BIOGEOGRAPHIA
The Journal of Integrative Biogeography

Biogeographia – The Journal of Integrative Biogeography 2026, 41 (1): a060

https://doi.org/10.21426/B6.61410

On the distribution of the rare Andean snakes, *Saphenophis tristriatus* (Rendahl & Vestergreen, 1940), and *Saphenophis sneiderni* Myers, 1973, with an analysis on the snake endemism in the Cauca River basin, Colombia

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Keywords: Endemism areas, Squamata, trans-Andean valleys, zoogeography.

SUMMARY

Saphenophis tristriatus and *Saphenophis sneiderni* are poorly known snake species endemic to the Northern Andes of Colombia. Based on a recently collected specimen and photographs, we present new records for both species in the Central and Occidental (Western) cordilleras of Colombia along an elevational range between 1,700 to 2,940 m a.s.l. We also discuss the representativeness of snake endemism in the Cauca River basin (63,300 km^2, 4.1% of the Northern Andes) using 0.5° x 0.5° grid cells. The record of *S. tristriatus* and *S. sneiderni*, plus additional photograph-based records, extends the known distribution approximately 200 km north from the previous known localities in southwestern Colombia. The review of additional snake species gathered 20 species which are endemic to this basin. A highly endemic snake concentration occurs at the middle Cauca River valley, where nine species are found in two grids. The fact that the Cauca River basin has such a high level of snake endemism's compared to other areas worldwide is highly significant in biogeographical terms, particularly for disentangling the Central America and Northern South America snakes phylogeography.

INTRODUCTION

Tropical mountains acting as global epicenters of endemism where a high biodiversity inhabits into relatively small geographic areas (Rahbek et al. 2019). However, this richness is shadowed because many montane specialists are classified as Data Deficient (DD) (IUCN 2019). While these species are often overlooked in conservation priorities due to a lack of population trends, Gumbs et al. (2020) suggests that DD non-avian reptile species are frequently as threatened as those listed as Critically Endangered (CR). In the context of tropical mountains where habitats are shrinking rapidly due to climate change and habitat transformation, studying these elusive species is imperative, aiming to document and protect unique lineages before they vanish.

The Northern Andes, extending from the Huancabamba deflection on the Peru-Ecuador border to Cordillera de Merida in Venezuela (Josse et al. 2009) constitutes a geomorphologically complex region with a geological history and paleoclimatic characteristics closely linked to the speciation and diversification of multiple flora and fauna lineages (van der Hammen et al. 1973, Gentry 1982a, b, 1995, van der Hammen 2000, Hoorn et al. 2010, Pérez-Escobar et al. 2022). In particular, across the Northern Andes Cordilleras, high elevation areas above 2,500 m a.s.l. are constituted by Andean and high Andean forests (Josse et al. 2009) which are characterized by elevated levels of plant and vertebrate endemism (Gentry 1982a, b, Kattan et al. 2004, Swenson et al. 2012, Ramírez-Chaves et al. 2021). The distribution of highly diverse groups, such as the snake genus *Atractus* Wagler, 1828, highlights the relevance of the Northern Andean cordilleras for understanding the distribution patterns of Neotropical biota (Morrone 2015, Antonelli et al. 2009, Pomar-Gómez et al. 2021).

Different regions across the lowland and mountainous areas of the Neotropics have been recognized as centers of phylogenetic snake endemism, including the Caribbean, Central America, the Andes, the Atlantic Forest, and scattered highlands in central Brazil (Azevedo et al. 2020, Pomar-Gómez et al. 2021, Serrano et al. 2024). In addition, Andean valleys have been identified as barriers separating closely related snake taxa (Esqueda et al. 2025). Based on Häffer's (1967, 1969) Pleistocene refugia hypothesis, Müller (1972, 1973) identified 40 Neotropical areas as centers of species dispersal. Müller (1973) designated the Cauca and Magdalena centers to encompass the inter-Andean valleys of northwestern Colombia, primarily based on bird distribution data. Later, Hernández-Camacho et al. (1992) proposed that portions of the Cauca and Alto Patía River valleys correspond to dry remnants containing possible interglacial wet enclaves in their middle sections (within the departments of Caldas, Risaralda, and Quindío). Hernández-Camacho et al. (1992) also defined the following biogeographic districts for the Cauca Basin: (i) Bosques Subandinos de la Cordillera Central Cauca-Valle, (ii) Planicie Alto Cauca, and (iii) Cañón del Cauca. However, the authors did not provide details regarding the biotic elements that define these units.

Recently, Morrone et al. (2015) defined the Cauca Province as stretching from western Colombia to Northern Peru. This province is defined by endemic flora and fauna, including vertebrates identified by Müller (1973) in the Cauca Center such as birds: Apodidae (*Cypseloides lemosi* Eisenmann & Lehmann, 1962), Cracidae (*Ortalis guttata guttata* Spix, 1825), Picidae (*Picumnus granadensis* Lafresnaye, 1847), Rhamphastidae (*Aulacorhynchus albivitta griseigularis* Chapman, 1915), Tinamidae (*Nothocercus julii* (Bonaparte, 1854)); and mammals: Cervidae (*Pudella mephistophiles* (de Winton, 1896)), Leporidae (*Sylvilagus andinus* (Thomas, 1897)), Procyonidae (*Nasua olivacea* Gray, 1865), Sciuridae (*Leptosciurus pucheranii* (Fitzinger, 1867)). For other vertebrate groups, such as non-avian reptiles, the information is, however, lacking or limited.

For snakes, one genus restricted to Andean and high Andean forests within the Northern Andes is *Saphenophis* Myers, 1973 (Serpentes: Dipsadidae). This genus comprises five recognized species: *S. antioquiensis* (Dunn, 1943), *S. atahuallpae* (Steindachner, 1901), *S. boursieri* (Jan, 1867), *S. sneiderni* Myers, 1973, and *S. tristriatus* (Rendahl & Vestergren, 1940). Species within *Saphenophis* are oviparous, terrestrial-diurnal species, feeding on a wide variety of prey, from invertebrates to lizards (Cisneros-Heredia 2005), but no additional ecological traits are known for the genus. All *Saphenophis* are restricted to the Andean Cordilleras of Colombia and Ecuador in elevations over 1,200 m (Myers 1973), excepting *S. boursieri* whose geographic distribution include Andean-Pacific foothills up to 1,000 m (Pazmiño-Otamendi 2020). Speciation in *Saphenophis* is presumed to have occurred during the Pleistocene (Myers 1973),

particularly in the Central and Occidental (Western) Cordilleras of Colombia where four species are found: *S. antioquiensis*, *S. boursieri*, *S. sneiderni* and *S. tristriatus*. Three species (*S. antioquiensis*, *S. sneiderni* and *S. tristriatus*) are endemics to the Cauca River basin (Myers 1973, Bolívar-García et al. 2015, Bernal 2025).

Saphenophis tristriatus and *S. sneiderni* are poorly known snake species for which little information has been published since their original descriptions (Bolívar-García et al. 2015, Vera-Pérez et al. 2018). The former is among the snake species reaching highest elevations in the Northern Andes (2,500–3,200 m a.s.l.) (Myers 1969, 1973, Vera-Pérez et al. 2018, Bernal 2025). However, due to a lack of ecological and population data coupled with few records through its range, *S. tristriatus* is classified as Data Deficient (DD) by the International Union for Conservation of Nature - IUCN (Bolívar and Arredondo 2016). In contrast, *S. sneiderni* is listed as Endangered (EN) both nationally (Bolívar-García et al. 2015), and globally by the IUCN Redlist (Bolívar and Velasco 2017). In this study, we report new records for *S. tristriatus* and *S. sneiderni* and discuss the endemism of snakes in the Cauca biogeographical province, particularly the Cauca River basin, emphasizing its importance for understanding the zoogeography of South American snakes.

MATERIALS AND METHODS

Study area

The Cauca River basin (63,300 km^2) is the main affluent of the Magdalena River, the largest trans-Andean River of Colombia. The Cauca River originates at an altitude of approximately 3,200 m a.s.l., in the Paletará valley, Department of Cauca (2°12' N, 76°29' W) and flows downhill south-north direction, running parallel to the Occidental Cordillera at the west, and the Central Cordillera at the east (Fig. 1). It is 1,360 km long and empties into the Magdalena River at the Ciénaga El Floral, Department of Bolívar (8°53' N, 74°27' W, 20 m a.s.l.). The Cauca basin emerged for the collision of an intra-oceanic island arc against the irregular continental margin of the northwestern part of South America. Age relationships of deposits that were folded and thrusted show that diachronous collision was completed from south to north during late Cretaceous to Neogene (López and Toro-Toro 2020). This has been a tectonically active intramountain basin during the Neogene (Nivia 2001; López and Toro-Toro 2020). The Cauca River valley (18,000 km2 spanned from Jamundí, Valle del Cauca to La Virginia, Risaralda) corresponds to the first mid-section of the basin. Along this area, a southern volcanic segment (Cauca-Patía valley, Occidental Cordillera) and northern volcanic segment (Los Nevados, Central Cordillera) have influenced the physiography, soils composition and climate over Quaternary (Monsalve-Bustamante 2020). From La Virginia (5° N), to the north (7° N), the Cauca River valley narrows, with mountain ranges running transversely.

Distribution update of *Saphenophis striatus* and *S. sneiderni*

To update the distribution of these two species, we first compiled locality records from literature (Myers 1973, Castro-Herrera and Vargas-Salinas 2008, Bolívar-García et al. 2015, Bolívar-García and Arredondo 2016, Bolívar-García and Velasco 2017, Vera-Pérez et al. 2018) and the Global Biodiversity Information Facility (GBIF 2025) including recent photographs for the species (Table 1). The inclusion of photographs was validated by verifying their identification accuracy on the iNaturalist platform and by comparing the photos to prevent confusion with similar species, such as *Erythrolamprus lamonae* (Dunn, 1944), with which *S. tristriatus* geographically overlaps. Furthermore, we added new records obtained during herpetological monitoring in the CHEC forests at Department of Risaralda, Colombia. During this monitoring, one individual of an unidentified snake was captured on August, 2015. The snake (Fig. 2) was ethically euthanized, collected and deposited in the Colección de Reptiles, Museo de Historia Natural of the Universidad de Caldas (MHN-UCa-R). Collection permit was provided by the ANLA (Autoridad Nacional de Licencias Ambientales de Colombia) through the Resolution N° 02497 of 31 December 2018 to the Universidad de Caldas. Species identification was made following Myers (1969) and Myers (1973) descriptions. The snout-vent length (SVL) and tail length (TL) were obtained with a ruler to the nearest 1 mm. Head length and head width were measured using a digital caliper Mitutoyo to the nearest 0.01. Also, head and body color traits, besides standard scale counting's are given. We follow Dowling (1951) for the counts of ventral scales.

Table 1. Snake species with restricted known distribution to the Cauca River Basin, Colombia.

Species	Elevation (m a.s.l.)	Andean Cordillera	IUCN	Source
Anomalepis colombia Marx, 1953	500-1,700	Central and Occidental	DD	Vanegas-Guerrero et al. (2019), Bernal (2025)
Atractus andinus Prado, 1944	1,200-1,400	Occidental	DD	Prado (1946)
Atractus biseriatus Prado, 1941	1,200-2,200	Central	DD	Ramírez-Chaves et al. (2022), Bernal (2025)
Atractus lasallei Amaral, 1931	1,700-2,700	Central	LC	Passos & Arredondo (2009), Rojas-Morales et al. (2023), Bernal (2025)
Atractus loveridgei Amaral, 1930	1,700-2,000	Occidental	DD	Passos et al. (2009), Bernal (2025)
Atractus manizalesensis Prado, 1940	1,500-2,200	Central	LC	Rojas-Morales et al. (2017), Bernal (2025)
Atractus nasutus Passos, Arredondo, Fernandes & Lynch, 2009	2,600	Central	DD	Passos et al. (2009), Bernal (2025)
Atractus nicefori Amaral, 1930	1,600-2,700	Occidental	VU	Passos et al. (2009)
Atractus obesus Marx, 1960	1,200-2,800	Occidental	DD	Vera-Pérez et al. (2018)
Atractus oculotemporalis Amaral, 1932	1,800-2,000	Occidental	DD	Bernal (2025)
Atractus paisa Passos, Arredondo, Fernandes & Lynch, 2009	2,100-2,600	Central	LC	Passos et al. (2009), Bernal (2025)
Atractus sanguineus Prado, 1944	1,100-2,400	Central	DD	Passos & Arredondo (2009), Passos et al. (2009)
Atractus titanicus Passos, Arredondo, Fernandes & Lynch, 2009	1,800-2,400	Central	LC	Passos et al. (2009), Vanegas-Guerrero et al., (2016), Bernal (2025)
Dipsas sanctijoannis (Boulenger, 1911)	900-2,300	Central and Occidental	LC	Ramírez-Chaves et al. (2022), Bernal (2025)
Geophis betaniensis Restrepo & and Wright, 1987	1,650	Occidental	DD	Myers (2003), Castro-Herrera & Vargas-Salinas (2008), Savage and Watling (2008), Valencia-Zuleta et al. (2014)
Mastigodryas danieli Amaral, 1935	600-2,400	Central and Occidental	LC	Montingelli et al. (2018)
Saphenophis antioquiensis (Dunn, 1943)	2,500-2,600	Central	DD	Myers (1969), Myers (1973)
Saphenophis sneiderni Myers, 1973	1,500-2,300	Occidental	EN	Myers (1973), Bolívar-García et al. (2015), Bernal (2025), this work
Saphenophis tristriatus (Rendahl & Vestergren, 1940)	2,500-3,200	Central and Occidental	DD	Myers (1973), Bernal (2025), this work
Trilepida joshuai (Dunn, 1944)	1,100-2,300	Central and Occidental	LC	Pinto et al. (2010), Rojas-Morales et al. (2011), Bernal (2025)

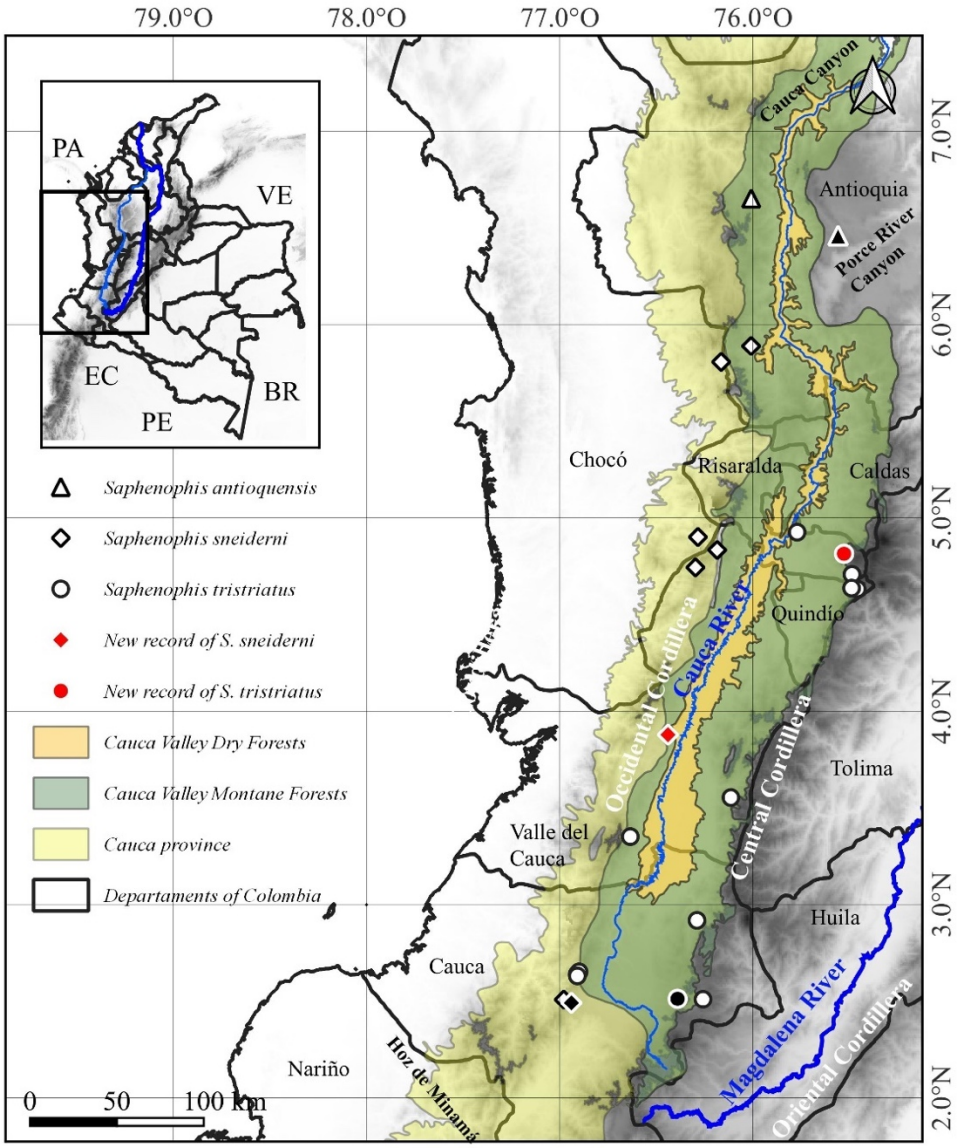

Figure 1. Map of Northwestern Colombia depicting records of the snake genus *Saphenophis*, based on voucher specimens and photo records from GBIF (see Table 1), and remarking geographical features possibly related to their evolution. The type localities for the species are indicated with black polygons. Acronyms of the countries corresponds to a: PA (Panama), VE (Venezuela), EC (Ecuador), PE (Peru), BR (Brazil).

Biogeographic analysis

To explore snake endemism patterns along the Cauca River Basin of Colombia we follow the framework proposed by Kreft and Jetz (2010). First, we built a dataset with records of snake species whose geographic distribution is restricted to the eastern slope of the Occidental and the western slope of the Central Cordillera of Colombia (i.e., the Cauca Basin). The dataset includes three sources of information: (1) specialized literature (see Supplementary material: Table S1); (2) GBIF records only including voucher specimens for Andean species, and (3) specimens from biological collections such as the MHN-UCa-R; Coleccion de Anfibios y Reptiles de la Universidad del Quindío (ARUQ), Colección de Ofidios of the La Salle Museum (MLS-Ofi), and the Colección de Reptiles of the Instituto Alexander von Humboldt (IAvH-R) (Supplementary material: Appendix 1). We sub-divided the records as: i) present in the western slopes of the Central Cordillera, ii) present in the eastern slopes of the Occidental Cordillera, and iii) present in both Central and Occidental Cordilleras across the Cauca River Basin (Table 1). We also mapped all records over the Cauca Province

shapefile provided by Morrone et al. (2022). Geographic coordinates were extracted for those records lacking it using the centroid method. This procedure involves determining the geometric center of the locality or administrative unit described in the primary source (Chapman and Wieczorek 2020). This allows the geographic location to be standardized when exact field coordinates are unavailable. To explore the relationship between endemic species richness and elevation, we assigned the snake records to three elevation zones based on phytosociological regionalization's of the Colombian Andes by Cuatrecasas (1958), Gentry (1982a, b), and Rangel-Ch et al. (1997): Low zone (600–1,000 m a.s.l.), corresponding to the Cauca Valley Dry Forests. The intermediate zone is 1,000–2,400 m a.s.l. and corresponds to the sub-Andean forests (Gentry 1982a, b, Rangel-Ch et al. 1997). The upper zone (2,400–3,500 m a.s.l.) corresponding to the Andean and high Andean forests and their transition to the Páramo biome (Cuatrecasas 1958, Rangel-Ch et al. 1997).

To analyze variation in endemic snake richness, we identified areas of species concentration by establishing 0.5° latitude by 0.5° longitude cells (operative geographically units - OGU´s). We estimated 35 OGUs for this area by taking into account the total spatial area of the Cauca River basin (63,300 km²). The southern limit is the Hoz de Minamá (Occidental Cordillera, Department of Nariño), and the northern limit is the Cañón del Río Cauca (Department of Antioquia) (Fig. 1). Then, OGUs were subjected to phenetic classification (Sneath and Sokal, 1962) through Ward´s agglomerative hierarchic cluster analyses based on the species incidence matrix. The Ward measure with a Euclidean distance was selected to diminish variance (Kreft and Jetz 2010).

RESULTS

Distribution of *Saphenophis tristriatus* and *S. sneiderni* in Colombia

Based on the sources examined, for *S. tristriatus* we compiled 11 records from nine localities documented in the literature and GBIF. All records come from inter-Andean Cauca River Basin. In addition, we documented an additional locality representing a new record for the species described below.

For *S. sneiderni*, we compiled nine records from two localities documented in the literature, and four records from GBIF. All records come from inter-Andean Cauca River Basin. In addition, we documented an additional locality representing a new record for the species.

New record of *Saphenophis tristriatus*. COLOMBIA – Risaralda, Santa Rosa de Cabal, Distrito de Conservación de Suelos Campoalegre, vereda San Ramón, predio CHEC-Los Alpes; 04°48′54.5″N, 075°31′40.7″W; 2,940 m a.s.l. (Fig. 2); 26.VIII.2015; collected by Héctor F. Arias Monsalve; manual capture;1 ♀, MHN-UCa-R 1207. Snout-vent length (SVL) 588 mm, tail length (TL) is 172 mm or 22.6 % of the total length. Head width 10.56 mm and head length 17.21 mm (Fig. 2). The dorsal scales are smooth, lacking apical pits, and in 17-17-15 rows; scale row reduction occurs by fusion of rows 3 and 4 at level of ventral 91 (right). There are 1 pre-ventral, 173 ventrals followed by a divided anal plate and 70 divided subcaudals; 8-8 supralabials with the third, fourth and five contacting the orbit; 9-9 infralabials, from one to fifth contacting the chin shields. The first four infralabial scales are in contact with the first pair of chin shields; the fifth infralabials contacting the second pair of chin shields (Fig. 2). Loreal scale higher than wider. Two postoculars; superior postocular is three times larger than inferior one. Temporals 1+1+2 (right) and 1+2 (left) (Fig. 2C). Left maxillae with 21+2 teeth with a small diastema.

The head and body are dark brown. The dorsal surface of the head and body is dark brown, gradually turning grayish toward the tail. The back has a pattern of longitudinal lines and bands arranged as follows: a median, narrow black stripe on the vertebral scale row occurs along the body but incontiguous at the tail. Two lateral, pale tan stripes behind dorsal black stripe, occupies two scale rows (5-6 anteriorly, 4-5 posteriorly); the encroachment of dark pigment posteriorly gives it the appearance of two adjacent rows of staggered light spots. Another dark line is on the side of the neck, reaching the mid-anterior of the body length (20-25 ventrals), on the upper third of row 2 (Fig. 2). All of the stripes start on the neck and run unbroken but uncontinuous posteriorly to the tip of the tail. The snake's head is brown with black spots. The cream-colored supralabial and infralabial scales have dark spots that follow a banded pattern connecting with the

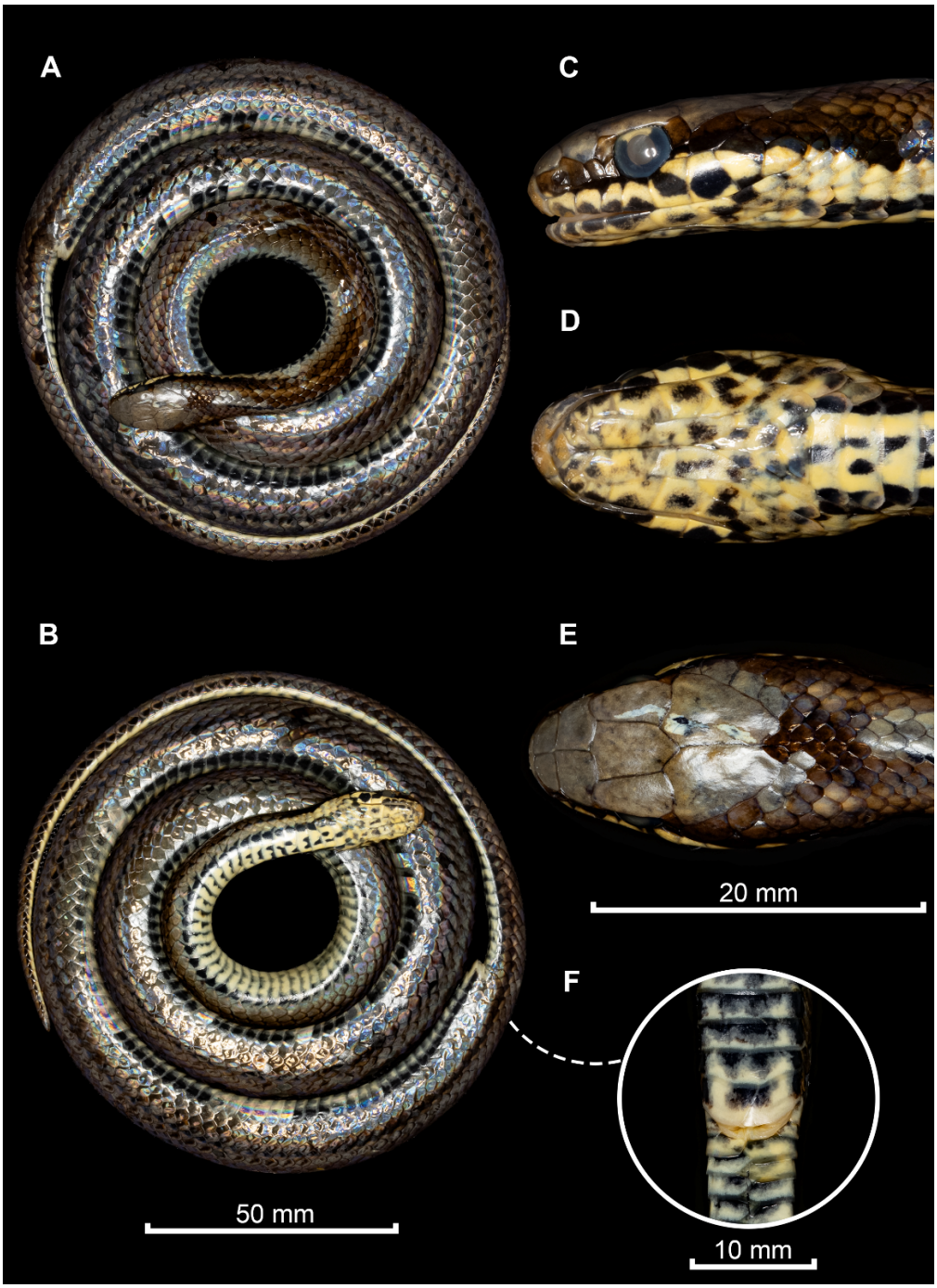

Figure 2. Female of *Saphenophis tristriatus* (MHN-UCa-R 1207) from Santa Rosa de Cabal, Risaralda Department, Colombia, 2,940 m a.s.l. (A) Dorsal, and (B) Ventral views of the specimen. Head detailed in lateral (C), inferior (D) and superior (E) views. (F) Detail of the cloacal plate. Photographs: Jose J. Henao-Osorio.

dorsolateral lines (Fig. 2C). The first four supralabial and the first five infralabial scales have black spots forming a pattern as if the snake were wearing "lipstick." The ventral surface of the head and body is yellowish cream, with black spots covering all the body's scales. The ventral scales have black edges, forming a semi-continuous line to the tail. The posterior ventral scales are more covered with black, including the cloacal plate. This color pattern continues to cover the subcaudal scales (Fig. 2F).

New record of *Saphenophis sneiderni*. COLOMBIA – Valle del Cauca, Yotoco, Reserva Forestal Protectora Bosque de Yotoco; 03°52′46.12″N, 076°26′21.51″W; 1,800 m a.s.l.;

26.VIII.2011; photographs by Julián A. Rojas-Morales; undetermined sex (Supplementary material: Figure S1). Unhandled individual; approximately 450-500 mm total length. The ground color of the dorsum is brownish red, and the ground color of the lower sides (below the lateral dark stripe) is a paler brown. There is no vertebral line. No continuous lateral dark lines the neck to the tail. It becomes broader and darker posteriorly and is not bordered above by a pale line or spots. The supralabials are mostly obscured by black big spots. There is a vivid whitish-yellow horizontal line margined above by a black stripe that extends along the side of the head and fuses with the lateral body stripe on the side of the neck.

Endemic snakes of the Cauca River basin

Twenty species of snakes belonging three families (Anomalepididae, Dipsadidae, and Leptotyphlopidae), and seven genera were identified as restricted —i.e. endemics — to the Cauca River Basin (Supplementary material: Table S1, Fig. S2). In terms of species composition, snake's endemic to the Cauca River basin mainly belong to the genus *Atractus* (13 species, accounting for 60% of the total), followed by the genus *Saphenophis* with three species (15%), and other genera (*Anomalepis*, *Dipsas*, *Geophis*, *Mastigodryas*, *Trilepida*) with one species each (Table 1, Fig. 3).

The species recorded at lower elevations are *Anomalepis colombia* and *Mastigodryas danieli*, both of which with records up to 1,000 m a.s.l. In contrast, *S. tristriatus* is the only species recorded at elevations above 3,000 m a.s.l. (Table 1). The endemic species are primarily found in the Cauca Valley Montane Forests belt and the upper zone of high Andean forests in both Cordilleras (Fig. 3). In total, five species are shared between the slopes of the Central and Occidental Cordilleras, seven restricted to the eastern slopes of the Occidental Cordillera, and nine to the western slopes of the Central Cordillera (Table 1, Fig. 3A, B).

According to the analyzed records, areas of high species concentration stand out in the middle Cauca basin, with 7-9 endemic species. Other areas of intermediate richness, with 3–5 species, were identified in the upper basin (Fig. 4A). The rest of the areas depict two or three species. The distribution patterns suggest the presence of a core endemism area within the Cauca River Basin, but the Central and Occidental Cordilleras were not clearly differentiated in the hierarchic clustering of the OGUs (Fig. 4B). Hierarchical cluster analysis using Ward's method revealed the formation of two distinct groups among the 35 OGUs (Fig. 4). The dendrogram shows deeply dissimilarity on the vertical axis. OGUs merged at the lowest distance observed —i.e., more similar —, forming very heterogeneous subgroups that, upon examination of the data, corresponds to areas of both Central and Occidental cordilleras (Fig. 4). The first group depicts nine empty OGUs (11–13, 24, 25, 28, 31, 46, 54), or cells without endemic snake records. The second group depicts two main clusters, all containing OGU´s from the Central and Occidental Cordilleras, and the Cauca River valley (CRV) (Fig. 4B). OGUs with endemic species richness values greater than seven (OGUs 41–45 and 55–58) were found to be associated with the middle basin of the Cauca River (Fig. 4A). OGU 43 (see Supplementary material: Fig. S3) had the highest endemic snake richness, with nine species.

DISCUSSION

Snakes' endemism in the Cauca River Basin

Based on the sources of information, we compiled records of 20 species (including *S. tristriatus* and *S. sneiderni*) restricted to the Cauca River Basin. The records presented in this study extend the geographic range of *S. tristriatus* and *S. sneiderni* (see Fig. 1), two poorly known snake species endemic to the Cauca River basin, Colombia. The voucher specimen of *S. tristriatus* from the Department of Risaralda is, at the best of our knowledge, the only known for this locality (Risaralda, 2,940 m a.s.l.) (Fig. 1, Supplementary material: Table S1). Records for both species in the Andean forests of the Central and Occidental cordilleras suggests that their distribution is wider than previously known (Myers 1973, Bolívar-García et al. 2015, Bolívar and Arredondo 2016, Bolívar and Velasco 2017). For *S. tristriatus*, the record extends the known distribution of this species by about 200 km north of previously known locations in the upper Cauca River valley (Supplementary material: Table S1). Regarding *S. sneiderni*, the analyzed photographic records extend its distribution by approximately 150 km to the north from the type locality (El Tambo, Department of Cauca), along the eastern flank of the Occidental Cordillera (see Fig. 1).

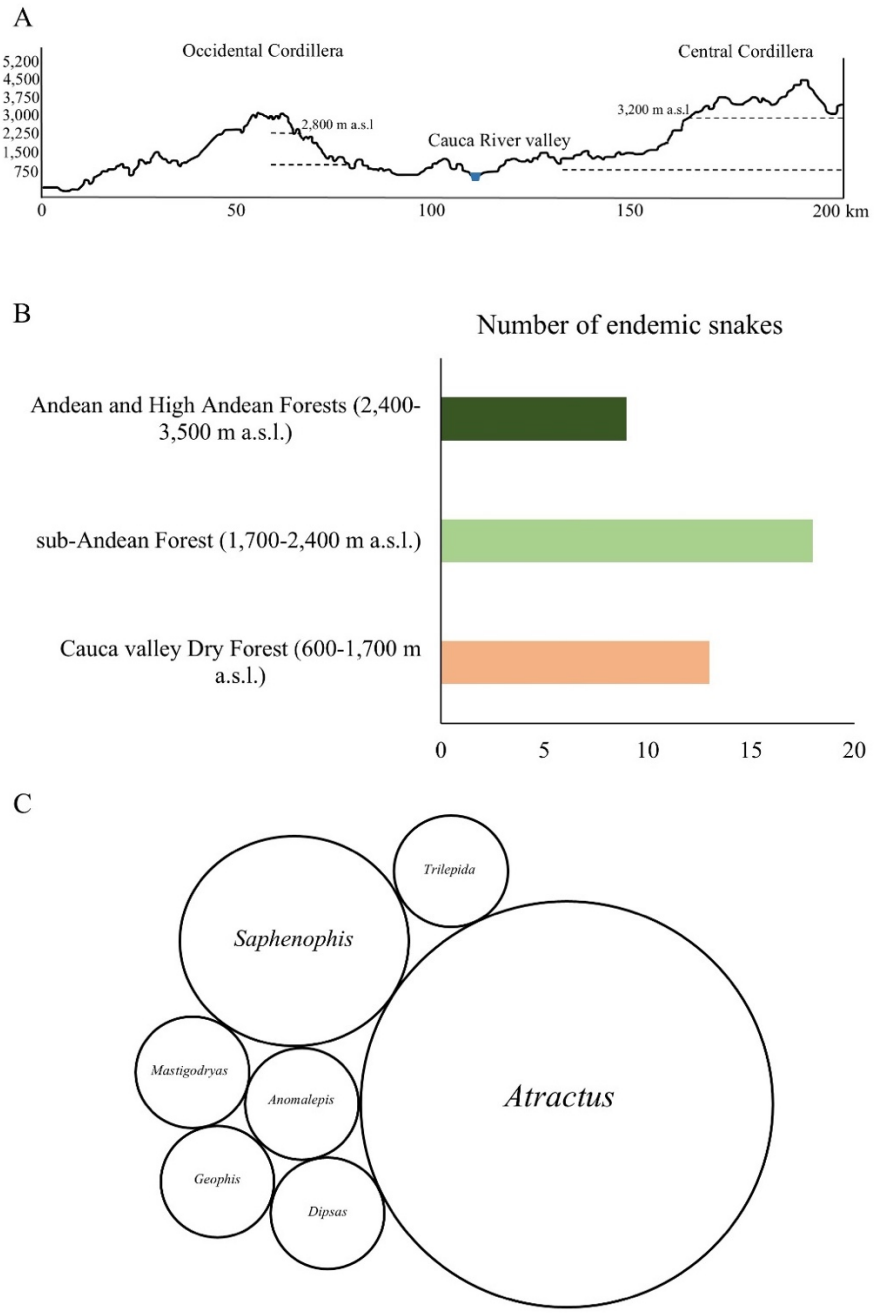

Figure 3. (A) Altitudinal profile at the middle Cauca River valley depicting lower and upper elevation limits for endemic snake species -dash lines- at the western flank of the Central and the eastern flank of the Occidental cordilleras, respectively (Google Earth Pro 7.3.6.10201.). (B) Snakes' endemic richness by main vegetation types along the elevation gradient. (C) Circular tree map showing the proportion of the endemic snake genus at the Cauca River basin.

This information is biologically novel and contributes to the biogeographic definition of the Cauca Province, for which there is a lack of data on non-avian reptiles (Müller 1974, Morrone 2015). Reptile diversity in this biogeographic province is considerably lower than in the Magdalena Province, which corresponds to the lower and middle basins of the Magdalena River (Medina-Rangel 2011, Rojas-Morales et al. 2023). However, a macroecological analysis of the Cauca-Magdalena basin is still needed to identify areas of fine-scale endemism (i.e., biogeographic districts), and test biogeographic regionalization hypotheses (Hernández-Camacho et al. 1992, Morrone 2015).

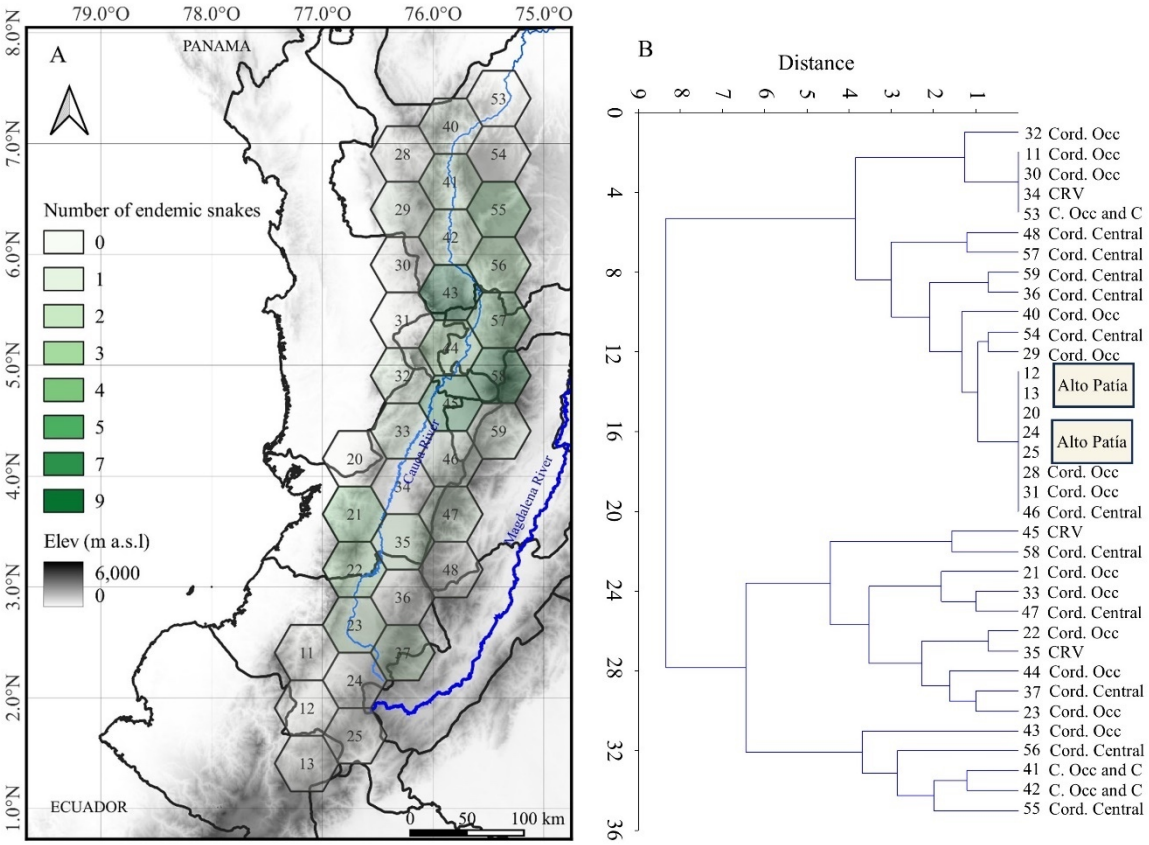

Figure 4. (A) Species richness map for the snake endemic species to the Cauca River Basin (see Table S2). (B) Agglomerative hierarchical cluster analysis using Ward's method for the OGU´s (0.5° lat x 0.5° long) defined in the study area. Acronyms are: Cord. Occ -Occidental Cordillera - and CRV -Cauca River Valley-.

At this point, it is important to state the difference among the Areas and Centers of Endemism. Areas of Endemism (AOEs) are defined as "areas delimited by the congruent distribution of at least two species of restricted range" (Nelson and Platnick 1981, p. 468, Hausdorf 2002). AOEs are often used as geographical units in testing hypotheses in historical biogeography (Kreft and Jetz 2010). Instead, Centers of Endemism (COEs) are areas where endemic species concentrate. They usually have more endemics than the surrounding areas and are often termed "hotspots". COEs are units of concern for conservation biogeography (Whittaker et al. 2005). The results of this study show that the Cauca River basin is home to a high diversity of endemic snakes (20 species), despite being relatively small in size (63,300 km² or 5.51% of Colombia's continental territory). This is a highly diverse region compared to areas of endemism of considerably greater size, such as the Caatinga in Brazil (22 species) (Guedes et al. 2014), and the Greater Maputaland-Pondoland-Albany in southeast Africa (13 species) (Perera et al. 2018), as well as the Gulf of California (11 species) (Arnaud et al. 2024) (Table 2), possibly related to a latitudinal gradient.

Most of the species restricted to the Cauca River Basin belong to the genus *Atractus* (13 species, 62% of the endemic snake fauna) (Fig. 3C). The *Atractus* genus is characterized by a South American origin and a high degree of endemism, particularly in the Andes and peripheral mountain ranges, with the genus extending north into Panama and to isolated locations of the Amazonia and the Pantepui in South America (Passos et al. 2009, Passos and Lynch 2011, Pomar-Gómez et al. 2021, Esqueda et al. 2025). Species distribution of *Atractus* is influenced by complex topography, and while some species are widespread, many are highly endemic known from only a few specimens. The *Atractus* of the Cauca River Basin, and the Cauca province are found usually in a very small, specific geographic area, such as a particular mountain range or inter-Andean

Table 2. Some snake endemism areas identified worldwide comparing their extension and basic environmental information with the Cauca River basin, Colombia.

Zoogeographical region / Endemism area	Area (km²)	Latitude	Dominant vegetation	Climate	Snake endemic species	Source
Saharo-Arabian						
Sinai Peninsula	61,000	27°N-31°N	Xeric	Dry arid	2	Milto (2017)
Afrotropical						
Greater Maputaland-Pondoland-Albany (GMPA), South east Africa	274,136	34°S-22°S	subtropical thicket	Dry subtropical	13	Perera et al. (2018)
The southern African Great Escarpment						
Mt. Nlonako, Cameroon	150		Moist broadleaf forest	Humid tropical	3	Herrmann et al. (2005)
Nearctic						
Gulf of California, Mexico	283,000	24°N-32°N	Xeric	Dry arid	11	Arnaud et al. (2024)
Neotropical						
Merida Cordillera, Venezuela	40,000	7°N-10°N	Dry Tropical Forest to Paramo	Dry-arid to humid tropical	17	La Marca and Soriano (2005); Rivas et al. (2012)
Pernambuco Endemism Center, Brazil	56,000	5°S-10°S	semi-deciduous forests	Humid tropical	7	França et al. (2020)
Caatinga, Brazil	844,453	3°S-18°S	Mosaic	Dry arid	22	Guedes et al. (2014)
Chocó Biogeográfico, Colombia	187,400	1°N-8°N	Moist broadleaf forest	Humid tropical	11	Rojas-Morales (2012)
Cauca River Basin, Colombia	63,300	2°N-7°N	Moist broadleaf forest	Warm and humid tropical	20	This work
Palearctic						
Taiwan	35,800	22°N-25°N	Temperate forests	Humid subtropical	14	Lee et al (2019), Jiang (2024)
Indomalayan						
Nortwest Uplands	132,140	17°N-22°N	Moist broadleaf forest	Humid tropical	12	Bain and Hurley (2011)

valley. This is especially true for the species in the Cauca Valley Montane Forests (e.g., *A. nicefori*, *A. manizalesensis*, *A. obesus*, *A. titanicus*), which could represent an interesting case of evolution related to vicariant events by orogeny and climatic changes (Pomar-Gómez et al. 2021).

For *Saphenophis*, the phylogenetics relationships to other Neotropical Dipsadids are poorly understood. Abbeg et al. (2022) recovered *S. antioquiensis* as the sister group of a clade including Tropidodryadini and Philodryadini (<70%) but no comments were provided at this respect. Zaher et al. (2019) could not assess the monophyly of *Saphenophis* and other snake genera due to missing samples for mostly species, restricting biogeographic comparisons with other snake's endemic to the Cauca River basis such as species within *Atractus*. Myers (1973: 24) stated that "Probably the various populations of the *S. boursieri* group are distributional relicts from a more favorable time, as perhaps a period of Pleistocene glaciation during which some species of the tropical highlands had wider horizontal and vertical distributions than today (Haffer 1967)". In light of Quaternary paleoclimatic and paleoecological evidence for the Cauca River basin (Berrío et al. 2002, Hoogiemstra and Flantua 2019), Myers' hypothesis on the evolution and geographic distribution of *Saphenophis* makes sense. However, the lack of phylogenetic support for most of the species within *Saphenophis* prevents directly acceptance or rejection of Myers' proposal. To assess whether *S. antioquensis*, *S. sneiderni*, and *S. tristriatus* are derived from a wider elevation distributed ancestors, such as *S. boursieri* (Myers 1973), it is necessary to analyze intrageneric relationships, besides another related South American taxa of Xenodontinae snakes (Zaher

2019). It is particularly important to collect additional *S. antioquiensis* and *S. tristriatus* specimens to analyze interspecific variation and define species boundaries.

Finally, the Cauca River basin has experienced extensive habitat transformation, with approximately 80% of this original forest cover lost to agriculture, livestock farming, and urban expansion. The montane forests between 1,700 and 3,000 m a.s.l. harbor the highest diversity of endemic snakes in this basin, but are particularly vulnerable to deforestation driven by coffee plantations, avocado crops, and pastureland expansion. The lack of ecological and demographic data for nearly all endemic snake species, coupled with limited representation in protected areas within the middle Cauca River basin (Supplementary material: Fig. S4), underscores the need for targeted surveys. For *S. sneiderni*, Bolívar and Velasco (2017) stated that the fragmentation of montane forests in the Occidental Cordillera represents a critical threat to population viability. Despite *S. tristiatus* reaching higher elevations, habitat loss in the high Andean forests, are increasingly impacted by climate change and agricultural frontier expansion (Bolívar and Arredondo 2016).

Preserving areas of high endemism, particularly in tropical mountain ranges such as the Cauca Province, is a critical global priority because these zones act as the primary repositories for the planet's unique evolutionary history. However, these face a convergence of threats including intensive land conversion for agriculture, expanding infrastructure, and climate change effects. The conservation challenge is exacerbated by the lack of knowledge of range-restricted endemics classified as Data Deficient (DD), such as *S. tristriatus*. Yet, as reinforced by Gumbs et al. (2020), DD non-avian reptile species often possess biological traits and face human pressures that make them functionally comparable to Critically Endangered (CR) species. In the Cauca Province, DD species such as *S. tristriatus* and CR species such as *S. sneiderni* should therefore be interpreted as a precautionary indicator of ecologically and biogeographically rarity and imminent peril.

CONCLUSION

The genus *Saphenophis* is endemic to the northern Andes. Three species are restricted to the Andean mountain forests of the Cauca River basin in Colombia. The restricted distribution of *S. tristriatus* and *S. sneiderni* to the Cauca River Basin, combined with their current conservation status (DD and EN, respectively), underscores the urgent need for monitoring efforts in areas where both species have been identified. Further studies are needed to reduce Linnean and Wallacean shortfalls through phylogenetic population analysis. This analysis should include the exploration of remote areas in the Cauca River basin, such as the Tatamá, Los Nevados, and Las Orquídeas National Natural Parks, where additional cryptic snake species may be discovered. The fact that the Cauca River basin has such a high level of snake endemism compared to other endemism areas worldwide is highly significant in biogeographical terms, particularly for disentangling the Central America and northern South America snakes phylogeography.

ACKNOWLEDGEMENTS

To the Central Hidroeléctrica de Caldas (CHEC) S.A. ESP and Vicerrectoría de Investigaciones y Posgrados of the Universidad de Caldas "Convocatoria de apoyo con recursos económicos a Grupos de Investigación de la Universidad de Caldas Año 2024" for financial support. This study was partially funded by the Ernst Mayr Grant, Museum of Comparative Zoology, Harvard University. To Fernando Vargas (ARUQ), Sandra Galeano (IAvH), Julieth Cárdenas Hincapié (MLS), Esteban Franco and Danny Zurc (CSJ), for the permit to access specimens under their care. JARM received a doctoral fellowship (BPIN 2022000100055 – Becas V) from the Colombian Ministerio de Ciencia, Tecnología e Innovación.

AUTHOR CONTRIBUTIONS

Conceptualization: JARM, HERCh; Data curation: JARM, JJHO, LSCM; Formal analysis: JARM; Manuscript writing, revision and editing: JARM, EACG, JJHO, LSCM, HERCh; Funding acquisition: JARM, HFAM, HERCh; Project administration: HERCh.

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Submitted: 11 December 2025

First decision: 16 February 2026

Accepted: 18 February 2026

Published online: 26 February 2026

Edited by Matteo Riccardo Di Nicola