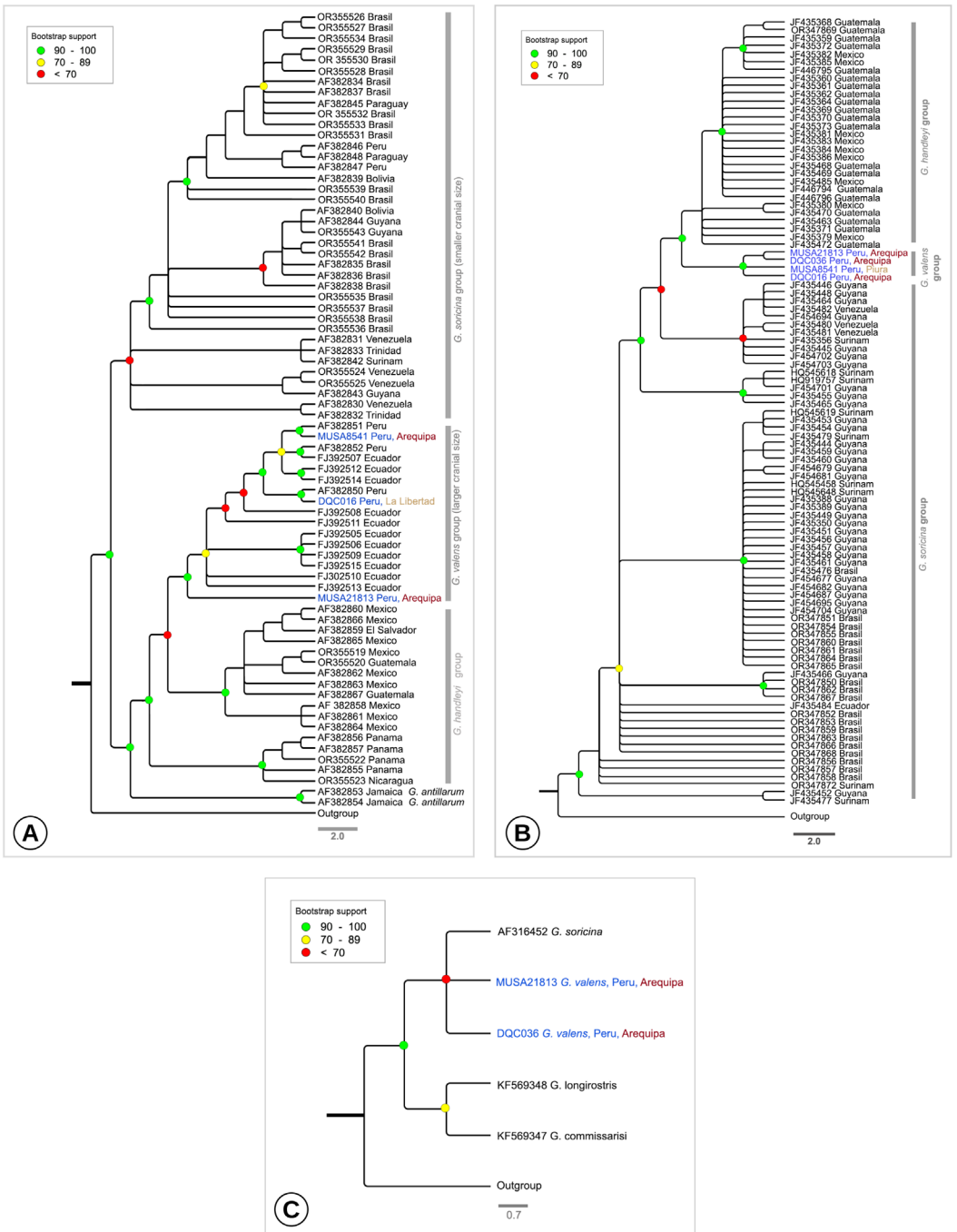

Fig. 3. **A**. **C**yt **B** Explain explain explain. **B**. Coi. Explain explain explain. **C**. RAG2. Explain explain explain.

sizes (ESS) greater than 500 for all parameters. The resulting trees were summarized into a majority-rule consensus tree and visualized with FigTree v1.4.3 (Rambaut *et al.*, 2016).

Analysis of mitochondrial and nuclear DNA sequences

We analyzed the same specimens described in the previous section using sequences from the mitochondrial COI gene (105 taxa) and the nuclear RAG2 gene (11 taxa). These markers were selected due to their widespread use in systematic studies and their capacity to capture divergence at different evolutionary scales. The analyses began with the COI gene, which included the highest number of taxa, and subsequently incorporated Cyt b and RAG2. This stepwise approach was implemented using Mesquite (Maddison & Maddison, 2017), and the final dataset was formatted in NEXUS. Bayesian inference was conducted in MrBayes (Ronquist *et al.*, 2012) using partitioned models to accommodate the heterogeneity among gene regions. These analyses aimed to integrate mitochondrial and nuclear evolutionary signals and to assess whether the *Glossophaga* records from Arequipa correspond to currently recognized species or represent an independent evolutionary lineage.

Morphometric analyses

We examined a total of 142 *Glossophaga* specimens from Peru, including 29 individuals assignable to *G. soricina* and 113 to *G. valens*. Only adult specimens with fully erupted and functional dentition were considered (Porto *et al.*, 2009). A full list of examined specimens is provided in the Appendix.

Quantitative morphological analysis was based on measurements of forearm length and 13 craniodental dimensions (Fig. 2), recorded in millimeters (mm). Measurements were taken using a precision caliper (±0.1 mm), following the protocols of Barquez *et al.* (1999), Díaz *et al.* (2011, 2016), and Marchán-Rivadeneira *et al.* (2012). Qualitative morphological comparisons were based on the following external and cranial characters: (i) presence and visibility of the lambdoid crest, (ii) development of the mastoid processes, (iii) robustness of the zygomatic arches, (iv) shape and alignment of the upper incisors, (v) posterior skull profile, and (vi) pelage coloration, with color terms capitalized in accordance to Ridgway (1912).

Principal Component Analysis (PCA) was used to identify major patterns of variation in skull size and shape and to explore the distribution of individuals in morphospace. Linear Discriminant Analysis (LDA) was conducted to compare skull morphometrics between *G. valens* and *G. soricina*. Both analyses were performed in R (RStudio Team, 2020) using the MASS, FactoMineR, and ggplot2 packages (Venables & Ripley, 2002; Husson *et al.*, 2021; Wickham, 2016). All morphometric variables were log10-transformed prior to analysis. Specimens of both sexes were pooled for morphometric analyses, as previous tests for sexual dimorphism revealed no significant differences and showed overlapping cranial measurements. These findings are consistent with results reported for other *Glossophaga* species (see Calahorra *et al.*, 2021).

RESULTS

Molecular analyses.

Phylogenetic inference based on the Cyt b (775 bp, no gaps), COI (509 bp, no gaps), and RAG2 (479 bp, no gaps) using BI method provided robust support for a consistent relationship among populations for each gene. Moreover, the branching patterns indicate relatively low genetic distances between *G. valens* specimens from Arequipa and those from northwestern Peru.

Alignment of the Cyt b sequences (Fig. 3A) revealed a close common ancestry between *G. soricina* and other *Glossophaga* species. The sequences formed a hierarchical structure in which *G. valens* and *G. handleyi* grouped as sister species, while G. antillarum occupied a basal position within the clade, reflecting greater genetic differentiation. The genetic distance based on Cyt b, as estimated using the K2P model, indicated an average divergence of 7.1% between *G. valens* from Arequipa and the sister clade formed by *G. soricina*. The genetic distance between *G. valens*

from Arequipa and samples from northwestern Peru was approximately 1%, while the divergence between *G. valens* from southern Peru and *G. valens* sequences retrieved from GenBank was 7.5%. The genetic distance between *G. valens* from Arequipa and the remaining *Glossophaga* species averaged approximately 3%.

The COI gene alignment (Fig. 3B) yielded similar results. *G. valens* and *G. handleyi* were recovered as sister taxa, while *G. soricina* was placed in a more basal position. Genetic distances based on the COI dataset (Table 1), estimated using the K2P model, showed low divergence between *G. valens* from Arequipa and northwestern Peru, supporting a recent common ancestry and the formation of a well-supported clade. In contrast, the divergence between *G. valens* from Arequipa and *G. soricina* averaged 6.9%. The distance between northern *G. valens* and Arequipa specimens was less than 2%.

The RAG2 gene analysis (Fig. 3C) revealed a well-defined phylogenetic structure, with *G. valens* from Arequipa and *G. soricina* recovered as sister taxa based on the available RAG2 sequences. This result indicates a strong evolutionary relationship between the two species in the context of this nuclear marker, with high support values (bootstrap = 100%, posterior probability = 1.00). Genetic variation between *G. valens* from Arequipa and *G. soricina* was minimal, with a mean pairwise divergence (Table 3) of less than 1%. The genetic distance between *G. valens* from Arequipa and *G. longirostris* and *G. commissarisi* ranged from 0.6% to 0.8 %.

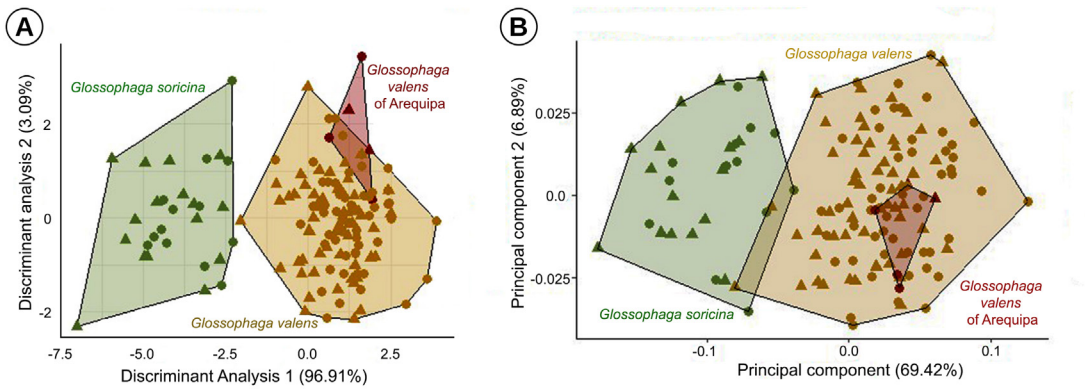

Fig. 4. A. Explain explain explain. B. Explain explain explain

Morphometric analysis

Principal Component Analysis (PCA) based on cranial measurements of *Glossophaga* provided a general overview of skull morphological variation. The first three principal components accounted for 81.7% of the total variation, with a clear spatial separation of *G. valens* from Arequipa relative to the *G. soricina* group. In contrast, *G. valens* specimens from Arequipa showed substantial overlap with other *G. valens* specimens (Fig. 4).

The first two Linear Discriminant Analysis (LDA) functions (LD1 and LD2) explained 96.91% and 3.09% of the total cranial variation, respectively. Palate length (PL) contributed most strongly to group differentiation, while condylobasal length (CIL) and maxillary toothrow length (MXTR) also played significant roles in the distribution of specimens in morphospace (Table 4).

Quantitative comparisons (Table 5) indicated that the skulls of *G. valens* from northwestern Peru and Arequipa differ in both size and shape from those of *G. soricina*. While there was some partial overlap in cranial and forearm measurements, slight differences were alsoobserved between the *G. soricina*, *G. valens* populations from northwestern regions of Peru and Arequipa region, with the latter exhibiting marginally larger skulls on average.

The morphological similarities shared between *G. valens* from Arequipa and other *Glossophaga* species in Peru are informative for characterizing the genus. The recurrent presence of these feature may reflect a shared evolutionary pattern, possibly associated with common ecological adaptations such as feeding strategies. Key shared features include, a comparatively smaller third premolar within the premolar series; presence of a cingulum on the upper canine; a well-developed

connection between the uropatagium and the feet; and absence of fur on the tibia and forearm. The most distinctive morphological traits that differentiate *G. valens* from Arequipa from other *Glossophaga* species in Peru are summarized in the Table X.

DISCUSSION

This study represents the first integrative taxonomic assessment of *Glossophaga valens* from the Arequipa region in southwestern Peru, combining molecular and morphometric data. Phylogenetic analyses based on both nuclear (RAG2) and mitochondrial markers (Cyt b and COI) recovered well-supported clades (bootstrap support = 100%, posterior probability = 1.00), confirming the phylogenetic placement of the Arequipa specimens within the *G. valens* lineage.

Previous studies (Hoffmann & Baker 2001; Dias *et al.*, 2017; Hoffmann *et al.*, 2019) established the species-level distinction between *G. soricina* and *G. valens* using Cyt b sequences, a conclusion later reinforced by Calahorra *et al.* (2021). However, those studies focused exclusively on populations from northwestern Peru and did not account for potential cryptic diversity within the genus *Glossophaga* (Ruelas *et al.*, 2016). In our study, we integrated mitochondrial (Cyt b and COI; Clare 2011) and nuclear (RAG2; Rojas *et al.*, 2012) markers to more accurately resolve the phylogenetic position of the Arequipa samples and assess their relationship to other Peruvian populations.

The Arequipa specimens were consistently grouped within the clade that includes *G. valens* individuals from the western slopes of northwestern Peru. This result supports their inclusion within *G. valens* and confirms their status as a sister lineage to *G. soricina*, consistent with previous findings by Calahorra *et al.* (2021). The inclusion of nuclear data (RAG2) strengthens this inference and helps to mitigate the potential effects of mitochondrial introgression and incomplete lineage sorting.

A significant outcome of this study is the documented southward expansion of the known distribution range of *G. valens* into the arid and semi-arid environments of the Arequipa region. This distributional extension suggests ecological tolerance and intraspecific variation, consistent with earlier suggestions by Tuttle (1970), and highlights the species' ability to occupy diverse habitats along environmental gradients. The Andean topography, characterized by complex elevational corridors acting as ecological filters, may be facilitating genetic divergence and contributing to the emergence of differentiated lineages that may warrant taxonomic recognition.

Cranial morphometric analyses revealed subtle but consistent differences between *G. valens* specimens from Arequipa and those from northwestern Peru. These findings contrast with previous studies by Calahorra *et al.* (2021) and Hoffmann &d Baker (2001), which were based solely on northwestern samples and led to the hypothesis of an undescribed species. Earlier morphological observations by Ortiz de la Puente (1951) described female *G. valens* with slightly larger total skull length compared to males. Our results align with this pattern and also show slight differences in the shape of the posterior skull profile and forearm length. Based on our current dataset, *G. valens* from Arequipa can be distinguished from *G. soricina* by differences in pelage coloration, overall body size, and the shape of the cranial roof, which is squared in *G. valens* but domed in *G. soricina*. These morphological differences may reflect phenotypic plasticity in response to local environmental conditions, rather than full speciation (Calahorra *et al.,* 2021). Overall, our findings support the presence of cryptic diversity within *G. valens*, a pattern repeatedly suggested in previous studies (Ruelas *et al.,* 2016; Dias *et al.,* 2017; Hoffmann *et al.*, 2019; Calahorra *et al.*, 2021).

Molecular and phylogenetic analyses confirm the presence of *Glossophaga valens* in the Arequipa region, with this population showing genetic differences compared to those from northern Peru. This study also emphasizes its broad distribution along the western slopes of the Andes, from northern Ecuador to southern Peru, is also emphasized. Given its specialized nectar-feeding diet and its restricted occurrence in the coastal desert of western Peru, we suggest further ecological studies to assess its potential inclusion in a conservation category. Following the approach applied to similar species, such as *Platalina genovensium*.

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Table 1. Average genetic distances of 2 Kimura parameters between *Glossophaga* species according to COI. The values in bold on the diagonal indicate intrapopulation distances. Distances expressed as percentages.

Species	1	2	3	4
1. *G. soricina*	**0.4**			
2. *G. handleyi*	5.7	**0.6**		
3. *G. valens* north	5.7	2.7	**-**	
4. *G. valens* of Arequipa	6.9	3.8	1.2	**1.4**

* The script indicates groups with a single sequence.

Table 2. Average genetic distances of 2 Kimura parameters between *Glossophaga* species according to Cyt b. The values in bold on the diagonal indicate intrapopulation distances. Distances expressed as percentages.

Species	1	2	3	4	5	6
1. *G. soricina*	**0.4**					
2. *G. valens*	7.5	**1.2**				
3. *G. antillarum*	6.6	3.5	**1.2**			
4. *G. handleyi*	6.8	3.0	3.7	**0.4**		
5. *G. valens* north	8.3	1.5	4.2	4.0	**1.1**	
6. *G. valens* of Arequipa	7.1	0.5	3.2	2.7	1.2	**-**

* The script indicates groups with a single sequence.

Table 3. Average genetic distances of p-distance between *Glossophaga* species according to RAG2 gene sequences. The values in bold on the diagonal indicate intrapopulation distances. Distances expressed as percentages.

Species	1	2	3	4
1. *G. soricina*	**-**			
2. *G. longirostris*	1.0%	**-**		
3. *G. commissarisi*	0.8%	0.6%	**-**	
4. *G. valens* Arequipa	0.2%	0.8%	0.6%	**0.0%**

* The script indicates groups with a single sequence.

Table 4. Vector correlation loading with original variable of principal component (PC1 and PC2) and discriminant functions (DF1 and DF2) for selected samples of *G. soricina*, *G. valens*, and *G. valens* from Arequipa. See Appendix for variable abbreviations.

	PC 1	PC 2	DF 1	DF 2
BRW	0.16707	0.030118	-30.639	-29.118
CC	0.23282	0.027852	15.693	28.309
POW	0.27564	0.17021	-4.658	-0.17735
ZB	0.20672	0.058324	-9.7543	-43.369
PL	0.369	-0.18232	-20.414	-9.1497
MM	0.24871	0.18288	0.64356	13.702
ABB	0.16074	0.90621	-7.6709	8.9216
MB	0.2033	-0.018038	35.04	67.69
GLS	0.28682	-0.064172	42.702	173.95
MXTR	0.31735	-0.14095	-13.853	-45.534
CIL	0.33398	-0.075049	62.609	-79.302
ML	0.30679	-0.13559	40.224	-94.272
MLT	0.3007	-0.16581	10.828	45.874
FA	0.23436	-0.047112	-11.445	-8.4613

Table 5. Selected measurements (mm) of *Glossophaga*. The numbers indicate: mean, range (in parentheses), and sample size.

Measurements	*G.soricina*	*G. valens*	*G. valens* de Arequipa
GLS	20.6 (19.5-21.4) 29	22.4 (21.16-23.69) 108	22.5 (21.99-22.9) 5
CIL	19.1 (16.89-20.05) 29	21.1 (19.73-22.53) 108	21.5 (21.06-21.83) 5
MXTR	7.0 (6.64-7.5) 29	7.7 (7.2-8.22) 108	7.8 (7.74-7.92) 5
MB	8.7 (8.29- 9.1) 29	9.2 (8.48-9-69) 108	9.2 (9.09-9.5) 5
ABB	3.3 (3.02-3.53) 29	3.4 (3.11-3.8) 108	3.4 (3.19-3.53) 5
MM	5.3 (4.99-5.57) 29	5.7 (4.18-6.21) 108	5.7 (5.52-5.92) 5
PL	10.5 (9.48-11.24) 29	11.7 (10.41-12.6) 108	11.9 (11.75-12.06) 5
ZB	9.1 (8.69-9.58) 29	9.7 (8.75-10.27) 108	9.8 (9.57-10.25) 5
BRW	8.6 (8.28-9.02) 29	9.0 (8.56-9.32) 108	9.0 (8.89-9.22) 5
POW	4.0 (3.71-4.82) 29	4.3 (3.67-4.75) 108	4.4 (4.27-4.44) 5
CC	3.9 (3.54-4.21) 29	4.2 (3.93-4.72) 108	4.2 (3.99-4.32) 5
ML	13.8 (13.22-14.65) 29	15.2 (14.15-16.08) 108	15.5 (15.29-15.67) 5
MLT	7.4 (7.07-7.95) 29	8.1 (7.49-8.68) 108	8.2 (8.12-8.34) 5
FA	35.1 (32.3-38.6) 29	37.3 (32.9-40.38) 108	37.8 (35.49-40) 5

Table 6. Morphological comparison of *G. soricina*, G. valens, and *G. valens* from Arequipa.

	G. soricina	*G. valens*	*G. valens* de Arequipa
Braincase	Domed braincase	Square braincase	Square braincase
Visibility of the Lambdoid Ridge	Slightly visible	Moderately visible	Visible
Mastoid processes	Poorly developed, ventrally almost imperceptible	Poorly developed, visibly ventral	Poorly developed, ventrally visible
Zygomatic arches	Subparallel zygoma	Anteriorly converging zygoma	Anteriorly converging zygoma
Incisor	Inner upper incisor larger than outer in bulk (occlusal view)	Extremely procumbent upper incisors	Extremely procumbent upper incisors
Variation in external cranial morphology	Posterior profile of the skull not bulging, continuous	Slightly bulging posterior profile of the skull	Noticeably bulging posterior profile of the skull
Foramen magnum	Anteroventral margin of the foramen is rounded	Anteroventral margin of the foramen in the shape of a “U/V”	Anteroventral margin of the foramen in the shape of a “V”
Color bands on dorsal pelage (from base to tip)	Dark hair. Two stripes, cream-colored base and dark brown tips.	Pelage lighter, with two bands; each with a cream-colored base and light brown tips	Pelage lighter, with two bands; each with a cream-colored base and light brown tips
Ventral pelage	Pelage dark, with two stripes; each with a cream-colored base and dark brown tips	Lighter pelage with two bands, cream at base and light brown at tips	Lighter pelage with two bands, cream at base and light brown at tips
Dorsal pelage (variable)	Hair tips ranging from Argus Brown to Brussels Brown	Hair tips ranging from Antique Brown to Sudan Brown	Hair tips ranging from Antique Brown to Sudan Brown