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Systematics of the dwarf red brocket, *Mazama rufina* (Pucheran, 1851) (Mammalia: Artiodactyla: Cervidae), with the description of a new genus

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Abstract

The dwarf red brocket, *Mazama rufina* (Pucheran, 1851) is a small deer with a fragmented distribution in the montane forests of the Andes of Peru, Ecuador, Colombia, and Venezuela. Little is known about the phylogenetic relationships and the haplotype diversity of its populations, which show distribution gaps. Here we elucidate the phylogenetic relationships of *M. rufina* and other neotropical deer using mitochondrial data, and analyze genetic geographic variation of this taxon by using haplotype networks of the Cyt-*b* gene from northern South America. Our analyses recovered *M. rufina* as independent clade that is not part of *Mazama*, and sister to a clade composed of *Mazama* species (except *Mazama chunyi*) and *Odocoileus*. The morphometric data of cranial traits confirms that the dwarf red brocket is among the smallest species of deer in South America, only overlapping with small cis-Andean gray brockets (genus *Passalites*). Based on these results, we provide a new generic classification for this taxon by placing the dwarf red brocket in a new genus found only in the Andes of northern South America. The Cyt-*b* haplotype network of the dwarf red brocket showed a strong geographic structure caused by the interplay of Cordilleras and lowland river valleys. The genetic distances between the geographic groups were between 1.4 % (Central Cordillera of Colombia vs. Andes of Ecuador) to 2.52 % (Mérida Cordillera vs. Ecuador). The species range using Extent of Occurrence (EOO) and Area of Occupancy (AOO) was 443,764 and 796 $km^{2,}$ respectively, suggesting that the species could be listed as Near Threatened. However, additional information on population changes and susceptibility to habitat transformation is crucial to evaluate whether the dwarf red brocket can be deemed Vulnerable along its distribution. Compared with previous distribution hypotheses, the revised map suggests less extensive distribution gaps in Colombia and highlights priority areas for future sampling in Colombia, Ecuador, and Venezuela.

Key words: Andes, Capreolinae, Haplotypes, Neotropics, Odocoileini, South America

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Introduction

Deer (Artiodactyla, Cervidae) are represented in South America by the genera *Blastocerus*, *Bisbalus*, *Hippocamelus*, *Mazama, Odocoileus*, *Ozotoceros*, *Subulo*, *Passalite*s, *Pudella*, and *Pudu*, all of them grouped in the tribe Odocoileini of subfamily Capreolinae (Bernegosi *et al*. 2023; Escobedo-Morales *et al*. 2023; Sandoval *et al*. 2024; Mammal Diversity Database 2025). The members of morphologically diagnosed genera, differentiated by antler shapes, body size, among other attributes, such as *Hippocamelus* and *Mazama*, have been recovered as paraphyletic using molecular and total evidence approaches (Duarte *et al*. 2008; Heckeberg 2020; Sandoval *et al*. 2024).

Historically, the genus *Mazama* has included members of morphologically cohesive species that exhibit intricate evolutionary relationships (Duarte *et al*. 2008; Heckeberg 2020) and include taxa which validity has been controversial (Groves & Grubb 2011; Mammal Diversity Database 2025). In the last decade, several studies have clarified the taxonomic status of *Mazama* species and closely related genera (Gutierrez *et al*. 2015; Escobedo *et al*. 2016; Cifuentes-Rincón *et al*. 2020; Bernegossi *et al*. 2023; Sandoval *et al*. 2024). However, there are still gaps in the knowledge of their distributions, phylogenetic relationships, biogeography, and taxonomy (Gutierrez *et al*. 2015; Ramírez-Chaves *et al*. 2021; Sandoval *et al.* 2024).

Recent reviews of the phylogenetic affinities of *Mazama* (sensu lato), based only on mitochondrial DNA, have resulted in the revalidation of: i) the genus *Subulo*, to include the gray brocket, *Mazama gouazoubira* (Bernegosi *et al*. 2023); and ii) the genus *Passalites*, to include *Mazama nemorivaga* (Morales-Donoso *et al*. 2023); studies have also iii) proposed the new genus *Bisbalus*, to include *Mazama cita* (Sandoval *et al*. 2024); and iv) restricted *Mazama* to red brockets, i.e., *M. americana*, *M. chunyi*, *M. jucunda*, *M. nanus*, *M. rufa*, and *M. temama*; but *M. chunyi* is recovered as sister to *Subulo gouazoubira*. Erecting *Bisbalus, Passalites*, and *Subulo* partially solved the polyphyly of *Mazama.* However, the Andean-endemic dwarf red brockets, currently *Mazama rufina* (Pucheran, 1851), with *Mazama bricenii* O. Thomas, 1908 considered a junior synonym, are still paraphyletic relative to the *M. americana* species group (Heckenberg *et al.* 2016; Escobedo-Morales *et al.* 2023).

Mazama rufina is characterized by its reddish-brown pelage with blackish coloration on the face and legs (Hershkovitz 1982). It is, together with *Pudella mephistophiles*, one of the smallest deer species occurring in the northern Andes of South America. *Mazama rufina* is endemic to the Andes of Colombia, Ecuador, Peru, and Venezuela (Gutiérrez *et al.* 2015), where it inhabits páramo (high-elevation grassland dominated by plants of the genera *Espeletia* and *Calamagrostis*) and Andean cloud forests (Lizcano 2006), at an elevational range between 1,000 and 4,000 m (Groves & Grubb 2011; Solari *et al*. 2013; Jasper *et al*. 2022). The species is currently classified as Vulnerable (VU) because it apparently has small and fragmented populations with a trend to decrease under climatic, biological, and anthropogenic pressures (Lizcano 2016). However, this assessment predates the taxonomic revision that suggested *M. bricenii* as a junior synonym. As a result, the current conservation status requires re-evaluation with updated data.

The taxonomy of *M. rufina* has been assessed based on morphology and Cytochrome *b* (Cyt-*b*) gene sequences of specimens from Venezuela, Colombia, and Ecuador. With the new concept that includes *M. bricenii,* the distribution of *M. rufina* is now extended to the Oriental (Eastern) Cordillera of Colombia and the Mérida Cordillera of Venezuela (Gutiérrez *et al*. 2015). However, the distribution of the species has several gaps in the north of the Oriental (Eastern) Cordillera. Apparently, the populations of the north of the Colombian Central and Oriental Cordilleras, the Serranía del Perijá (Colombia–Venezuela), and the Mérida Cordillera of Venezuela are isolated (Jasper *et al*. 2022). Besides these distribution gaps, the knowledge of the morphology, phylogenetic relationships, and haplotype diversity of these isolated populations is still scarce. Therefore, confirming the phylogenetic position of *M. rufina,* and including additional samples of specimens from northern Colombia, is crucial to resolve taxonomical problems and is critical for conserving potentially fragmented populations. For this reason, we analyzed morphological, morphometric, and molecular traits, and we present a proposal for the classification of *M. rufina*, considering the paraphyly of *Mazama*.

Methods

Phylogenetic analyses

We used two datasets for separate analyses: one consisting of complete mitogenomes, and the other including only sequences of the Cytochrome *b* (Cyt-*b*) mitochondrial gene, to allow for broader taxonomic coverage. For the mitogenome, we retrieved 44 mitogenomes of 10 genera and 17 species of Neotropical deer from GenBank (Supplementary Data SD1). We aligned Ribosomal RNA (rRNA), transfer RNA (tRNA), and protein-coding genes with MUSCLE in Geneious *v.* 10.2.3 (www.geneious.com). We excluded the control region from the analyses. The control region has a higher mutation rate than the rRNA and protein-coding genes of the mitochondrial genome (Gong *et al*. 2015), and in *Mazama*, it frequently has multiple insertions and deletions and the presence of repetitive sections that are difficult to align, increasing the risk of substitution saturation, introducing homoplasy, and reducing phylogenetic signal (Escobedo-Morales *et al*. 2023). The final data matrix comprised 37 loci (two rRNA, 13 protein-coding, and 22 tRNA genes). We used *Alces alces* (KP405229), *Capreolus capreolus* (JN632610), and *Cervus nippon* (AB211429) as outgroups.

For the Cyt-*b*- only analysis, we extracted DNA from the muscle of five specimens of *M. rufina*, and one of *M. americana*, two of *M. temama,* and two of *O. virginianus* from Colombia (Appendix 1; Supplementary Data SD2) by using the Wizard® Genomic DNA Purification kit (Promega Corporation), following the manufacturer's instructions. Tissues are deposited at the Colección de Mamíferos del Museo de Historia Natural, Universidad de Caldas (MHN-UCa-M), in Manizales, Colombia, and come from either road-killed or deceased individuals held at the Center for Attention, Valuation, and Rehabilitation (CAVR) of the Regional Autonomous Corporation (Corpocaldas), or from individuals hunted by locals (Appendix 1). Sampling was conducted under the framework permit granted by the National Authority for Environmental Licenses (ANLA) as stipulated in resolution No. 00854 of May 20, 2019, and updated by resolution No. 00519 of March 3, 2022, and donations made by Corpocaldas to the Universidad de Caldas.

Amplification of mitochondrial gene Cyt-*b* was performed using primer pair LGL765F and LGL766R, targeting a ≈1140 bp (Bickham *et al*. 1995, 2004). The final amplification reaction volume was 30 µL, which contained 20.24 µL ultrapure water, 3 µL 10X buffer, 0.9 µL MgCl2 (50 mM), 2.4 µL dNTP mix (10 mM), 0.36 µL of each primer (25 µM), 1.2 U of Taq DNA Polymerase, and 2.5 µL DNA (approximately 110 ng of DNA). The amplification was performed on a Techne TCPLUS thermocycler: initial denaturation of 3 min at 94°C, followed by 35 cycles of 95°C for 45 s of denaturing, 50°C for 40 s of annealing, 72°C for 45 s of extension, completing the reaction with a final extension cycle at 72°C for 7 min. The PCR products were quantified by fluorometry using a Quantus Fluorometer™ (Promega®). PCR products were sent to Macrogen Inc. (South Korea) for purification and DNA sequencing. The sequencing chromatogram was evaluated and edited using the Geneious® Prime 2022.1 software (Kearse *et al*. 2012). To avoid stop codons and investigate the correct translation frame, the resulting sequence was translated to protein using the Translate option in the web tool Expasy (at https://web.expasy.org/translate/). For the ingroup, we gathered 196 sequences representing 23 deer species to construct a matrix of 206 Cyt-*b* sequences (Supplementary Data SD2). We included three additional sequences—*Alces alces* (NC020677), *Capreolus capreolus* (NC020684), and *Hydropotes inermis* (JN632649)—as outgroups, resulting in a total matrix of 209 Cyt-*b* sequences, which includes the 10 sequences we generated. We aligned all the sequences using the default parameters of the Clustal W algorithm in BioEdit 7.2.6 software (Hall 1999). The data underpinning the analysis reported in this paper are deposited in the Mendeley Repository at: http://dx.doi.org/10.17632/d6pnhd5bgd.1

For the mitogenome dataset, we analyzed a partitioned scheme for the different coding and non-coding regions of the mtGenome, selecting the best-fit partition scheme and the best model of substitution rates for each partition using ModelFinder (Kalyaanamoorthy *et al*. 2017) in IQ-TREE (Nguyen *et al*. 2015; Supplementary Data SD3). For the Cyt-*b* dataset, we selected TN+F+I+G4 as the best-fitting model of sequence evolution according to the Bayesian Information Criterion (BIC) estimated using ModelFinder (Kalyaanamoorthy *et al*. 2017) in IQ-TREE (Nguyen *et al*. 2015). We conducted maximum-likelihood inferences for both datasets using IQ-TREE (Nguyen *et al.* 2015), with 20,000 replicates to find the best tree. We used nonparametric SH-aLRT and ultrafast-bootstrap (UFBoot; Hoang *et al.* 2018) values as the branch support measure.

Haplotype analysis

We explored the relationships among the different Cyt-*b* haplotypes of *M. rufina.* We trimmed all sequences to equal length, removing sites containing ambiguities that could not be interpreted as heterozygotes, and constructed a haplotype network under the TCS algorithm (Clement *et al*. 2000) in PopArt software (Leigh & Bryant 2015). For the analyses of genetic distances and haplotypes network, we considered the geographic reference of the sequences as Ecuador, Eastern Cordillera, Central Cordillera, Colombian Massif (a mountainous region in south-central Colombia, where the Central and Oriental Cordilleras of Colombia begin), and Mérida Cordillera. We calculated average uncorrected *p*-distances within the haplotypes of *M. rufina*, considering partial deletion, where positions with less than 95% site coverage in the alignment were eliminated using MEGA 11 software (Tamura *et al*. 2021). The percentage of genetic divergence was computed as genetic distance × 100.

Morphological comparisons

We preserved the specimens of *M. rufina* sequenced as study skins with associated skull, postcranial skeleton, and tissues in ethanol (96%) at the MHN-UCa-M. All specimens originated from the Central Cordillera of the Department of Caldas, Colombia. We also examined 41 additional deer specimens housed at the MHN-UCa, the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN) in Bogotá, and at the Museo de Historia Natural of the Universidad del Cauca (MHNUC) in Popayán, Colombia (Appendix 1). For the morphometric comparisons, we also used selected measurements of specimens from South America available in the literature (e.g., Sandoval *et al.* 2022; Sandoval *et al*. 2024). We considered discrete morphological traits that allow the identification of *M. rufina* such as the reddish pelage, black head and legs, white mental and narial patches, extremely large preorbital glands, round and excavated preorbital fossa, and size (Hershkovitz 1982). We also took linear measurements of the cranium and mandible (following von Den Driech 1976; Groves & Grubb 2011; Gutiérrez *et al*. 2015, Sandoval *et al*. 2022). Measurements were taken to the nearest 0.01 mm with a digital caliper. We compared the measurements with available data for other Neotropical deer taxa (e.g., Gutiérrez *et al*. 2015; Peres *et al.* 2021; Sandoval *et al.* 2022; Sandoval *et al*. 2024) and assessed morphometric gaps separating *M. rufina* and *P. mephistophiles* as discrete groups by using a Principal Component Analysis (PCA). For the PCA, we selected 11 cranial variables (Table 2) of 53 specimens of Neotropical deer, including data from the literature of recently validated taxa (Sandoval *et al.* 2022; Sandoval *et al*. 2024): GLS = greatest length of the skull; CBL = condylo-basal length, SSL = short skull length, PR = premolare–prostion, LP = lambda–prostion, AK = akrokranium, LCR = length of the cheektooth row, GILO = greatest inner length of the orbit, GIHO = greatest inner height of the orbit, LFB = Least frontal breadth, LBBO = least breadth between the orbits, and ZB = zygomatic breadth.

Distribution analyses

We compiled available localities from the literature (e.g., Gutiérrez *et al.* 2015, Jasper *et al*. 2022), online databases such as the Global Biodiversity Information Facility (GBIF), and our new records to the dataset available in Appendix 1. We also estimated the species range using the Extent of Occurrence (EOO) and Area of Occupancy (AOO). We calculated the EOO using the minimum convex polygon method (the shortest continuous boundary drawn to encompass all known occurrences of the species) and the AOO by summing the area of grid squares in which the species is known to occur (adopting the standard grid cell size of 2 km, as recommended by the International Union for the Conservation of Nature (IUCN 2010), using GeoCAT (Bachman *et al.* 2011).

We tested the allopatric distribution of *M. rufina* hypothesis presented in Jasper *et al*. (2022) by exploring the presence of the species in intermediate localities by performing ecological niche models (ENM) on the R package Wallace (Kass *et al*. 2018, 2023) and using the Maxent algorithm (Phillips & Dudík 2008; Phillips *et al.* 2017). We reduced spatial biases by applying spatial filtering and retaining only occurrences separated by more than 2 km^2 by using "spThin" package in R (Aiello-Lammens *et al.* 2015). We selected a five-degree buffer area around localities as our study area to build the model, and sampled 10,000 random "background" pixels. We used 20 predictor layers from WorldClim data version 2.1, including the elevation and 19 Bioclimatic variables (https://www.worldclim.org/data/worldclim21.html; Fick & Hijmans 2017). We used all variables, as excluding highly correlated predictors

does not significantly affect model performance. Moreover, this strategy has limited impact because Maxent can account for redundancy among variables (Feng *et al*. 2019).

We ran a non-spatial partition modeling approach ("*n* − 1 jackknife"; Pearson *et al.* 2007; Shcheglovitova and Anderson 2013) and estimated optimal model complexity considering values of regularization multiplier between 0.5 and 3.5 by 0.5 and five feature classes combinations (linear [L], quadratic [Q], and hinge [H]: L, LQ, LQH, H, LQHP), using ENMeval (Muscarella *et al.* 2014). We chose Cloglog output format to describe the species suitability (Phillips *et al*. 2017) in a continuous range between 0 (unsuitable) and 1 (the most suitable). The best-fit ecological niche models were selected based on AICc = 0, and Area Under the Curve (trainAUC > 0.75) of the Receiver Operating Characteristic curve based on the test records (Muscarella *et al*. 2014).

Results

Based on the mitogenome (Figure 1) and Cyt-*b* (Figure 2), we recovered *M. rufina* as a monophyletic group sister to a clade containing *Mazama* + *Odocoileus*, but not part of *Mazama* (sensu stricto) or other genera of Neotropical deer. The phylogenetic analysis recovered for the mitochondrial mitogenome showed the dwarf red brocket as an independent clade from *Mazama* sensu stricto, indicating that it represents a separate undescribed genus. This highly supported clade shares an exclusive common ancestor with the also highly supported genera *Mazama* and *Odocoileus*, all grouped in the clade representing the sub-tribe Odocoileina. The relationship between Odocoileina and Blastocerina, the two subtribes of Neotropical deer, is also fully supported, which the latter comprising the genera *Blastocerus*, *Bisbalus*, *Hippocamelus*, *Oztocerus*, *Passalites*, *Pudu*, and *Subulo* (Figure 1). All the nodes are well supported under all partitions except for those within the *Bisbalus*-*Subulo* clade and within *M. americana* (Figure 1).

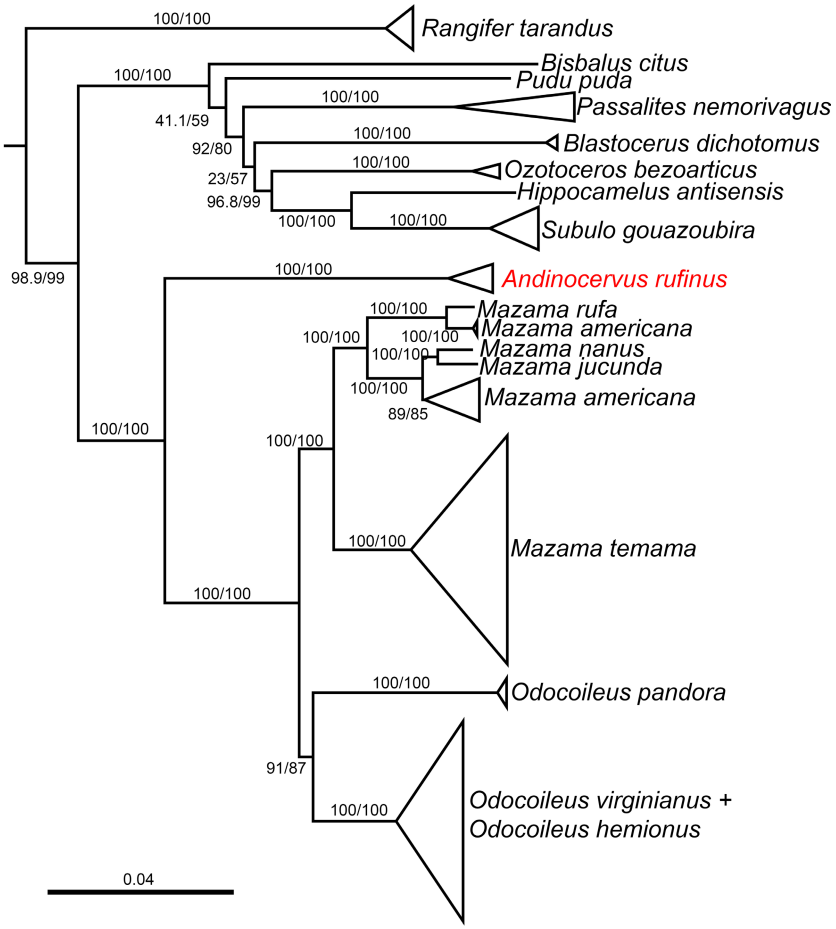

FIGURE 1. Phylogeny of Neotropical deer based on the mitochondrial genomes (nucleotide sequences) using the best partition scheme. Values of branches indicate the maximum likelihood inference's nonparametric (SH-aLRT; left) and ultrafast (UFBoot; right) bootstrap values.

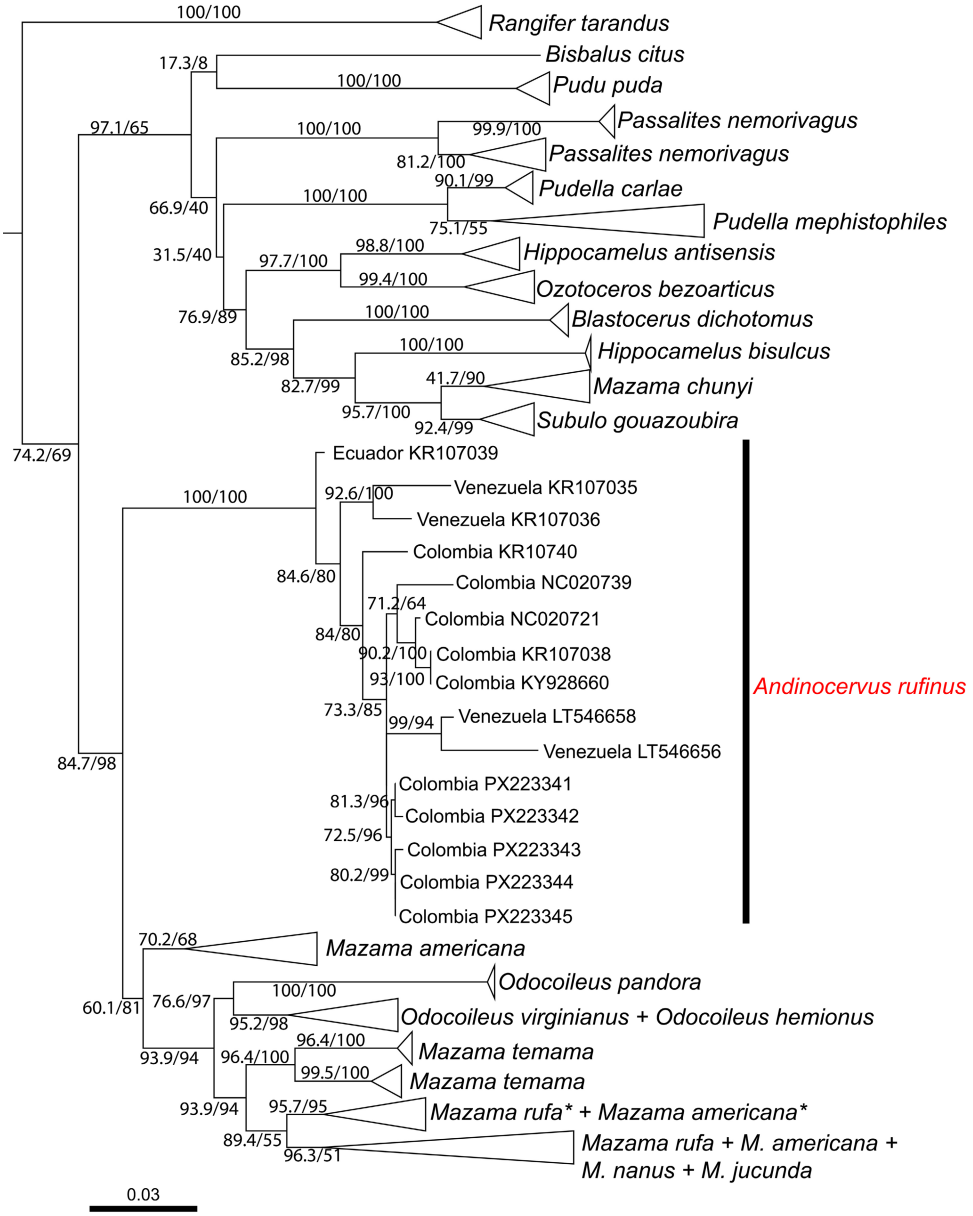

FIGURE 2. Phylogenetic tree using Cytochrome *b* sequences of Neotropical deer taxa. Values of branches indicate the maximum likelihood inference's nonparametric (SH-aLRT; left) and ultrafast (UFBoot; right) bootstrap values.

Similarly, in our Cyt-*b* tree (Figure 2), the dwarf red brocket formed a highly supported clade separate from *Mazama* sensu stricto. The dwarf red brocket clade is the first diverged clade in a more inclusive clade that is strongly supported by ultrafast bootstrap (UFBoot = 98), but has medium support in the nonparametric bootstrap (SH-aLRT = 84.7). The dwarf red brocket clade is sister to a clade composed of *Mazama* species (except "*M." chunyi*) and *Odocoileus*. In the Cyt-*b* tree, most of the species' clades received strong support except for the genus *Mazama*, where several clades within *M. americana* species groups appeared polyphyletic (Figure 2). "*Mazama" chunyi* formed a poorly supported clade (UFBoot = 90; SH-aLRT = 41.7), being sister (UFBoot = 100; SH-aLRT = 95.7) to the *S. guazoubira* clade and not part of the other members of *Mazama*. Finally, the genus *Hippocamelus* did not form a monophyletic group (Figure 2).

The haplotype network showed strong geographic structure, containing unique haplotypes for each locality (Figure 3b). Sequences from the Central Cordillera of Colombia formed a distinct cluster, separated by 14 and 31 mutational steps from sequences from other localities. The most distinctive haplotypes were both sequences from Mérida Cordillera, separated by nineteen and thirty-one mutational steps from other localities; and one sequence

from Colombia (NC020739), without specific geographic information, that has between 19 and 31 mutational steps from other dwarf red brocket haplotypes. The genetic distances between the geographic haplotypes using a total of 774 base pairs were between 1.4 % (Central Cordillera of Colombia vs. Ecuador) and 2.52 % (Mérida Cordillera vs. Ecuador). In general, the genetic distances of the sequences from the Mérida Cordillera are greater compared with the distances between the other haplotypes (Table 1).

All the specimens revised exhibited diagnostic morphological traits of the dwarf red brocket including large preorbital glands, round and excavated preorbital fossa (Figure 4), reddish pelage, black head and legs (Figure 5), and white mental and narial patches. Cranial and body mass measurements (GLS: 170–172 mm; weight up to 15 kg) confirm that the dwarf red brocket is among the smallest of South American deer. In the Andean region of Ecuador and Colombia, it is the second smallest deer after *Pudella mephistophiles*. Cranially, it is generally smaller than other sympatric or allopatric deer species (Table 2; Figure 6), being larger only tha *P. mephistophiles*. The PCA (Figure 6) showed that the dwarf red brocket slightly overlaps in skull size with *Mazama nanus* and gray brockets

TABLE 1. Genetic distances in percentages based on 774 bp of Cyt-*b* gene between different populations of *Andinocervus rufinus*.

	Central Cordillera	Oriental Cordillera	Colombian Massif	Ecuador
Eastern Cordillera	1.52			
Colombian massif	1.52	2.33		
Ecuador	1.40	1.94	1.42	
Mérida Cordillera	2.49	2.52	2.26	2.13

TABLE 2. Cranial measurements of *Andinocervus rufinus* and other similar-sized deer species. *Mazama temama* (Colombia) includes specimens from trans-Andean Colombia (sensu Escobedo-Morales *et al*. 2025), that can be sympatric with *A. rufinus*. Data of *Mazama nanus*, *Passalites nemorivagus* and *Subulo gouazoubira* were taken from Sandoval *et al.* (2024) and Bernegossi *et al.* (2023).

	A.rufinus	*Pudella mephistophiles*	*M. temama* (Colombia)	*Mazama nanus*	*Passalites nemorivagus*	*Subulo gouazoubira*
Measurement						
GLS	167.14 (156.37–172.56) 8	128.15 (124.99–132.25) 3	196.54 (190.93–205.21) 3	167.68 (163.7–172.4) 4	173.71 (171.25–176.02) 3	172.34 (166.43–178.40) 3
CBL	159.53 (147.75–165.68) 8	121.12 (117.54–125.64) 3	186.25 (182.56–189.76) 4	158.44 (149.90–164.48) 4	164.19 (162.93–165.57) 3	163.07 (156.94–170.17) 3
SSL	99.25 (92.94–102.66) 8	81.86 (77.20–87.66) 3	115.52 (11.83–117.73) 4	98.75 (95.30–101.70) 3	102.75 (100.93–104.00) 3	100.48 (98.99–102.40) 3
PR	51.05 (45.63–56.28) 8	33.17 (31.83–34.20) 3	61.54 (60.19–64.39) 4	48.84 (44.43–52.00) 4	51.69 (50.13–54.02) 3	54.17 (50.18–58.94) 3
LP	157. 21 (148.03–165.54) 8	119.77 (114.74–124.13) 3	186.74 (180.78–195.73) 4	162.19 (157.33–169.04) 4	168.17 (151.58–175.51) 3	169.24 (157.96–177.87) 3
AK	119.61 (113.98–123.66) 8	81.48 (52.53–98.79) 3	136.44 (130.25–144.87) 4	119.95 (117.06–122.20) 4	123.01 (120.30–125.51) 3	123.20 (118.66–127.75) 3
GILO	29.44 (27.99–31.19) 8	22.11 (20.27–23.69) 3	32.64 (31.68–33.11) 4	29.58 (28.53–30.58) 4	30.52 (29.51–31.10) 3	32.03 (31.90–32.13) 3
GIHO	27.92 (25.65–29.67) 8	22.00 (20.98–23.68) 3	32.15 (31.15–33.72) 4	31.25 (27.77–34.16) 4	30.34 (29.47–31.05) 3	32.28 (28.98–37.53) 3
LFB	45.14 (32.78–54.85) 8	33.91 (29.47–42,67) 3	57.54 (50.20–71.07) 4	51.03 (48.09–54.64) 4	47.10 (43.80–53.50) 3	48.09 (45.54–52.57) 3
LBBO	36.17 (33.37–38.03) 8	33.31 (32.89–33.89) 3	45.84 (45.00–46.52) 4	44.30 (43.62–45.03) 4	45.58 (43.29–46.92) 3	45.80 (44.86–47.04) 3
ZB	67.06 (50.89–77.87) 8	43.86 (41,96–45.37) 3	86.75 (82.54–92.00) 4	74.46 (71.98–75.89) 4	73.80 (69.51–78.09) 2	72.39 (72.09–72.62) 3

(i.e., *Passalites nemorivagus*, *Subulo gouzoubira*). The dwarf red brocket is cranially smaller than *Bisbalus citus,* and other species of *Mazama* and *Odocoileus virginianus*. The first three components explain about 96.49% of the total variability observed. The first principal component (PC1) explains 93.62% of the variation, and the second (PC2) explains 1.78%. All variables contributed positively to PC1, showing that the first principal component reflects variation in overall cranial size (Table 3). The variables that contributed most strongly to PC1 were the CBL (0.4898) and GLS (0.4880). The other principal components had positive and negative variable contributions (Supplementary Data SD5) and reflected variation in cranial shape. In the scatter plot, both forms have overlapping morphometric distributions. Linear measurements of Colombian specimens are provided in Table 2.

We found a total of 186 records of the dwarf red brocket from Colombia, Ecuador, Peru, and Venezuela (Supplementary Data SD4), with all records occurring within an elevational range of 1,000 to 3,700 meters. The AOO of the species is 796 $km^{2,}$ and the EOO is 443,764 km^2. There are at least three allopatric metapopulations: Mérida Cordillera, northeast of the Táchira depression; Oriental Cordillera south of Tachira depression and north of Las Cruces pass; and Central Cordillera to potentially northern Peru (Figure 3). However, additional genetic and geographic information is needed to determine whether other populations exist, and to test the cause of potential barriers causing allopatry in the species.

The best-performing model was LQHP 1.5, based on AICc values, and demonstrated strong predictive performance (AUC = 0.95) with a low omission rate (OR = 0.124; Supplementary Data SD6). This model accurately predicted species presence across the evaluated localities (Figure 3a), and the most influential predictors are detailed in the Supplementary Data SD7. High suitability areas were identified across the northern Andes, including regions to the north of the Marañón River in Peru and the Mérida Cordillera in Venezuela. The model also suggested that the species occupies several allopatric ranges, which correspond with the geographic structure observed in the haplotype network. The Mérida Cordillera, isolated by the Táchira Depression, contains the most divergent haplotypes. The Oriental (Eastern) Cordillera, between the Táchira Depression and Las Cruces Pass, harbors distinct, unique haplotypes. Additionally, the model predicted a continuous distribution across the Central Cordillera, the Colombian Massif, and the Andes of Central Ecuador, each area also containing unique haplotypes. Lowland river valleys such as the Magdalena, Cauca, and Patía likely contributed to the observed geographic genetic structure (Figure 3).

The model showed some over-predicted areas in some regions of Colombia, Ecuador, and Venezuela that we consider crucial for sampling to discover new populations or related taxa (Figure 3). These areas (Supplementary Data SD4) were: i) the Oriental Cordillera of Colombia, south of Las Cruces pass, between the departments of Huila and Cundinamarca; ii) the Perijá Massif of Colombia and Venezuela, in the departments of Cesar and La Guajira, and the Zulia state; iii) the Central Cordillera of Colombia, in the Department of Valle del Cauca; iv) the Occidental Cordillera of Colombia, in the departments of Nariño, Cauca, and Valle del Cauca; v) the area between the provinces of Cotopaxi and Cañar in Ecuador; vi) the southwestern portion of Mérida Cordillera in the states of Táchira and Mérida in Venezuela., vii) the Sierra Nevada de Santa Marta, Colombia.

TABLE 3. Loadings of the measurements of the Principal Component Analyses results for 11 cranial measurements of 53 specimens of 10 Neotropical deer species. In bold are indicated the variables that most contributed to the variation.

Measurement	PC1	PC2
GLS	0.488	-0.1626
CBL	**0.4898**	-0.3628
SSL	0.2545	-0.09155
PR	0.177	-0.09594
LP	0.4644	-0.1261
AK	0.3182	0.2744
GILO	0.05107	0.09395
GIHO	0.06576	0.1033
LFB	0.1548	**0.6093**
LBBO	0.1284	0.2162
ZB	0.248	**0.5437**

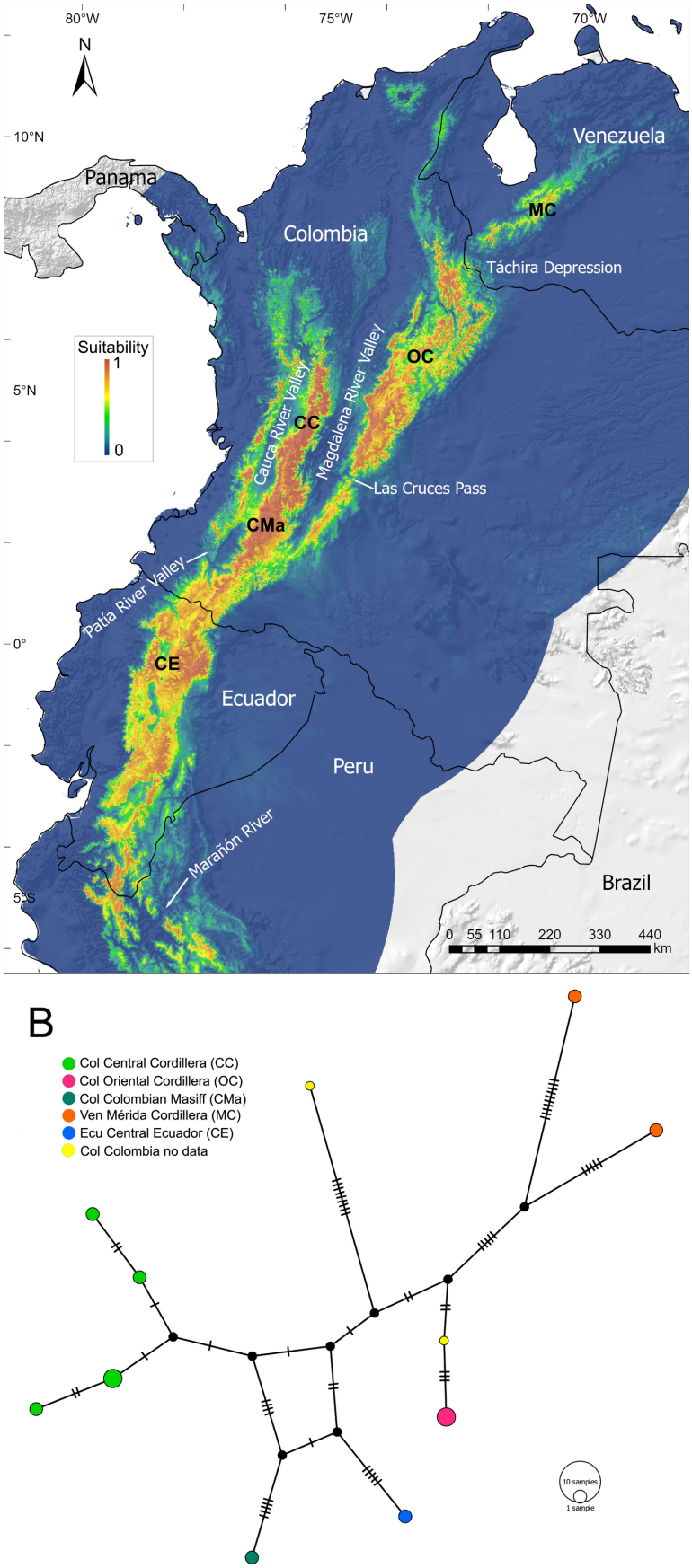

FIGURE 3. A. Bioclimatic distribution models using Maxent for *Andinocervus rufinus* and allopatric breaks in the northern Andes. B. Haplotype network of the Cyt-*b* of *A. rufinus* constructed under TCS algorithm.

FIGURE 4. Morphological details of the skull of male *Andinocervus rufinus* from the Central (left) and Oriental (right) cordilleras of Colombia. Note the deeply excavated lacrimal fossae (arrow).

FIGURE 5. An adult female and a juvenile of *Andinocervus rufinus* in southwestern Colombia. Photographs obtained using trail cameras at Santa Rosa, Cauca, Amazon foothills of the Oriental Cordillera of Colombia, by the Grupo de Monitoreo Fundación de Monitoreo de la Vida Silvestre Villalobos FUNCMOVIS.

Considering the evidence compiled in the phylogenetic analyses, and the presence of unique morphological traits such as the excavated deeply excavated lacrimal fossae, we propose a new genus for the dwarf red brocket (*Mazama rufina,* including *M. bricenii*):

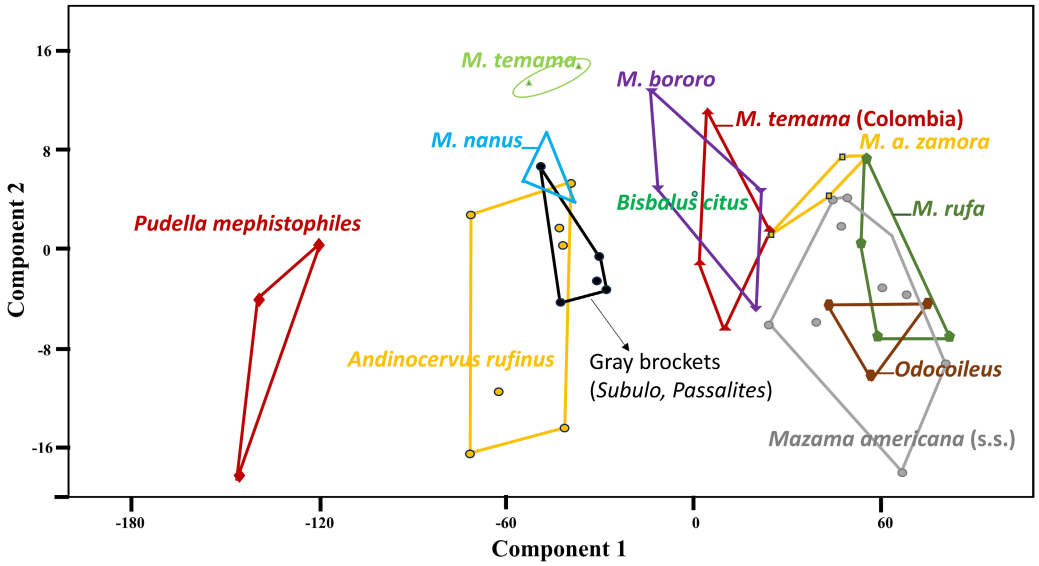

FIGURE 6. PCA biplot for specimens of *Andinocervus, Bisbalus, Mazama, Odocoileus*, *Subulo*, *Passalites*, and *Pudella. Andinocervus rufinus* is among the smallest deer species in the Andes of northern South America. *Mazama temama* (Colombia) includes specimens of red brockets from the Andean landscapes and inter-Andean valleys of Colombia sensu Escobedo-Morales *et al*. (2025). *Mazama americana zamora* includes specimens of red brockets from the Amazon Region of Colombia.

Systematics

Class Mammalia

Order Artiodactyla

Suborder Ruminantia

Family Cervidae

Subfamily Capreolinae

Tribe Odocoileini

Genus *Andinocervus* Ramírez-Chaves, Morales-Martínez, Cardona-Giraldo, Ossa-López, Rivera-Páez & Noguera-Urbano, gen. nov.

Type species: *Cervus rufinus* Pucheran, 1851:561.

Etymology: *Andinocervus* (Latin *andinus* = Andean; *cervus* = deer). The prefix Andino is a Spanish word meaning "of the Andes," which itself is derived from *Andes*, the mountain range of South America, in which the species inhabits. The suffix cervus is a Latin word for "deer", and honors the original name in which the nominal species was described (*Cervus rufinus*). The proposed genus name *Andinocervus* is to be treated as a masculine noun.

Diagnosis: Because *Andinocervus* is monotypic, this diagnosis applies to both the genus and to *A. rufinus*. It represents a monophyletic lineage sister to a clade formed by *Mazama* and *Odocoileus*. A small brocket, with body length smaller than 900 mm, and hind legs longer than forelegs. Cranial measurements include a skull length of less than 175 mm and an upper toothrow of up to 57 mm. The skull has a deep and well-excavated lacrimal fossa. The antlers are short (> 80 mm) and unbranched (Figure 4), with the shape of small spikes. Dorsal pelage coloration is reddish brown and becomes blackish on the legs, reaching down to the hoofs. Ventral fur coloration is lighter that the dorsum but not very countershading. The face is also blackish forming a mask that includes the chin but not the

cheeks, surrounding the eyes. It also has whitish mental and narial patches. Ears with internal borders and part of the posterior half of the pinnae whitish. Abdomen and ventral side of legs vary between ochre and reddish brown with long (~ 70 mm near the genitals) and cottony pelage. Tail is short, up to 150 mm including hairs, with the ventral area whitish.

Distribution: It occurs throughout the northern Andes, from Peru north of the Marañón depression through Ecuador, Colombia, and Venezuela (Figure 3), at elevations ranging from 1,000 to 3,700 m.

Species account

Andinocervus rufinus (Pucheran, 1851:561), comb. nov.

Synonyms:
Cervus rufinus Pucheran, 1851:561. Type locality "la vallée de Lloa, sur le versant occidental de la Cordillière du Pichincha;"
Mazama bricenii Thomas, 1908:349: Type locality "Paramo de la culata, Merida, Venezuela. Altitude 3000 m."
Mazama rufinus: Thomas, 1908:349. Name combination.
See Hershkovitz (1982) and Jasper *et al.* (2022) for a complete list of synonyms.

Type locality: "la vallée de Lloa, sur le versant occidental de la Cordillière du Pichincha;" Ecuador.

Holotype: Muséum national d'Histoire naturelle (MNHN)—MNHN-ZM-MO-1851-61, by monotypy.

Diagnosis: As for the genus.

Common names: dwarf red brocket; little red brocket (English). Venado de páramo, venado chonta, soche de páramo (Spanish).

Description: A small brocket (head and body length, 85–90 cm; height at shoulders, 45 cm; weight, 10–15 kg); pelage reddish brown and becomes blackish on the legs, reaching down to the hoofs. The tail is short with white hairs in the ventral side. Approximately ¾ of the hairs exhibit a cream-gray band and the tips are reddish. Dorsal hairs are long (~ 45 mm). Neck shorter than the head´s length. Fur over the head is shorter (~ 20 mm) than in the back. The hairs of the nape are not reversed. It has four inguinal teats. Males with small tuffs around the antlers. Approximately six superciliary (up to 35 mm in length), seven mystical, and more than 15 interramal vibrissae. *Andinocervus rufinus* is the second smallest deer species in the Andean region of Colombia and Ecuador (greatest length of the skull: 170–172 mm), and the smallest brocket in Venezuela. Cranially, it is smaller than other sympatric or allopatric species, and exhibits round and excavated preorbital fossa (Table 2).

Comparisons: *Andinocervus rufinus* is similar in size to *Mazama nanus* and the gray brockets, i.e., *Passalites nemorivagus*, *Subulo gouazoubira*, but can be easily differentiated by a more excavated lacrimal fossae and smaller vacuities. Externally, juveniles of *A. rufinus* are similar to adults of *P. mephistophiles* (Figure 5), but they can be differentiated by the reduced tail of the latter. Adults of both species are easily differentiated based on the larger external and cranial size and the lack of vestigial canines of the *A. rufinus*. Other small deer such as *Pudu puda,* and both *Pudella carlae* and *P. mephistophiles* are smaller in external and cranial measurements and exhibit upper vestigial canines. *Mazama temama* lacks the excavated preorbital fossa, does not have the black mask and the general coloration is lighter. "*Mazama*" *chunyi* is similar in size than *A. rufinus*, but lacks the dark brown face.

Discussion

Despite advances in understanding the diversity of Neotropical deer, morphological and mitochondrial DNA evidence suggests that the current taxonomic classification of the cervid tribe Odocoileini does not fully reflect their evolutionary history (Barrio *et al*. 2024). For instance, our phylogenetic analysis recovered the dwarf red brocket, historically placed within the genus *Mazama,* as an independent lineage (see also Heckeberg 2020). This finding supports the need to propose a new generic name, as no available names are applicable, as previously noted by Allen (1915), Hershkovitz (1982), and Jasper *et al*. (2022). Names such as *Coassus* Gray, 1843, and *Homelaphus* Gray, 1872, have been associated with *Mazama* sensu stricto, while *Nanelaphus* Fitzinger, 187, refers to a taxon currently included within *Subulo*. A case similar to that of *Andinocervus* applied to other lineages now recognized as separate genera, such as *Bisbalus* (Sandoval *et al.* 2024).

Due to the demonstrated polyphyly of *Mazama*, based on a single genetic locus, the mitochondrial DNA, Gutiérrez *et al.* (2017) recommended restricting the use of *Mazama* to the clade containing *M. temama* and *Mazama americana* sensu lato. The recent reassignment of the genus *Subulo* to include *M. gouazoubira* and possibly *M. chunyi* (Bernegossi *et al*. 2022; Barrio *et al.* 2024), and the description of *Andinocervus* align with this proposal and has further implications for the taxonomy of Neotropical deer.

Our results further point out to the need for an expanded integrative assessment of the diversity of cervids in northern South America (from Peru to Venezuela) especially in Colombia, where the number of deer species in unclear (Solari *et al.* 2013; Ramírez-Chaves *et al.* 2021). The identification of deer in the northern Andes is still controversial, where species such as *M. americana* have unclear distribution limits and likely represent species complexes (Barrio *et al.* 2024; Mammal Diversity Database 2025). Similarly to recent and historical studies, including morphometric information of Neotropical brockets (Hershkovitz 1982; Gutiérrez *et al*. 2015; Sandoval *et al*. 2022; Peres *et al*. 2021), our results show that cranial morphology is a valuable tool for establishing species-level identity among deer in the northern Andes—consistent with findings from other South American deer species (e.g., De Lima *et al.* 2024). The skull measurements of *A. rufinus* available in the literature (Gutiérrez *et al.* 2015) are alike to those of the present study, except for some of them, namely the CBL, BL and UTRL, which are longer in four (CBL and BL: MHN-UCa-M 196; M 3290, M 3345, M 4187), and two (UTRL: MHN-UCa-M 196 and M 3290) specimens (Table 2).

Genetic distances support the taxonomic reconsideration of *M. bricenii* as a synonym of *A. rufinus* (Gutiérrez *et al.* 2015) because the values of the genetic distance between the sequences of Mérida Cordillera and other localities are lower than the values proposed in the genetic concept of species (Bradley & Baker 2001), and are also lower than the values of the genetic distances between *A. rufinus* and other Neotropical deer (3.7%–8.3%; Gutiérrez *et al.* 2017). Nevertheless, the presence of very distinctive haplotypes from the Mérida Cordillera may indicate that the populations of Venezuela are currently isolated from the other populations of the species, and additional analyses should explore the presence of subspecies. Additionally, using ecological niche modeling, Gutiérrez *et al*. (2017) concluded that the Táchira depression does not act as an ecological barrier for dwarf red brockets. In contrast, our model revealed low suitability values for *A. rufinus* in the Táchira depression, supporting its role as an important allopatric barrier isolating populations of the Mérida Cordillera from those of the Oriental (Eastern) Cordillera in Colombia. The discrepancy with Gutiérrez *et al*. (2017) likely arises from their smaller dataset, which was concentrated in Venezuelan localities and may have overestimated the species' distribution, as well as from their use of the minimum training presence threshold, which tends to incorporate marginally suitable habitats. By contrast, our broader dataset indicates that raw suitability values in the Táchira depression are consistently very low ($p < 0.5$).

Haplotype analyses of the limited available sequences revealed evidence of geographic structure. This pattern may reflect both the small number of sequences and the restricted geographic sampling. However, considering that the species is restricted to mid and high Andean elevations with small and fragmented populations (Jasper *et al.* 2022), it is plausible that there is a high genetic diversity along its distribution. Testing that scenario is crucial for the conservation of the species because each population could represent a distinct genetic conservation unit or subspecies, as suggested for *M. bricenii* (Gutiérrez *et al.* 2015).

The geographic information presented here is key for planning conservation strategies. *A.rufinus* is listed as Vulnerable by the International Union for Conservation of Nature—IUCN (Lizcano & Álvarez 2016). Based only on AOO, this species might be Endangered (Least Concern based only on EOO); however, it has been suggested that, due to hunting, it needs to be locally and regionally recognized as a potentially threatened species (Lizcano & Álvarez 2016). Road-killed specimens are relevant because they represent a new threat to *A. rufinus* populations, affecting individuals also near protected areas such as the Los Nevados National Park, where indeed one of the road-killed specimens was found.

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APPENDIX 1. Specimens examined. Museum acronyms are explained in Material and methods. *Specimens included in the Principal Component Analyses. PX numbers indicate the GenBank accession numbers of the specimens. New records are indicated in bold.

Pudella mephistophiles: Colombia: Cauca, Guanacas (MHNUC 167*, 168*); Páramo de Guanacas, sector Totoró-Inzá (MHN-UCa-M 5161); Cauca? (MHNUC 171*).

Andinocervus rufinus: Colombia: Caldas, Villamaría, Reserva Forestal Protectora CHEC, sector El Topacio (MHN-UCa-M 2049; PX223342); Caldas, Villamaría, Gallinazo, RFP Bosques de la CHEC, sector El Topacio, quebrada Termales cerca de La Gruta (MHN-UCa-M 2777; PX223343); Caldas, Villamaría, Reserva Forestal Protectora Bosques de la CHEC, camino de la Fe (MHN-UCa-M 3148); Caldas, Villamaría, Reserva Forestal Protectora Bosques de la CHEC, camino de la Fe (MHN-UCa-M 3149); Caldas, Villamaría, Gallinazo (**MHN-UCa-M 4282**); Caldas, Oriente de Caldas (MHN-UCa-M 3290*; PX223344); Caldas, Manizales, Torre 4 (MHN-UCa-M 3296; PX223345); Caldas, Manizales, Finca El Diamante, Vía Manizales-Bogotá (**MHN-UCa-M 3345***); Caldas, Manzanares, Vereda Centro, sector San Luis (MHN-UCa-M 2024*; PX223341); Caldas, Manzanares, a 20 minutos del casco urbano, aserradero, bosque de pinos (**MHN-UCa-M 4754**); Caldas, Marulanda, (**MHN-UCa-M 4187***); Caldas, Marulanda, Vereda San Isidro, arroyo Las Palomas, finca Berlín (MHN-UCa-M 1921); Caldas, Pensilvania, Vereda Quebrada Negra (MHN-UCa-M 2946). Cauca (MHNUC 174*; MHNUC 170*). Nariño, Puerres, Momopamba (MHNUC 1957); Cauca, Páramo de las Papas (MHNUC 166*). Norte de Santander, Toledo, Vereda Belchite, zona del rio Jordan (**MHN-UCa-M 4134**). Risaralda, Pereira, Vereda El Bosque (MHN-UCa-M 822*). Risaralda, Santa Rosa de Cabal, Vereda San Ramón, predio de conservación CHEC, Los Alpes (MHN-UCa-M 3157). Tolima, Rioblanco, Vereda La Albania, Finca Nuevo Mundo (MHN-UCa-M 3179); Tolima, Herveo, Páramo de Letras (MHN-UCa-M 196*). Valle del Cauca, Palmira, Vereda La Nevera, sector Quebrada Toche, Parque Nacional Natural Las Hermosas (MHN-UCa-M 3404). No locality data (MHN-UCa-M 4393; MHN-UCa-M 4394).

Mazama temama (*included in the morphometric analyses as *M. temama* (Colombia)): Colombia: Caldas, Riosucio (**MHN-UCa-M 3807***). Cauca, Popayán, Quintana (MHN-UCa-M 4542; **MHN-UCa-M 4993**); Cauca? (MHNUC 175* skull; 178 dentary). Nariño, Chachagüí, La Ensillada (MHN-UCa-M 3799*); Nariño, Consacá, Vereda Cariaco Bajo (MHN-UCa-M1859*). Risaralda, Santuario, Parque Nacional Natural Tatamá (MHN-UCa-M 3381). Valle del Cauca, El Águila, Vereda Judea, finca La Solita (MHN-UCa-M1798, MHN-UCa-M1799).

Mazama americana zamora: Colombia: Meta, Municipio de Mesetas, vereda San Isidro, cuenca media del rio Duda, 420 m (ICN 11626*); Meta, Sierra de La Macarena (ICN 503*). Vaupés, Laguna del Churuco, rio Apaporis (ICN 504, ICN 505*); Vaupés, Rio Apaporis, campamento La Aventura (ICN 507*). No data (ICN 2895*).

Gray brockets (*Subulo, Passalites*): Colombia: Amazonas, La Chorrera, cabildo Okaina, Puerto Oriente (collector number D3M 1125*). Meta, La Macarena (Paratype of *Mazama gouzoubira medemi*; ICN 780*). Vaupés: La Providencia, rio Apaporis (ICN 746 *). Caquetá, Parque Nacional Natural Chiribiquete, caño Cuñare, raudal de la Víbora (ICN 14927). La Guajira, Cerca de Siapana (ICN 797).

Odocoileus virginianus: Colombia: Caldas, Manizales (MHN-UCa-M 2942*; PX223341). Arauca, Arauca (MHN-UCa-M 3734*; MHN-UCa-M 2061*).

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary Data SD1. GenBank accession numbers and locality of the mitogenome sequences used in our analysis.

Supplementary Data SD2. GenBank accession numbers and country of the Cytochrome *b* sequences used in our analysis. SG = Submitted to GenBank.

Supplementary Data SD3. best partition scheme and the best model for each partition of the Mitogenome analysis estimated by ModelFinder (Kalyaanamoorthy *et al.* 2017) on IQtree (Nguyen *et al.* 2015).

Supplementary Data SD4. Distribution of records of *Andinocervus rufinus* in South America. The green polygon represents the Extent of Occurrence.

Supplementary Data SD5. Eigenvalue and percentage of variance for 11 cranial measurements of 11 cranial measurements of 53 specimens of 10 Neotropical deer species. In bold are indicated the variables that most contributed to the variation. CBL and GLS contributed the most in the PC1 and LFB and ZB in the PC2.

Supplementary Data SD6. Results of the evaluation of different models for the ecological niche modeling, the model used was LQHP 1.5 considering the high AUC values and lowest AICc values.

Supplementary Data SD7. Lambdas of the contribution of bioclimatic variables associated with Maxent models of climatic suitability. Variables with the largest contribution are shown in bold.